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# Wildlife population changes across Eastern Europe after the collapse of socialism

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When political regimes fall, economic conditions change and wildlife protection can be undermined. Eastern European countries experienced turmoil following the collapse of socialism in the early 1990s, raising the question of how wildlife was affected. We show that the aftermath of the collapse changed the population growth rates of various wildlife taxa. We analyzed populations of moose (*Alces alces*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), and gray wolf (*Canis lupus*) in nine countries. Population growth rates changed in 32 out of 49 time series. In the countries that reformed slowly, many species exhibited rapid population declines, and population growth rates changed in 83% of the time series. In contrast, in countries with fast post-socialism reforms, many populations increased rapidly, and growth rates changed in only 48% of time series. Our results suggest that the direction and frequency of the changes were associated with socioeconomic conditions, and that wildlife populations can be greatly affected by socioeconomic upheavals.

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Economic upheavals and changes in political regimes can have major detrimental effects on wildlife when rising poverty drives the growth of subsistence hunting and poaching, and the enforcement of wildlife protection laws diminishes (Brashares *et al.* 2004). Even peaceful political transitions can cause major declines in wildlife populations (Bragina *et al.* 2015). However, economic and political change may also have positive effects on wildlife, such as when human access to wilderness becomes unsafe because of a war (Hallagan 2009). This

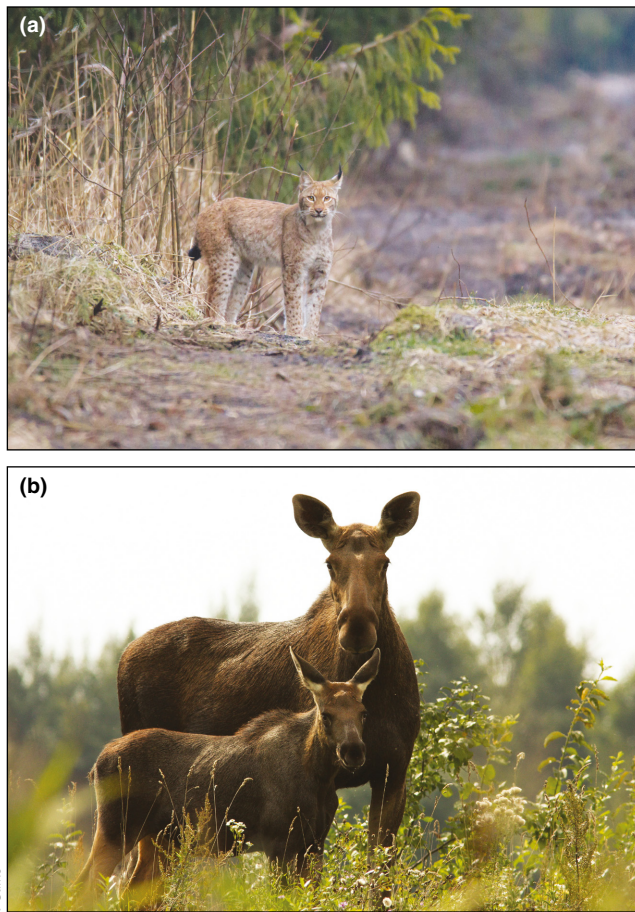
raises the question of how wildlife populations are affected during times of political and economic disturbance, and where population declines are most likely.

Here, we investigate the effects of the collapse of socialism on large mammal populations throughout Eastern Europe since the 1980s (Figure 1). We focus on large mammals because they are especially vulnerable to poaching during times of upheaval (Polishchuk 2002; Neronov *et al.* 2013). The consequences of the collapse of socialism were diverse, including armed conflict and land restitution. Rather than parse out how specific events may have affected specific species, we instead provide a general summary of changes in mammal population dynamics among countries. Many countries experienced major economic and social turmoil after the collapse of the Soviet Union but each varied greatly in their respective economic conditions and the speed of reforms toward becoming open-market economies. We therefore suspected that there would be differences in the magnitude of changes in wildlife population dynamics among different countries. To investigate these differences, we analyzed time series for seven wildlife species – specifically, moose (*Alces alces*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), and gray wolf (*Canis lupus*) – in nine countries to identify broad patterns in population growth rates among various wildlife species living in economically and politically diverse countries.

