Forest Ecology and Management 366 (2016) 53–64

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Long-term study of damage to trees by brown bears *Ursus arctos* in Poland: Increasing trends with insignificant effects on forest management

E. Zyśk-Gorczyńska [a], Z. Jakubiec [b], B. Wertz [c], A. Wuczyński [a,*]

[a] *Institute of Nature Conservation, Polish Academy of Sciences, Lower-Silesian Field Station, Podwale 75, 50-449 Wrocław, Poland*
[b] *University of Zielona Góra, Faculty of Biological Sciences, Szafrana 1, 65-516 Zielona Góra, Poland*
[c] *University of Agriculture in Kraków, Faculty of Forestry, Al. 29-listopada 46, 31-425 Kraków, Poland*

ARTICLE INFO

Article history:
Received 18 September 2015
Received in revised form 2 February 2016
Accepted 3 February 2016

Keywords:
Damage to forests
Long-term trends
Tree damage
Foraging behavior
Forest economy
Carpathians

ABSTRACT

We present a long-term quantitative analysis of forest damage caused by the brown bear (*Ursus arctos*) in the biggest refuge of this species in Poland. Based on questionnaires distributed to the relevant authorities we estimated the number of trees damaged by bears in 1991–2013, changes in the tree species composition and large-scale factors potentially affecting the extent of damage. We also discuss the importance of bear tree damage to forest management. Throughout the 23 years of the study we recorded 6937 trees damaged by bears: a clearly increasing trend and distinct fluctuations in tree numbers and species composition were discernible. Conifers (91.7% – fir 70.0%, larch 11.3%, spruce 9.5%, pine 0.9%) were more frequently damaged than deciduous species (2.9%). Larch and spruce were preferentially affected during the whole study period, and the preference for larch was distinct when collated with its availability in forest stands – a forage ratio of 0.50 compared to 0.35 for fir, 0.17 for spruce and 0.13 for pine. In 2003, however, bears suddenly switched to fir and it is this species that now predominates among the damaged trees, reaching 96.5% in 2013.

Two models based on minimum AIC_c values were best explaining damage to trees. The most parsimonious model contained one explanatory variable: brown bear population size. The second best model included both bear population size and the average fir tree-ring width. Neither fluctuations in daily temperatures nor the number of days with snow cover had any influence on the scale of damage. Our findings suggest that damage caused by bears is not to be regarded as a serious problem by forest management in Poland and it is unlikely to reach a level of economic significance in the short term.

1. Introduction

Biotic and abiotic factors can affect forest health and productivity. Damage to a tree trunk can disrupt its mechanical structure and hence the transport pathways linking the elevated and underground parts of the tree (Vasiliauskas, 2001). The life processes of a wide variety of organisms from fungi to insects and mammals may cause the death or reduce the growth of individual trees or their stands (Bobiec et al., 2005; Hegland et al., 2013; Jędrzejewski and Sidorovicz, 2010; Vospernik, 2006). Wild ungulates are most commonly identified with damage to forest stands in Europe and elsewhere (Bergqvist et al., 2014; Gill, 1992; Jędrzejewski and Sidorovicz, 2010). Moreover, in some European forests, animals with a high conservation priority, such as European bison *Bison bonasus*, Eurasian beaver *Castor fiber* or brown bear *Ursus arctos*, may be responsible for damage. In view of the rarity of these species and the difficulties in studying tree damage over large areas, this phenomenon is still poorly understood, even though tree damage may significantly affect forest health and productivity (Flowers et al., 2012; Lowell et al., 2010; Manning and Baltzer, 2011).

This study discusses the characteristics of tree damage caused by the brown bear (*U. arctos*). Tree damage is observed throughout the distribution range of this species and other *Ursidae*, and is done for marking, feeding, and play. Marking behavior relates to single trees and is thought to be associated with body care (Meyer-Holzapfel, 1968) or social communication (Green and Mattson, 2003). Tree marking may be repeated by bears over the years and generally does not lead to tree death (Jakubiec, 2001; Sato et al., 2013). Foraging behavior usually relates to many trees and consists in stripping the bark from the trunk and then feeding on

* Corresponding author.
E-mail address: a.wuczynski@pwr.edu.pl (A. Wuczyński).

http://dx.doi.org/10.1016/j.foreco.2016.02.007
0378-1127/© 2016 Elsevier B.V. All rights reserved.

the tree cambium (Ziegltrum and Nolte, 2001; Zyśk-Gorczyńska and Jakubiec, 2010). This behavior has been reported mainly from North America in black bears (*Ursus americanus*) (Flowers et al., 2012; Nolte and Dykzeul, 2002; Ziegltrum, 2005), but also from Asia in Japanese black bears (*Ursus thibetanus japonicas*) (Watanabe, 1980; Watanabe et al., 1970; Yamada and Fujioka, 2010) and from Europe in brown bears (Jakubiec, 2001; Kunovac et al., 2008; Krapinec et al., 2011a,b; Zyśk-Gorczyńska and Jakubiec, 2010, 2014). Bark stripping by bears can result in the complete girdling of the stem, which normally leads to tree death. Nonetheless, wounds are usually small and the damaged trees live on in the ecosystem until their natural death, providing a range of ecological niches for different organisms (Kanaskie et al., 1990; Ziegltrum and Nolte, 2001; Zyśk-Gorczyńska et al., 2015).

Recently, an increase in the intensity of tree damage by brown bears has been observed in different parts of their European distribution (Krapinec et al., 2011b). Clearly, the phenomenon is dynamic and ought to be better understood. Unfortunately, however, long-term trends in the extent of damage, its causes, ecological characteristics and significance for forest management, have been largely neglected in Europe. For instance, a wide variety of tree species are known to be damaged, although conifers are definitely preferred (Barnes and Engeman, 1995; Kanaskie et al., 1990; Krapinec et al., 2011a,b; Sullivan, 1993; Witmer et al., 2000; Zyśk-Gorczyńska and Jakubiec, 2014). In the USA the black bear readily forages on *Pseudotsuga menziesii*, *Pinus contorta*, *Larix occidentalis* (Barnes and Engeman, 1995; Sullivan, 2009; Witmer et al., 2000), Japanese black bears regularly damage Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*) (Watanabe, 1980; Yamada and Fujioka, 2010), while brown bears in Europe mostly forage on fir (*Abies alba*), larch (*Larix decidua*) and spruce (*Picea abies*) (Jakubiec, 2001; Krapinec et al., 2011a,b; Zyśk-Gorczyńska and Jakubiec, 2014). However, data from Poland indicate that these preferences have changed in recent decades (Jakubiec et al., 1993; Jakubiec, 2001; Zyśk-Gorczyńska and Jakubiec, 2014), possibly as a result of long-term changes in the condition of particular tree species (=nutritional value of cambium) (Kimball et al., 1998a,b; Radwan, 1969), changes in alternative food supply in forest stands (Noble and Meslow, 1998), or in bear population size (Krapinec et al., 2011b; Nolte and Dykzeul, 2002). However, no quantitative analyses have been carried out to verify these conjectures.

In North America, the foraging of black bears on tree cambium is known to have a substantial impact on the forest economy (Flowers et al., 2012; Nolte and Dykzeul, 2002). For instance, in NW Oregon the area of damaged stands is estimated at approximately 1400 ha per year (corresponding to a loss of $11.5 million). The related high economic losses are generated by the necessity of removing the damaged trees, by the preferences of bears for trees in good condition, subject to earlier costly treatments (Flowers et al., 2012; Kanaskie et al., 1990; Sullivan, 2009; Witmer et al., 2000), by reduced tree growth following bear damage (Lowell et al., 2010; Manning and Baltzer, 2011), and also by indirect costs associated with damage prevention.

In Europe the damage caused by bears is incomparably smaller than in North America, although in Croatia financial losses due to bear damage have increased (Krapinec et al., 2011b). Similar trends also pertain to Poland, but they are not considered a serious problem by forest management. Bear damage is not even assessed by forest administrations, in contrast to damage caused by other large mammals (Zyśk-Gorczyńska and Jakubiec, 2014; Zyśk-Gorczyńska et al., 2015). In Poland damage caused by bears is usually identified as domestic damage, comparable with the killing of farm animals or damage to apiaries (Jakubiec, 2001).

