

Contributed Paper

# **Effects of Economic Downturns on Mortality of Wild African Elephants**

# GEORGE WITTEMYER\*†‡

\*Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, U.S.A., email g.wittemyer@colostate.edu

†Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, U.S.A. ‡Save the Elephants, Nairobi, Kenya

Declines in economic activity and associated changes in buman livelihood strategies can increase threats of species overexploitation. This is exemplified by the effects of economic crises, which often drive intensification of subsistence poaching and greater reliance on natural resources. Whereas development theory links natural resource use to social-economic conditions, few empirical studies of the effect of economic downturns on wild animal species have been conducted. I assessed the relations between African elephant (Loxodonta africana) mortality and human-caused wounds in Samburu, Kenya and (1) livestock and maize prices (measures of local economic conditions), (2) change in national and regional gross domestic product (GDP) (measures of macroeconomic conditions), and (3) the normalized difference vegetation index (NDVI) (a correlate of primary productivity). In addition, I analyzed household survey data to determine the attitudes of local people toward protected areas and wild animals in the area. When cattle prices in the pastoralist study region were low, human-caused wounds to and adult mortality of elephants increased. The NDVI was negatively correlated with juvenile mortality, but not correlated with adult mortality. Changes in Kenyan and East Asian (primary market for ivory) GDP did not explain significant variation in mortality. Increased buman wounding of elephants and elephant mortality during periods of low livestock prices (local economic downturns) likely reflect an economically driven increase in ivory poaching. Local but not macroeconomic indices explained significant variation in mortality, likely due to the dominance of the subsistence economy in the study area and its political and economic isolation. My results suggest economic metrics can serve as effective indicators of changes in human use of and resulting effects on natural resources. Such information can help focus management approaches (e.g., antipoaching effort or proffering of alternative occupational opportunities) that address variation in local activities that threaten plant and animal populations.

**Keywords:** Africa, development, economic incentives, illegal wildlife use, natural resource economics, poaching, poverty, protected areas

Efectos de las Recesiones Económicas sobre la Mortalidad de Elefantes Africanos Silvestres

Resumen: Las declinaciones de la actividad económica y los cambios asociados en las estrategias de sustento bumano pueden incrementar las amenazas de cosecha no sostenible de especies. Esto está ejemplificado por los efectos de las crisis económicas, que a menudo conducen a la intensificación de la cacería de subsistencia furtiva y a una mayor dependencia de los recursos naturales. Mientras que la teoría del desarrollo relaciona el uso de recursos naturales con las condiciones sociales- económicas, existen pocos estudios empíricos del efecto de las recesiones económicas sobre especies de animales silvestres. Evalué las relaciones entre la mortalidad de elefante africano (Loxodonta africana) y beridas provocadas por bumanos en Samburu, Kenya con (1) precios de ganado y maíz (medidas de condiciones económicas locales), (2) cambio en el producto interno bruto (PIB) nacional y regional (medidas de condiciones macroeconómicas), y (3) índice normalizado de diferencia de

vegetación (INDV) (un correlato de la productividad primaria). Adicionalmente, analicé datos de encuestas para determinar las actitudes de babitantes locales bacia las áreas protegidas y animales silvestres en el área. Cuando los precios del ganado en la región de estudio eran bajos, incrementaron las beridas provocadas por bumanos en y la mortalidad de elefantes. EL INDV se correlacionó negativamente con la mortalidad de juveniles, pero no se correlacionó con la mortalidad de adultos. Los cambios en el PIB en Kenia y Asia Oriental (mercado primario de marfil) no explicaron variación significativa en la mortalidad. El incremento de beridas en elefantes provocadas por bumanos y la mortalidad de elefantes durante períodos de precios de ganado bajos (recesiones económicas locales) probablemente refleja un incremento en la cacería furtiva de marfil debido a causas económicas. Los índices locales, no los macroeconómicos, explicaron variación significativa en la mortalidad, probablemente debido a la dominancia de la economía de mercado en el área de estudio y su aislamiento político y económico. Mis resultados sugieren que las medidas económicas pueden servir como indicadores efectivos de los cambios en el uso bumano de los recursos naturales y los efectos resultantes sobre los mismos. Tal información puede ayudar a enfocar los métodos de manejo (e.g., esfuerzos para evitar la cacería furtiva o el ofrecimiento de oportunidades ocupacionales alternativas) que atienden la variación en actividades locales que amenazan a poblaciones de plantas y animales.

