Conservation Biology

Contributed Paper

Rapid declines of large mammal populations after the collapse of the Soviet Union

Eugenia V. Bragina,*† ¶ A. R. Ives,‡ A. M. Pidgeon,* T. Kuemmerle,§ L. M. Baskin,** Y. P. Gubar,†† M. Piquer-Rodríguez,§ N. S. Keuler,‡‡ V. G. Petrosyan,** and V. C. Radeloff*

*Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, U.S.A.
†Faculty of Biology, Lomonosov Moscow State University, 1-12 Leninskie Gory, Moscow, 119991, Russia
‡Department of Zoology, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, U.S.A.
§Geography Department, Humboldt-Universitat zu Berlin, Unter den Linden 6, 10099 Berlin, Germany
**Severtsov Institute of Ecology and Evolution, 33 Leninsky pr., Moscow, 117071, Russia
††FGU 'Thentrohotcontrol', 4 Zoologicheskaya str., Moscow, 123056, Russia
‡‡Department of Statistics, University of Wisconsin-Madison, 1300 University Avenue, Madison, WI 53706, U.S.A.

Abstract: *Anecdotal evidence suggests that socioeconomic shocks strongly affect wildlife populations, but quantitative evidence is sparse. The collapse of socialism in Russia in 1991 caused a major socioeconomic shock, including a sharp increase in poverty. We analyzed population trends of 8 large mammals in Russia from 1981 to 2010 (i.e., before and after the collapse). We hypothesized that the collapse would first cause population declines, primarily due to overexploitation, and then population increases due to adaptation of wildlife to new environments following the collapse. The long-term Database of the Russian Federal Agency of Game Mammal Monitoring, consisting of up to 50,000 transects that are monitored annually, provided an exceptional data set for investigating these population trends. Three species showed strong declines in population growth rates in the decade following the collapse, while grey wolf* (Canis lupus) *increased by more than 150%. After 2000 some trends reversed. For example, roe deer* (Capreolus spp.) *abundance in 2010 was the highest of any period in our study. Likely reasons for the population declines in the 1990s include poaching and the erosion of wildlife protection enforcement. The rapid increase of the grey wolf populations is likely due to the cessation of governmental population control. In general, the widespread declines in wildlife populations after the collapse of the Soviet Union highlight the magnitude of the effects that socioeconomic shocks can have on wildlife populations and the possible need for special conservation efforts during such times.*

Keywords: change point, game mammals, population trend, Russia, socioeconomic shock

Declinación Rápida de las Poblaciones de Mamíferos Mayores después del Colapso de la Unión Soviética

Resumen: *La evidencia anecdótica sugiere que los shocks socio-económicos afectan fuertemente a las poblaciones silvestres, pero la evidencia cuantitativa es escasa. El colapso del socialismo en Rusia en 1991 causó un gran shock socio-económico, incluido un incremento repentino en la pobreza. Analizamos las tendencias poblacionales de ocho mamíferos mayores en Rusia a partir de 1981 y hasta 2010 (es decir, antes y después del colapso). Propusimos la hipótesis de que el colapso primero causaría declinaciones poblacionales, principalmente por causa de la sobreexplotación, y después incrementos debido a la adaptación de la vida silvestre a nuevos ambientes. La Base de Datos a largo plazo de la Agencia Federal Rusa del Monitoreo de Mamíferos de Caza, que consiste en hasta 50, 000 transectos que se monitorean anualmente, proporcionó un conjunto excepcional de datos para investigar estas tendencias poblacionales. Tres especies mostraron fuertes declinaciones en la tasa de crecimiento poblacional en la década después del colapso, mientras que las poblaciones de lobo gris* (Canis lupus) *incrementaron por más del 150%. Después del año 2000 algunas*

¶*email e.bragina@gmail.com*
Paper submitted March 17, 2014; revised manuscript accepted October 3, 2014.

DOI: 10.1111/cobi.12450

tendencias fueron revertidas. Por ejemplo, la abundancia del venado de corzo (Capreolus spp.) *en 2010 fue la más alta de cualquier periodo de nuestro estudio. Las razones probables de la declinación poblacional en la década de 1990 incluyen a la caza furtiva y a la degradación de la aplicación de la protección de vida silvestre. El incremento súbito en la población de lobos grises probablemente se debe al cese del control poblacional por parte del gobierno. En general, las amplias declinaciones de las poblaciones silvestres después del colapso de la Unión Soviética resaltan la magnitud de los efectos que los shocks socio-económicos pueden tener sobre las poblaciones silvestres y la posible necesidad de esfuerzos especiales de conservación durante estos tiempos.*

Palabras Clave: mamíferos de caza, punto de cambio, Rusia, shock socio-económico, tendencia poblacional

Introduction

Rapid changes in governmental and social institutions can greatly affect conservation efforts because they are often accompanied by overexploitation of natural resources (Wittemyer 2011). Overexploitation is a particular threat when poverty forces people to rely on wildlife for their income (Brashares et al. 2004; Sinclair 2005; Ehrlich & Pringle 2008) or when institutional regulations governing exploitation are lacking (e.g., Sinclair 2005; Barrett et al. 2006; Wittemyer 2011). Conversely, times of change also entail opportunities for conservation. Land-use intensity often declines, allowing vegetation to recover (Kuemmerle et al. 2011), and the designation of major protected areas often coincides with institutional and social upheaval (Radeloff et al. 2013). Thus, socioeconomic shocks may hinder or help conservation. However, there have been too few comprehensive broad-scale studies to predict possible consequences of future socioeconomic changes.

A prime example of a socioeconomic shock is the collapse of the Soviet Union in 1991. Per-capita GDP in the Russian Federation plummeted after 1991 and stayed below 1990s levels until 2004 (United Nations Statistics Division 2013). Countries gained independence, land was privatized (Lerman & Shagaida 2007), previously state-controlled economies folded (Kolesnikov 2003), and governmental funding for wildlife management vanished (Williams 1996). Concomitantly, there were major land-use changes, most notably widespread farmland abandonment (Ioffe & Nefedova 2004) and steep declines in livestock numbers (Kolesnikov 2003) and forest harvesting (Filiptchouk et al. 2001). The collapse of the Soviet Union thus represents a perfect opportunity to examine how socioeconomic shocks affect wildlife populations both immediately (e.g., from poaching) and in the long term (e.g., from habitat change and human migration).