The objectives of this study were to evaluate the long-term dynamics of tree damage caused by brown bears in their most important refuge in Poland, and to determine which factors might be affecting the scale of damage and the choice of damaged tree species. We expected that the total number of trees damaged by bears would be directly affected by the size of the brown bear population. However, we also hypothesized that factors related to climate and tree condition could affect on the extent of damage. Finally, we discuss the role of brown bears in forest management. In particular, we ask whether this species might be regarded as a pest in Polish forest stands, given its present numbers and the current and potential future extent of damage to trees.

2. Material and methods

2.1. Study area

The study was carried out in the Bieszczady Mountains (SE Poland), which are situated in the North-Eastern Carpathians, in the borderland between Poland, Ukraine and Slovakia. The study area covered 1628.9 km^2 and extended over seven forest districts administered by the Regional Directorate of the State Forest Administration (RDSFA) in Krosno (Baligród, Cisna, Komańcza, Lesko, Lutowiska, Stuposiany, Ustrzyki Dolne) and the Bieszczady National Park (BNP) (Fig. 1, Table 1). Montane mesophilous forest is the predominant type of habitat in this region. The forests consist mainly of beech (>40%) and silver fir (>26%), spruce and alder are locally important, and there are accompanying species like sycamore and larch. The forests are very fertile (Marszałek, 2011; Winnicki and Zemanek, 2009), which has a direct impact on the annual current increment, the age of stands and abundance of trees. The annual current increment in the study area amounted to 6.83 m^3/ha/year, the stands have an average age of 79 years, and the abundance is 317 m^3/ha (Table 1). Notably, the latter two figures are much higher than the national averages (55 years and 245 m^3/ha, respectively) (Krameko, 2010; Marszałek, 2011). Consequently, the forests in the Bieszczady Mountains are of significant value for nature conservation. The Bieszczady are part of the Natura 2000 network (PLC180001) and include both Special Protection Areas and Special Areas of Conservation. The Bieszczady are also part of the UNESCO East Carpathians Biosphere Reserve. Because of the high level of habitat heterogeneity and fertility, this region is inhabited by a variety of animals. A unique feature of the Bieszczady is the coexistence of a wide spectrum of large ungulates, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), European bison and wild boar (*Sus scrofa*), with carnivores like brown bear, wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), wild cat (*Felis rufus*) and red fox (*Vulpes vulpes*). The populations of the large carnivores are relatively stable or increasing (in the brown bear, see below), while those of the ungulates are gradually increasing (Chapron et al., 2014; Marszałek, 2011; Winnicki and Zemanek, 2009).

2.2. The brown bear in Poland

The north-westernmost range of the Carpathian brown bear population, currently estimated at 7200 individuals, extends over Poland, Slovakia, Ukraine, Romania and Serbia. According to the IUCN red list categories the whole Carpathian population has been classified as "vulnerable", and in some regions as "endangered" (Chapron et al., 2014; Linnell et al., 2008). The brown bear population that we studied is of a transboundary character and its protection status varies: in Poland it is strictly protected, in Slovakia it is both protected and treated as game, but in Ukraine it is only game (Jakubiec, 2001; Koreň et al., 2011; Ševčenko and Škvirâ, 2009; Rigg and Adamec, 2007).

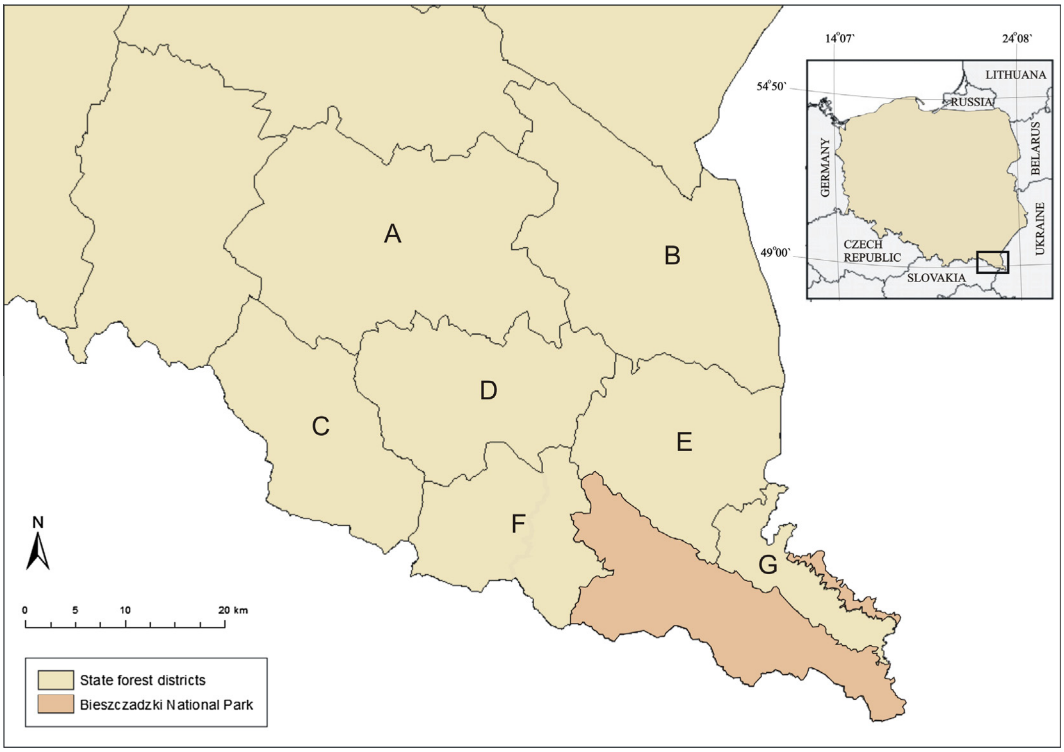

Fig. 1. Study area showing the location of the Forest Districts: Lesko (A), Ustrzyki Dolne (B), Komańcza (C), Baligród (D), Lutowiska (E), Cisna (F), Stuposiany (G) and the Bieszczady National Park in the Bieszczady Mountains (SE Poland, NE Carpathians). Data on tree numbers were obtained from all Forest Districts (A–G); data on brown bear population size were obtained from Baligród, Cisna, Komańcza and Stuposiany forest districts and from BPN.

Table 1
Characteristics of forest stands in the forest districts and the BNP (Krameko, 2010; Marszałek, 2011).

Forest districts	Total area (km^2)	Proportion of montane mesophilous forest (%)	Average age (years)	Average current increment (m^3/ha/year)	Average abundance of trees (m^3/ha)
Baligród	192.99	92.07	79	7.02	319
Cisna	201.64	97.71	78	7.75	283
Komańcza	216.44	97.93	77	7.80	330
Lesko	181.37	63.75	78	7.25	344
Lutowiska	207.25	95.70	72	3.50	256
Stuposiany	94.45	98.50	84	6.02	267
Ustrzyki Dolne	242.79	86.01	74	7.70	334
BNP	292.02	76.64	93	7.6	404
Total	1628.95		79	6.83	317

The whole area of Poland lies within the historical range of the brown bear. However, by the end of the 17th century, following intensive hunting, the species almost disappeared from most regions of the country, and the population was estimated at just a few individuals. After the Second World War, bears were present only in the Bieszczady and Tatra Mountains, and their total numbers were estimated at 10–14 individuals. Thereafter, the population began to recover slowly (Buchalczyk, 1980; Jakubiec, 2001). Currently, the numbers are estimated at 80–147 individuals, depending on the source (Chapron et al., 2014; Jakubiec, 2001; Selva et al., 2011; Śmietana et al., 2014), and are continuing to increase. The most important refuges of the brown bear in Poland are its two reproductive areas: the Bieszczady Mts., with the largest population (55–83 individuals) and the Tatra Mts. (12–15 individuals). The third and westernmost region in Poland where bears live and occasionally reproduce is the Beskid Żywiecki mountain range.