## Materials and methods

We analyzed publicly available time series of wildlife population size, with one estimate per country per

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**Figure 1.** European lynx (*Lynx lynx*) (a) and a female moose (*Alces alces*) with a calf (b) in Lithuania.

species per year: Bulgaria (five species), Czech Republic (3), Estonia (6), Hungary (3), Latvia (6), Lithuania (6), Poland (7), Slovakia (6), and Ukraine (7), for a total of 49 time series (WebTable 1). Time series were typically 30–50 years long. Although some datasets span up to 92 years, we did not analyze time series longer than 60 years, to better focus on the period before and after the collapse. We wanted to analyze all post-socialist European countries but were limited to nine countries by data availability. All datasets were produced by state-sponsored surveys specifically designed to estimate wildlife abundance. Wildlife survey methods included expert estimates, sample plots, winter track counts, and others; a full description of each dataset is provided in WebPanel 1 and WebTable 1.

### Country ranking

We used nine indices to describe how quickly countries reformed (WebPanel 1 and WebTable 2). These included two corruption control indices from the World Bank (<http://bit.ly/2cHS3d8>) and Transparency International (<http://bit.ly/1cdgWMM>), one index of per capita GDP from the World Bank ([www.worldbank.org](http://www.worldbank.org)), and six

transition indicators from the European Bank for Reconstruction and Development (<http://bit.ly/1PoFaXN>). We summed all indices to rank each country's pace and efficiency of transition, and then classified the nine countries into two groups based on overall score (WebTable 2). The first group, the slow-transitioning countries, included the Czech Republic, Estonia, Hungary, Poland, and Slovakia; the second group, the fast-transitioning countries, included Bulgaria, Latvia, Lithuania, and Ukraine.

### Changes of population growth rates through time

To evaluate changes in population growth, we fit a time-varying autoregressive state-space model of order 1 termed TVARSS(1) (Ives and Dakos 2012):

$$\begin{aligned}x(t) &= r(t-1) + bx(t-1) + \varepsilon(t) \\ r(t) &= r(t-1) + \phi(t)\end{aligned}\quad (1)$$

where  $x(t)$  is the logarithm of species abundance in year  $t$ , and  $r(t)$  is the exponential intrinsic rate of increase for the population in year  $t$ ; because population abundance is on a log scale, the intrinsic rate of increase  $r(t)$  enters as an additive term. In equation (1),  $b$  is the first-order autoregressive coefficient,  $\varepsilon(t)$  is the process error associated with changes in  $x(t)$ , and  $\phi(t)$  is the change in  $r(t)$  from one year to the next (Ives and Dakos 2012). If  $r(t)$  were constant, then the first equality of equation (1) would give an autoregressive model of order 1, AR(1). This is identical to the Gompertz model of population growth (Dennis and Taper 1994), which is  $N(t) = N(t-1) \exp(a + c \ln N(t) + E(t))$ , which on a logarithmic scale becomes  $x(t) = x(t-1) + a + cx(t-1) + \varepsilon(t) = a + bx(t-1) + \varepsilon(t)$  where  $b = c + 1$  (Dennis *et al.* 2006).

The second part of equation 1 allows the intrinsic rate of increase  $r(t)$  to vary as a random walk, with the rate of the random walk dictated by the variance  $\sigma^2$  of  $\phi(t)$ . Although the value of  $r(t)$  is in principle unbounded (because it follows a random walk), the values are constrained by fitting to the data. To account for possible measurement error (uncertainty in the estimates of population abundances), we included a measurement equation

$$x^*(t) = x(t) + \alpha(t)\quad (2)$$

in which  $x^*(t)$  is the observed value of log population abundance, and  $\alpha(t)$  is a random variable with mean zero and variance  $\sigma^2_\alpha$  that captures measurement error variance; this variance is estimated from the time-series data during model fitting. The model was fit by maximum likelihood using a Kalman filter (Harvey 1989). To ensure that the global maximum likelihood was found (Dennis *et al.* 2006), we initiated the optimization of the likelihood function with values of  $\sigma^2$  ranging from  $-10$  to  $0.2$ , performed optimization by simulated annealing, and finally polished the estimates using Nelder-Mead optimization (Ives and Dakos 2012).

