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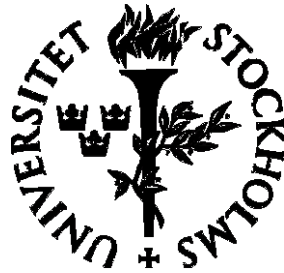
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Grey wolf (*Canis lupus*) density and ecosystem productivity: The relationship in theory and reality, and conservation implications

Författare: Shayer Mahmood Ibney Alam

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Grey wolf (*Canis lupus*) density and
ecosystem productivity:
The relationship in theory and reality, and
conservation implications

Författarens namn: **Shayer Mahmood Ibney Alam**

Handledare: **Bodil Elmhagen**

Forskningsämne: **Biodiversity and Conservation**

Granskningskommitté: **Birgitta Tullberg, Ulrika Alm-Bergvall**

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Grey wolf (*Canis lupus*) density and ecosystem productivity: The relationship in theory and reality, and conservation implications

Author: Shayer Mahmood Ibney Alam; Supervisor: Bodil Elmhagen
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Abstract

Both bottom-up exploitation (ecosystem productivity) and top-down control (predation) determine the abundance and distribution of species. The Exploitation Ecosystem Hypothesis (EEH) predicts that both predator biomass (carnivore densities) and the impact of predation (top-down ecosystem function) increase with productivity when the top trophic level remains unexploited. Top predators, therefore, play a significant role in maintaining ecosystem functions as well as local biodiversity and this can be an important issue for their conservation. This study focused on Grey Wolf (*Canis lupus*) as the top predator and investigated the theoretical relationship between wolf density and productivity and compared it with the real case scenario at continental scale, in Europe and North America separately. All available data on home range sizes and density were searched and analyzed in this regard. A positive theoretical relationship was indicated between wolf density and ecosystem productivity since home range size decreased asymptotically with the increasing productivity. The real scenario showed a complex pattern ranging from no relationship to positive linear and asymptotic relationships. The study assumed that these variations are due to the fact that wolves are controlled and managed by humans under their carrying capacity and hence might not be maintaining critical ecosystem functions.

Introduction

The abundance and distribution of species are determined both by bottom-up exploitation and top-down control. Bottom-up control is guided by the productivity of an ecosystem whereas predation is the mechanism for top-down control (Oksanen *et al.* 1981, Leibold 1989, Oksanen & Oksanen 2000, Melis *et al.* 2009). This is explained by the Exploitation Ecosystem Hypothesis (EEH) (Oksanen *et al.* 1981, Oksanen & Oksanen 2000), which predicts that when the top trophic level remains unexploited, both predator biomass (carnivore densities) and the impact of predation (the top-down ecosystem function) increase with productivity (Fretwell 1977, Elmhagen *et al.* 2010) and thereby reflect proper ecosystem functioning. Top predators are also known to play a significant role in maintaining ecosystem functions as well as local biodiversity (Sergio *et al.* 2005, Srivastava & Vellend 2005, Sergio *et al.* 2006, Schmitz 2008). Therefore, if the predictions of EEH are correct, maintaining ecosystem functions carried out by the top predators can be an important conservation issue.

There are studies which have shown that species biomass distributions follow predictions of EEH (Crete 1999, Aunapuu *et al.* 2008) but it has also been shown that the strength of top-down control in relation to productivity differs. Elmhagen & Rushton (2007) found stronger top-down impact from wolves/lynx on red fox at high productivity in Sweden, Melis *et al.* 2009 found stronger top-down impact from wolves/lynx on roe deer in unproductive Eurasia and Elmhagen *et al.* 2010 found stronger top-down impact from lynx on foxes in unproductive parts of Finland. So, the question arises on what is the 'theoretical' relationship between predator biomass (density) and productivity.

Home-range size is one of the most fundamental ecological parameters for a species that is often used for estimating population size and density (Herfindal *et al.* 2005, Nilsen *et al.* 2005) and variation in home range size is often due to prey population density and environment productivity (Carbone & Gittleman 2002, Nilsen *et al.* 2005). Productivity, however, is a primary determinant of variation in home range size between populations (McLoughlin & Ferguson 2000) and home range size increase with decreasing productivity (Harestad & Bunnell 1979, Carbone & Gittleman 2002, Nilsen *et al.* 2005).

Further to that, the variation in home range size within the same carnivore species is also related to latitude as it can be considered as an alternative measure of ecological productivity (Jedrzejewski *et al.* 2007). A northwards increase in home-range size has been observed in

wolves reflecting a positive relationship with latitude (Okarma *et al.* 1998, Mech & Boitani 2003, Jedrzejewski *et al.* 2007).