2.3. Questionnaires to forest districts

Long-term data on brown bear population size, biology and conservation were collected within the framework of the Bear Monitoring Programme in Poland (Jakubiec, 2001), coordinated by the Lower Silesian Field Station of the Institute of Nature Conservation of the Polish Academy of Sciences. One aspect of this programme were the questionnaires sent out each March to all forest administration districts and national parks that come within the distribution range of the brown bear in Poland. They asked for information, gathered by the forestry service all the year round, relating to various aspects of bear biology, including population size, productivity, occurrence of dens, winter activity, and also tree damage.

The survey concerning tree damage started in 1991, since such damage had rarely been recorded before then. Therefore, this study basically covers the period 1991–2013. We summarized the information from seven forest districts covering the Bieszczady Mts., and thus the local range of the brown bear (Fig. 1, Table 1). As the BNP does not sell timber, it did not record tree damage as precisely as the forestry service, so we did not include data concerning tree damage from the BNP. However, data from BNP were used to access brown bear population size (see below).

Data on tree damage were collected mainly by the foresters, during their daily service, supplemented with information gathered from hunters and forest workers. The number of foresters did not change significantly during the study period and was proportionate to the area of district, moreover each year the foresters were obliged to exploring the subordinate area evenly. For these reasons it was likely that the sampling effort was roughly the same between districts and years, although it could not be controlled. In protocols we have asked about trees damaged by bears only in a given year (fresh wound). Foresters recorded which part of the tree was damaged, which tree species were affected and the number of damaged trees. Although the foresters were not asked to classify the type of damage (e.g. marking, foraging) it was obvious that most data concerned the feeding oriented damage. This stemmed from the provided characteristics of the wounds (large, situated at the butt-end of the trunk) and the typical concentration of many damaged trees in a small area of the forest stand. We therefore implicitly treat the bear damage as foraging behavior throughout this paper, although some reported trees could have been damaged for other purposes. Moreover, in populations of the brown bear where the cambium-feeding occurs the damage for other purposes (marking and game) is relatively rare and can be neglected (Green and Mattson, 2003; Sato et al., 2013).

To quantify the data we first summed the numbers of damaged trees in each district and year, and then calculated the totals for the Bieszczady Mts. Occasionally, respondents approximated the number of individual damaged trees, so to quantify the data we assumed "a few" damaged trees to be five, and "a dozen or so" to be fifteen. Such approximations related to no more than 6% of the total number of damaged trees. If a tree was not named as to species, we identified it as "unknown species", and excluded it from the analyses of the species composition of damaged trees.

The questionnaire data were also used to assess the population size of the brown bear in Poland and more specifically, to calculate an index that was used to relate trends in tree damage and bear numbers (Section 2.4). The bear population in Poland was determined with the modified method of systematic, year-long observations of animals (Fruziński, 2002) which compiled various methods of bear monitoring. All available information on bear occurrence within each forest district, i.e. casual observations, counts at feeding sites, snow tracking, dens, counts of females with cubs and more recently data obtained from radio telemetry and trial cameras, were gathered from people regularly associated with forests – hunters, foresters, forest workers, researchers. Then, an approved person, usually biologist or game specialist, verified these data and prepared an expert assessment on bear numbers. Transient and resident individuals were distinguished, the latter were assumed to be bears that stayed in the same area more than 3 months, females with cubs, and denning individuals. The results were presented in the questionnaires and submitted to the national coordinators who re-examined all data. Additionally, annual summary reports were prepared for internal needs of the forest districts and national parks (e.g. Pirga, 2014, www.bdpn.pl/dokumenty/nauka/2014/2014_monitoringdrapieżników.pdf?v=2).

The method of systematic observations of animals has been used for years in Poland, especially in game management, however, it is often criticized as being difficult to the scientific evaluation (Okarma and Tomek, 2008). To minimize the disadvantages of this method and make the assessments of the bear population credible, over the entire study period we undertook a number of corrective measures (see Jakubiec, 2001, 2010 for detail, http://siedliska.gios.gov.pl). Initially, in 1991, an instruction on how to collect bear data, expanding the questionnaire points, has been sent to all forest district in the Polish Carpathians. In particular, the foresters were asked to measure, whenever possible, the width of the foreleg since this measure allows minimum individual bears to be recognized (Bromlej, 1965), hence an over-counting can be lessen. Particular attention has been given to the spring observations when the activity of bears is limited to relatively small wintering areas, and to simultaneous counts at bait stations. The accuracy of the information gathered from the observers and submitted in protocols was always requested (place, day, sometimes time of observation). The questionnaire forms did not change over years, also the respondents to the questionnaires remained the same, being in regular contact with the coordinators what allowed to consult any current doubts. As a result, the method appeared reliable and useful to the long-term monitoring of the brown bear, providing official statistics on the population metrics of this species in Poland (Boitani et al., 2015).

2.4. Statistical analyses

Standardized data collection protocols were used for assessing bear population size and trees damage. We standardized data spatially (among forest districts) by divided number of damaged trees and bears number per unit area (10 km^2). Than we used simply standardized method to standardize data temporally (along the study duration):

$$z = \frac{x - \mu}{\sigma}$$

where

x – $(x_1, \ldots, x_n)$,
μ – the average of the population,
σ – the standard deviation of the population.

The Spearman rank correlation was used to test possible relationships between the "damage variables" (i.e. total number of trees damaged by bears, the number and percentage of damage to individual tree species, where the percentages were calculated excluding the "unknown species", see above) and time (years). The Spearman correlation was also used to test the relationship between bear numbers and time.

To test the bears' preferences for particular tree species we calculated a forage ratio, using the B_{i1} index of Manly et al. (1972), i.e. by dividing the proportion of damaged trees by the proportion of trees available in the stand. The index was calculated for six tree species, (fir, larch, spruce, pine, ash and beech), and the category of "others", i.e. all the other tree species in the Bieszczady stands. The availability of these species was based on official statistics regarding the distribution of the forest area according to species and age classes, obtained from RDSFA. We used only stands >80 years old, since younger trees are rarely damaged by bears in the Bieszczady Mts. (Zyśk-Gorczyńska and Jakubiec, 2014). The forage ratio was calculated separately for each tree species and forest district. Afterward, we obtained the mean forage ratio by dividing the forage ratio for each tree species by the sum of forage ratios for all tree species (Sutherland et al., 2004).

Linear regression models were used to test the potential drivers of bear damage to trees. This part of the analysis was restricted to fir for several reasons (see Discussion – Section 4.5): in particular because of the disproportionately large amount of damage to this species, and because we had precise long-term data on tree condition only for this species. The standardized number of damaged firs (log + 1 transformed) in 1991–2013 was tested against four explanatory variables: (1) standardized numbers of bears, (2) fir condition as expressed by a standardized ring formation (mm) (log transformed), (3) number of days with snow cover in November–April, and (4) average daily temperature for May and June (°C). The explanatory variables are explained in greater detail below. We selected best model using Akaike information criterion corrected for small samples and associated statistics (AIC_c) (Burnham and Anderson, 1998, 2004). Lower AIC_c value indicates a more parsimonious model and we present results for models with $\Delta AIC_c < 2$ (the difference between the models with lowest AIC_c and the given model). Statistical significance for all tests was accepted at $P < 0.05$. We present the linear model results in graphs, where the explanatory variables are shown against a background of years. Trend lines are fitted to results. For the statistical analyses, we used STATISTICA version 12 (StatSoft, Inc., 2014) and Excel software.

To relate trends in tree damage and the number of bears, we used an index of population size, i.e. the most reliable assessment of the number of resident individuals in the best surveyed area. To calculate the index we selected, firstly, questionnaires from five forest districts with the most complete data regarding bear numbers: Baligród, Cisna, Wetlina, Komańcza, Stuposiany and from the BNP. In this area the average bear population was 48 individuals and increased significantly between 1991 and 2013 (R_s = 0.89, $P < 0.001$) (Table 2). Secondly, gap years – regarding data of bear numbers – 2008 in all districts and 2011 in BNP – were omitted from analyses. Finally, we considered only the number of bears described in questionnaires as residents, i.e. we cut the number of transient individuals which potentially could distort the district-based population assessments. With such an approach we obtained an index that reliably reflected bear abundance and trends and was useful for the purpose of linear models.

