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POPULATION DYNAMICS OF THE LYNX (*LYNX LYNX*) IN THE BIALOWIEZA PRIMEVAL FOREST REVISITED: A STATISTICAL ANALYSIS OF DENSITY-DEPENDENT MIGRATION

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ABSTRACT

This paper applies a two-patch model to the population dynamics of the lynx which lives in the Bialowieza Primeval Forest (BPF) that extends along the Poland–Belarus border, and discusses the implications of the results obtained. In the estimation process, we performed a unit root test to avoid spurious correlation, and subsequently, we estimated the parameter values for the model. We obtained a relatively high instantaneous growth rate. The ecological parameter values in Poland were higher than those in Belarus, suggesting that the policy applied in Poland is more conservative than the one applied in Belarus. Finally, we conclude the paper by suggesting that the conservation of the BPF and the extension of the reserve area are crucial for the wildlife in the region.

Key words: Bialowieza Primeval Forest, lynx, two-patch model, transboundary, spurious correlation

INTRODUCTION

One of the most controversial issues regarding wildlife management is its transboundary nature. In this paper, we outline two separate situations. Firstly, wild animals belonging to a local population may crossover artificial boundaries such as national borders, boundaries between several local governments and/or boundaries between private/public lands. This is considered problematic because there is a possibility that this will result in some inefficiency of management, unless the bodies in charge of these lands cooperate with each other with regard to management. One of the possible problems is the so-called free ride, where only some management bodies spend money for the reduction of agricultural/forestry damage caused by ungulates, resulting in unfair and inefficient management.

Secondly, wild animals may crossover different types of lands such as cultivated lands or hunting and protected areas. If the hunting in a particular area intensifies to the point where it crosses the critical level, it may result in the displacement of wild animals. This causes new agricultural/forestry damages to the land to which the wild animals have migrated to. For example, Maillard [11] reported on the forced wild boar displacement resulting from hunting related activities in France. He reports the influence of hunting dogs on the home range of wild boars which increased from 1,390 ha to 5,139 ha after the opening of the hunting season. In the case of the Hokkaido sika deer (*Cervus nippon yesoensis*) found in the Northern region of Japan, its home range has spread from the east to the west [9]. One of the reasons for this expansion appears to be the result of hunting pressure. Moreover, some of the displaced sika deer have escaped into protected areas and/or game reserves.

Therefore, the transboundary nature of wildlife should be taken into consideration in wildlife management. Recently, some existing studies in varying fields have begun investigating migration between two habitats. For example, Bhat and Huffaker [3] examine the management of transboundary wildlife from an economic perspective. Armstrong and Skonhoft [1] and Greenville and MacAulay [6,7] consider marine reserves, and the latter incorporate the predator-prey relationship in their model.

This paper re-examines the Bialowieza Primeval Forest (BPF) (Fig. 1), which has already been examined by Jędrzejewski *et al.* [10]. Applying the data collected by Jędrzejewski *et al.* [10], this paper primarily aims to demonstrate that (1) the displacement of the lynx in this forest can be explained fairly appropriately by using a two-patch model, and (2) the results obtained are statistically significant. Further, the implications of the results are discussed. Former studies employing two-patch models have calibrated or set parameter values based on other researches. However, this paper differs from the earlier studies in that the parameter values used in it have been estimated. Further, as part of the procedure, we statistically examined whether the time series data may have caused a spurious correlation [8], and to avoid this undesirable scenario, statistical tests were conducted.