This study focused on top predators and Grey Wolf (*Canis lupus*) as the model species and investigated the theoretical relationship between wolf density and productivity in Europe and North America. Since wolves are highly regulated by man (Mech & Boitani 2003), I approach the question by exploring the relationship between wolf home range size and productivity, under the assumption that this relationship should be fairly ‘constant’ irrespective of regulation by man, and therefore, indicates the possible theoretical relationship. I also explored the relationship between actual wolf density and productivity as the real case scenario.

All available data on home range sizes were searched and the relationship between these variables and productivity were tested to answer the question ‘Do wolf densities follow the predictions of EEH or is there a ‘saturation level’ where wolf densities no longer increase’? That is, what would be the likely form of the relationship between wolf home range size and productivity in Europe and North America (theoretical relationship)?

All available data on wolf densities were also searched to assess the actual relationship between densities and productivity in areas where wolves are present today. These were compared with the estimated ‘theoretical’ relationships and I discuss implications in terms of the conservation of wolves and ecosystem functions.

Methods

Data collection

I searched for all available data (published data from papers in journals and reports, unpublished data from masters theses) on home range sizes and densities of Grey wolf (*Canis lupus*) in Europe and North America.

Home range

In this study, I defined home range as the area defended by at least a pair or a pack of wolves. Therefore, home ranges of lone wolves were excluded from analysis. I considered all papers containing either the home range or territory size of wolves, since home range and territory are synonymous for wolf packs as they strictly defend the area they roam about (Mech & Boitani 2003).

Data obtained from different articles showed wide variation in how they analyzed home range data. Some articles provided home ranges for the male and female of a pack separately, while others, summer and winter home ranges separately. In both cases, I calculated the mean home ranges and used them to represent pack home range. Some articles provided a range instead of a single number. In those cases, I calculated the mean values of the range. Different articles used different methods for obtaining home range size that included satellite transmitters (PTT – platform transmitter terminals), conventional VHF transmitters, radiotracking using minimum area method, Minimum Convex Polygon (MCP 95% & 100%) and Kernel method. All of them were included for analysis.

While collecting data, emphasis was given on wolf packs that depend on resident and natural prey. Wolves that depend on migratory prey have excessively large home ranges compared to those that depend on resident prey and were excluded from the analysis (e.g. Walton *et al.* 2001).

Density

Density in this study was defined as the number of wolves/1000 km². Data given in number of wolves/hectar or number of wolves/100 km² were converted to the number of wolves/1000 km². I used two alternative sources of data to see whether they show similar results – data from the IUCN/SSC Canid Specialist Group's Status Survey and Conservation Action Plan of

the Canid species (Mech & Boitani 2004) and data from different published papers from scientific journals.

Mech & Boitani (2004; in this paper as IUCN data) provides the population size and the percentage of area occupied by wolves within countries in Europe and state or provinces in North America. I obtained data on the total area for the given country, state or province (CSP) from <http://www.britannica.com/> or government websites of the respected provinces (e.g. <http://www.gov.sk.ca/Default.aspx?DN=f80c0ebb-f1c6-497e-8bc0-30c215a5441f>). These were used to calculate the area occupied by the wolves and their density in the following way:

Area occupied by wolves (A) = Area of CSP * Range occupied (%) of that CSP / 100

$$\text{Density of wolves (wolves/1000 km}^2\text{)} = \frac{\text{Population}}{\text{Area occupied (A)}} \times 1000$$

In the case of data collected from published papers, when density for several years was given, the mean was calculated and used for analysis. Both average annual density and density at any point of the year were used for analysis.

Coordinates

I collected the coordinates of each location primarily from the respective articles. If not provided in the articles, the coordinates were obtained through visual impression from the study area map given in the articles and using the website <http://itouchmap.com/latlong.html> and Google Earth. To get country coordinates, I searched for the probable distribution of wolves within the country and chose the coordinates from the area of wolf distribution close to the centre of the distribution.

Productivity

For each coordinate, I used the average productivity for the past five years (2005 to 2009) as a measure of productivity for that location. The average productivity refers to the mean of Fraction of Photosynthetically Active Radiation absorbed by vegetation (FPAR) of 1×1 km squares for an area of 11 ×11 km² centered on the location's coordinates. Each of these means was an 8 day composite from the same time duration.

FPAR global 1×1 km MOD15A2 data sets were downloaded from MODIS and MISR website at Boston University <http://cliveg.bu.edu/modismisr/>.

Statistical analysis

The relationship of wolf density (number of wolves/1000 km²) and home-range size (km²) with productivity and latitude were estimated by fitting linear and non-linear models. For non-linear relationships, suitable curves were searched using different formulas representing exponential, asymptotic or sigmoid relationships.