Evaluation of the radial increment of silver fir was carried out on the basis of an irregular network of 16 sample plots, covering the range of this species along the entire Polish Carpathians. All the sampling plots were located in stands with silver fir as the main stand-forming species aged around 100 years in optimal habitat. On each site, 20–30 individual dominant firs in the stand, according to class I or II in Kraft's classification (Kraft, 1884), were selected and cored once at the dbh. After standard sample preparation, tree-ring widths were measured and cross-dated with the CooRecorder and CDendro programs (v.7.8, Cybis Elektronik & Data AB, Sweden) and COFECHA (Grissino-Mayer, 2001; Holmes, 1986). Next, using the dplR plugin (Bunn, 2010, 2008) in the R environment (R Development Core Team, 2015), the real regional chronology of the radial increment as well as the standardized one for firs in the Polish Carpathians was constructed on the basis of local chronologies from all 16 sites. To compute a standardized chronology and emphasize mid-term changes of the increment, a moving average filter with a 15-year window was applied, and the incremental index was calculated by dividing the real tree-ring width by the corresponding value of the moving average filter.

We selected two climate variables which could potentially influence bear damage. The number of days with snow cover between November and April was selected because we thought that this parameter could influence bear activity in spring. Furthermore, the number of days with snow cover could have an impact on tree condition. The average daily temperatures for May and June (°C) were chosen because most damage caused by bears in Poland occurs in these two months (Jakubiec, 2001; Zyśk-Gorczyńska and Jakubiec, 2014). Long-term climate data were obtained from the weather station situated in the study area (the Baligród forest district, N 49°21′, E 22°17′, 430 m amsl). The station belongs to the Institute of Meteorology and Water Management – National Research Institute, the official Polish meteorological service performing regular meteorological measurements all over the country. The figures relating to climate data are listed in Table 2.

3. Results

3.1. Damage characteristics and dynamics

A total of 6937 trees were damaged by bears in 1991–2013; the trend was an increasing one ($R_s = 0.89$, $P < 0.001$), with noticeable fluctuations in particular years, from six damaged trees in 1991–1076 in 2005 (mean 302 per year) (Table 3; Fig. 2). Damage occurred in each year of the study period, and the frequency of years with damage was high (>70%) in most districts. Moreover, the increasing trend was significant in all but two districts. However, the extent of damage was unequally distributed among districts: 86.8% of damage was recorded in only three districts, situated in the central part of the study area, whereas relatively small amounts of damage were reported in the peripheral districts, only recently colonized by bears (Lesko, Komańcza, Ustrzyki Dolne) (Table 3).

3.2. Changes in the species composition of damaged trees

Six tree species – fir, larch, spruce, pine, beech, and ash – were damaged by brown bears. Damage was more frequent on conifers (91.7% – fir 70.0%, larch 11.3%, spruce 9.5%, pine 0.9%) than on deciduous trees (2.9%). Damage to "unknown tree species" amounted to 5.4% (Table 4). Fir was the most damaged species in all forest districts, assuming fir to be the main tree in the category of "unknown species" with a high numbers in two districts (Table 3).

Interestingly, the proportions and composition of damaged tree species changed significantly during the study period. The percentage of larch and spruce declined even though the total number of damaged trees did not significantly change in these species. In contrast, there were significant increases in the total tree number and percentage of fir and pine, although the latter species was rarely damaged and both increases in pine were marginally significant (Table 4; Fig. 3). A substantial increase in damaged firs occurred in 2003; thereafter, fir was the most frequently damaged species, reaching 96.5% in 2013. Only beech among the deciduous species suffered a significant increase in the total number and percentage of damaged trees (Table 4). A significant increase in the total number of damaged trees was also recorded in the category of

Table 2
Summary data of candidate explanatory variables influencing bear damage used in the linear models.

Variables	Min	Max	Average (±SD) (1991–2013)
Number of bears	29 (1991)	90 (2013)	48 (17.8)
Fir growth rings (mm)	2.48 (1991)	3.36 (2004)	3.06 (0.22)
Number of days with snow cover November–April	34 (2006/2007)	114 (1995/1996)	85.5 (18.3)
Average daily temperatures May–June (°C)	9.5 (2013)	15.7 (2003)	13.6 (1.25)

Table 3
Summary statistics on damage to trees in the Bieszczady Mts. during a 23-year study period (1991–2013), divided into forest districts.

Forest districts	% years with bear damage	Total number of damaged trees	Numbers of damaged trees per 10 km^2	Average ± SD (min–max) number of trees per 10 km^2 per year	Spearman rank correlation (R_s)	P	Damage to tree species per 10 km^2						
							Fir	Larch	Spruce	Pine	Beech	Ash	Unknown
Baligród	78.26	1582	82.0	3.56 ± 4.93 (0–24.7)	0.79	<0.001	62.7	4.51	4.61	0.62	8.75	0.72	0.05
Cisna	91.30	2199	109.1	4.74 ± 4.45 (0–14.08)	0.29	0.174	49.7	31.1	25.84	<0.01	0.74	<0.01	1.69
Komańcza	73.91	119	5.5	0.24 ± 0.4 (0–1.9)	0.25	0.248	1.02	0.23	1.75	0.65	0.05	<0.01	1.8
Lesko	26.08	71	3.9	0.17 ± 0.42 (0–1.65)	0.44	0.033	1.65	<0.01	<0.01	<0.01	0.05	<0.01	2.21
Lutowiska	69.56	2238	108.0	4.7 ± 7.87 (0–29.43)	0.63	<0.001	101.3	<0.01	<0.01	0.24	<0.01	<0.01	6.41
Stuposiany	86.95	186	19.7	0.86 ± 1.03 (0–4.34)	0.62	<0.001	12.5	5.51	0.85	0.85	<0.01	<0.01	<0.01
Ustrzyki	72.72	542	22.2	0.97 ± 1.34 (0–4.53)	0.68	<0.001	15.4	0.54	0.25	0.86	<0.01	0.04	5.23
Total	100	6937	51.9	2.26 ± 2.07 (0.04–8.05)	0.89	<0.001	36.32	5.86	4.95	0.45	1.39	0.11	2.79

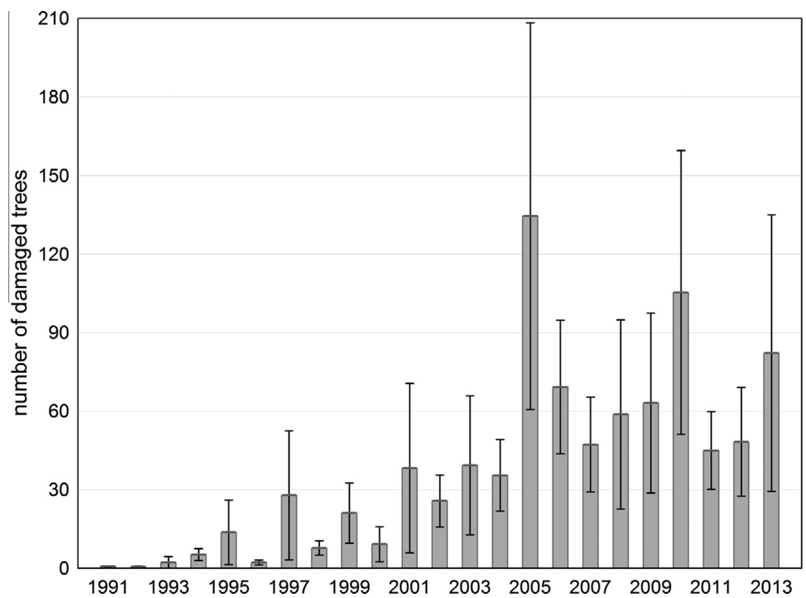

Fig. 2. The average number of trees damaged (±SE) from seven forest districts across years (all tree species pooled, $N = 6937$).

Table 4
Trends in bear damage to individual tree species during 1991–2013, expressed by a Spearman rank correlation.

Tree species	Tree number	Tree number in years		% trees in years	
		R_s	P	R_s	P
Fir	4856	0.89	<0.001	0.91	<0.001
Larch	784	−0.16	0.45	−0.91	<0.001
Spruce	662	0.1	0.66	−0.36	0.09
Beech	186	0.57	0.005	0.56	0.006
Pine	60	0.49	0.017	0.352	0.099
Ash	15	0.07	0.75	0.05	0.81
Unknown	374	0.64	<0.001	0.156	0.476
Total	6937	0.89	<0.001		

"unknown species"; however, as fir was probably the dominant species in this group, the results were treated as being collinear.