Prior studies of wildlife populations after the collapse of the Soviet Union reported varying trends. The dramatic decline of saiga antelope (*Saiga tatarica)* population began even before the collapse (Milner-Gulland et al. 2001). Also declining were red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus* and *Capreolus pygargus*), moose (*Alces alces*) (Petrosyan et al. 2012), reindeer (*Rangifer tarandus*) (Danilkin 1999), and wild boar (*Sus scrofa*) (Danilkin 2002; Petrosyan et al. 2012). A negative trend in wildlife populations was also reported for countries adjacent to Russia, including Mongolia (Pratt et al. 2004), Estonia (Valdmann 2001), the Czech Republic (Hladikova et al. 2008), and Romania (Micu et al. 2005). However, sika deer (*Cervus nippon*) (Stephens et al. 2006), argali (*Ovis ammon*) (Fedosenko & Weinberg 2001), and steppe raptors (Sánchez-Zapata et al. 2003) increased at least locally in post-Soviet area. This variation among species was likely caused by case-by-case differences in drivers and by differences in species' capacity to respond. For example, species with high reproductive rates are better equipped to recover rapidly from low population levels (Polishchuk 2002). The collapse of the Soviet Union appears to have been associated with both positive and negative outcomes for wildlife, highlighting the need for a systematic and comprehensive analysis.

We analyzed population trends of 8 large mammal species: European and Siberian roe deer (grouped together), red deer, reindeer, moose, wild boar, brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), and grey wolf (*Canis lupus*) from 1981 to 2010 in Russia, which encompasses periods before and after the collapse of the Soviet Union in 1991. We asked whether changes in population trends occurred coincidently with the Soviet Union collapse. We expected that all large mammals except wolves would show declines immediately after the 1991 collapse but increase after 2000 as socioeconomic conditions began to improve (United Nations Statistics Division 2013). Among the ungulate species, wild boar and roe deer possess greater fecundity than moose and red deer and thus have high population growth rates (Danilkin 1999; Geisser & Reyer 2005). We thus expected that wild boar and roe deer populations would rebound after an initial decline.

Methods

Data Set

Our source of data was the database of Russian Federal Agency of Game Mammal Monitoring. About 20 mammal species are counted annually. The monitoring

Table 1. Number of Russian regions studied and total population size for each species.[a]

Species	Number of regions in analysis	Total population in 2010 (thousands)	Published total population in 2010 (thousands)	Percent of 2010 total population[b]
Roe deer	47	791.3	845.5	93.6
Red deer	16	173.8	187.2	92.8
Wild reindeer	11	783.1	939.5	83.4
Moose	61	645.0	656.7	98.2
Wild boar	59	387.5	404.4	95.8
Brown bear	40	180.2	183.0	98.5
Eurasian lynx	50	18.5	20.7	89.1
Wolf	69	48.9	49.7	98.5

[a] *Includes only regions in which there were data for at least 27 of the 30 study years. For comparison, total population estimated from these regions and published total population size in Russia are included.*
[b] *Percentage of the estimated total our data represents.*

methods include winter track counts (WTC) (Mirutenko et al. 2009), accompanied and verified by aerial surveys, surveys on established plots, written surveys completed by hunters, and fall surveys of upland game (Gubar 2007).

The WTC is conducted in regions with stable snow cover. It measures the density of each species based on the number of tracks which cross a transect and the average daily movement distance of each species: $D = \pi * A/2L$, where D is the average number of animals per 10 ha, A is average track number which cross a transect per 10 km, and L is the average daily movement distance of an animal. This means WTC includes track counts and measurements of daily movement distance, which are measured by following animal tracks.

Statistical summaries at the regional level are available from 1981 to the present in the form of one estimate per year and per region for each species surveyed (Game Mammals of Russia 1992–2011).

We examined brown bear, Eurasian lynx, wolf, European and Siberian roe deer, red deer, reindeer, moose, and wild boar. Large carnivores and herbivores require large areas (Garshelis 1992) that are difficult to conserve in human-dominated landscapes (Woodroffe 1998; Gordon 2009). While other species are also counted in the WTC, we excluded species from our analyses that have narrow distributions (e.g., muskox [*Ovibos moschatus*]) or are not highly prized game species (e.g., red squirrel [*Sciurus vulgaris*]).

We analyzed the time series of WTC data for those regions which had no more than 3 years of missing data for the period 1981–2010. We analyzed the population of brown bear, wolf, and lynx in 40, 70, and 49 regions, respectively, and the population of moose, reindeer, roe deer, red deer and wild boar in 61, 11, 47, 16, and 57 regions, respectively. This translated to 83.4–98.5% of the total population for each species in Russia for 2010 (Table 1). Hereafter, we used the term *total population size* to designate total number of animals of each species summed for all these regions.

Change Point Selection

During the study period, the year 1991 was the key turning point in institutional and socioeconomic conditions, so we set this as our initial change point. To separate the potential immediate versus longer term effects of the socioeconomic shock, we divided the period after 1991 in 2 at the point when Russian GDP changed direction from negative to positive (i.e., after the year 2000 [United Nations Statistics Division 2013]). Thus, we divided each time series into 3 periods: before the Soviet Union collapse (1981–1991), directly after the collapse (1992–2000), and 10–20 years after the collapse (2001–2010).

Data Analyses

To estimate absolute population trends for the 30-year period, we calculated per-capita population growth rates λ_t as N_{t+1}/N_t, where N_t and N_{t+1} are population number in year t and in year $t+1$, respectively. In this case, $\lambda_1{}^* \lambda_2{}^* \ldots \lambda_t = N_{t+1}/N_1$ and a geometrical average $\lambda_{\text{aver}} = (\lambda_1{}^* \lambda_2{}^* \ldots \lambda_t)\hat{}(1/t) = (N_{t+1}/N_1)\hat{}(1/t)$. We computed these values for the 3 periods of our study. A $\lambda < 1$ implies population decline, and $\lambda > 1$ implies population growth.