The following formulas were used for non-linear models (Crawley 2007):

1. Exponential, $y = ae^{bx}$
2. 2-parameter asymptotic exponential, $y = a(1 - e^{-bx})$
3. 3-parameter asymptotic exponential, $y = a - be^{-cx}$
4. Gompertz, $y = ae^{-be^{-cx}}$
5. 3-parameter logistic (sigmoid), $y = \frac{a}{1 + be^{-cx}}$

The obtained non-linear models were then compared with a linear model ($y = ax + c$) to find out the relationship that fits the data best. For comparing and attaining best fitted curves, the highest-ranking model was selected based on the lowest 'Akaike's Information Criterion (AIC)' value (Burnham & Anderson 2001, Herfindal *et al.* 2005, Hebblewhite *et al.* 2007).

The European and North American data were analyzed separately due to the different prey types (Fuller *et al.* 2003, Garrott *et al.* 2007) and to explore and compare the trends separately at continental level. All data were analyzed using statistical software R (version 2.10.1).

Results

A total of 30 home range sizes of grey wolves were included in the final analysis, out of which, 12 were from Europe and 18 from North America (Appendix I). From the IUCN data, a total of 28 densities were calculated of which 18 were from Europe and 10 from North America (Appendix II). Of 24 densities from journal papers used for the analyses, 7 were from Europe and 17 from North America (Appendix III). The relationship models that best fit each particular data set are summarized in Table 1. Home ranges followed the prediction of EEH but in an asymptotic way whereas the density followed more complex patterns, which to some extent reflects the fact that they are under human management and are not contributing properly in ecosystem functioning.

Table 1. Models fitted for different data sets. To note, models with the lowest dAIC values were chosen as the best fitted for the specific criterion, but to nullify other models, the difference between the dAIC values should be at least 2. The multiple models shown under single criterion are with differences less than 2 from the lowest value and in ascending order. EU = Europe, NA = North America, asymp II = 2- parameter asymptotic model, asymp III = 3- parameter asymptotic model, exp = exponential model, lin = linear model, sig = sigmoid model

Response variable	Explanatory variable	Continent	Relationship (best fitted models)	d AICc
Home range	Productivity	EU	neg asymp II	0.0
		NA	neg asymp II > neg sig > lin	0.0 > 0.4 > 0.7
	Latitude	EU	exp	0.0
		NA	exp > sig > lin	0.0 > 1.7 > 1.9
Density (IUCN data)	Productivity	EU	linear	0.0
		NA	No relation	0.0
	Latitude	EU	neg asympII > lin	0.0 > 1.6
		NA	No relation	0.0
Density (Journal data)	Productivity	EU	linear	0.0
		NA	No relation > lin	0.0 > 0.1
	Latitude	EU	No relation > lin	0.0 > 1.1
		NA	neg asymp II > neg asymp III	0.0 > 0.3

Home range

In Europe, a negative asymptotic model fitted as the best model to explain the relationship between the home range and productivity while exponential models best explained the relationship between home range and latitude. The same relationships were also found in case of North America (Fig 1).