Beech (53.1%) and fir (34.4%) were the dominant species in the forest stands studied. Larch, spruce and pine were admixed species (0.7%, 2.5% and 2.9% respectively). However, the mean forage ratio was higher for larch than for fir, spruce and pine (larch 0.50 > fir 0.35 > spruce 0.17 > pine 0.13), whereas the preference of brown bears for deciduous trees was marginal (Fig. 4).

3.3. Variables influencing bear-caused damage

We found two models with ΔAIC_c values below 2 (Tables 5 and 6). More parsimonious model contained one explanatory variable: the brown bear population size, whereas the second best model contained additionally the variable "the average fir tree-ring width". These two models had comparable evidence ratios and good fit to the data (adjusted $R^2 = 0.44$ and 0.48, respectively) (Table 5). The number of days with snow cover and the average daily temperatures in May–June (°C) had no effect on the bear caused damage (Table 5; Figs. 5 and 6).

4. Discussion

4.1. General findings

On the basis of long-term data on the occurrence of the brown bear in Poland we attempted a comprehensive review of tree damage caused by this species in one of its important refuges in Europe. Our data showed that tree damage for foraging purposes is a new and dynamic phenomenon, recorded in Poland from the end of the 1980s and significantly increasing ever since. It is the growing numbers of bears in Poland, reflecting trends across the whole European population (Ionescu, 2002; Kindberg et al., 2011; Rigg and Adamec, 2007; Solberg et al., 2006), that are thought to be the main driver of the observed increase in tree damage. However, as the damage patterns could also be driven by other factors operating at different scales (e.g. local), they are less clear. For example, we recorded, for the first time, an interesting switch in species preferences of damaged trees. Firs, rarely damaged before 2003,

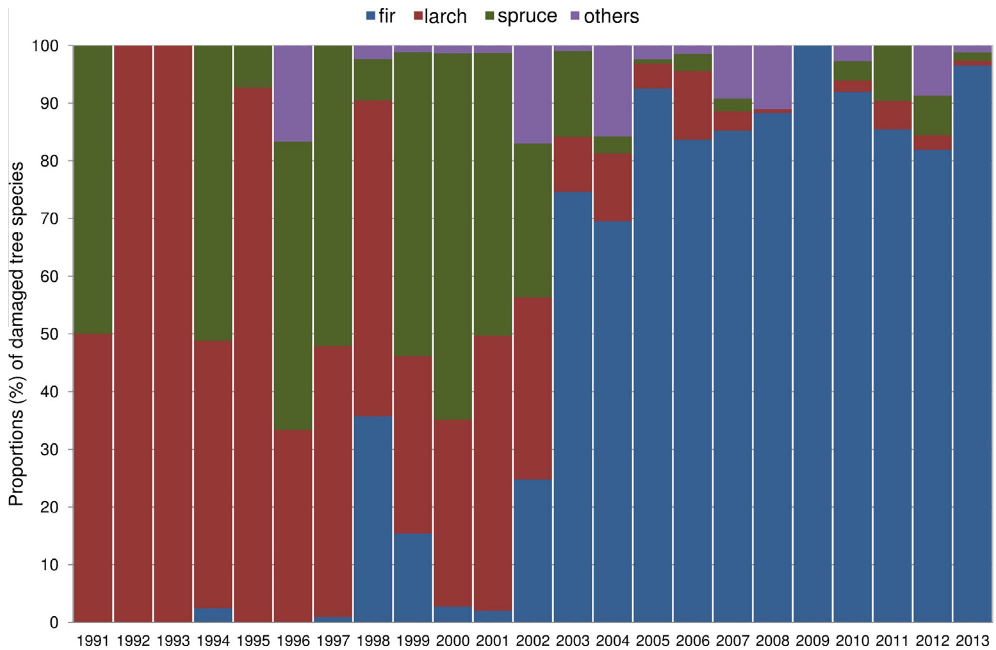

Fig. 3. Changes in tree species structure damaged by brown bears during 1991–2013 in the Bieszczady Mts. (the category “others” includes the sum of ash, beech and pine).

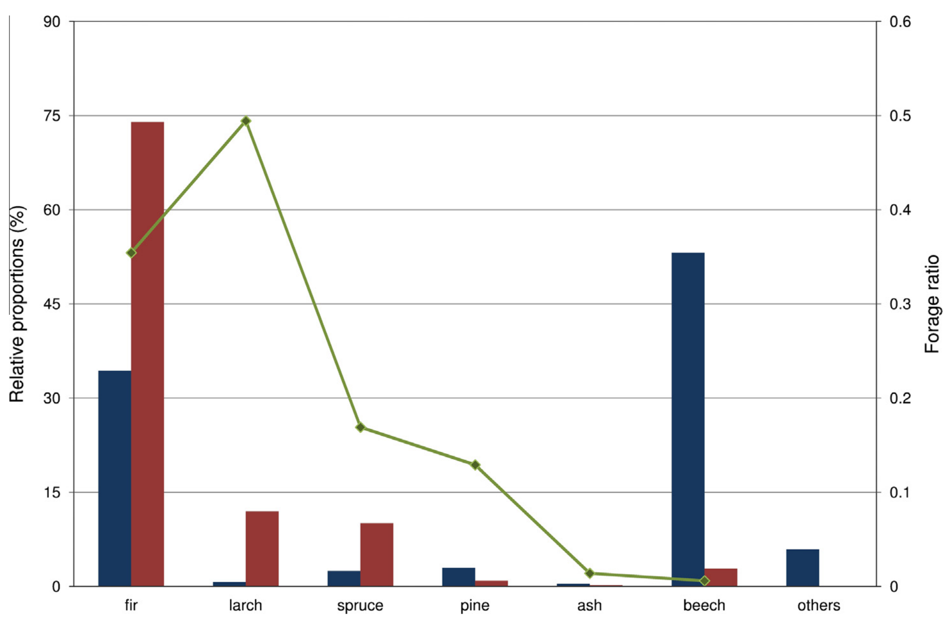

Fig. 4. Relative proportions (%) of tree species in stands potentially vulnerable to bear damage in the Bieszczady Mts. (blue bars); proportions of trees actually damaged by bears (red bars); mean forage ratio per species (green line). Note: the category “others” in this figure includes the overall availability of other tree species in the Bieszczady stands. As there are insufficient data regarding damage to other species, only the availability of these species in the stands is shown (blue bar). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are now the main species among the damaged trees in the Bieszczady Mts. This switch coincided with a long-term improvement in the condition of firs in the Carpathians (Wertz et al., 2014); however, the particular attributes of this species which suddenly attracted bears remain unknown.

4.2. Potential biases

Our results were based on a questionnaire survey, so they involved some unavoidable approximations (Anderson, 2001), especially regarding the extent of tree damage. We believe that the average numbers of damaged trees (302 trees/year) may have been underestimated. At the Bieszczady refuge scale this underestimation could be due to the lack of data from the BNP. In our assessment, it could be 65–70 additional trees per year, considering the average extent of damage in the four worst affected forest districts and accounting for the larger area of the BNP (Tables 1 and 3). At the district scale, the underestimation could have resulted from the field data being insufficiently precise (foresters did not find all the damaged trees) (Krapinec et al., 2011b). However, our data concerned trees damaged for foraging purposes, normally a serious problem (Jakubiec, 2001; Sullivan, 2009; Ziegltrum, 2005), in contrast to marking, which usually affects single trees only (Green and Mattson, 2003; Jakubiec, 2001; Sato et al., 2013).

Table 5
AIC_c-based rankings from best to worst for 15 potential linear regression models testing the effect on damaged firs of fir growth rings (fir rings), brown bear population size (bear population), average daily temperatures in May and June (average temp.), and the number of days with snow cover in winter (snow cover). Rankings were based upon model probabilities (ω_i) and evidence ratios ($E_{i,j}$). Δ_i shown difference in Akaike values between the first and the actual model (Burnham and Anderson, 1998, 2004).