**Palabras Clave:** África, áreas protegidas, cacería furtiva, desarrollo, economía de los recursos naturales, incentivos económicos, pobreza, utilización ilegal de vida silvestre

#### Introduction

Whereas affluent sectors of society tend to have greater ecological effects than lower-income sectors (Dietz et al. 2007), the rural poor often rely directly on natural resources for food, shelter, and fuel to a greater extent than other sectors of societies (Mainka & Trivedi 2002; Barbier 2005). Major economic downturns (e.g., multiple quarter declines in gross domestic product [GDP]) increase the number of poor (Jalan & Ravallion 2000; Suryahadi & Sumarto 2003), and extreme downturns elicit urban-torural migration and increasing dependence on natural resources (Pallot & Moran 2000; Chan 2010). Among some rural, poor communities, increasing use of natural resources during economic downturns is a recognized economic diversification strategy (Barrett et al. 2001; Fisher 2004; Barbier 2005).

The disintegration of the Soviet Union and associated reductions in abundance of saiga antelope (Saiga tatarica) across extensive areas provides an empirical example of how major political and economic transitions can drive changes in human use of natural resources and thus strongly affect an animal species (Kuhl et al. 2009). The hypothesis that economic fluctuations are correlated with human hunting of wild animals is supported by the association between the price and consumption of bushmeat and the corresponding effects of this consumption on abundance and distribution of animals (Brashares et al. 2004; de Merode et al. 2004). Although typically focused on deterrents to poaching and the elasticity of the price of harvested species, theoretical investigations of illegal harvesting of wild animals have considered the relation between harvesting effort and social and economic conditions (Leader-Williams et al. 1990; Milner-Gulland & Leader-Williams 1992; Bulte & van Kooten 1999). Results of a recent work project increases in poaching of rhinoceros (Rbinocerus unicornis) on the basis of macroeconomic indices (national and regional GDP), although the authors acknowledge the need to explore local economic metrics (Poudyal et al. 2009).

Assessments of the relation between economic trends and human hunting or collection of wild species is most rigorous when salient economic metrics or income and unemployment records for the people interacting with a natural system can be monitored accurately. The pastoralist communities in East Africa (Kenya, Uganda, and Tanzania) in and around rural protected areas offer such a study opportunity. In these largely noncash, nonhorticultural societies, economic wealth is invested in livestock holdings because livestock are the means to maximize milk production (the primary product of such systems) for household use, maintaining livestock is a cultural norm, and financial institutions for the safe keeping or accrual of cash resources are few, inaccessible, and often expensive (Quam 1978; Livingstone 1986; McPeak 2005). The pastoralism of these communities principally contributes to subsistence rather than the market economy (Davies 2008), and livestock sales are the common manner in which these communities interact with formal markets (Livingstone 1986; McPeak & Barrett 2001). Low market prices for livestock are concomitantly a function of decreased physical condition of the livestock (usually in response to dry seasons or drought) (ALRMP 2009) and increased proportion of nonlactating females that are sold to augment household incomes in response to seasonal or drought-related cessation of milk production (Davies & Bennett 2007). Thus, prices of livestock, particularly cattle, offer a robust metric of general household economic conditions that can be linked to local declines in abundance or increased offtake of wild species.

I examined whether local livestock prices, monitored by the Arid Lands Resource Management Project (ALRMP) (ALRMP 2009), national maize prices, and national and East Asian GDP growth rates (indices of macroeconomic conditions) were associated with mortality and human-induced wounds in a population

Wittemyer 3

of African elephants (*Loxodonta africana*) inhabiting Kenya's Samburu and Buffalo Springs national reserves (Wittemyer 2001; Wittemyer et al. 2005). In addition, I used household survey data to quantify attitudes toward wild animals and the nature reserves in the study area, which provided insight into the mechanisms driving the observed relation between economic conditions and elephant mortality.

## Methods

## Demographic Data

Individuals in the elephant population inhabiting the semiarid savanna of Samburu and Buffalo Springs national reserves in northern Kenya have been monitored since 1997 (Wittemyer 2001). These elephants are not always present in the national reserves (combined area 260 km<sup>2</sup>) (Wittemyer et al. 2007a), which represent <10% of the animals' known range (Wittemyer et al. 2005). Outside the protected areas, the elephants occur in largely unpatrolled, communally owned lands, where the probability of illegal killing is relatively high (Kahindi et al. 2010). The presence of government rangers in these unprotected areas during the study was constant and low, approximately 1 ranger/250 km<sup>2</sup> (i.e., a single security platoon for 5,000 km<sup>2</sup>), relative to theoretically effective levels of 1 ranger/20 km<sup>2</sup> in savanna ecosystems (Leader-Williams et al. 1990). My field team and I recorded the presence or absence of known individual elephants (all elephants that use the reserves are known) and observations of human-induced wounds during weekly travel along fiveestablished transects (approximately 20 km long) in the protected areas (as described in Wittemyer et al. 2005).