To estimate relative population trend, we fitted first-order autoregressive models of the form $(n_{r,t+1} - \mu_r) = \rho_r(n_{r,t} - \mu_r) + \varepsilon_{r,t}$ to the time series of each population in each region across Russia (Table 1), where $n_{r,t}$ is the log-transformed population density in region r in year t that is standardized to have variance 1, μ_r is the mean regional population density, ρ_r is the autoregression coefficient, and $\varepsilon_{r,t}$ represents the region-specific residuals. Because densities were log-transformed, differences between consecutive years provided the annual per-capita population growth rates. By standardizing $n_{r,t}$ to have variance 1, all regions were weighted equally in the analyses, even though they contained different mean densities; the overall conclusions were the same when $n_{r,t}$ was not

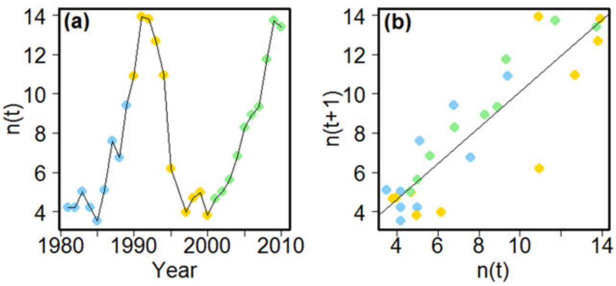

Figure 1. An example of autoregressive model ($n_{r,t+1} - \mu_r) = \rho_r(n_{r,t} - \mu_r) + \varepsilon_{r,t}$ fit, where $n_{r,t}$ is the log-transformed population density in region r in year t (blue, 1981–1991; yellow, 1992–2000; green, 2001–2010): (a) time series data for wild boar in Pskov region and (b) fit of the model to the data for wild boar in Pskov region (points above the line, i.e., most of blue and green points from the first and third periods, respectively, indicate a growing population; points below the line, i.e., most of yellow points from 2nd period indicate a declining population).

standardized. We analyzed mean residuals of the model in each of the 3 periods (1981–1991, 1992–2000, and 2001–2010), that is, the mean of the values of $\varepsilon_{r,t}$. We considered the per-capita population growth rate in a given period to be low if the mean residual for this period was negative and high if it was positive because the mean value of all residuals was zero. The basic idea is shown in Fig. 1, where some points have $n_{t+1} > n_t$. These points correspond to years when the number of animals was higher in a given year than in the previous year. Similarly, when $n_{t+1} < n_t$, the number of animals was lower in a given year than in the previous year. Our method thus measures the relative per-capita population growth rates among periods because total residuals equaled zero whether population trend was positive or negative overall. Therefore, the mean residual for a given period shows only the sign and magnitude of a population size change relative to other periods.

For statistical inference, we conducted a parametric bootstrap procedure. First, we fitted the autoregressive model $(n_{r,t+1} - \mu_r) = \rho_r(n_{r,t} - \mu_r) + \varepsilon_{r,t}$ to every region separately and collected residuals. Second, we computed the covariance matrix of residuals among regions to account for spatial correlation. Third, using this covariance matrix, we generated spatially covarying random residuals with the package mvtnorm for R statistical software (Genz & Bretz 2009; Genz et al. 2012) and simulated data using the autoregressive model with parameters estimated from the original data. Thus, these simulated data sets included both spatial correlations through the covariance matrix of ε_t and temporal autocorrelation through the coefficient ρ_r. Fourth, we applied the autoregressive model again to the simulated data and computed mean residuals from 3 periods, as we did for the original data. We repeated the third and fourth steps 20,000 times so that the resulting values approximated the distribution of mean residuals under the null hypothesis that there is no difference in per-capita population growth rates in the 3 periods (although there was both spatial and temporal autocorrelation). We calculated p values from this distribution. For example, if the mean residual calculated from the original data was >97.5% of values in the bootstrap distribution of 20,000 residuals, we concluded that p was <0.05 (2-tailed).

Lambda and mean residuals together provide a comprehensive description of population trend in cases of populations with $\lambda > 1$ but negative mean residuals (population increase but more slowly than in other time periods).

To investigate the possibility that broad-scale climate fluctuations explain these population trends, we obtained temperature and precipitation data for 1981–2005 from the website thermograph.ru. We performed similar analyses with untransformed annual precipitation and annual average mean, minimum, and maximum temperatures from 45 meteorological stations in 45 regions of Russia (1 station/region). We divided data into 3 periods (1981–1991, 1992–2000, and 2001–2005). As we did for the population data, we fitted first-order autoregressive models to the time series of each climate variable in each region and analyzed mean residuals of the model in each of the 3 periods.

Results

Population Trends Across Russia

From 1981 to 2010 populations of all 8 species exhibited strong population fluctuations (Fig. 2). Most notably, population trends of roe deer, moose, wild boar, brown bear, Eurasian lynx, and wolf all changed around 1991, and all species except wolf declined immediately after the collapse. Six of the 8 species (wild boar, moose, roe deer, brown bear, lynx, and red deer) had the lowest λ in the period following collapse, and wolf had the highest λ (Fig. 2).

In the 2000s, 6 of our 8 mammal species populations increased again. At the end of 2000s wild boar, brown bear, and roe deer reached their highest population levels during the study period, accompanied by increasing population rates ($\lambda = 1.09$, 1.04 and 1.02, respectively). Populations of moose and red deer also increased ($\lambda = 1.01$ for both species). Only Eurasian lynx ($\lambda = 0.98$) and wild reindeer ($\lambda = 0.99$) continued to decline.

Population Trends for the Each Region

For most species, populations changed synchronously across regions. Accordingly, there were statistically

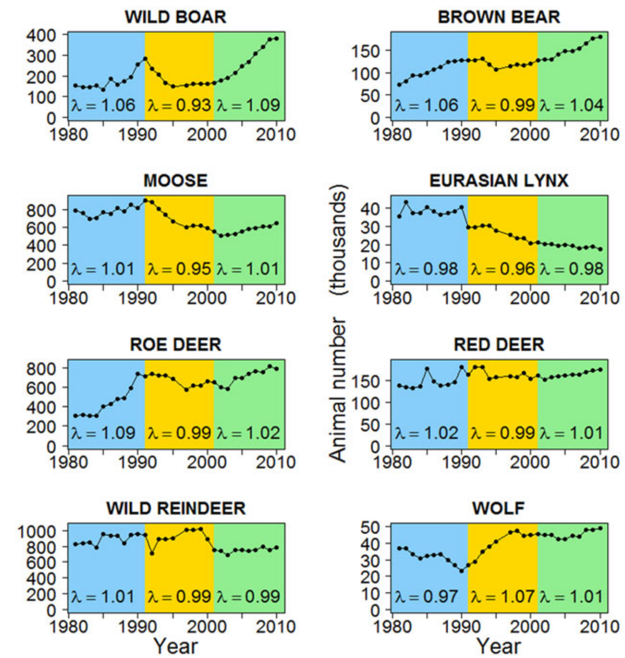

Figure 2. Changes in population size of 8 species from 1981 to 2010 (blue, 1981–1991; yellow, 1992–2000; green, 2001–2010) (λ, per capita population growth rate).

significant declines in per-capita population growth rates immediately following collapse for wild boar, moose, and roe deer and a statistically significant increase for wolf (Table 2). For example, in 38 of the 47 regions where roe deer occurred (94% of the entire roe deer population), populations declined from 1991–2000. However, population trends for species varied among regions (see Fig. 3 for moose and Supporting Information for the other species). We applied a parametric bootstrap test and found significant differences in population trends among regions ($p = 0.001$ for 7 species; $p = 0.22$ for wild reindeer).

