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ESTIMATION OF CARRYING CAPACITY AND GROWTH RATE OF WOLF IN LITHUANIA

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Abstract. The purpose of this paper is to estimate ecological carrying capacity (K) and growth rate (r) of Lithuanian wolf based on the estimated population sizes and number of harvests from 1966 to 2007. We used the modified Schaefer model where population dynamics is described by the logistic-equation-type growth function with time lag operator (τ) and harvest. We statistically selected the best model whose τ value was 4 and estimated value of K and r were 626 heads for the total Lithuanian territory and 0.776/ year, respectively. Then we examined the appropriateness of the values from the ecological point of view and concluded that ecological carrying capacity is supported by the prey base of wild animals, mainly cervids, and also by depredation on domestic animals. In 1994–1998, the population was near ecological carrying capacity or exceeding it, what we explain by high ecological plasticity of the species and increased use of domestic animals.
Key words: *Canis lupus*, ecological carrying capacity, growth rate, Schaefer model

Introduction

The wolf (*Canis lupus*) inhabits the Baltic States and their neighbouring countries such as Finland, Russia and Poland. LCIE reports the population size of wolf in the Baltic States as 400–500 heads in Lithuania, 300–500 in Latvia and 100–150 in Estonia (LCIE 2008). The numbers are changing though and in 2008 the official wolf population in Lithuania was 409 individuals while the minimum population count showed only 273 (Monitoring data 2008). The ecological carrying capacity of Latvia for wolf is quite high – over 1,000 individuals (Kawata 2008). In Lithuania, it has not been known to date. Thus, our study aims to give basic information on the estimated values of ecological carrying capacity and growth rates of wolf in Lithuania for scientific monitoring. Although the estimated values for parameters K and r are based on a simple model, they can be used as a candidate of index for wolf ecology. They can be used in consulting about the current wolf status in Lithuania and for comparison with values of other countries.

Material and methods

Our study was based on an official wolf survey and bag numbers in Lithuania in 1965–2007 (Table 1). However for 2006 and 2007, the minimum population count based on two-day snow tracking in all forest districts for two days was used. Because the numbers of wolves hunted are not available from 1994–1995, we substituted them with the arithmetic average of 1993 and 1996 ((148 + 122)/2 = 135). In 2005–2007, the hunting seasons' quota was set at 20 individuals. In 2007 it was not fulfilled (18 individuals hunted), but we have data on two wolf individuals lost in road accidents; thus, the number of 20 was used (Balčiauskas, unpubl.).

Table 1. Wolf numbers (N – survey, h – hunted) in Lithuania, 1965–2007.

Year	N	h	Year	N	h	Year	N	h
1965	34	43	1980	290	152	1995	600	135
1966	38	48	1981	290	137	1996	590	122
1967	36	26	1982	240	103	1997	623	117
1968	40	42	1983	250	180	1998	609	98
1969	54	33	1984	300	125	1999	477	87
1970	56	45	1985	290	144	2000	545	48
1971	65	47	1986	300	135	2001	425	76
1972	73	34	1987	290	156	2002	355	64
1973	100	55	1988	350	179	2003	150	53
1974	120	45	1989	350	120	2004	250	50
1975	130	61	1990	350	122	2005	182	20
1976	180	68	1991	420	94	2006	193	20
1977	180	94	1992	480	111	2007	205	20
1978	220	118	1993	485	148			
1979	250	109	1994	684	135			

Source: Official wolf survey and bag numbers in Lithuania.

We supposed the population dynamics of Lithuanian wolf can be described by a logistic equation with time lag and harvest. We used the following Schaefer model because it is widely used not only in fishery science but also in wild animal science, especially recently (Bulte & van Kooten 1999; Skonhoft 1999; Rondeau & Conrad 2003). Our model is described as follows:

$$N(t+1) = N(t) + r\left[1 - \frac{N(t-\tau)}{K}\right]N(t) - h(t)$$

where N, r, K and h are population size, growth rate, ecological carrying capacity and number of harvests, respectively. We set the interval of time period t as 1 year. τ is the time lag operator, which takes non-negative integral numbers.

For the estimation of K and r, we rewrote the above equation as follows:

$$Y = \beta_1 X_{1\tau} + \beta_2 X_{2\tau} + \varepsilon_\tau$$

where $Y = N(t + 1) - N(t) + h(t)$, $X_{1\tau} = N(t)$ and $X_{2\tau} = N(t - \tau)N(t)$; β_i ($i = 1, 2$) and ε_τ denote parameters and unobserved errors, respectively; $\beta_1 = r$ and $\beta_2 = -r/K$. Firstly, we estimated β_1 and β_2, and subsequently we calculated the values of K and r using above relationships.