Model	K	AIC_c	Δ_i	ω_i	$E_{i,j}$	R^2
Bear population	2	16.30	0.00	0.48	1.00	0.44
Bear population + fir rings	3	17.51	1.21	0.22	0.46	0.48
Bear population + average temp.	3	19.50	3.20	0.08	0.17	0.41
Bear population + snow cover	3	19.51	3.21	0.08	0.17	0.41
Bear population + fir rings + average temp.	4	19.71	3.41	0.06	0.13	0.45
Bear population + fir rings + snow cover	4	20.13	3.83	0.05	0.10	0.44
Bear population + average temp. + snow cover	4	22.59	6.29	0.01	0.03	0.38
Bear population + fir rings + average temp. + snow cover	5	23.20	6.90	0.01	0.02	0.42
Fir rings	2	25.86	9.56	0.00	0.01	0.15
Fir rings + average temp.	3	26.35	10.05	0.00	0.01	0.17
Fir rings + snow cover	3	28.50	12.20	0.00	0.00	0.11
Average temp.	2	29.54	13.24	0.00	0.00	0.03
Fir rings + average temp. + snow cover	4	29.29	12.99	0.00	0.00	0.12
Snow cover	2	30.11	13.81	0.00	0.00	0.04
Average temp. + snow cover	3	32.20	15.91	0.00	0.00	0.08

Table 6
Estimates of the most parsimonious linear regression models ($\Delta AIC_c < 2$), relating the extent of tree damage to the population size of the brown bear and the width of fir growth rings.

Variable	Estimate	SE	Lower 95% CL	Upper 95% CL	P
I model					<0.001
Bear population	+0.31	0.08	0.15	0.47	
II model					<0.001
Bear population	+0.28	0.08	0.12	0.44	
Fir rings	+3.29	2.2	−1.33	7.9	

This means that damage for foraging purposes is probably rarely overlooked by foresters, especially in managed woodlands. Moreover, the importance of potential biases is also lessened by the general purpose of our analyses. We focused in particular on the long-term changes relating to tree damage, so, despite some approximations in our data, they provide a good illustration of the general trends over the 23 years, i.e. the dynamics of damage, and changes in the species composition of damaged trees.

The questionnaire survey associated with expert assessments could not give precise information on bear numbers, therefore, we introduced several corrective measures (see Methods). In particular, for the purposes of this paper we removed all the data difficult to interpret, i.e. regarding transient individuals and forest districts with incomplete protocols. The resulting index of population size was then appropriate to analyze trends. Overall, it should be underlined that the science-based routine data collection was in practice the only possible way to assess the populations of large carnivores in large remote areas of Poland and other Central European countries, especially in the past. In particular, most of the field data were collected from a diverse, numerous, and changing group of observers whose observation effort could not be determined with accuracy. Hence, the large datasets obtained over years were not appropriate to advanced modelling procedures applied to population assessments (Kindberg et al., 2009). From the other side the sampling effort did not differ significantly between the forest districts and years. The data were gathered mainly by qualified forest service, whose numbers was balanced during the study period, and whose responsibilities included good overview of the subordinate forest units. This allowed the bear population size and detection of damaged trees to be made with more accuracy.

It should also be noted that the questionnaire based monitoring programs on the brown bear have been widely used in several European countries, such as Sweden: Zedrosser and Swenson, 2005; Kindberg et al., 2009; Finland: Kojola and Laitala, 2000, Slovakia: Hell and Slamecka, 1999; Spain: Wiegand et al., 1997; Poland: Jakubiec, 2001), as well as in North America (Knight et al., 1995). Clear increasing trend of bear population presented in this paper is consistent with other studies carried out in the Bieszczady Mts. (Buchalczyk, 1980; Jakubiec, 2001), including the more recent research incorporating genetic methods and telemetry (Selva et al., 2011; Śmietana et al., 2014). Increases have also been noted in the neighboring countries supporting regional bear population, Slovakia (Chapron et al., 2014) and Ukraine (Khoyetskyy, 2013). For all these reasons we can safely assume that the indices of bear population used in this paper were sufficient to be related with trends in tree damage.

4.3. Scale and dynamics of brown bear damage in Poland

The data collected showed an interesting pattern of brown bear damage in the Bieszczady stands. Firstly, thanks to long-term monitoring we registered a spectacular increase in the extent of damage, from just a few trees in 1991 to more than 500 in the last decade. Several hundred damaged trees per year may be

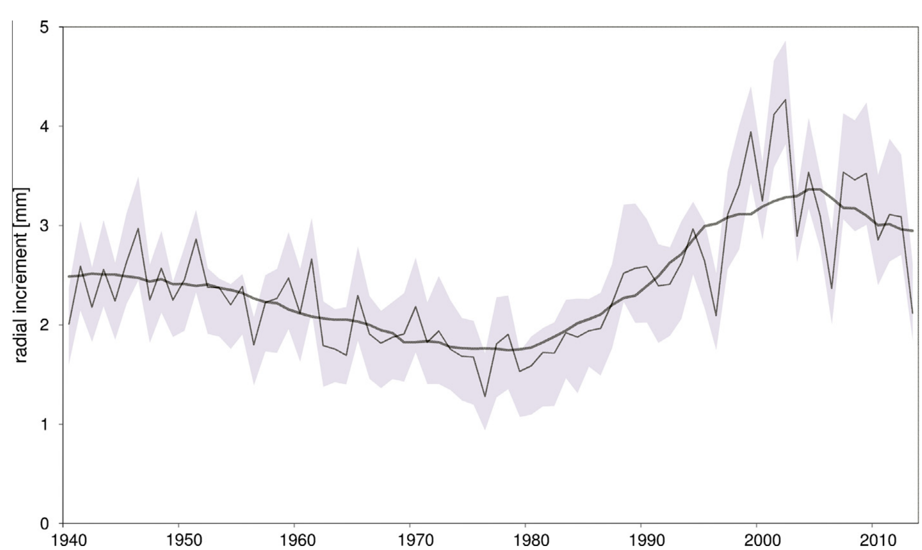

Fig. 5. Mean tree-ring chronology of silver fir in the Polish Carpathians (thin line) with its 95% confidence interval and 15-year moving-average (thick line).