From 2001–2010, regional trends exhibited patterns similar to national trends. The overall per-capita population growth rates for roe deer, wild boars, and brown bears were higher than the averages for 1981–2010 in, respectively, 39 of 47 regions, 53 of 59 regions, and 30 of 40 regions though only wild boar per-capita population growth rate was significantly higher than average across the country ($p = 0.009$). Roe deer, wild boar, brown bear, and wolf populations all peaked in either 2009 or 2010.

Climate Variable Trends

We found no significant trend in maximum, minimum, and mean temperatures or annual precipitation for the first 2 periods. In 2001–2005, there was no significant trend for minimum temperature or annual precipitation, but maximum and mean temperatures increased significantly faster than average ($p = 0.039$ and 0.045, respectively).

Discussion

Our results indicate that major changes in the population trends of 4 species of large mammals occurred during the first decade after the collapse of the Soviet Union in 1991 (Table 2). Wild boar, moose, and brown bear had lower per-capita population growth rates, while wolves increased in the 1990s. Increased poaching, low enforcement of protection laws, loss of crops as forage, an increase wolf abundance (Danilkin 2002), and other factors associated with the collapse of the Soviet Union together likely caused the rapid population changes. These results concur with other findings from the former Soviet Union (Danilkin 1999, 2002; Trepet & Eskina 2012). The magnitude of the socio-economic changes in countries of the former Soviet Union was astounding. Post-Soviet changes happened quickly, causing a "poverty shock" (Dudwick et al. 2003) and a "suicide epidemic" (Brainerd 2001). Poverty increased many fold in a very short period after 1991 (Grootaert & Braithwaite 1998). The death rate among working age men increased by 74% (Brainerd 2001). While we did not analyze economic variables and causal relationships between human behavior and wildlife decline, it is clear that given the circumstances, wildlife management institutions were challenged to provide adequate protection for wildlife (Wells & Williams 1998). Social turmoil can result in population declines of vulnerable and endangered species (e.g., saiga antelope [Milner-Gulland et al. 2001] and African elephant [*Loxodonta africana*]). However, the mammals we studied are widespread and are not endangered or threatened (IUCN 2014). Even species with otherwise healthy populations like wild boar (Geisser & Reyer 2005) decreased in population size by half (from 1991 compared with 1995). One of the main conservation messages stemming from our study is that even abundant species may need careful monitoring during times of turmoil. Similarly, wildlife conservation and monitoring efforts may need international assistance during times of turmoil.

In the second decade after the collapse (2001–2010), wild boar populations increased significantly, whereas there was an increasing but not significant trend for brown bear, moose, roe deer, and red deer. For example, wild boar abundance increased by 150% from 1995 to 2010; brown bear abundance increased by 70% between 1995 and 2010, and roe deer increased by 37% from the lowest number in 1997–2010. Conversely, Eurasian lynx continued to decline. Russia's rural population started to decline in 1995 (Ioffe et al. 2004), and Russia's GDP started to rebound in the late 1990s (United Nations Statistics Division 2013). About 40% of farmland in European Russia was abandoned after the collapse and had become early successional forest by the 2000s (Baumann et al. 2012; Potapov et al. 2012; Prishchepov et al. 2012). Succession provided cover and forage for species like bear and moose (Martin et al. 2010; Baskin &

Table 2. Relative and absolute population trends and mean residuals (rows 1 and 2) for real and simulated data, respectively, to show that it is unlikely to achieve a given result with randomly simulated data (in case of $p < 0.05$).

Year		*Roe deer*	*Red deer*	*Wild reindeer*	*Moose*	*Wild boar*	*Brown bear*	*Eurasian lynx*	*Wolf*
1981–1991	Resid. from actual data	−0.087	0.169	−0.121	−0.1	−0.037	−0.064	0.22	−0.091
	Resid. from simulation $\bar{x}$ (SD)	−0.08 (0.03)	−0.08 (0.04)	0.03 (0.03)	0.17 (0.03)	−0.05 (0.04)	−0.04 (0.02)	0.17 (0.03)	−0.01 (0.03)
	p	0.71	0.43	0.56	**0.01**	0.77	0.45	**0.01**	0.68
	N(-) (%)[a]	19 (40)	9 (56)	4 (36)	8 (13)	26 (44)	19 (48)	10 (20)	36 (61)
	$\lambda \geq 1$ (%)[b]	36 (77)	13 (81)	6 (55)	39 (64)	49 (83)	34 (85)	21 (42)	22 (32)
1992–2000	Resid. from actual data	−0.022	−0.17	0.334	−0.118	−0.283	−0.067	−0.184	0.075
	Resid. from simulation $\bar{x}$ (SD)	0.03 (0.04)	0.09 (0.05)	0.04 (0.04)	0.00 (0.05)	−0.13 (0.05)	−0.07 (0.03)	−0.08 (0.04)	0.12 (0.04)
	p	0.43	1	0.59	**0.03**	**0.01**	**0.008**	0.32	**0.01**
	N(-) (%)	38 (81)	7 (44)	5 (45)	54 (89)	52 (88)	34 (85)	36 (72)	9 (13)
	$\lambda \geq 1$	23 (49)	6 (38)	81 (73)	9 (10)	13 (22)	20 (50)	18 (36)	43 (62)
2001–2010	Resid. from actual data	0.105	−0.034	−0.147	0.194	0.263	0.117	−0.073	0.031
	Resid. from simulation $\bar{x}$ (SD)	0.06 (0.03)	0.01 (0.04)	−0.06 (0.03)	−0.17 (0.03)	0.16 (0.04)	0.09 (0.02)	−0.11 (0.03)	−0.09 (0.02)
	p	0.28	0.18	0.58	0.23	**0.009**	0.09	0.18	0.09
	N(-) (%)	8 (17)	5 (31)	6 (55)	36 (59)	6 (10)	10 (25)	35 (70)	49 (71)
	$\lambda \geq 1$	38 (81)	9 (56)	6 (55)	39 (64)	52 (88)	34 (85)	22 (44)	28 (41)
Pop. Size ($N(-)_{2period}$)/Total Pop. size (N[tot]) in 1991[c]		94	58.1	95.2	83.7	90.4	94.3	66.7	4