The procedure of the estimation of K and r is largely based on Kawata (2008) with minor modifications. For the estimation, we used *EViews* Ver. 6 by Quantitative Micro Software. To be brief, we made the estimation based on the following procedures (Fig. 1):

1. We set the value of τ; τ is the time period influential to the dynamics of wolf population size. We limited the upper value to 5 years because most of wolves in neighbouring Latvia die until that age (Ozoliņš & Andersone 2002; Ozoliņš *et al*. 2008). In Belarus, only 11 percent of wolves were older than 4 years (Sidorovich *et al*. 2007). Therefore, we set τ between 0 and 5 and used the following procedures for 6 cases.
2. We conducted the Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test to detect if explanatory variables $X_{i\tau}$ s ($i = 1, 2$, and $\tau = 0,\ldots,5$) and explained variable Y are stationary or not. The null hypothesis (H_0) of the KPSS test is 'variable is stationary'. If H_0 was rejected at more than 5%, we regarded the variable as non-stationary. If both explanatory (at least one) and explained variables were non-stationary, we moved on to procedure 3. Otherwise (in our case, none or at most one variable was non-stationary), we moved on to procedure 4.
3. We conducted a co-integration test. For this test, we adopted Johansen's test. If co-integration was detected, we applied the dynamic ordinary least square (DOLS) method and had the estimated value of K and r. Otherwise, we finished estimation without estimating K and r.
4. We estimated K and r using OLS. Then we conducted F test and LM test for serial correlation. Null hypotheses (H_0) of F test and LM tests are 'there is no serial correlation'. If H_0 was rejected at more than 5%, we regarded there was serial correlation and we applied the Cochrane-Orcutt method when estimating K and r using OLS.

Results

We followed the procedures mentioned above. In procedure 2, we conducted the KPSS test. The results are tabulated in Table 2. For 6 cases of τ, we supposed two types of test equations: only intercept was included (denoted 'I') and both intercept and trend were included (denoted 'I & T'). Default was selected for a spectral estimation method, and Bartlett kernel was selected au-

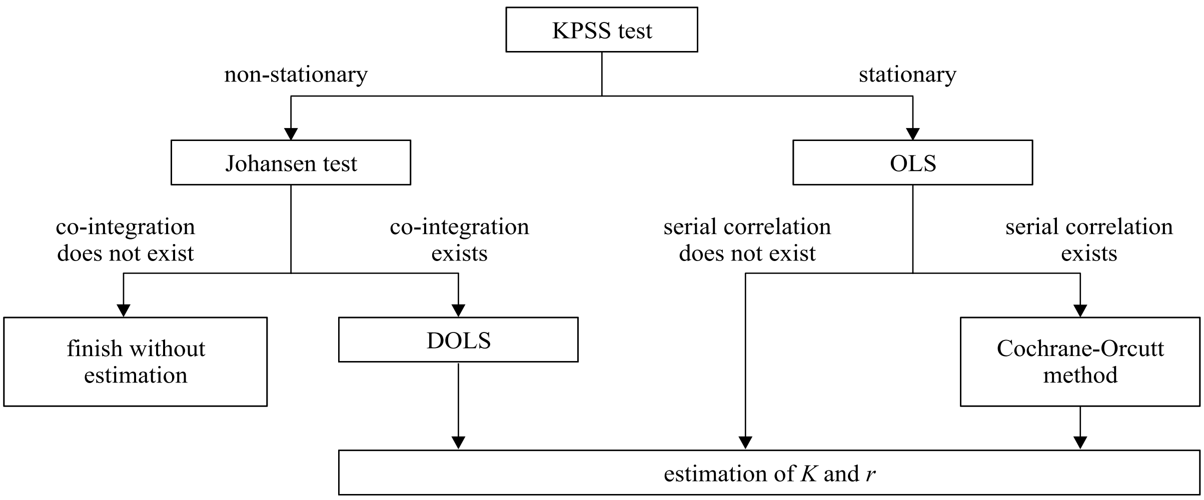

Figure 1. Procedures for estimation of K and r.

Table 2. Results of KPSS test.

	I			I & T		
name of variable	KPSS test statistic	bandwidth	result	KPSS test statistic	bandwidth	result
$\tau = 0$						
Y	0.186	5	stationary	0.183**	5	non-stationary
X1	0.518**	5	non-stationary	0.128*	5	stationary
X2	0.421*	5	stationary	0.097	5	stationary
$\tau = 1$						
Y	0.213	4	stationary	0.203**	4	non-stationary
X1	0.494**	5	non-stationary	0.130*	5	stationary
X2	0.427*	5	stationary	0.094	5	stationary
$\tau = 2$						
Y	0.219	4	stationary	0.201**	4	non-stationary
X1	0.471**	5	non-stationary	0.132*	5	stationary
X2	0.445*	5	stationary	0.097	4	stationary
$\tau = 3$						
Y	0.229	4	stationary	0.196**	4	non-stationary
X1	0.445*	5	stationary	0.144*	4	stationary
X2	0.456*	5	stationary	0.096	4	stationary
$\tau = 4$						
Y	0.241	4	stationary	0.193**	4	non-stationary
X1	0.419*	5	stationary	0.144*	4	stationary
X2	0.490**	5	non-stationary	0.093	4	stationary
$\tau = 5$						
Y	0.261	4	stationary	0.186**	4	non-stationary
X1	0.393*	5	stationary	0.145*	4	stationary
X2	0.507**	5	non-stationary	0.094	4	stationary