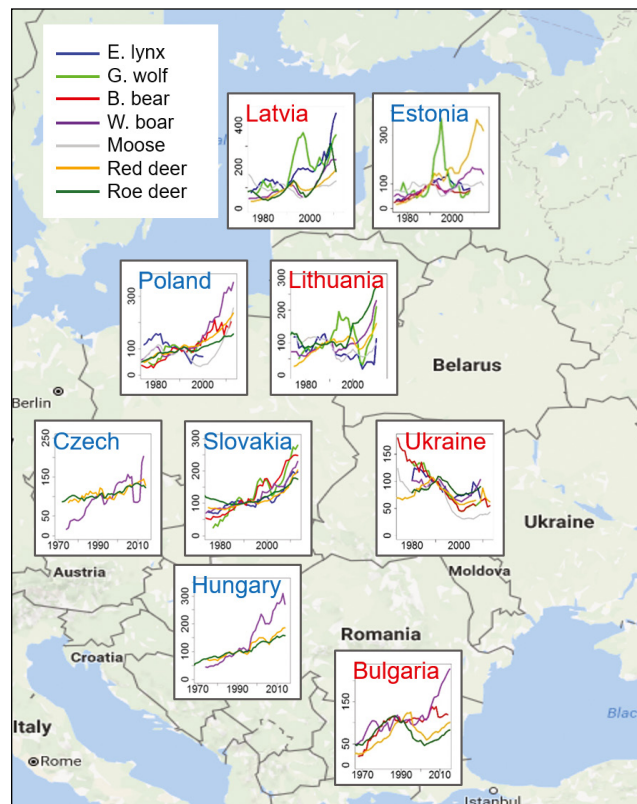
The null hypothesis that the population growth rate of a time series does not change through time can be tested using the variance  $\sigma^2$  of  $\phi(t)$ . Because  $\phi(t)$  represents changes in  $r(t)$ ,  $\sigma^2 = 0$  implies that the intrinsic rate of increase does not change through time. For each time series, we estimated  $\sigma^2$ , and we regressed  $\sigma$  over the country rankings, including species as a factor. Because there were many zero values of  $\sigma$ , we confirmed the  $P$  values using a permutation test in which  $\sigma$  values were permuted among countries for each species. We also performed similar analyses dividing countries into groups of slow- and fast-transitioning countries. Because we compare wildlife dynamics in different countries, we used the point estimates of  $\sigma$  for each time series; although the individual estimates of  $\sigma$  might or might not be statistically significant at a given alpha confidence level, using the best estimates of  $\sigma$  is appropriate when comparisons are made among time series.

Our statistical analyses focused on changes in the intrinsic rate of increase  $r(t)$ , rather than changes in population abundance, because changes in growth rates reflect more fundamental changes in population dynamics. The TVARSS(1) model identifies any pattern of change in population growth rate that occurs, and does not require predetermining a time point at which population growth rates changed in each country. While we assumed that the collapse of socialism affected population growth rates, these effects could have exhibited different forms and time lags in different countries and for different species, and we wanted to avoid making a priori assumptions about the effects of the collapse. Furthermore, our methods focused on multi-year changes because wildlife population estimates tend to fluctuate considerably within single years. Finally, our model accounted for internal dynamics, such as density dependence. Therefore, our approach targets the dynamic patterns that are most likely due to external factors.

## Results

Many wildlife species in Eastern Europe exhibited marked population growth or decline during the transition from socialism to market-driven economies (Figure 2). Interestingly, the direction of those changes differed between fast-transitioning and slow-transitioning countries. In slow-transitioning countries, the populations of some species declined rapidly. In contrast, in fast-transitioning countries, the populations of most species increased – substantially so in many time series (Figure 2).

Population growth rates also changed discernably between the 1980s and the 2010s. We found that 32 of the 49 time series had estimates of  $\sigma^2 > 0$  (25 of the 32 were significant, without correcting for multiple comparisons), implying that their intrinsic population growth rates changed (Table 1; Figure 3). Again, the frequency of changes in intrinsic rates of increase clearly differed between the two groups of countries. In slow-transitioning



**Figure 2.** Wildlife population dynamics in Eastern Europe. Countries that transitioned quickly through post-socialist reforms are named in blue, whereas slow-transitioning countries appear in red. The y axis depicts the percentage of population change relative to population size in 1990, which we defined as 100%. In “red” countries, either wildlife populations declined during the 1990s (eg Ukraine) or changes differed among species (eg Latvia), while in “blue” countries, populations generally increased (eg Slovakia).

countries, 20 of 24 (83%) time series showed changes in the intrinsic rate of increase ( $\sigma^2 > 0$ ), whereas in the fast-transitioning countries only 12 of 25 (48%) exhibited changes. The regression of  $\sigma$  against the summed ranks of country transition indices, including species as a factor, was significant (coefficient = 0.0022,  $P = 0.032$ , permutation test  $P = 0.034$ ). Dividing countries into slow- and fast-transitioning groups produced similar results (coefficient = 0.10,  $P = 0.0035$ , permutation test  $P = 0.0033$ ).