[a] *Relative trends: number of regions for which autoregressive model output was a negative mean residual (N[-]). The percentage of total analyzed regions in which the mean residual was negative is included in parentheses. For example, for roe deer, 19/47 analyzed regions (see Table 1) results in 40% of regions with a negative mean residual.*
[b] *Absolute population trends show number and percentage of regions in which λ ≥ 1 (i.e., population was growing in that period). If in a given time period a population shows an absolute increase but increases more slowly than the average increase for 1981–2010, λ is larger than 1 but the mean residual from the autoregressive model is negative.*
[c] *A percentage of population number in the regions with negative mean residuals in 2nd period related to total population size in 1991. For example, number of roe deer had low per-capita population growth rate in 38 regions of Russia in 1992–2000, and these 38 regions amount for 94% of total population size of roe deer in 1991.*

Prishchepov 2011; Bjørneraas et al. 2011). We cannot exclude the possibility, however, that the increase of brown bear abundance in 2001–2010 reflects changes in monitoring procedures over time, not an actual increase in individual animals (Y.P.G., unpublished data).

The rapid growth of wolf populations after 1991 was likely due to the cessation of control measures. According to historical data, wolf populations increased after each social turmoil. After the Civil War of 1917–1922 and during WWII in 1941–1945, Russian wolf populations increased rapidly (Bibikov 1985). In the following stable periods, however, incentives were used to reduce wolf population (Bibikov 1985). After 1991 wolf control efforts stopped (Game Mammals of Russia 2000; Valdmann 2001), and our results show significant population increase (by 80% between 1991 and 2010; Table 2). We hypothesize that the increasing wolf population, among other factors, contributed to ungulate decline.

In contrast to the significant patterns we found for mammal species, we found no significant trends in climate time series for 1991–2000. Thus, it is unlikely that climate played an important role in driving the observed population changes. Of course, we cannot exclude other possible unknown drivers of population changes. Nonetheless, the magnitude and spatial extent of the patterns we documented argues in favor of the high-magnitude changes in human impacts that were brought about by socioeconomic forces.

We reviewed the literature to informally assess the degree to which other countries' wildlife populations changed during times of socioeconomic shocks and human conflict. We searched for all studies on wildlife trends in post-Soviet countries and African and Asian countries which underwent societal turmoil. We also examined case studies from multiple western countries that did not experience social turmoil. On one hand, other postsocialist countries exhibited similar patterns of mammal declines. On the other hand, western countries which did not go through social turmoil did not experience mammal population trends similar to those that had. In African and Asian countries that experienced societal turmoil, wildlife populations usually declined. We