Note 1: 'I' means intercept is included in test equation and 'I & T' means intercept and trend are included in test equation.
Note 2: Asymptotic critical values are 0.739, 0.463, 0.347 for 1%, 5% and 10%, respectively in case of 'I', 0.216, 0.146 and 0.119 for 1%, 5% and 10%, respectively in case of 'I & T'.
Note 3: * – significant at 10% and ** – significant at 5%.

tomatically. Bandwidth was also automatically selected, and Newey-West Bandwidth was used.

When $\tau = 3$ and type of test equation is 'I', all variables were regarded as stationary. For other cases, only one variable was regarded as non-stationary and two variables were regarded as stationary. Therefore, we moved to procedure 4 and applied OLS for all 6 cases[1].

In procedure 4, we applied OLS to all 6 cases of τ values. When null hypotheses (H_0) of F test and LM tests are rejected at 1% level, we also conducted OLS with the Cochrane-Orcutt method. The results are tabulated in Table 3.

When $\tau = 0$, 1 and 2, OLS was applied, and when $\tau = 3$, 4 and 5, OLS with the Cochrane-Orcutt method was applied. Based on AIC and adjusted R^2, we selected $\tau = 4$ case as the best model, where estimated values of *K* and *r* were 626 heads for all Lithuanian territory and 0.776/year, respectively.

Discussion

In general, the population size should be less than carrying capacity (Odum 1953), which was confirmed by the wolf population in Latvia (Kawata 2008). In Lithuania, ecological carrying capacity was exceeded in 1994 (684 wolf individuals) and nearly reached in 1995–1998 (590–623 individuals). Does this mean our estimation is not valid?

Wolf numbers increased in the 1990s after restoration of independence in all three Baltic countries, reaching the maximum in the middle of the decade. As one of

[1] We should add the following: Our results of the KPSS test (here we discuss only when the type of test equation is 'I') suggest that spurious correlation did not occur because the explained variable was stationary. However, if the explanatory variable is non-stationary, *t*-values are no longer reliable. Nevertheless, we will leave these explanatory variables in our estimation models because these variables are necessary in our models and spurious correlation is denied.

Table 3. Results of OLS and estimated values of *K* and *r*.

	τ = 0	τ = 1	τ = 2	τ = 3	τ = 4	τ = 5
X1	0.708*** (5.813)	0.638*** (5.116)	0.725*** (6.465)	0.778*** (11.615)	0.776*** (13.047)	0.748*** (12.437)
X2	-0.001*** (-3.932)	-0.001*** (-3.263)	-0.001*** (-4.464)	-0.001*** (-8.163)	-0.001*** (-9.216)	-0.001*** (-8.645)
AR (1)				-0.449*** (-2.906)	-0.449*** (-2.916)	-0.506*** (-3.367)
adjR^2	0.085	-0.001	0.160	0.363	0.464	0.391
AIC	11.683	11.791	11.634	11.414	11.256	11.406
D. W.	1.684	2.353	2.441	1.902	2.159	2.211
F test	0.316	0.232	0.153	0.007***	0.006***	0.002***
LM test	0.310	0.255	0.146	0.007***	0.007***	0.003***
type	OLS	OLS	OLS	OLSwithCO	OLSwithCO	OLSwithCO
r	0.708	0.638	0.725	0.778	0.776	0.748
K	738	761	691	657	626	599

Note 1: *t* values are in parentheses.
Note 2: * – significant at 10%, ** – significant at 5% and *** – significant at 1%.
Note 3: F test and LM test were conducted for the results of OLS.

the reasons was the weakening of wolf control (Andersone *et al*. 2001).

Of three Baltic countries, Lithuania is characterised as having the smallest forest area/percent. Forests covered approximately 2.05 million ha or 33% of the territory of Lithuania in 1996, 3.0 million ha or 48% of the territory of Latvia in 1997, and 2.2 million ha or 48% of the territory of Estonia in 1996 (Baltic 2000). Stable distribution of wolves (Balčiauskas *et al*. 1999) was based on the use of unusual habitats formed after destruction of intensive agriculture and other human activities such as abandoned and re-grown fields, restoring exploited peat-lands, closed military areas, unused fish pond complexes, also new protected areas established after 1992 (Balčiauskas 2002, 2008).