I examined data on known mortalities (n=126) registered by the team within the national reserves from 2000 through 2006. Mortalities were identified in 1 of 3 ways: known individuals were found dead; repeated (>3) observations established individuals were missing from their family group (i.e., mothers repeatedly observed without their offspring or absent mothers despite repeated observation of their calves in their family groups); and no observations for >3 years of individuals that had been observed by the monitoring team on a regular basis (i.e., at least annually). None of the elephants recorded as dead had been observed as of mid-2011. Because subadult males (8-16 years old) regularly leave their family groups and appear to wander widely, they were recorded as dead only when their carcasses were observed.

I divided mortalities into 2 age classes: juveniles ( $\leq$ 5 years) (n=45) and subadults and adults (n=81). I used visual characteristics established from elephants of known age to estimate the age of individuals (Moss 2001) and validated these age estimates in the study population by comparing visual estimates of age with ages of dead or anesthetized individuals determined from dentition (Ras-

mussen et al. 2005). I excluded from analyses juveniles that died at the same time as their mothers.

Carcasses of over half the registered mortalities were never found; therefore, their dates of death were unknown. Dates of death for these animals were estimated by subtracting half the time since the last observation of the animal from the first date when death was suspected, typically 1-2 months for females and calves missing from their families. Date of death for adult males, which generally use the protected areas seasonally, were assigned after the animal had not been observed for 3 years as half the time between the last observation and expected return date. To account for potential errors in estimated dates of death, I analyzed mortalities seasonally after assigning deaths to the 7-month wet to dry season that occurs from April through October or to the 5-month wet to dry season that occurs from November through March (14 seasons in my 7-year study) (Fig. 1).

I also examined records of observations of wounds inflicted by humans (n=29) recorded in the study area between 2000 and 2006. Such wounds were primarily from bullets, spears, and arrows and occasionally from snares. The first observation of a fresh wound was recorded. I excluded old wounds (i.e., scars) from analyses. These wounds are the principal metric of the direct effects of humans on the study population given poaching did not occur within the national reserves during the study period.

# **Metrics of Economic Conditions**

I used market prices of cattle and goats and national market prices of maize as metrics of local economic conditions and annual changes in national GDP and East Asian (China, Hong Kong, Japan, Macau, Mongolia, North Korea, South Korea, and Taiwan) GDP as macroeconomic metrics. Average prices of cattle and goats were provided for each month and district by the ALRMP, a joint venture of the government of Kenya and the World Bank to monitor key livelihood indices to inform famine-relief efforts (ALRMP 2009). Because Isiolo was the closest livestock market to the reserves (other markets were >100 km from the study area) and near an area where many elephants have been killed illegally (Kahindi et al. 2010), I focused on the correlation between elephant mortality and livestock prices from Isiolo district. I averaged inflation-adjusted, monthly prices of livestock for April through October and November through March from 2000 through 2006 (Fig. 1).

Maize is a staple among the communities in the study area. Maize prices are monitored by the World Food Program (ALRMP 2009), but information on local maize prices for the duration of the study was not available. Because the study region has little to no horticulture, maize prices are assumed to be primarily a function of the national market. Therefore, I incorporated the

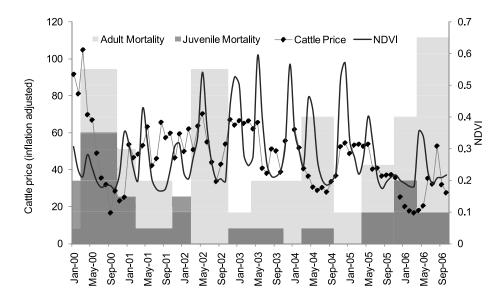


Figure 1. Monthly average (2000-2006) normalized difference vegetation index (NDVI), monthly average cattle price, and the number of elephant deaths per wetdry season (juveniles in dark gray and adults in light grayscaled from 0 at the bottom of the graph to 13 in the last bar on the far right).

commodity price of maize (U.S. dollars per metric ton adjusted for inflation) on the Nairobi exchange in analyses. Monthly price data were averaged for April through October and November through March for each year.

I incorporated the annual rate of change in Kenya's GDP (U.N. 2009) in models of annual elephant mortality. I used annual rates of GDP change in East Asia (the primary ivory-purchasing region) (U.N. 2009) as a measure of global demand for ivory (Poudyal et al. 2009). The U.N. releases annual rates of GDP change for specified areas by fiscal year, January-December (U.N. 2009). Because elephant mortality data were collated by season (biannually starting in April or November), data on mortality (November-October) and GDP were mismatched by 2 months.