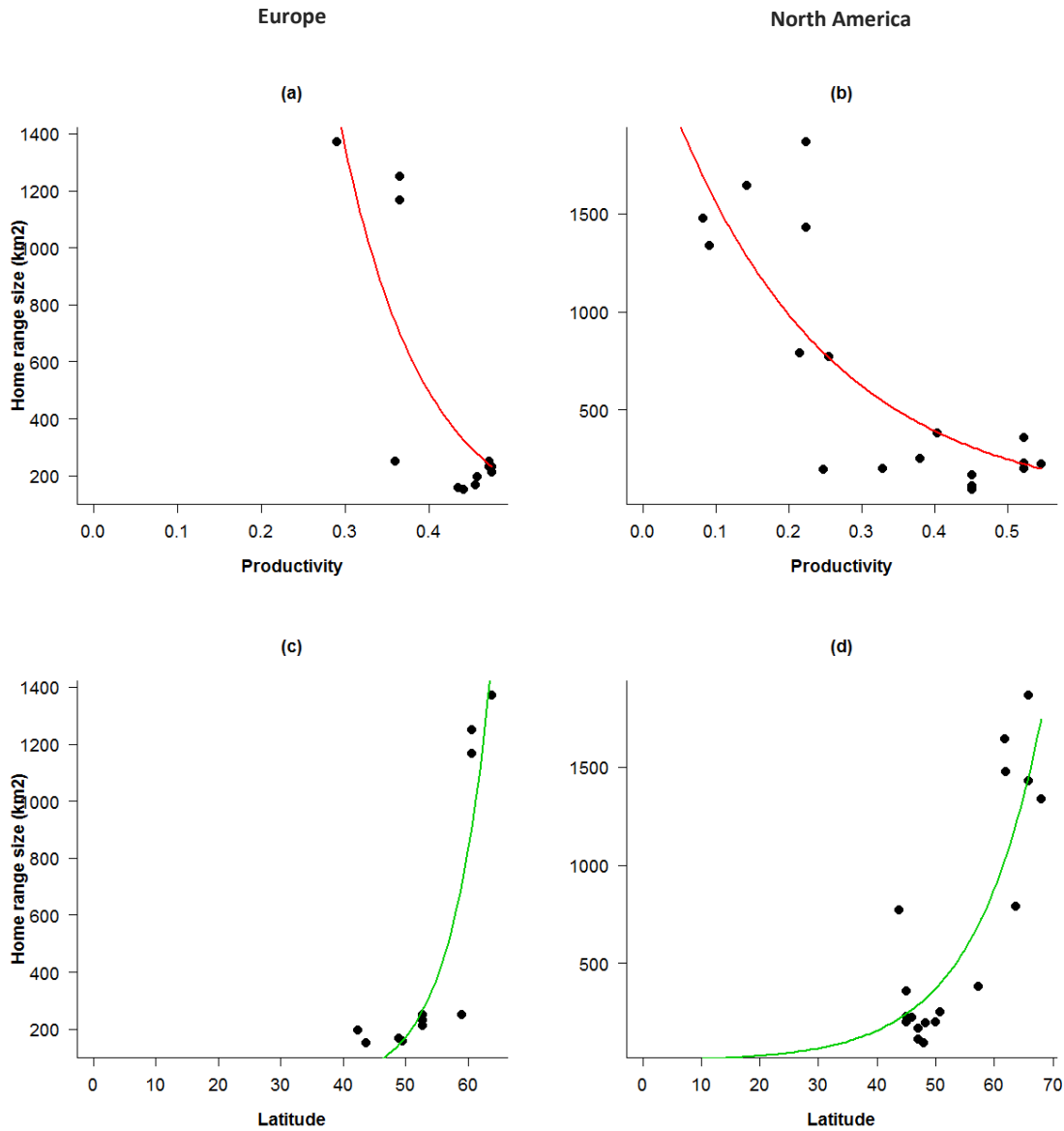


Fig 1. Models for relationship between home range and productivity (above) and home range and latitude (below). Home range showed a negative asymptotic relationship with productivity both in Europe (a) and North America (b). Exponential relationships were found between home range and latitude in both continents, Europe (c) and North America (d).

Density

Both IUCN and journal data showed similar relationships – with productivity, positive linear in Europe and no relationship in North America (Fig 2). However, the results are different with latitude. Europe shows negative asymptotic relationship in IUCN data but no relationship in journal data (Fig 3). On the other hand, North America shows the opposite trend, that is, no relationship in IUCN data but negative asymptotic relationship in journal data (Fig 3).