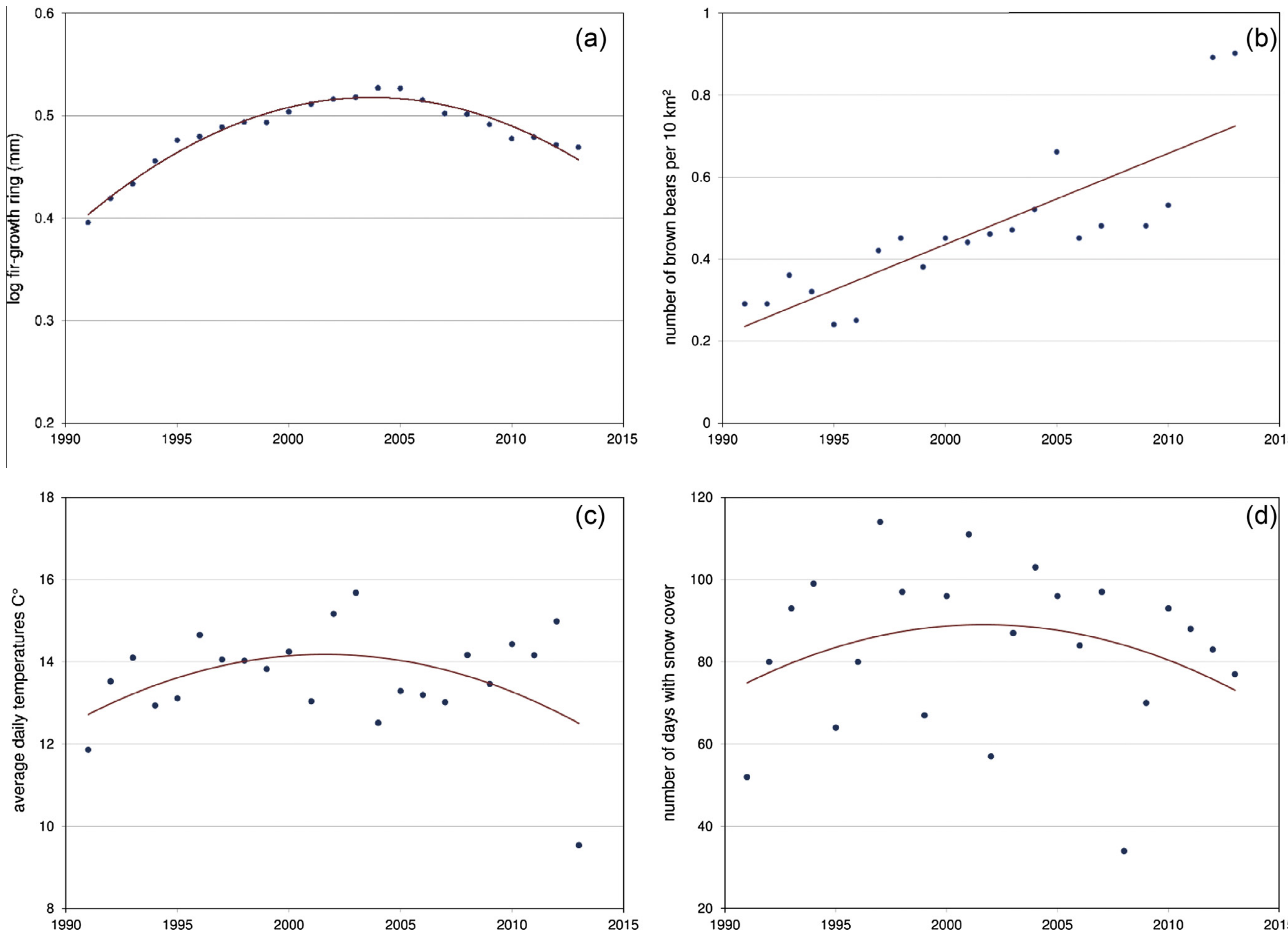

Fig. 6. Changes in fir growth rings (a), brown bear population size (b), average daily temperatures in May and June (c), and number of days with snow cover in November–April (d) between 1991 and 2013.

considered the current level of brown bear damage to trees in Bieszczady, and also in Poland, since the phenomenon does not occur elsewhere in the country (pers. comm.). Over the study period, there was a modest but stable increase, albeit with some fluctuations, such as the rapid and scarcely explainable leaps in 2005 and 2010. The increase is continuing and is accompanied by a concomitant growth in the bear population. Therefore, in the near future we can assume that the number of damaged trees will be sustained at the current level or will further increase. Secondly, despite the recorded trend, the figure of several hundred damaged trees must be considered insignificant at both the Bieszczady scale, and even more so at the nationwide scale, given the large area of Poland (>312,000 km^2) and the percentage of the country covered by woodland (29.3%) (Leśnictwo, 2013). This minimal significance of tree damage is a consequence of Poland's location – at the edge of the distribution range of the brown bear's Carpathian population; this means a small national population of this species (<100 individuals, Chapron et al., 2014). It is also a consequence of the multispecific, unevenly-aged stands in Poland, and selective timber management, which prevents serious damage (Sullivan, 2009). Thirdly, we demonstrated the uneven spatial distribution of damage intensity in the Bieszczady. In central forest districts, with the highest brown bear density, more damage was recorded compared to the edge districts, despite both having similar stand compositions. Similar results have been obtained in Asia and North America (Giusti, 1990; Noble and Meslow, 1998; Poelker and Hartwell, 1973; Sullivan, 2009; Watanabe, 1980; Watanabe et al., 1970).

4.4. The brown bear's preferred tree species

Based on our findings, bears in Poland prefer conifers; this is consistent with results from Europe, North America and Japan (Krapinec et al., 2011a,b; Kunovac et al., 2008; Noble and Meslow, 1998; Sullivan, 2009; Watanabe, 1980; Witmer et al., 2000; Yamada and Fujioka, 2010). In Poland, fir, larch and spruce are the species suffering the most damage by bears (Jakubiec, 2001; Jakubiec et al., 1993; Zyśk-Gorczyńska and Jakubiec, 2010, 2014). In Croatia and in Bosnia and Herzegovina fir and spruce are the most frequently damaged trees (Krapinec et al., 2011a,b; Kunovac et al., 2008). However, as the concept of the total number of damaged trees of particular species might be misleading, preference ratios concerning the availability of tree species in stands seem be more useful. In Poland the highest preference ratio was found for larch and was higher than for fir, spruce or pine (Fig. 4). In spite of larch being an admixture in the Bieszczady stands (0.7%), it was often recorded during study period as a species damaged by bears. Selective damage, incompatible with stand availability, was also recorded in other studies (Barnes and Engeman, 1995; Sullivan, 1993, 2009; Witmer et al., 2000).

Bear populations commonly show a preference for conifer species because of the high sugar levels in freshly-developing vascular tissues (Kimball et al., 1998a,b; Radwan, 1969). On account of these features of conifers, the foraging of bears on deciduous trees is considered a curiosity. Deciduous trees, probably because of their bark structure, which is more difficult to remove than that of conifers, are rarely damaged (Watanabe et al., 1970). In contrast, our findings showed that beech and ash, though few in number, were quite regularly damaged by bears in the Bieszczady Mts. The percentage of these species in the overall numbers of trees was only 2.9%; interestingly, however, during the study period there was an increase in the number and percentage of damaged beech trees. The factors affecting the extent of damage to beeches are not clearly understood, so it would be important to observe this trend in the future.

The interesting and novel results of our study revealed changes in the preferences of bears for particular tree species. Nowadays, fir is the main species damaged by bears in Poland, whereas formerly it was rarely damaged. For instance, at the beginning of the 1990s Jakubiec et al. (1993) found that most damage in the Bieszczady occurred on larch, pine and spruce. These authors also found that larch and pine were the tree species most frequently damaged by bears (>84%), even though they comprised only 18% of the tree stands. Fir was the dominant coniferous species (18%) but sustained no damage. The latest studies, from a different area of the Bieszczady Mts., showed damage only to firs, although other conifers were present (Zyśk-Gorczyńska and Jakubiec, 2010). Data from the last ten years show that bears have switched almost completely to fir (96.5% in 2013), with additional increases in the total number and percentages of beech and pine (Table 4, Fig. 3). In consequence, we recorded a significant decrease in the percentages of larch and spruce affected, even though the total number of trees of these species remained at a similar level. This means that bears still readily forage on larch and spruce (as shown by the forage ratio), but that they have also started to forage on fir on a massive scale. As mentioned above, fir is the dominant species damaged by bears in certain areas of Europe. To date, however, there have been no results demonstrating species-specific damage over the years. Hence we have no precise knowledge of whether, as in Poland, bears have switched their foraging preferences to fir throughout their distribution range in Europe.

4.5. Variables influencing bear damage

While seeking the reasons for noticeable trends in damage we restricted our assessment to fir, because of the dominant role of fir in coniferous stands, the importance of this species to forest management and ecosystem protection, and because we were able to access long-term, abundant data on the condition of fir in the Polish Carpathians (Wertz et al., 2014). In addition, fir is recommended for introduction to suitable habitats, where it can produce durable, highly productive stands. Fir is one of the most shade-tolerant tree species and can grow in mono- or multi-specific stands (Wertz et al., 2014). The latter seem particularly interesting.

For approximately half a century since the 1940s fir had experienced a decline in many European countries, expressed e.g. by the decline in the number of natural and artificial renewals and narrower annual ring widths (Wertz et al., 2014; Zawada, 2001). The trend changed in the 1980s, since when dynamic increases in tree ring width have been recorded (Elling et al., 2009; Wertz et al., 2014; Zawada, 2001). The reasons behind fir revitalization are to be sought in the drastic reduction in air pollution (mainly by SO_2), climate change and the eutrophication of habitats (Bošela et al., 2014; Dobrowolska, 2008; Elling et al., 2009; Hauck et al., 2012). Nowadays, fir revitalization is proceeding apace in the Carpathians and, as elsewhere in Europe (Wertz et al., 2014; Zawada, 2001) (Fig. 5). During our study, the largest ring width (3.36 mm) in firs was achieved in 2004; interestingly, this was one year after the abrupt increase in the number of firs damaged by bears (Fig. 3). Based on minimum AIC values two models were best explaining damage to fir. The variable 'the fir tree-ring width' was not included in the more parsimonious model, but it was included in the second best model. Then, we inferred that the improvement in fir condition and the rise in brown bear numbers had a significant influence on the numbers of damaged firs.