### **Primary Productivity**

I used the normalized difference vegetation index (NDVI) as a measure of primary productivity in the study system. The NDVI is derived from remotely sensed spectral images and is the ratio of visual (VIS) to near infrared (NIR) reflection NDVI =  $\frac{NIR - VIS}{NIR + VIS}$ . The NDVI is correlated with green biomass and, therefore, provides an estimate of the abundance of vegetation (Pettorelli et al. 2005). I used the mean 10-day composite NDVI value, recorded by the SPOT (Satellite Probatoire d'Observation de la Terre) system at 1-km resolution, for an approximately 1200-km<sup>2</sup> area defined from radio-tracking data on 12 female elephants (Wittemyer et al. 2007b) to represent time-specific vegetation productivity. Because productivity during the wet season affects biomass of vegetation for the following dry season, I used the seasonal maximum NDVI value (i.e., the highest, 10-day composite value averaged for the 1200-km<sup>2</sup> area during a wet-dry seasonal cycle) in my analyses, as recommended by Rasmussen et al. (2006) (Fig. 1).

# **Household Survey Data**

As part of a Global Environment Facility (GEF) project conducted in July 2002, household survey data were collected from 100 randomly selected households living on the boundary of Samburu and Buffalo Springs national reserves. Open-ended questions were asked regarding each household's attitudes toward the nature reserves, problems they encounter related to the location of the reserves, the relative severity of these problems, and their current number of cattle and goats (Supporting Information). I used data from this survey to assess the relative importance of human-wildlife conflict and general attitudes toward wildlife and management bodies.

#### **Statistical Analyses**

Poisson regression is commonly used to analyze count data, but the residual deviance of my models indicated overdispersion by a factor of 2-3. Therefore, I used negative binomial generalized linear models, for which the relation between residual deviance and degrees of freedom  $(\varphi \sim 1)$  indicated almost no overdispersion. Temporal independence of the 3 response variables (adult mortality, juvenile mortality, and human-caused wounds) at seasonal and annual time lags was established with partial autocorrelation functions; therefore, time was not incorporated in the model structure. Independent variables were maximum current and previous wet-dry season averaged composite NDVI value; average seasonal market prices of cattle, goats, and maize; and annual change in GDP for Kenya and East Asia. I conducted separate analyses for each response variable. I conducted analyses with data from 14 seasons, except for analyses that incorporated GDP growth, for which all data were collated annually (7 years).

I used information theoretic approaches to compare the performance of models on the basis of bias-adjusted Wittemyer 5

Table 1. Bias-adjusted Akaike's information criterion (AIC<sub>c</sub>) values, weights  $(w_j)$ , and associated independent variables for the top negative binomial generalized linear models of seasonal and annual elephant mortality (juvenile and adult) and seasonal human-caused elephant wounds.

Relative model performance <sup>a</sup>	$AIC_c$	$\Delta_{\mathbf{i}}$	$w_i$
Adult elephant mortality			
(–)cattle price**	75.19	0	0.68
(–)cattle price** + (+)goat price	77.31	2.13	0.23
(-)cattle price* + (-)NDVImax <sub>t</sub> <sup>b</sup>	79.22	4.03	0.09
Juvenile elephant mortality			
$(-)$ NDVIma $x_t^{***}$	47.96	0	0.60
$(-)$ NDVIma $x_t^{***} + (+)$ goat price	48.90	0.95	0.37
(-)NDVImax <sub>t</sub> ** + $(+)$ goat price +	53.82	5.86	0.03
$(+)$ NDVImax $_{(t-1)}^{c}$			
Human-induced elephant wounds			
(–)cattle price*** + (+)goat price**	57.02	0	0.37
(-)NDVImax <sub>t</sub> *	57.03	0.15	0.36
(–)cattle price*	58.52	1.64	0.17
$(+)$ NDVImax $_{(t-1)}$	59.66	2.64	0.10
Annual adult elephant mortality			
(-)cattle price*** + (+)goat price**	42.56	0	0.70
(-)cattle price*+ (+) GDP <sub>Asia</sub> *d	45.47	2.91	0.16
(–)cattle price*	45.73	3.17	0.14

<sup>&</sup>lt;sup>a</sup>Signs in parentheses indicate the direction of coefficients. Units of cattle and goat prices are inflation-adjusted Kenya shillings; p = 0.05; \*\*p = 0.01; \*\*\*p = 0.001.

Akaike's information criterion (AIC<sub>c</sub>) (the use of which is suggested when the ratio of the sample size to the number of model parameters is <40) and AIC weights (the contribution of a candidate model to the sum of the relative weights of all models compared). Models with weights <10% of the best-fit model are considered weakly supported; therefore, I do not present them in the results (Burnham & Andersen 1998). For analyses of seasonal data, I compared AICc among all possible models; full models contained all 5 independent variables and interactions between prices of cattle, goats, and maize plus all constitutive terms (i.e., interaction components) and current- and previous-season NDVI. The full model for annual data, analyzed following the same procedure, did not incorporate NDVI, but included interactions between prices of cattle, goats, and maize. I used R (version 2.9.1) (R Development Core Team 2008) for all statistical analyses.