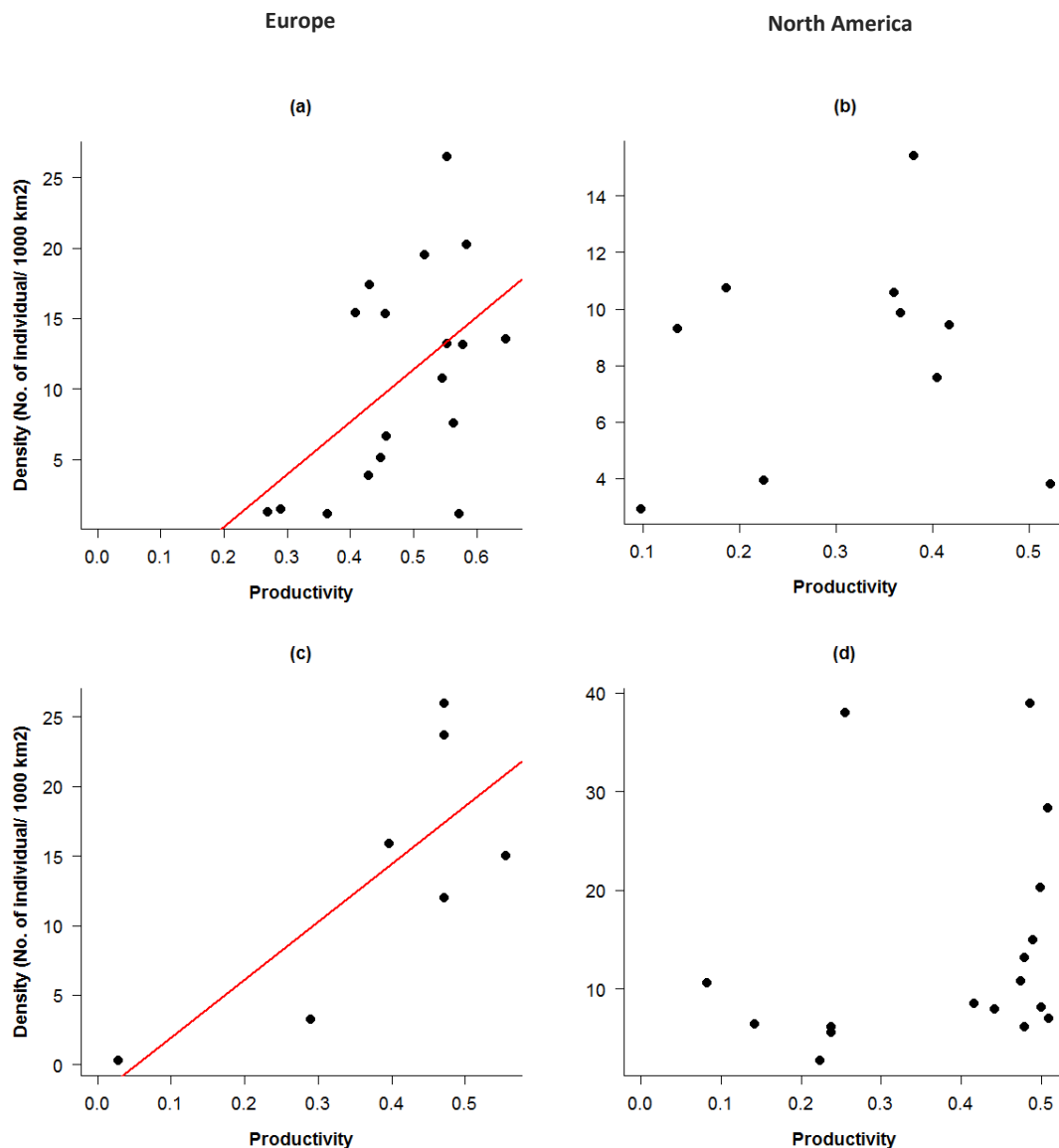


Fig 2. Relationship between density and productivity of grey wolves from IUCN 2004 data (above) and journal data (below). Positive linear relationships were found in Europe (a & c) and no relationship in North America (b & d). For 'd', linear model was the second best model with the AIC value difference of 1.1.