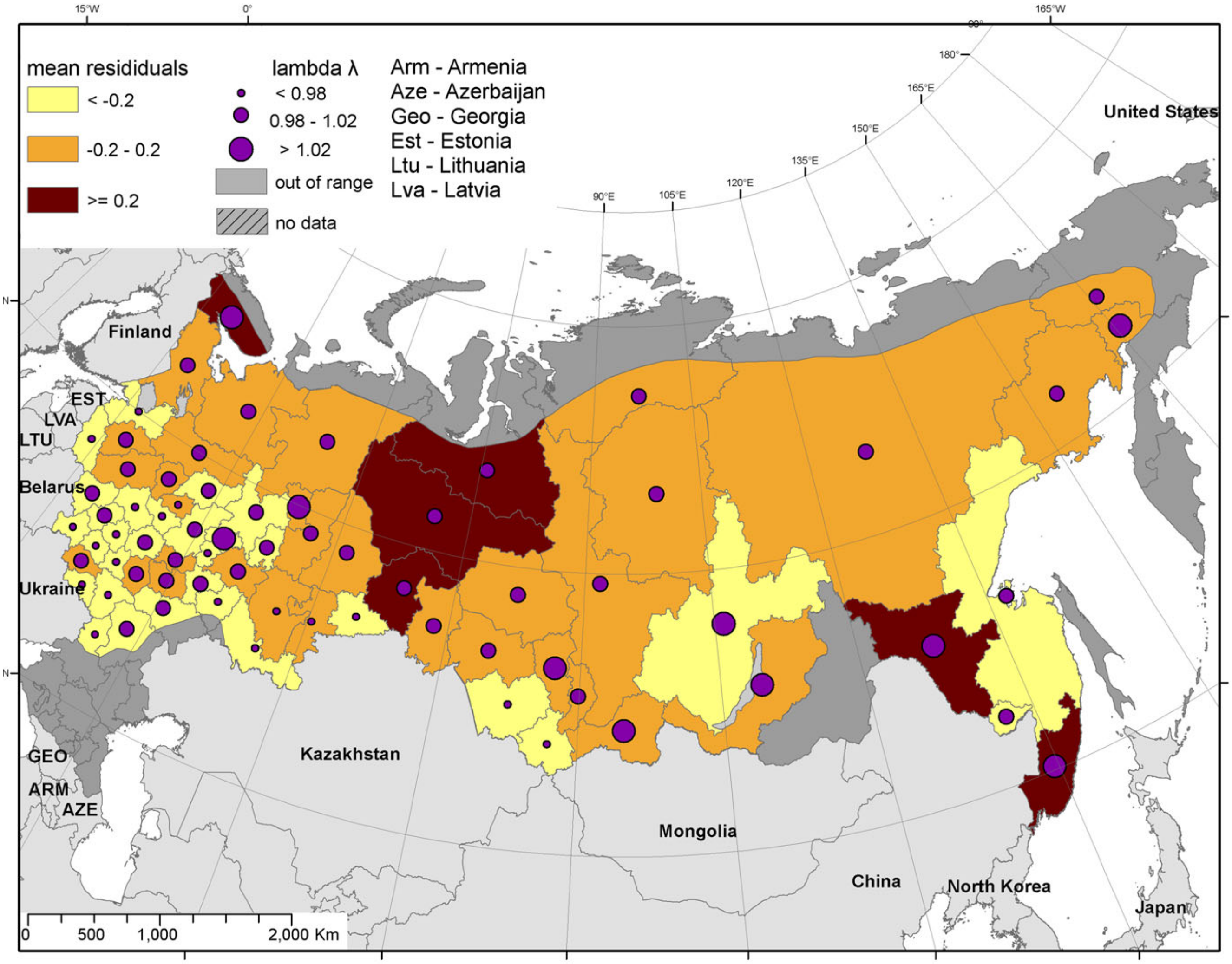

Figure 3. Map of moose population trends after the collapse of the Soviet Union. Magnitude of mean residuals reflects population growth rate in 1990s. Per capita population growth rate (λ) shows absolute population trend in 1990s. For similar maps for the other species, see Supporting Information.

also found several examples of when social downturn benefitted wildlife. In most cases it was because people were restricted from visiting wildlife areas (Draulans & Van Krunkelsven 2002) (e.g., increase of elephants in the Hangwe National Park, Zimbabwe, when it was dangerous to poach them [Hallagan 2009]).

With regard to post-Soviet countries, wild boar in the Czech Republic declined from 1991–1995 (Hladikova et al. 2008), as did roe deer in Estonia, Eurasian lynx in both Estonia and Lithuania (Valdmann 2001; Matyushkin & Vaisfeld 2003), and brown bear in Romania (Micu et al. 2005) and Estonia (Valdmann 2001). In some post-Soviet countries large mammals rebounded after initial postcollapse declines. For example, wild boar populations in the Czech Republic increased rapidly after 1996 (Hladikova et al. 2008), as did brown bear populations in Romania after 1997 (Micu et al. 2005). An increase in wolf populations following the collapse of socialism also occurred in other post-communist countries. Wolf abundance after 1991 increased in Estonia (Valdmann 2001), Latvia (Ozolins et al. 2008), and Lithuania (Balciauskas 2008). Conversely, we could find only 2 documented cases of wildlife trend patterns in post-Soviet countries that differed from the patterns in Russia. Roe deer and Eurasian lynx populations in the Vitebsk region of Belarus increased from 1985–2004, and especially after 1995 (Sidorovich 2006), and wolf populations in Kyrgyzstan decreased by half from 1988 to 1999 (Hazell 2001). In general though, wildlife trends in other post-Soviet countries were similar to the trends we documented for Russia.

The rapid changes in large mammal populations that we found are even more striking when compared with concomitant population trends of the same species in countries without socioeconomic shocks. Populations of large mammals in North America increased or were stable (e.g., moose [Timmermann 2003; Wattles & Destefano 2011], grizzly bear [*U. arctos*] [e.g., Brodie & Gibeau

2007]; American black bear [*Ursus americanus*] [Garshelis & Hristienko 2006]). Similarly, brown bear and European lynx populations in Scandinavia did not decline in the 1990s (e.g., Nyholm et al. 1998; von Arx et al. 2004), and wild boar populations in many European countries increased in recent decades (Goulding et al. 2003; Massolo & Della Stella 2006). In Norway, the total moose harvest (a proxy for population size) increased slightly in the 1990s. Only Finland and Sweden had declining moose harvests in the 1990s (Lavsund et al. 2003). The wolf population in Canada has been stable during recent decades (Mech & Boitani 2003). The wolf population in France, Italy, Sweden, Poland, Czech Republic, and Romania increased following legal protection (Boitani 2000).

Our findings for Russian mammals concur with population trends in other countries during times of socioeconomic shocks. For example, the breakup of the East African Community in 1977 was followed by sharp declines of African buffalo, African elephant, and black rhinoceros (*Diceros bicornis*) population (Sinclair 2005). Elephant wounding and juvenile mortality in Kenya increased during periods of low livestock prices, suggesting that the local economy drives poaching (Wittemyer 2011). In Ghana, years of increased hunting and sharp declines in many wildlife species coincide with years of poor fish supply (Brashares et al. 2004). During the Rwandan civil war, poaching posed a major threat to the mountain gorilla (*Gorilla gorilla beringei*), sitatunga (*Tragelaphus spekii*), and other species (Plumptre et al. 1997; Kanyamibwa 1998). Similarly, the civil war in the Democratic Republic of Congo led to increased poaching of bonobos (*Pan paniscus*) and gorillas (Vogel 2000). In Cambodia, war, conflict, and turmoil were associated with a shift in villagers wildlife-trading behavior in markets outside the country; this trading included endangered species like tiger (*Panthera tigris*) (Loucks et al. 2009). In Mongolia, poaching pressure for brown bear, saiga antelope, red deer, argali, musk deer (*Moschus moschiferus*), Siberian marmot (*Marmota sibirica*), and Mongolian Gazelle (*Procapra gutturosa*) increased dramatically at the time of the 1990 Democratic Revolution in Mongolia (Zahler et al. 2004).

Our results on population declines of large mammal populations in Russia after the collapse of the Soviet Union, especially when compared with population trends in other countries, provide compelling evidence for the magnitude of the effect of socioeconomic shocks on large mammals. Times of socioeconomic shocks can be critical periods for wildlife and may warrant special attention by conservationists.

Acknowledgments

We acknowledge support from FGBU TsentrOkhotkontrol, which collects and processes WTC data. We appreciate the help of Y. Dgebuadze, D. Helmers, B. Borisov, M. Dubinin, and A. Allstadt. Comments by 2 anonymous reviewers improved the manuscript substantially. We gratefully acknowledge support by the German Science Foundation (DFG), the Russian Foundation for Fundamental Investigations (RFFI), the Russian Academy of Sciences Biological Resources of Russia program, the Einstein Foundation Berlin, and the NASA Land Cover and Land Use Science Program.

Supporting Information

Procedure of WTC data collection, additional exploratory analyses, and maps of brown bear, Eurasian lynx, roe deer, and grey wolf population trends after the collapse of the Soviet Union (Appendix S1) are available online. The authors are 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

Balciauskas L. 2008. Wolf numbers and distribution in Lithuania and problems of species conservation. Annales Zoologici Fennici **45**:329–334.

Barrett CB, Gibson CC, Hoffman B, McCubbins MD. 2006. The complex links between governance and biodiversity. Conservation Biology **20**:1358–1366.