#### Results

Inflation-adjusted cattle prices explained over 40% of the deviance in mortality of adult elephants and demonstrated the greatest weight of evidence among the assessed independent variables (Table 1). On the basis of

Table 2. Negative binomial generalized linear model results for the model with the best fit (see Table 1) of adult or juvenile seasonal mortality, human-caused wounds, and annual adult mortality of elephants.

Best-fit model parameters	Estimate	SE	Z	р
Adult montality				
Adult mortality	2.00	0 /=	( <b>-</b> /	0.01
intercept	3.08	0.47	6.54	< 0.01
cattle price	-0.03	0.01	-2.89	< 0.01
Juvenile mortality				
intercept	3.17	0.69	4.62	< 0.01
NDVI*	-5.93	1.69	-3.50	< 0.01
Human wounds				
intercept	1.82	0.63	2.90	< 0.01
cattle price	-0.07	0.02	-3.36	< 0.01
goat price	0.25	0.09	2.78	< 0.01
Annual adult mortality				
intercept	3.08	0.57	5.39	< 0.01
cattle price	-0.05	0.02	-2.50	0.01
goat price	0.19	0.07	2.81	< 0.01

<sup>\*</sup>Normalized difference vegetation index (NDVI).

model fit, the negative correlation predicted the number of deaths of adult elephants in a season decreased from 13 to 1 across the observed range of cattle prices (Table 2 & Fig. 2). The NDVI was not significantly correlated with adult mortality (Table 1). This covariate appeared in the third best-supported model, which had nearly 8 times less support than the model with cattle prices alone (Table 1). Consistent with these results, the best-fit model of human-inflicted wounds contained both cattle (z = -3.36, p < 0.01) and goat prices (z = 2.78, p< 0.01; Table 2). In this model the negative correlation predicted the number of adult elephants wounded in a season decreased from nearly 5 to 1 across the observed range of cattle prices. The model containing currentseason NDVI was approximately equivalent to the model with livestock prices ( $\triangle AIC = 0.01$ ), but the negative association between human-inflicted wounds and cattle prices was 1.48 times more plausible than that between human-inflicted wounds and NDVI (Table 1).

In contrast to adult mortality, the variable most strongly associated with juvenile mortality was current NDVI (Table 1 & Fig. 3). The best-fit model contained only a negative association with current season NDVI (z=-3.50, p<0.01; Table 2), for which the negative correlation predicted the number of deaths of juvenile elephants in a season decreased from 6 to 1 across the observed range of NDVI. The second best model contained both current-season NDVI and goat prices (Table 1), but as an explanation of juvenile mortality current-season NDVI was 3 times more plausible than goat prices.

The best model of annual adult mortality contained both cattle ( $z=-2.50,\,p<0.05$ ) and goat prices ( $z=2.81,\,p<0.01$ ; Table 2) and explained over 95% of the deviance in annual adult mortality. Cattle price was the covariate most strongly associated with annual adult

<sup>&</sup>lt;sup>b</sup>Current-season maximum normalized difference vegetation index (NDVI).

<sup>&</sup>lt;sup>c</sup>Previous-season maximum normalized difference vegetation index (NDVI)

<sup>&</sup>lt;sup>d</sup>Annual change in East Asian gross domestic product (GDP).

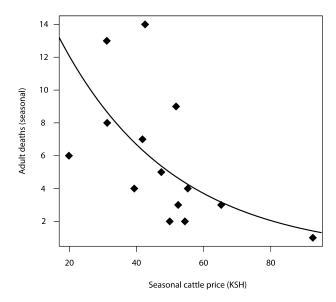


Figure 2. Negative binomial generalized linear model fit (line) between recorded deaths of adult elephants for each wet-dry season and local, averaged cattle prices (inflation-adjusted Kenya shillings [KSH]) over the same period.

elephant mortality, and the negative correlation predicted that the number of adult elephant deaths in a year decreased from nearly 14 to 11 across the observed range of cattle prices. Although East Asia's GDP growth was positively associated with adult mortality, the relation was not significant and the weight of evidence for

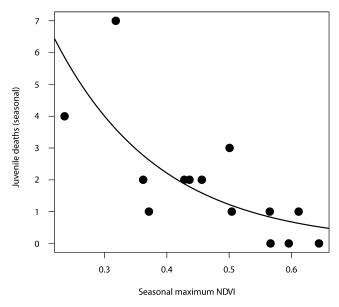


Figure 3. Negative binomial generalized linear model fit (line) between recorded deaths of juvenile elephants for each wet-dry season and the maximum normalized difference vegetation index (NDVI) for the study area over the same period.

the model incorporating East Asia's GDP was over 4 times less than that of the best-fit model (Table 1).