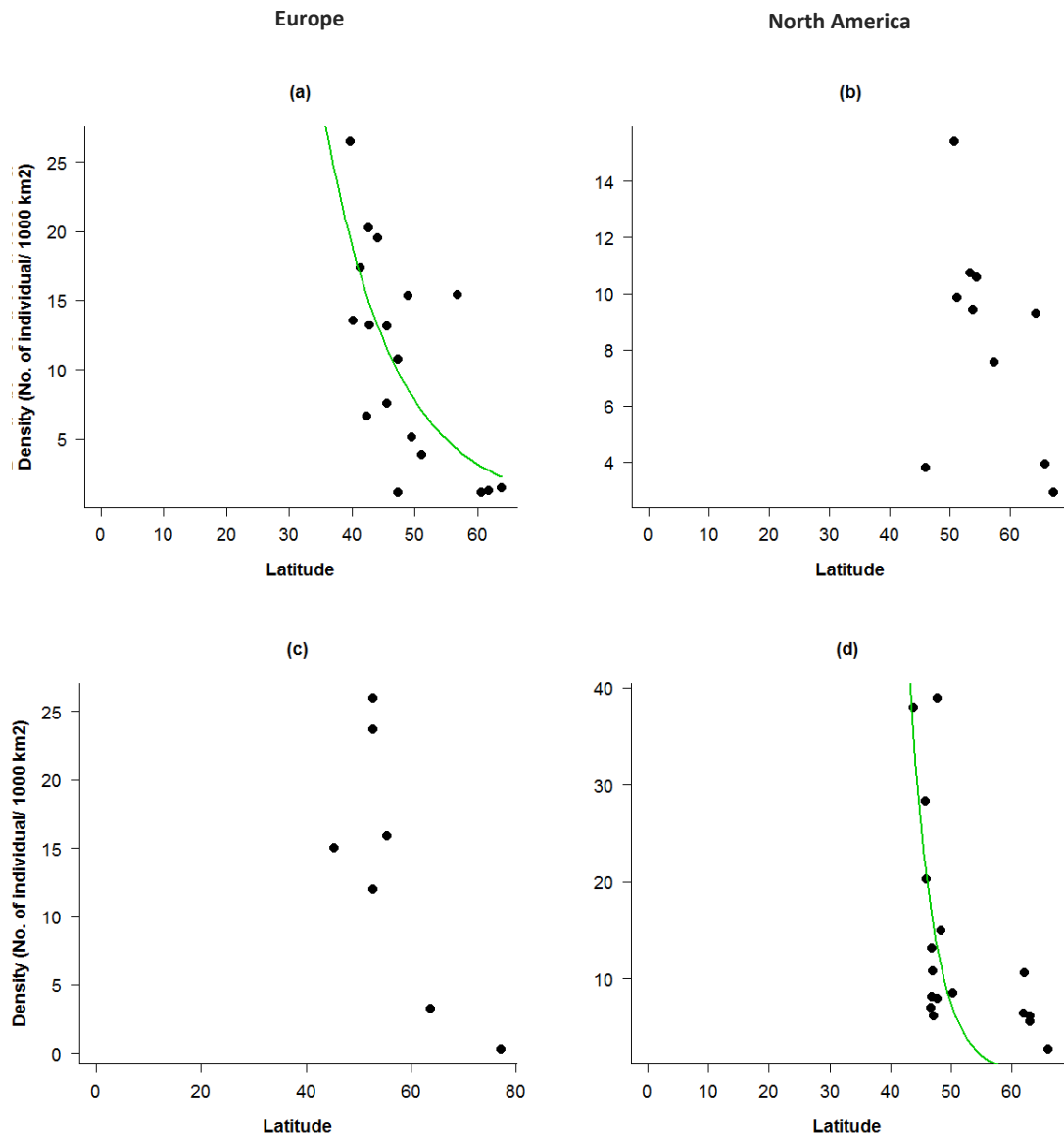


Fig 3. Relationship between density and latitude of grey wolves from IUCN 2004 data (above) and journal data (below). Negative asymptotic models fit for Europe (a) in IUCN data and for North America (d) in journal data; no relationship was found North America (b) in IUCN data and Europe (c) in journal data. For 'c', however, linear model was the second best model with the AIC value difference of only 0.1.

Discussion

The results from the present study follow the prediction of EEH that predator density follows ecosystem productivity. Theoretically, analyzing home range data, the study found that there exists an asymptotic relationship between wolf density and productivity (both with FPAR and latitude) but in varying magnitude. In the real case scenario, analyzing the density data, the results follow the EEH only in some cases. Therefore, it can be assumed that wolves, at present, are not contributing to ecosystem functioning according to their potential, at least in some places, and imply the conservation perspective that they are under human exploitation/management.

The theoretical relationship

Productivity is one of the major factors that affect intraspecific variation in home range size (McLoughlin & Ferguson 2000). Harestad & Bunnell (1979) showed that home range size is inversely proportional to ecosystem productivity, that is, areas with greater productivity usually have smaller home ranges. The present study supports this but, in addition, shows that the relationship is asymptotic, both in Europe and North America (Fig 1). Though, Nilsen *et al.* (2005) found a similar (negative asymptotic) trend for wolf, brown bear and leopard in general, the present study showed the trend only for wolves and at a continent level (Europe and North America separately). Harestad & Bunnell (1979) also found a positive correlation between home range size and latitude. Several other studies found a northwards increase in home-range size in wolves reflecting a positive relationship with latitude (Okarma *et al.* 1998, Mech & Boitani 2003 and Jedrzejewski *et al.* 2007). This trend is evident from the present study but the relationships are exponential, both in Europe and North America.

The asymptotic and exponential relationships (Fig 1) indicate that there is a minimum home range size below which there is no decrease with increasing productivity. One possible explanation behind this could be intraspecific interactions, such as territoriality.

For a given area, it is expected that the larger home range sizes will result in less wolf packs and vice versa (given that the pack sizes are equal throughout), and thus imply that home range size is inversely proportional to density. Population density is positively correlated with prey biomass density within carnivore species (Carbone & Gittleman 2002) and prey (herbivore) biomass in turn with the ecosystem productivity (McNaughton *et al.* 1989, Crête 1999, Nilsen *et al.* 2005, Bråthen *et al.* 2007). From this point of view also it can be assumed that carnivore density is positively correlated to the ecosystem productivity, and therefore, can suggest a

theoretical relationship between density and productivity, which is opposite to the relationship between home range and productivity.