Baskin LM, Prishchepov AV. 2011. Dynamics of moose (*Alces alces*) populations in the Volga River basin. Povolzhskii Ekologicheskii Zhurnal **2**:218–222.

Baumann M, Ozdogan M, Kuemmerle T, Wendland KJ, Esipova E, Radeloff VC. 2012. Using the Landsat record to detect forest-cover changes during and after the collapse of the Soviet Union in the temperate zone of European Russia. Remote Sensing of Environment **124**:174–184.

Bibikov DI. 1985. The wolf. Page 609 in History, systematics, morphology, ecology. Nauka, Moscow.

Bjørneraas K, Solberg EJ, Herfindal I, Van Moorter B, Rolandsen CM, Tremblay J-P, Skarpe C, Sæther B-E, Eriksen R, Astrup R. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology **17**:44–54.

Boitani L. 2000. Action plan for the conservation of the wolves (*Canis lupus*) in Europe. Council of Europe Publishing, Strasbourg.

Brainerd E. 2001. Economic reform and mortality in the former Soviet Union: a study of the suicide epidemic in the 1990s. European Economic Review **45**:1007–1019.

Brashares JS, Arcese P, Sam MK, Coppolillo PB, Sinclair A, Balmford A. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science **306**:1180–1183.

Brodie JF, Gibeau ML. 2007. Brown bear population trends from demographic and monitoring-based estimators. Ursus **18**:137–144.

Danilkin AA. 1999. Deer (Cervidae). GEOS, Moscow.

Danilkin AA. 2002. Pigs (Suidae). GEOS, Moscow.

Draulans D, Van Krunkelsven E. 2002. The impact of war on forest areas in the Democratic Republic of Congo. Oryx **36**:35–40.

Dudwick N, Gomart E, Marc A, Kuehnast K, editors. 2003. When things fall apart. Qualitative studies of poverty in the former Soviet Union. The World Bank, Washington, D.C.

Ehrlich P, Pringle R. 2008. Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. Proceedings of the National Academy of Sciences of the United States of America **105:**11579–11586.

Fedosenko AK, Weinberg PJ. 2001. On the status of the *Pamir argali* populations in Tadjikistan and Kirghizstan. Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologicheskii **106:**3–12.

Filiptchouk AN, Strakhov VV, Borisov VA. 2001. Forest and forest products country profile. Geneva Timber and Forest Study Papers, Russian Federation. United Nations, Economic Commission for Europe, Geneva, Switzerland.

Game mammals of Russia. 1992, 1996, 2000, 2004, 2007, 2011. Status of resources game animals in Russian federation. Information & analytical materials. Issues 1–9. FGU TsentrOkhotkontrol', Moscow.

Garshelis D, Hristienko H. 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. Ursus **17:**1–7.

Garshelis DL. 1992. Mark-recapture density estimation for animals with large home ranges. Pages 1098–1111 in McCullough RH, Barrett DR, editors. Wildlife 2001: populations. Elsevier Applied Science, London.

Geisser H, Reyer H-U. 2005. The influence of food and temperature on population density of wild boar Sus scrofa in the Thurgau (Switzerland). Journal of Zoology **267:**89–96.

Genz A, Bretz F. 2009. Computation of multivariate normal and t probabilities. Springer-Verlag, New York.

Genz A, Bretz F, Miwa T, Mi X, Scheipl F, Bornkamp B, Hothorn T. 2012. mvtnorm. Multivariate Normal and t Distributions. R package version 0.9-9992. Available from http://cran.r-project.org/package=mvtnorm (accessed May 2013).

Gordon IJ. 2009. What is the future for wild, large herbivores in human-modified agricultural landscapes? Wildlife Biology **15:**1–9.

Goulding, M, Roper T, Smith G, Baker S. 2003. Presence of free-living wild boar *Sus scrofa* in southern England. Wildlife Biology **9:**15–20.

Grootaert C, Braithwaite J. 1998. Poverty correlates and indicator-based targeting in Eastern Europe and the former Soviet Union. The World Bank Social Development Department and Europe and Central Asia Poverty Reduction and Economic Management Sector Unit. Washington, D.C.

Gubar YP. 2007. Status of Resources game animals in Russian federation in 2003–2007. Page 164. in Information and analytical materials/Game animals of Russia (biology, protection, study of resources, rational use). Issue 2. FGU TsentrOkhotkontrol', Moscow.

Hallagan JB. 2009. Elephants and the War in Zimbabwe. Oryx **16:**161–164.

Hazell C. 2001. The status of the wolf population in post-Soviet Kyrgyzstan. Endangered Species Update **18:**142–146.

Hladikova B, Zboril J, Tkadlec E. 2008. Population dynamics of the Wild Boar (Sus scrofa) in central Moravia, Czech Republic (Artiodactyla: Suidae). Lynx **39:**55–62.

Ioffe G, Nefedova T. 2004. Marginal farmland in European Russia. Eurasian Geography and Economics **45:**45–59.

Ioffe GT, Nefedova T, Zaslavsky I. 2004. From Spatial Continuity to Fragmentation: the case of Russian farming. Annals of the Association of American Geographers **94:**913–943.

IUCN (International Union for Conservation of Nature). 2014. The IUCN Red List of threatened species. Version 2014.1. IUCN, Gland, Switzerland. Available from http://www.iucnredlist.org (accessed June 2014).

Kanyamibwa S. 1998. Impact of war on conservation: Rwandan environment and wildlife in agony. Biodiversity & Conservation **7:**1399–1406.

Kolesnikov SV, editor. 2003. Regions of Russia. Socio-economic variables. 2003. Federal State Statistical Service, Moscow. Available from http://www.gks.ru/bgd/regl/B03_14/Main.htm.

Kuemmerle T, et al. 2011. Predicting potential European bison habitat across its former range. Ecological Applications **21:**830–843.

Lavsund S, Nygrén T, Solberg EJ. 2003. Status of moose populations and challenges to moose management in Fennoscandia. Alces **39:**109–130.

Lerman Z, Shagaida N. 2007. Land policies and agricultural land markets in Russia. Land Use Policy **24:**14–23.

Loucks C, Mascia MB, Maxwell A, Huy K, Duong K, Chea N, Long B, Cox N, Seng T. 2009. Wildlife decline in Cambodia, 1953–2005: exploring the legacy of armed conflict. Conservation Letters **2:**82–92.