Although direct information on poaching was not available, household survey data indicated that conflict with wild animals in general (i.e., not specific to elephants) was not a primary concern among communities bordering the national reserves. Only 12% of households identified general wild animal conflict as a problem, and all households indicated the magnitude of other problems related to their location was greater. A greater percentage of poorer households (17%) (i.e., those with livestock holdings below the average) than wealthier households (9%) identified conflicts with wild animal as a problem; however, livestock holdings did not differ significantly between households that identified conflict with wild animals as a problem and those that did not (Z = 0.37, p =0.71). Those households indicating that they derived benefits from the national reserves (n = 71), however, tended to have more livestock than those that did not indicate the reserves provided benefit (Z = 2.47, p < 0.05).

## **Discussion**

Although studies and models of illegal harvesting of animals often focus on the relation between deterrents (e.g., patrolling and fines) and harvest levels (Hilborn et al. 2006), there have been few direct assessments of social and economic factors related to illegal offtake (Gavin et al. 2010). I found that adult elephant mortality and human-induced wounding of elephants were closely correlated with indices of economic conditions in local pastoral communities (Table 1 & Fig. 2). Human hunting of elephants, the only source of predation on adults in the study system (Wittemyer et al. 2005), generally targets adult animals as a function of the size of their tusks and their weight (meat) (Milner-Gulland & Mace 1991). In pastoral systems, changing forms of income generation is a common response to environmental stochasticity (Mc-Peak 2005; McPeak et al. 2006; Davies & Bennett 2007). Thus, my results may reflect a change to high risk but potentially lucrative poaching for ivory or meat in response to the downturn in traditional revenue sources. Comparable increases in the use of natural resources (plant and animal) triggered by economic shocks (Pallot & Moran 2000; Fisher & Shively 2005) and elevated food prices (Brashares et al. 2004; Wilkie et al. 2005) has been observed in other ecosystems.

Amplified conflict between humans and wild animals during economic recessions could also drive the correlations I found. Livelihoods may be more sensitive to conflict with wild animals or tolerance of wild animals may decrease as a function of stress on local communities caused by economic hardship. In the study system, conflict between humans and wild animals was not identified in surveys as a primary concern by local people;

Wittemyer 7

therefore, it is unlikely the observed increase in adult elephant mortality during economic downturns was caused by conflict. There are stiff penalties associated with illegal killing of elephants, which makes direct information on illegal killing difficult to attain. Because this study is correlative, my results only offer insight into possible causal links. Determining causes of illegal activities is often challenging, but the focused sociological study of illegal activity through indirect interview methods can provide useful information (Gavin et al. 2010). Little is known about the relations among economic cycles, conflict between humans and animals, and illegal harvesting, but identifying such connections may help optimize deterrent efforts (Gavin & Anderson 2007).

Differentiation in age-class-specific mortalities of elephants provides additional insight to the mechanisms driving mortality. The influence of economic factors on elephant mortality may be complicated by variation in environmental factors that affect elephant demography (Wittemyer et al. 2007b) and livestock-based economies (McPeak 2005) (e.g., poor recruitment in elephants and livestock is correlated with low primary productivity). Ungulate survival is strongly mediated by environmental stochasticity or population density (Gaillard et al. 2000), and younger age classes are more susceptible to resource limitations than adults (Gaillard et al. 1998). In my study, NDVI was the only statistically significant correlate of juvenile elephant mortality, and it was not associated with adult elephant mortality. Although 2 severe droughts during the study period likely caused the deaths of adult elephants, the dominant cause of known adult deaths in the study system was human killing (Wittemyer et al. 2005). The different patterns of elephant mortality between juveniles and adults likely stem from the strong influence of human selection for high-value adults.

Macroeconomic conditions also may be important indicators of elephant mortality where such conditions influence rates of illegal elephant harvesting. Changes in Kenya and East Asia's GDP, a potential indicator of ivory demand (Poudyal et al. 2009), however, had little explanatory power in my models. The lack of correlation between the latter macroeconomic metrics and elephant mortality in contrast to the correlation of mortality with local commodity prices may reflect the economic isolation of pastoral communities (McPeak & Barrett 2001) or the disparity between different sectors of Kenya's economy. Although not comparable to the subsistence-based economy in my study system, the utility of macroeconomic indicators for explaining observed patterns and predicting illegal harvest of wild animals has been shown in other studies (Poudyal et al. 2009) and may be effective for predicting larger scale mortality patterns.