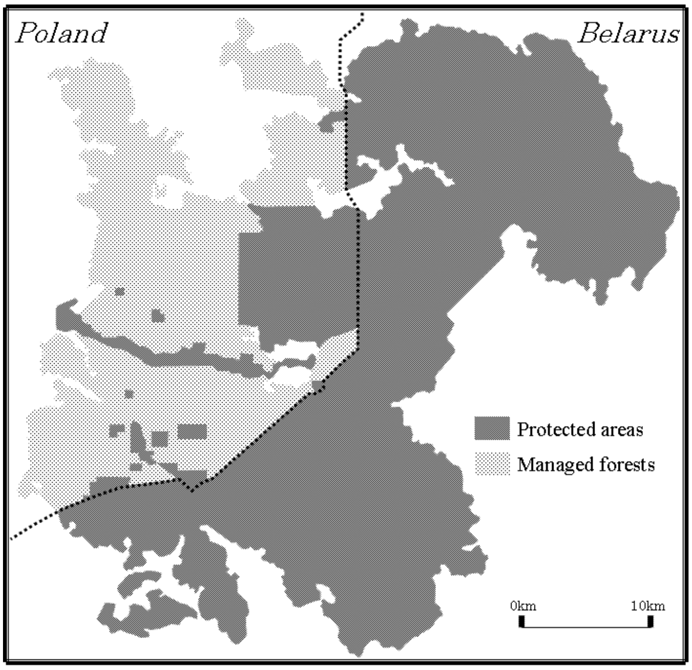

Fig. 1. Map of the study area

METHOD

Firstly, we outline the study area and the movement of the lynx based on Jędrzejewski *et al.* [10] (see also Table 1). According to Jędrzejewski *et al.* [10] (1) the BPF is located along the Poland–Belarus border (p. 123) and (2) a high, wire fence along the border, built in 1981, prevents the movement of ungulates but allows the lynx to pass through (p. 125). As a result of the dissimilarity stated in (2), we set parameter reflecting the different factors between the two patches in what follows.

We propose the following density-dependent migration model based primarily on Armstrong and Skonhoft [1].

$$N_{t+1}^{B} - N_{t}^{B} = r^{B}\left[1 - \frac{N_{t}^{B}}{K^{B}}\right]N_{t}^{B} - m\left[\frac{nN_{t}^{B}}{K^{B}} - \frac{N_{t}^{P}}{K^{P}}\right] - H_{t}^{B} \quad (1)$$

$$N_{t+1}^{P} - N_{t}^{P} = r^{P}\left[1 - \frac{N_{t}^{P}}{K^{P}}\right]N_{t}^{P} + m\left[\frac{nN_{t}^{B}}{K^{B}} - \frac{N_{t}^{P}}{K^{P}}\right] - H_{t}^{P}, \quad (2)$$

where

N_{t+1}^{B} and N_{t}^{B} are the estimated number of lynx in the exploited part of the BPF forest in Belarus in the year $t+1$ and t.

N_{t+1}^{P} and N_{t}^{P} are the estimated number of lynx in the exploited part of the BPF forest in Poland in the year $t+1$ and t.

r^{B} and r^{P} are the instantaneous growth rates of the lynx in the Belarussian and Polish part of BPF, respectively.

K^{B} and K^{P} are the carrying capacities of the lynx in the Belarussian and Polish part of BPF, respectively.

m is the parameter reflecting the degree of dispersion.

n is the parameter reflecting the different factors between the two patches, which affect the degree of dispersion (for details, see [1]).

H_{t}^{B} and H_{t}^{P} are the hunting quotas for the lynx in the Belarussian and Polish part of the exploited forest in the year t.

Table 1. Summary of the study area. Based on Jędrzejewski *et al.* [10] and Bobiec [3]

	Belarussian part	Polish part
Area of BPF	670 km^2 Partly protected since 1945	580 km^2
National park	After 1991, the entire area	105 km^2
Data and its period	The estimated number of lynx Hunting quotas for lynx 1946–1994	The estimated number of lynx Hunting quotas for lynx 1946–1994
Transition of the lynx management	1946–1955: Sport hunting 1956–1967: Persecution 1968–1992: Sport hunting 1993–onwards: Protection	1946–1953: Protection 1954–1988: Sport hunting 1989– onwards: Protection

For estimating the numbers of (N_{t+1}^{B} and N_{t}^{B}) and the hunting quotas (H_{t}^{B} and H_{t}^{P}) for the lynx, we use the data between 1946 and 1994 provided in Jędrzejewski *et al.* [10].