Martin J, Basille M, Van Moorter B, Kindberg J, Allainé D, Swenson JE. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Canadian Journal of Zoology **88:**875–883.

Massolo A, Della Stella RM. 2006. Population structure variations of wild boar *Sus scrofa* in central Italy. Italian Journal of Zoology **73:**137–144.

Matyushkin EN, Vaisfeld MA. 2003. The lynx: regional features of ecology, use and protection. [Rys: regionalnye osobennosti ekologii, ispolzovaniya i okhrany.]. Nauka, Moscow.

Mech, LD, Boitani, L, editors. 2003. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

Micu I, Nahlik A, Uloth W. 2005. Situation of large predators in Romania. [Die Situation des Grossraubwildes in Rumaenien.]. Beitraege zur Jagd- und Wildforschung **30:**175–180.

Milner-Gulland EJ, Kholodova MV, Bekenov A, Bukreeva OM, Grachev IA, Amgalan L, Lushchekina AA. 2001. Dramatic declines in saiga antelope populations. Oryx **35:**340–345.

Mirutenko VS, Lomanova NV, Bersenev AE, Morgunov NA, Volodina OA, Kuzyakin VA, Chelintsev NG. 2009. Recommendations on methods of conducting and analysis of winter track count data of game animals in Russia (with algorithms of calculation of population size). FGNU "Rosinfomagrotech," Moscow, Russia.

Nyholm E, Nyholm K, Sørensen OJ, Swenson JE, Kvam T, Sandegren F, BjÄrvall A, Franzen R, SÖderberg A, Wabakken P. 1998. Brown bear conservation action plan for Europe (Finland, Norway, Sweden). Pages 55–122 in Servheen C, Herrero S, Peyton B, editors. Bears. Status survey and conservation action plan. IUCN, Gland, Switzerland.

Ozolins J, Zunna A, Pupila A, Bagrade G, Andersone-Lilley Z. 2008. Wolf (*Canis lupus*) conservation plan. Latvian State Forestry Institute "Silava," Salaspils, Latvia.

Petrosyan VG, Dergunova NN, Bessonov SA, Omelchenko AV. 2012. Analysis of population dynamics and spatial distributioin of important wild game ungulate species (moose, roe deer, boar) in Russia using long-term monitoring. Advances in Current Biology (Uspekhi sovremennoi biologii) **132:**463–476.

Plumptre AJ, Bizumuremyi J-B, Uwimana F, Ndaruhebeye J-D. 1997. The effects of the Rwandan civil war on poaching of ungulates in the Parc National des Volcans. Oryx **31:**265–273.

Polishchuk LV. 2002. Conservation priorities for Russian mammals. Science **297:**1123.

Potapov P, Turubanova S, Zhuravleva I, Hansen M, Yaroshenko A, Manisha A. 2012. Forest cover change within the Russian European north after the breakdown of Soviet Union (1990–2005). International Journal of Forestry Research **2012:**1–11.

Pratt D, Macmillan D, Gordon I. 2004. Local community attitudes to wildlife utilisation in the changing economic and social context of Mongolia. Biodiversity & Conservation **13:**591–613.

Prishchepov AV, Radeloff VC, Baumann M, Kuemmerle T, Müller D. 2012. Effects of institutional changes on land use: agricultural land abandonment during the transition from state-command to market-driven economies in post-Soviet Eastern Europe. Environmental Research Letters **7:**024021 (13 pp.).

Radeloff VC, Beaudry F, Brooks TM, Butsic V, Dubinin M, Kuemmerle T, Pidgeon AM. 2013. Hot moments for biodiversity conservation. Conservation Letters **6:**58–65.

Sánchez-Zapata J, Carrete M, Gravilov A, Sklyarenko S, Ceballos O, Donázar JA, Hiraldo, F. 2003. Land use changes and raptor conservation in steppe habitats of Eastern Kazakhstan. Biological Conservation **111:**71–77.

Sidorovich V. 2006. Relationship between prey availability and population dynamics of the Eurasian lynx and its diet in northern Belarus. Acta Theriologica **51:**265–274.

Sinclair A. 2005. Serengeti past and present. Pages 8–11 in Sinclair A, Arcese P, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago.

Stephens PA, Zaumyslova OY, Miquelle DG, Myslenkov AI, Hayward GD. 2006. Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Pereleshin formula. Animal Conservation **9:**339–348.

Timmermann H. 2003. The status and management of moose in North America–circa 2000–01. Alces **39:**131–151.

Trepet SA, Eskina TG. 2012. Effect of environmental factors on population dynamics and structure of the caucasian Red Deer (*Cervus elaphus maral*) in the Caucasian State Biosphere Reserve. Biology Bulletin **39:**1–12.

United Nations Statistics Division. 2013. National accounts main aggregates database. UN, New York. Available from http://unstats.un.org/unsd/snaama/selbasicFast.asp (accessed December 2013).

Valdmann H. 2001. Current situation of the large carnivores in Estonia. Pages 38–44 in Balčiauskas L, editor. Proceedings of BLCI symposium "Human Dimensions of Large Carnivores in Baltic Countries." Šiauliai University.

Vogel G. 2000. Conflict in Congo threatens bonobos and rare gorillas. Science **287:**2386–2387.

von Arx M, Breitenmoser-Würsten C, Zimmermann F, Breitenmoser U. 2004. Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. Page 330 in Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA Bericht no. 19. Muri, Switzerland.

Wattles DW, Destefano S. 2011. Status and management of moose in the Northeastern Unated States. Alces **47:**53–68.

Wells MP, Williams MD. 1998. Russia's protected areas in transition: the impacts of Perestroika, economic reform and the move towards democracy. Ambio **27:**198–206.

Williams M. 1996. Russia and Northern Eurasia: the last frontiers for biodiversity conservation. Natural Areas News **1:**1–5.

Wittemyer G. 2011. Effects of economic downturns on mortality of wild African elephants. Conservation Biology **25:**1002–1009.

Woodroffe R. 1998. Edge Effects and the extinction of populations inside protected areas. Science **280:**2126–2128.

Zahler P, Lhagvasuren B, Reading R, Ingard J, Amgalanbaatar S, Gombobaatar S, Nigel B, Onon Y. 2004. Illegal and unsustainable wildlife hunting and trade in Mongolia. Mongolian Journal of Biological Sciences **2:**23–31.