Although my results are from a single species in a single system, the correlation between threats to a species affected by trade and local economic recessions may be of broad relevance to species conservation and management bodies. In particular, such connections may influence conservation initiatives in communities in which local economics can influence harvest quotas of animal species (Barrett & Arcese 1995). Information on economic fluctuations can serve to focus management activities on, for example, enhancing employment opportunities during economic downturns or adjustment of antipoaching efforts in response to or anticipation of economically driven changes in natural resource reliance. Informative metrics may be system specific or general (with the latter being relevant where harvest of wild animals driven by economics is synchronized over large areas and multiple species), but such data may be easily and cheaply obtained through market surveys or publicly available economic data. Management responses to such economic indices, however, may be limited by the fact that conservation goals and associated resource allocations are often low priorities during economic crises (Pergams et al. 2004).

# Acknowledgments

I thank the Kenyan Office of the President; Kenya Wildlife Service; the Samburu and Buffalo Springs national reserves' county councils, wardens, and rangers; and D. Daballen, D. Lentipo, and I. Douglas-Hamilton of Save the Elephants. R. Kuriyan generously provided household survey data for this analysis and assisted in interpretation of results. J. Berger, C. Burton, H.T. Dublin, E. Fleishman, J. Goldstein, R. Kuriyan, M. McCarthy, and 2 anonymous reviewers provided helpful comments on this manuscript.

# **Supporting Information**

The household survey instrument (Appendix S1) is available online. The author is solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

#### Literature Cited

ALRMP (Arid Lands Resource Management Project). 2009. Arid Lands Resource Management Project II Early Warning System (EWS) bulletins. Ministry of State for the development of northern Kenya and Other Arid Lands, Nairobi. Available from http://www.aridland.go.ke/index.php (accessed January 2009).

Barbier, E. B. 2005. Natural resources and economic development. Cambridge University Press, New York.

Barrett, C. B., and P. Arcese. 1995. Are integrated conservationdevelopment projects (ICDPs) sustainable-on the conservation of large mammals in sub-Saharan Africa. World Development 23:1073-1084.

Barrett, C. B., T. Reardon, and P. Webb. 2001. Nonfarm income diversification and household livelihood strategies in rural Africa: concepts, dynamics, and policy implications. Food Policy 26:315-331.

- Brashares, J. S., P. Arcese, M. K. Sam, P. B. Coppolillo, A. R. E. Sinclair, and A. Balmford. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306:1180-1183.
- Bulte, E. H., and G. C. van Kooten. 1999. Economic efficiency, resource conservation and the ivory trade ban. Ecological Economics 28:171-181.
- Burnham, K. P., and D. R. Andersen. 1998. Model selection and inference: a practical theoretic approach. Springer, New York.
- Chan, K. W. 2010. The global financial crisis and migrant workers in China: 'There is no future as a labourer; returning to the village has no meaning.' International Journal of Urban and Regional Research 34:659-677.
- Davies, J. 2008. Turning the tide: enabling sustainable development for Africa's mobile pastoralists. Natural Resources Forum 32:175-184.
- Davies, J., and R. Bennett. 2007. Livelihood adaptation to risk: constraints and opportunities for pastoral development in Ethiopia's afar region. Journal of Development Studies 43:490-511.
- de Merode, E., K. Homewood, and G. Cowlishaw. 2004. The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. Biological Conservation 118:573–581.
- Dietz, T., E. A. Rosa, and R. York. 2007. Driving the human ecological footprint. Frontiers in Ecology and Evolution 5:13-18.
- Fisher, M. 2004. Household welfare and forest dependence in southern Malawi. Environment and Development Economics 9:135–154.
- Fisher, M., and G. Shively. 2005. Can income programs reduce tropical forest pressure? Income shocks and forest use in Malawi. World Development 33:1115-1128.
- Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Populations dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58-63.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.
- Gavin, M. C., and G. J. Anderson. 2007. Socioeconomic predictors of forest use values in the Peruvian Amazon: A potential tool for biodiversity conservation. Ecological Economics 60:752-762.
- Gavin, M. C., J. N. Solomon, and S. G. Blank. 2010. Measuring and monitoring illegal use of natural resources. Conservation Biology 24:89-100.
- Hilborn, R., P. Arcese, M. Borner, J. Hando, G. Hopcraft, M. Loibooki, S. Mduma, and A. Sinclair. 2006. Effective enforcement in a conservation area. Science 314:1266-1266.
- Jalan, J., and M. Ravallion. 2000. Is transient poverty different? Evidence for rural China. Journal of Development Studies 36:82-99.
- Kahindi, O., G. Wittemyer, J. King, F. Ihwagi, P. Omondi, and I. Douglas-Hamilton. 2010. Employing participatory surveys to monitor the illegal killing of elephants across diverse land uses in Laikipia-Samburu, Kenya. African Journal of Ecology 48:972–983.
- Kuhl, A., N. Balinova, E. Bykova, Y. N. Arylov, A. Esipov, A. A. Lushchekina, and E. J. Milner-Gulland. 2009. The role of saiga poaching in rural communities: linkages between attitudes, socio-economic circumstances and behaviour. Biological Conservation 142:1442-1449.
- Leader-Williams, N., S. D. Albon, and P. S. M. Berry. 1990. Illegal exploitation of black rhinoceros and elephant populations—patterns of decline, law enforcement and patrol effort in the Luangwa Valley, Zambia. Journal of Applied Ecology 27:1055-1087.
- Livingstone, I. 1986. The common property problem and pastoralist economic-behavior. Journal of Development Studies 23:5–19.
- Mainka, S., and M. Trivedi. 2002. Links between biodiversity conservation, livelihoods and security: the sustainable use of wild species for meat. International Union for Conservation of Nature, Species Survival Commission, Gland, Switzerland.
- McPeak, J. 2005. Individual and collective rationality in pastoral production: evidence from northern Kenya. Human Ecology 33:171-197.