In the estimation, we rewrite equations (1) and (2) as follows.

$$N_{t+1}^{B} - H_{t}^{B} = AN_{t}^{B} + B\{N_{t}^{B}\}^{2} + CN_{t}^{P} \quad (3)$$

$$N_{t+1}^{P} - H_{t}^{P} = DN_{t}^{P} + E\{N_{t}^{P}\}^{2} + FN_{t}^{B}, \quad (4)$$

where

$$A = 1 + r^{B} - \frac{mn}{K^{B}},\ B = -\frac{r^{B}}{K^{B}},\ C = \frac{m}{K^{P}},\ D = 1 + r^{P} - \frac{m}{K^{P}},\ E = -\frac{r^{P}}{K^{P}} \text{ and } F = \frac{mn}{K^{B}}.$$

Firstly, we estimate A to F, and subsequently, we calculate the values of r^{B}, r^{P}, K^{B}, K^{P}, m and n using these relationships.

ANALYSIS AND RESULTS

Firstly, we performed the Kwiatkowski, Phillips, Schmidt and Shin (KPSS) test, which is used to determine whether the time series variables have unit roots. We employed this test because it is more reliable than the other tests. Moreover, a former research in the field of ecology has also used this test in its estimation [4]. The null hypothesis of the KPSS test is that the time series does not have a unit root. We performed this test for the variables N_{t}^{B}, N_{t}^{P}, H_{t}^{B} and H_{t}^{P} by using the software *EViews 6*.

Results of the KPSS test are tabulated in Table 2, where the KPSS test statistic and bandwidth have been summarized. The following two types of test equations are available for the KPSS test: (1) with intercept but without trend and (2) with intercept and trend. Since the former is more suitable for our data, we employed the former for all variables. The lag length (bandwidth) was automatically selected by *EViews 6* using the Schwarz info Criterion. The asymptotic critical values were 0.347, 0.463 and 0.739 for the 10%, 5% and 1% levels, respectively; we employed the 5% significant level. The KPSS test statistics were 0.098 to 0.394, all of which are less than 0.463. This implies that we were unable to reject the null hypothesis for all the variables at the 5% level. Therefore, a spurious correlation did not arise.

Table 2. Results of the KPSS test. Individual coefficients are statistically significant at the *10% level. The bandwidth is automatically selected by Newey-West using Bartlett kernel.

Variables	Test stat.	Bandwidth
$N_{t+1}^B - H_t^B$	0.160	4
$N_{t+1}^P - H_t^P$	0.211	5
N_t^B	0.098	4
$\{N_t^B\}^2$	0.109	4
N_t^P	0.259	5
$\{N_t^P\}^2$	0.394*	5

Since our time series data was not affected by a spurious correlation, we applied several estimation methods for equations (3) and (4) using *EViews 6* and *S-PLUS 2000*. We employed the ordinary least square (OLS) method and the generalized least square method, which includes the weighted least square method, and obtained robust estimation results. We have only presented the results of OLS estimation method in Table 3. We used White's heteroscedasticity-consistent standard errors and covariance. Undoubtedly, the adjusted determination coefficient (adj. R^2) was 0.49 and 0.53 for equations (3) and (4), respectively. The Durbin-Watson statistics were 1.965 and 2.591. Since our models lack an intercept, we used the critical values presented in Farebrother [5]. The 1% and 99% critical values (the number of explanatory variable $k = 3$, and the number of sample n = 45) was 1.160 and 2.848, respectively. Therefore, we interpret that serial correlation did not occur in our model.

Table 3. Results of the estimation. Individual coefficients are statistically significant at the **5% level or ***1% level. t values are given in parentheses.