Lithuanian forests abound in ungulates, being the main prey of wolves in natural habitats. In 1990–2000 the average number of wild boar was over 20,000 (16,620–24,500), that of roe deer over 44,500 (36,300–68,600), and that of red deer near 13,500 (13,391–16,701) (Baleišis *et al*. 2003). The current population of ungulates is much larger, thus may support even higher numbers of wolves. In addition, Lithuania can boast of a very large population of beaver, which is food source for wolf in Latvia, too (Andersone & Ozoliņš 2004). Here we explain that the number of wild food items, irrespective of their share in wolf diet, may even separately support the current numbers of wolves. Our model did not evaluate food availability – but in Lithuania we have surplus of wild food for wolf.

As additional food source, there always have been numbers of domestic animals killed by wolves in Lithuania (Balčiauskas *et al*. 2002). In 1995–2002, the number of killed cattle and sheep was about 1,000 heads yearly (Bluzma 1999; Balčiauskas 2002). In 2002–2005, wolf depredation lessened considerably, approximated by one to several hundred heads, and in 2007–2008, wolf depredation started growing again (Balčiauskas, unpubl.). Thus, based on the estimation of ecological plasticity of the species and food resources (considering wild and domestic animals), we may conclude that ecological carrying capacity for wolves in Lithuania was calculated properly.

In this work we do not consider transboundary movements of wolf packs. In Latvia, migration of wolves from neighbouring areas in the east (Russia) is known (Andersone 2003; Andersone *et al*. 2005). In north Lithuania, a survey of wolves shows packs migrating to/from Latvia, while in south Lithuania to/from Byelorussia (Balčiauskas, unpubl.). Nevertheless, it is hardly believable these migrations to be intensive enough to influence ecological carrying capacity of the species. Contrary to Kawata (2008), we did not explain an extremely large proportion of hunted wolves in the 1970s and 1980s by immigration, but rather by underestimation of the population size. The possible reason could be political, as wolf was regarded as a pest and exterminated by all possible ways; thus, underestimation of pest numbers was politically 'sound'.

The growth rate ($r = 0.776$/year) seems acceptable, and is not necessarily based on immigration of wolves from neighbouring countries. For Latvia, growth rate was considered being higher (Kawata 2008), thus requiring support from the immigration process. At the moment, numerical estimation of transboundary wolf packs between the two countries is absent. Knowing this parameter may improve the power of our models.

The difference in response rate between Latvian and Lithuanian wolves – the latter being one year later – may be explained by different age structure between populations. The authors presume that a lower hunting pressure in Lithuania let wolves achieve older age – thus, response is also later. But for confirmation of this presumption we lack data on the age of hunted wolves in the bag. Also, our results point out to the lack of knowledge of wolf diet in Lithuania (killing rate and diet composition, for example). Additional data can improve discussion in the future.

Conclusions

Ecological carrying capacity for wolves in Lithuania is 626 individuals as estimated by the modified Schaefer model, and growth rate is 0.776 per year. High population numbers of wild boar, red deer and roe deer may support even higher wolf numbers (based on the average food requirements of the species); however, wolf diet studies are not being carried out in Lithuania currently.

High ecological carrying capacity is supported not only by wild prey base, but also depredation on livestock, which in the last decades varied from several hundred to approximately one thousand heads.

High depredation was the possible reason real numbers of wolves were close to ecological carrying capacity or even exceeded it in the period of 1994–1998.

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Vilkų aplinkos talpos ir populiacijos augimo greičio Lietuvoje įvertinimas

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Santrauka

Straipsnis skirtas įvertinti Lietuvos ekologinę talpą vilkams (*K*) ir jų populiacijos augimo greitį (*r*) remiantis populiacijos dydžiu ir sumedžiojimu 1966–2007 metais. Buvo pritaikytas modifikuotas Šeferio modelis, kuriame populiacijos dinamika aprašoma logistine augimo lygtimi su vėlinimo operatoriumi (metų skaičius, τ) ir sumedžiojimu. Buvo parinktas statistiškai geriausias modelis, kurio τ vertė buvo 4. Apskaičiuota, kad *K* reikšmė visai Lietuvos teritorijai yra 626 individai, o *r* – 0,776 per metus. Buvo įvertintas ir apskaičiuotų dydžių tinkamumas ekologiniu požiūriu. Padaryta išvada, kad ekologinė talpa priklauso nuo grobio – laukinių (ypač elninių) gyvūnų gausos ir nuo papjaunamų naminių gyvulių skaičiaus. 1994–1998 metais populiacija buvo beveik pasiekusi ekologinę talpą arba ją viršijo. Tai galima paaiškinti dideliu rūšies ekologiniu plastiškumu bei tuo, kad tais metais vilkai papjaudavo daugiau naminių gyvūnų.

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