- McPeak, J. G., and C. B. Barrett. 2001. Differential risk exposure and stochastic poverty traps among east African pastoralists. American Journal of Agricultural Economics 83:674-679.
- McPeak, J. G., D. R. Lee, and C. B. Barrett. 2006. Introduction: the dynamics of coupled human and natural systems. Environment and Development Economics 11:9-13.
- Milner-Gulland, E. J., and N. Leader-Williams. 1992. A model of incentives for the illegal exploitation of black rhinos and elephants: poaching pays in Luangwa Valley, Zambia. Journal of Applied Ecology 29:388-401.
- Milner-Gulland, E. J., and R. Mace. 1991. The impact of the ivory trade on the African Elephant Loxodonta-africana population as assessed by data from the trade. Biological Conservation **55:**215-229
- Moss, C. J. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. Journal of Zoology 255:145-156.
- Pallot, J., and D. Moran. 2000. Surviving the margins in post-Soviet Russia: forestry villages in northern Perm' Oblast. Post-Soviet Geography and Economics 41:341-364.
- Pergams, O. R. W., B. Czech, J. C. Haney, and D. Nyberg. 2004. Linkage of conservation activity to trends in the US economy. Conservation Biology 18:1617–1623.
- Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.
- Poudyal, M., K. Rothley, and D. Knowler. 2009. Ecological and economic analysis of poaching of the greater one-horned rhinoceros (*Rbinoceros unicornis*) in Nepal. Ecological Applications 19:1693–1707.
- Quam, M. D. 1978. Cattle marketing and pastoral conservatism: Karamoja District, Uganda, 1948-1970. African Studies Review 21:49-71.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rasmussen, H. B., G. Wittemyer, and I. Douglas-Hamilton. 2005. Estimating age of immobilized elephants from teeth impression using dental acrylic. African Journal of Ecology 43:215–219.
- Rasmussen, H. B., G. Wittemyer, and I. Douglas-Hamilton. 2006. Predicting time-specific changes in demographic processes using remotesensing data. Journal of Applied Ecology 43:366–376.
- Suryahadi, A., and S. Sumarto. 2003. Poverty and vulnerability in Indonesia before and after the economic crisis. Asian Economic Journal 17:45-64.
- U.N. (United Nations). 2009. National accounts main aggregates database. U.N. Department of Economic and Social Affairs, Statistics Division, New York.
- Wilkie, D. S., M. Starkey, K. Abernethy, E. N. Effa, P. Telfer, and R. Godoy. 2005. Role of prices and wealth in consumer demand for bushmeat in Gabon, central Africa. Conservation Biology 19:268–274.
- Wittemyer, G. 2001. The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. African Journal of Ecology 39:357–365.
- Wittemyer, G., D. K. Daballen, H. B. Rasmussen, O. Kahindi, and I. Douglas-Hamilton. 2005. Demographic status of elephants in the Samburu and Buffalo Springs national reserves, Kenya. African Journal of Ecology 43:44-47.
- Wittemyer, G., W. M. Getz, F. Vollrath, and I. Douglas-Hamilton. 2007a. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. Behavioral Ecology and Sociobiology 61:1919-1931.
- Wittemyer, G., H. B. Rasmussen, and I. Douglas-Hamilton. 2007b. Breeding phenology in relation to NDVI variability in free-ranging African elephant. Ecography 30:42-50.