Equation (3)			Equation (4)		
Variable	Coefficient		Variable	Coefficient	
N_t^B	1.339 (4.88)	***	N_t^P	1.611 (6.80)	***
$\{N_t^B\}^2$	–0.020 (–2.60)	**	$\{N_t^P\}^2$	–0.021 (–4.867)	***
N_t^P	0.028 (0.31)		N_t^B	0.311 (1.373)	
R^2	0.545		R^2	0.512	
Adj. R^2	0.525		Adj. R^2	0.490	
D. W. stat.	2.591		D. W. stat.	1.965	

Subsequently, we employed these values to calculate the parameter values. The results are as follows: r^B = 0.64/year, r^P = 0.65/year, K^B = 30.06 heads/670 km^2, K^P = 33.11 heads/580 km^2, m = 10.29 heads/year and n = 0.081 (Table 4). The sign condition of these parameters are r^B, r^P, K^B, K^P, $m > 0$ and $0 < n < 1$, all of which were satisfied in our results.

Table 4. Estimated values of the parameters

Variables	Values	Units
r^B	0.638	Year
r^P	0.649	Year
K^B	30.057	Heads/670 km^2
K^P	33.114	Heads/580 km^2
m	10.287	Heads/year
n	0.081	

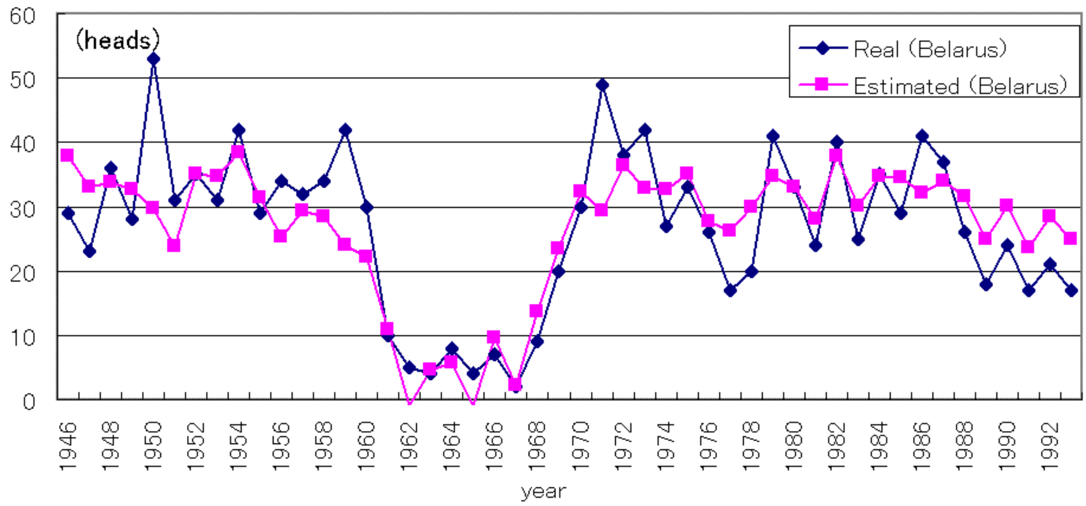

Fig. 2. Real and estimated numbers of the lynx in the Belarussian BPF

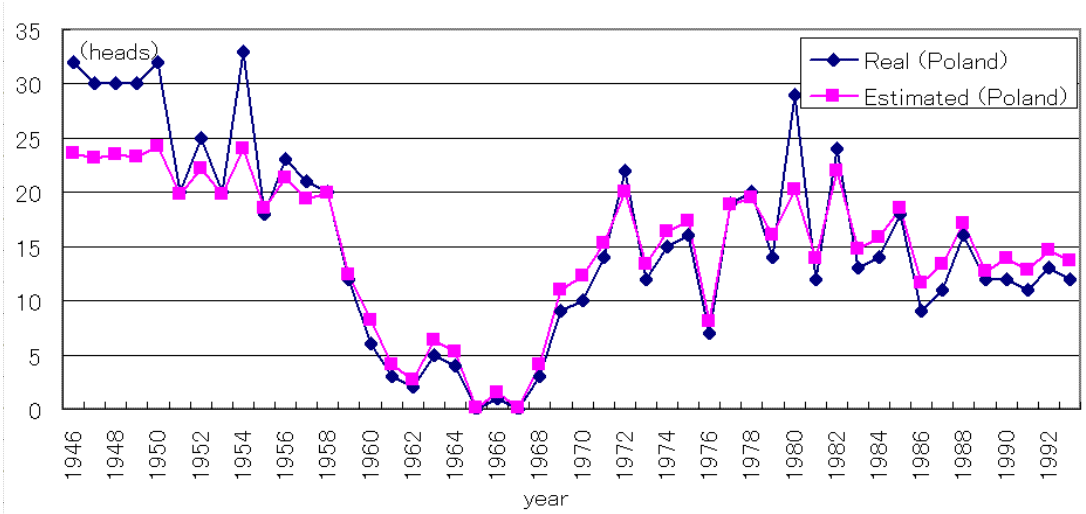

Fig. 3. Real and estimated numbers of the lynx in the Polish BPF

Finally, we verify our results by comparing the real time series data with the estimated ones. These have been presented in Figs. 2 and 3. The estimated time series values were considerably similar to the real values, with the exception of nearly one decade at the beginning of the period in case of Poland.

DISCUSSION

The validity of the parameter values have been discussed below. The instantaneous growth rates r^B and r^P are relatively high. This may indicate that the migration has occurred from outside the BPF. The possibility of migration can be further reinforced by the fact that n takes the value less than 1. This is because if $n < 1$, 'the circumstances outside the reserve [in our case, the BPF] are detrimental, creating less potential migration out of the reserve' [1, p. 469]. In addition, since the BPF is 'a remnant of a natural deciduous, temperate forest ecosystem' [3, p. 33] and has a large protected area for game animals, it may attract wild animals as being a potential habitat.