## Discussion

After the collapse of socialism in Eastern Europe, the population dynamics of selected wildlife taxa experienced widespread and pronounced changes, likely attributed to a range of causes, including poaching and reduced enforcement. For example, ungulate populations were harvested extensively and thereafter declined in Ukraine (Volokh 2009), Belarus (Sidorovich *et al.* 2003), and the Baltics (Baleishis *et al.* 1998; Andersone-Lilley *et al.* 2010). With disruptions to socioeconomic

**Table 1. Estimates of the variance ( $\sigma^2$ ) of the intrinsic rate of increase ( $r[t]$ ) for seven species in nine countries**

	<i>Eurasian lynx</i>	<i>Gray wolf</i>	<i>Brown bear</i>	<i>Wild boar</i>	<i>Moose</i>	<i>Red deer</i>	<i>Roe deer</i>	Summed ranking (WebTable 2)
Ukraine	0	0.048*	0.0332	0.030***	0.040***	0.033	0.037**	80
Bulgaria	–	0	0	0.076*	–	0.047*	0.025***	62
Lithuania	0	0.24*	–	0.058*	0.086***	0.052*	0.080***	56
Latvia	0.063*	0.11*	–	0.072***	0.067***	0.039*	0.12***	54
Poland	0.058	0	0	0.064**	0.078***	0.030*	0	37
Slovakia	0.0415*	0	0	0	–	0.0146***	0.00938***	36.5
Czech Republic	–	–	–	0	–	0	0.02	30.5
Estonia	0.028	0	0.032	0.089	0.087***	0	–	29
Hungary	–	–	–	0	–	0	0	20

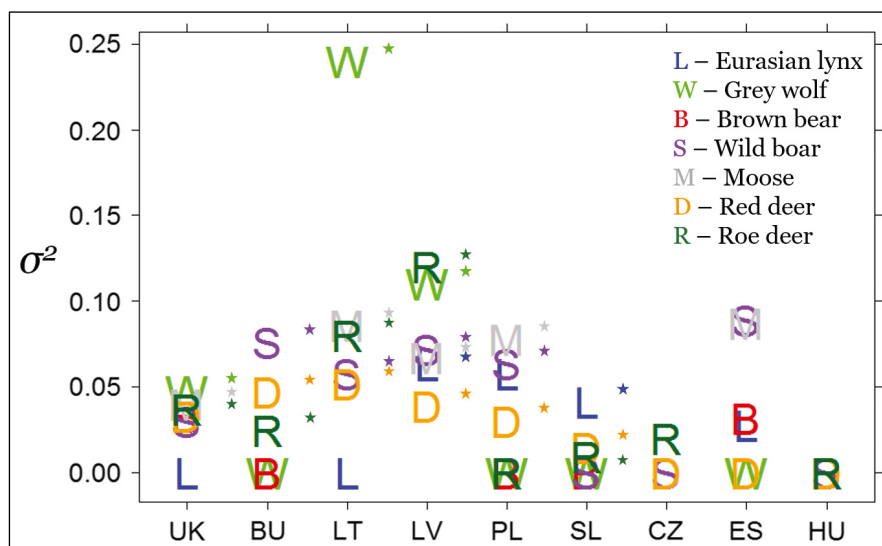
**Notes:** The right-most column displays the summed rankings of countries according to transition indicators (WebTable 2). By definition, if the variance of the intrinsic rate of increase  $\sigma^2 > 0$ , the per capita population growth rate is changing over time. Because our model accounts for density dependence, the changes reflect external drivers (eg overharvesting). In the countries above the horizontal line (ie in Bulgaria, Ukraine, Latvia, and Lithuania),  $\sigma^2$  is generally larger than zero, while in the other countries it is generally equal to zero. See also Figure 3. \*significant at  $P < 0.05$ , \*\*significant at  $P < 0.01$ , \*\*\*significant at  $P < 0.001$ ; no correction for multiple comparisons.

stability occurring throughout the world, our results call attention to the risk of large mammal declines during such events.