The real case scenario

From the present study, the two sets of data showed both similar (considering productivity) as well as dissimilar (considering latitude) results (Table 1). In Europe, I found a linear relationship with productivity in both cases but no relationship for North America (Fig 2). On the other hand, a negative asymptotic relationship was found with latitude in Europe from IUCN data and in North America from journal data (Fig 3) and no relationship in North America from IUCN data and in Europe from journal data. The asymptotic relationships (Fig 3) with the latitude, however, show level off denoting that there is a minimum density below which it does not decrease with increasing latitude (in other words, increase with productivity). This may be due to the fact that they reach the region where they start to follow the migratory prey or above that the places are so little productive that they are not suitable as wolf habitat.

In Europe, three out of four cases and in North America one out of four cases show relationship while the rest shows no relationship (Fig 2 & 3). Therefore, it can be said that in reality, wolf densities following EEH in some cases showing positive relationships while not in other cases where no relationship exist. It may be due to the fact that some of the data are from the protected areas where wolves are not exploited while some are from the population that are recolonizing or under human management (Elmhagen *et al.* 2010) below the level of carrying capacity and to the point from where they cannot contribute to maintain ecosystem function. The existence of relationships, however, indicates that at least in some places wolves are carrying out their ecological functions. But, to fulfill the EEH, it is a prerequisite that the top predator must remain unexploited. That may also be the cause why there is no support for EEH in some cases.

Some other factors may contribute to the results such as intraspecific competition (Carbone & Gittleman 2002), variation in pack size, prey availability, types and biomass (Crête, 1999, Lariviere *et al.* 2000, Mech & Boitani 2003), stochastic events and even interaction among these factors (Sinclair & Krebs 2002). Some of these factors, on the other hand, are related to productivity on regional as well as continental scale (Gompper & Gittleman, 1991, Carbone & Gittleman, 2002, Herfindal *et al.* 2005). Further, small sample size (Nilsen *et al.* 2005) and/or inappropriate coordinate estimation for FPAR measurement might have also influenced the results.

The productivity measurements

Though the present and several other studies used latitude as a proxy for productivity and found relationship both with density and home range, latitude may not be an appropriate indicator for judging relationships as it does not consider the local variation in geography and climate (Nilsen *et al.* 2005). On the other hand, use of FPAR as a productivity measurement is regarded as a powerful tool (McNaughton *et al.* 1989, Sellers *et al.* 1997, Nilsen *et al.* 2005). The results from the present study may also support this notion showing consistency with productivity (Fig 2) and inconsistency with latitude (Fig 3) in both IUCN and journal density data. But still, even FPAR has its drawback as it considers all areas irrespective of utilization by the species and can get biased by the surroundings (Nilsen *et al.* 2005).

Future directions

Since wolves are heavily impacted by human, it is a complicated species to deal with. To get more substantial support to the findings, it might be interesting to study how density influences on home range sizes and vice versa and the interaction between them. It should also be checked whether there remains any autocorrelation among the data points.

In this study, I took consideration of all method together. It might also be interesting to investigate whether the results vary with i) the methodology of obtaining the data (for example, may be according to Kernal vs. MCP or within MCP (95% vs. 100%), or between data obtained by GPS vs. VHS method), ii) number of observation points to estimate the home range (for karnel and/ MCP), which can be a confounding factor for the analysis of the present study, iii) populations, whether they are introduced or recolonized as in Yellowstone National Park, Scandinevia etc. or saturated as in Poland, Canada etc. and iv) types of main prey as moose in Scandinavia and elk, roe deer or wild boar in central Europe.

Conservation implications

It is a prerequisite of EEH that the top predator have to remain unexploited to maintain the ecosystem functions. Several studies have found that top predators play significant roles in maintaining local biodiversity and thus ecosystem function (Sergio *et al.* 2005, Srivastava & Vellend 2005, Sergio *et al.* 2006, Schmitz 2008) and they are often used as ‘flagship’ or ‘umbrella’ species for conservation of biodiversity (Linnell *et al.* 2000, Sergio *et al.* 2006). Therefore, to maintain biodiversity and ecosystem function, wolves (top predator) should remain unexploited.

For effective conservation and management of a carnivore species, home range size is considered as one of the most important parameter for planning and recovering populations, especially at the time of estimating carrying capacity for a given area (Herfindal *et al.* 2005, Nilsen *et al.* 2005). Protected areas (PA), however, are regarded as the central method of *in-situ* conservation strategies (Loyola *et al.* 2009). As we see from the study that home range size increase with latitude (decreasing productivity towards higher latitudes), therefore, theoretically, it can be assumed that smaller PAs can be enough in high productive areas of low latitudes while larger PAs are needed in less productive areas of higher latitude to maintain ecosystem function. At the present day situation where large PAs are scarce, and wolves are living mostly in human dominated multi-use landscapes, it would be a better strategy to conserve wolves in lower latitudes where their home ranges are smaller (Linnell *et al.* 2000).