The value of carrying capacity K^P is almost at the upper bound of the lynx fluctuation in the case of the Polish BPF; however, this is not necessarily the case with respect to K^B. The carrying capacity of and instantaneous growth rate in Belarus are less than those of Poland perhaps because of the difference in the management policies of the two countries. Half of the Bialowieza National Park (BNP) located in Poland is preserved as a strict nature reserve, which, in other words, is 'the most protected area' [3, p. 33]. On the other hand, in Belarus, the BPF 'was used as a special hunting ground for [the] Communist Party members until 1991' [3, p. 34], and the lynx was keenly hunted between 1956 and 1967 [10, p. 125]. Finally, the value of m appears appropriate when compared with the values of the carrying capacities.

The implications of the results obtained have been discussed as follows. The relatively high instantaneous growth rates and carrying capacities suggest the importance of BPF as a habitat for game animals. In addition, Bobiec [3, p. 35] states that ‘the BPF and BNP are the last lowland forest in Europe where wolves and lynx naturally control red and roe deer populations.’ Therefore, it is crucial to ensure the sustainability of the BPF not only as a forest but also as a habitat.

In addition, our paper suggests the following: (1) the possibility of the lynx migrating from the surrounding forests and (2) a relatively high superiority of the instantaneous growth rate and carrying capacity in Poland, where the management policy towards the lynx is more generous. The latter may imply that the Belarussian BPF has the potential of improving its quality as a habitat. Moreover, when considering the home range of the lynx, a larger area needs to be reserved, for instance, the sanctuary and the reserved area should be enlarged.

Given that the BPF is one of the last remaining large natural forests in Europe, one of the most crucial roles of the management of the BPF is the protection of its wilderness. Our results imply that the BPF has the potential to become a quality habitat.

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