In addition to poverty and poaching, changes in management goals and practices after the collapse of socialism in Eastern Europe may also have influenced some of the observed changes in population growth rates. In Baltic countries, populations of moose and other ungulates declined in the 1990s (Figure 2). During the Soviet era, high ungulate density led to widespread damage to forests (bark stripping of Norway spruce *Picea abies*) and

agriculture (Randveer and Heikkilä 1996), raising public concern (Andersone-Lilley et al. 2010). After the collapse of socialism, pre-Soviet private land was restituted and hunting management systems in the Baltics were reorganized (Andersone-Lilley et al. 2010; Hartvigsen 2014). In Lithuania, for instance, harvest of ungulates such as moose was deliberately intensified to protect saplings from browsing by moose (Andersone-Lilley et al. 2010).

Another possible cause of the observed changes in population dynamics was the widespread abandonment of agricultural land during the 1990s (Alcantara et al. 2013); in Latvia alone, “42% of all agricultural land in 1990 was abandoned by 2000” (Prishchepov et al. 2012), and the reduction in row crop agriculture led to a subsequent decline of wild boar populations due to loss of forage (Danilov and Panchenko 2012). Furthermore, as wolf populations increased in the absence of population control, so did predation rates on ungulates (Valdmann et al. 2005). However, the transition of former agricultural lands into early successional ecosystems also provided new habitat for wildlife, which may have contributed to some of the population increases during the 2000s. Thus, the observed changes in the population dynamics of large mammals after the collapse of socialism were likely attributable to several factors, including poaching, land ownership change, institutional changes, abandonment of agriculture, and increased predation.



**Figure 3.** Magnitude of variance ( $\sigma^2$ ) of the intrinsic population rate of increase ( $r[t]$ ) for nine countries in Eastern Europe. Estimates of  $\sigma^2 > 0$  indicate that a given population growth rate varied over time. A star designates statistical significance of whether  $\sigma^2$  differs from zero. Given that our model accounted for density dependence, the causes of changes are likely external. Countries are ordered by their summed transition indicators (Table 1). UK – Ukraine, BU – Bulgaria, LT – Lithuania, LV – Latvia, PL – Poland, SL – Slovakia, CZ – Czech Republic, ES – Estonia, HU – Hungary.

Despite the prospect of inherent sources of bias in the analyzed datasets, it is unlikely that these biases affected our conclusions. Official data may have exaggerated the number of moose in Poland (Bobek *et al.* 2005), lynx in Estonia (von Arx *et al.* 2004), and ungulates in the Baltics during Soviet times (Tönisson and Randveer 2003; Andersone-Lilley and Ozoliņš 2005; Andersone-Lilley *et al.* 2010). It is also possible that game mammal survey procedures were changed due to political turmoil, thereby affecting estimates (eg through modifications to the amount of effort dedicated to surveys). Finally, there may have been changes in management unrelated to the collapse of socialism. For example, the decline of moose in Poland was caused by legal overhunting after the hunting quota was increased, which coincided with but was not related to the collapse (Bobek *et al.* 2005) (Figure 2). Despite these and other potential sources of bias, our results should be fairly insensitive to consistent over- or underestimates of abundance, and to one-time changes in reporting methods, because we examined long-term variation in per capita population growth rates. For instance, a sudden switch in reporting methods would generate only a single change in  $r(t)$  between consecutive years, and would not result in changes in  $r(t)$  over the entire time series that would falsify the null hypothesis of no variation in  $r(t)$ . Although our statistical method is not prone to false positives (ie finding changes where they do not exist), false negatives could be caused by measurement error.

In summary, after analyzing the population dynamics of selected game species in Eastern Europe since the collapse of socialism, we detected major changes in population sizes as well as frequent changes in their intrinsic rates of increase. In general, in countries that transitioned slowly from a socialist to a market-driven economy, a greater number of wildlife populations exhibited rapid declines and more variable intrinsic rates of increase than populations in fast-transitioning countries. Socioeconomic disruptions are not particularly rare, and examining their effects is scientifically valuable and important for conservation efforts, given that wildlife populations can be highly vulnerable after such disturbances.

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## ■ Supporting Information

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