Conclusion

The present study shows that, theoretically, a positive relationship between wolf density and ecosystem productivity occurs where density increases asymptotically with productivity. The real scenario shows a range of patterns from no relationship to linear and asymptotic relationships. These variations verify the fact that wolves are highly controlled and managed by humans in many places across their range and thus are not being able to follow the predicted patterns that might be essential in maintaining critical ecosystem functions.

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Appendix I. Home ranges from different sources (journals, masters thesis and reports)

Continent	Reference	Home range size (km ²)
North America	Burch <i>et al.</i> 2005	787.0
	Adams <i>et al.</i> 2008	1336.5
	Ballard <i>et al.</i> 1997	1868.0
	Ballard <i>et al.</i> 1998	1430.0
	Ballard <i>et al.</i> 1987	1645.0
	Hayes and Harestad 2000	1478.0
	Jedrzejewski <i>et al.</i> 2007	382.5
	Carbyn 1983	252.5
	Kolenosky 1972	224.0
	Mills <i>et al.</i> 2006	228.0
	Mills <i>et al.</i> 2006	198.0
	Cook <i>et al.</i> 1999	355.7
	Potvin 1988	199.0
	Fuller <i>et al.</i> 1992	166.0
	Chavez & Gese 2006	193.5
	Van Ballenberghe <i>et al.</i> 1975	92.0
	Jedrzejewski <i>et al.</i> 2007	113.0
	Berger & Gese 2007	769.5
Europe	Kjell 2002	1251.0
	Sand <i>et al.</i> 2008	1166.0
	Kaartinen <i>et al.</i> 2005	1372.4
	Estonia 2001	250.0
	Jedrzejewski <i>et al.</i> 2007	250.0
	Jedrzejewski <i>et al.</i> 2001	232.0
	Nowak <i>et al.</i> 2008	158.0
	Theuerkauf <i>et al.</i> 2003	231.0
	Okarma <i>et al.</i> 1998	211.5
	Findo & Chovancova 2004	168.5
	Kusak <i>et al.</i> 2005	150.5
	Ciucci <i>et al.</i> 1997	197.0

Appendix II. Densities from IUCN 2004

Continent	Country/state/province	Density (Individual/ 1000 km ²)
North America	Alaska	3.93
	British Columbia	10.58
	Yukon Territory	9.31
	North-west Territories and Nunavut	2.91
	Alberta	7.55
	Saskatchewan	9.44
	Manitoba	15.43
	Ontario	9.87
	Labrador	10.73
	Minnesota	28.87
	Michigan and Wisconsin	3.81
Europe	Norway	1.24
	Sweden	1.11
	Finland	1.48
	Estonia. Latvia. Lithuania	15.39
	Poland	3.84
	Czech Republic	5.07
	Slovakia	15.3
	Hungary	10.75
	Romania	13.11
	Bulgaria	20.27
	Greece	26.52
	Croatia and Slovenia	7.59
	Albania	17.42
	Bosnia Herzegovina	19.53
	Spain	13.18
	Portugal	13.56
	France	1.1
	Italy	6.64

Appendix III. Densities from different journal papers

Continent	Reference	Density (Individual/ 1000 km ²)
North America	Ballard <i>et al.</i> 1997	2.70
	Hayes& Harestad 2000	10.60
	Fuller 1989	39.00
	Adams <i>et al.</i> 2008	5.55
	Berger <i>et al.</i> 2008	38.00
	Lariviere <i>et al.</i> 2000	20.30
	Lariviere <i>et al.</i> 2000	13.20
	Lariviere <i>et al.</i> 2000	10.80
	Lariviere <i>et al.</i> 2000	8.50
	Lariviere <i>et al.</i> 2000	8.10
	Lariviere <i>et al.</i> 2000	7.90
	Lariviere <i>et al.</i> 2000	7.00
	Lariviere <i>et al.</i> 2000	6.10
	Burch <i>et al.</i> 2005	6.10
	Ballard <i>et al.</i> 1987	6.45
	Bergerud <i>et al.</i> 1983	14.92
	Theberge <i>et al.</i> 2006	28.3
Europe	Jedrzejewski <i>et al.</i> 2007	26.00
	Sidorovich <i>et al.</i> 2007	15.90
	Marquard-petersen 2009	0.27
	Kusak <i>et al.</i> 2009	15.00
	Kaartinen <i>et al.</i> 2005	3.25
	Okarma <i>et al.</i> 1998	23.70
	Okarma <i>et al.</i> 1998	12.00