The condition of firs, as represented by annual ring width, may determine the extent of damage since it has a significant influence on the mass of vascular tissues (Kimball et al., 1998a,b; Nolte et al., 1998; Yamada and Fujioka, 2010). Indeed, Japanese black bears and American black bears preferred trees with greater masses of vascular tissue. These findings implied that when bears select a tree to damage, the mass of vascular tissue is a very important factor determining their choice.

In the study area the brown bear population has increased significantly, from 29 to 90 individuals; obviously, such a dynamic increase must lead to an increase in tree damage. A positive correlation between population size and extent of damage in stands was repeatedly found in ungulate studies (Bergqvist et al., 2014; Hörnberg, 2001), though rarely in bear studies (Krapinec et al., 2011a; Matthews, 2002). No relationship was found between the extent of damage and climate conditions in spring and winter. This may have been because the selected climate conditions, i.e. the average temperature for May and June, and the numbers of days with snow cover did not show any noticeable trends during the study period. Moreover, the tested series may have been too short for studying the influence of possible climate changes on brown bear behavior.

The variables we used in our study that potentially affect damage size partly coincide with results from North America as far as black bear damage is concerned. Based on these findings, the intensity of tree damage was determined by bear numbers and factors directly associated with tree phenology, e.g. tree condition, size, age and sugar/terpene concentrations in the vascular tissue. Different forest practices, e.g. thinning and fertilization, also had a significant impact on the extent of damage (Kimball et al., 1998a,b; Matthews, 2002; Nolte et al., 1998; Sullivan, 2009). The coincidence of results may show that tree damage is determined by certain universal factors that are independent of geographical regions or bear species.

4.6. Importance to forest management of bear damage to trees

Bear damage to trees has a significant impact on tree condition and health, as well as its value from the forest management point of view (Ziegltrum, 2005, 2006). Complete girdling is lethal to a tree, whereas partial girdling reduces growth and supplies pathways for insect and fungi infestation, which in consequence can also lead to tree death (Sullivan, 2009). However, in most cases wounds heal, but at the same time the value of the timber decreases and financial losses ensue (Krzysik, 1975; Lowell et al., 2010).

In Europe, including Poland there is still a general lack of detailed estimates of tree damage by bears. It has been suggested that in Europe such damage is not treated as seriously by the forestry authorities. This is probably for several reasons. Firstly, the extent of damage in individual European countries is not serious: this could be a consequence of the small number of bears, the abundance of tree stands in regions where damage occurs, and selective timber management (see above, chapter 3, discussion). Secondly, it is important that damaged trees do not drastically reduce the economic value of timber. Bears usually do not strip all the bark off a tree: in Poland 12% of damaged trees had their bark completely stripped away (Zyśk-Gorczyńska et al., 2015), while in Croatia the figure was 25% (Krapinec et al., 2011b). Consequently, trees damaged by bears can survive in forest ecosystems for many years, often without displaying physiological symptoms of stress (Ziegltrum, 2005). Moreover, damage to trees does not mean their timber cannot be sold. According to current regulations in Poland, the shortest useful part of coniferous timber logs for sawmills should be at least 2.7 m long. Bears damage trunks over average lengths of 100 cm (fir), 112 cm (larch) and 146 cm (spruce) (Zyśk-Gorczyńska and Jakubiec, 2014). Therefore, the average length of a wound does not normally prevent damaged trees from being processed in the sawmill; otherwise, the timber can always be sold as firewood. Thirdly, bear damage is marginal when compared with damage caused by other animals, especially by ungulates (Apollonio et al., 2010; Heinze et al., 2011). For instance, the extent of damage from bears in the Bieszczady region was barely 0.02% compared to that caused by ungulates (Zyśk-Gorczyńska et al. unpubl. data).

Finally, the ecological importance of trees damaged by bears should not be underestimated. We showed previously that in forest ecosystems brown bears might be viewed as ecological engineers (Zyśk-Gorczyńska et al., 2015). Through their foraging, bears initiate a cascade of biological processes that play an important part in ecosystem dynamics and in the maintenance of biodiversity. Ziegltrum and Nolte (2001) found similarly that trees damaged by American black bears are an important source of food for different animal species. For instance, severe black bear damage produces open patches in stands: the dead and dying trees within these patches allow more sunlight to reach the forest floor and support plant growth.

For these reasons, we believe that bear damage in Poland does not constitute a serious problem for forest management. In our opinion all damaged trees should remain in the forest stands. Removing a certain number of damaged trees should be undertaken only as a last resort, e.g. when large-scale bear damage occurs, but even then a good number of such trees should remain for conservation purposes.

5. Conclusion

Our results concern tree damage by bears in the Bieszczady Mountains – the largest and most important refuge of the brown bear in Poland. However, the scale of such damage should be compared with its extent over the whole country. Taking into account the size of Poland and the country's very extensive timber resources, we do not think that bear damage is of any practical significance for the national forest economy. Despite the increasing trend of bear damage, it is not anticipated that in the near future such damage will become a problem for forest management. It is significant that the forestry administration take a favorable approach to damage caused by bears. Trees damaged by bears are treated in the same way as those that are wind-thrown or have collapsed under the weight of heavy snow. Moreover, foresters take a pride in having brown bears in their stands, so the conservational importance of brown bears is respected and damaged trees are treated as a tourist attraction rather than a problem.

In view of the conservation priority of brown bears in Europe, their limited range of distribution, as well as the crucial ecological role of this species in forest stands, we conclude that trees damaged by bears should continue to be treated as a natural phenomenon in the forest ecosystem and as an integral aspect of the forest economy.

Acknowledgements

The comments of two anonymous Reviewers were very useful in preparing this paper. This paper is based on invaluable support from foresters from the Bieszczady forest districts. It is impossible to name them all, but for long-term cooperation we owe a special debt of gratitude to Wiktor Chojnacki (Lutowiska Forest District). The Regional Directorate of the State Forest Administration in Krosno provided data about the forest characteristics. Peter Senn kindly revised the English language. Grzegorz Gorczyński provided helpful comments on the statistical analyses. We are also grateful to Teresa Berezowska-Cnota for preparing the map of the study area. The study was in part supported by the Institute of Nature Conservation, Polish Academy of Sciences.

References

Anderson, D.R., 2001. The need to get the basics right in wildlife field studies. Wildl. Soc. Bull. 29, 1294–1297.
Apollonio, M., Andersen, R., Putman, R., 2010. European Ungulates and Their Management in the 21st Century. Cambridge University Press.
Barnes Jr., V.G., Engeman, R.M., 1995. Black bear damage to lodgepole pine in central Oregon. Northwest. Nat. 76, 127–129.
Bergqvist, G., Bergström, R., Wallgren, M., 2014. Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests – effects of forage availability, moose population density and site productivity. Silva Fenn. 48 (1), ID 1077.
Bobiec, A., Gutowski, J.M., Laudenslayer, W.F., Pawlaczyk, P., Zub, K. (Eds.), 2005. The Afterlife of a Tree. WWF Poland, Warszawa.
Boitani, L., Alvarez, F., Anders, O., et al., 2015. Key Actions for Large Carnivore Populations in Europe. Institute of Applied Ecology (Rome, Italy). Report to DG Environment. European Commission, Bruxelles (Contract No. 07.0307/2013/654446/SER/B3).
Bošela, M., Petráš, R., Sitková, Z., Priwitzer, T., Pajtík, J., Hlavatá, H., Sedmák, R., Tobin, B., 2014. Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. Environ. Pollut. 184, 211–221.
Bromlej, G.F., 1965. Medvedi juga dalnego vostoka SSSR. Moskwa – Leningrad (in Russian).
Buchalczyk, T., 1980. The brown bear in Poland. Int. Conf. Bear Res. Manage. 4, 229–232.
Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.
Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258.
Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference. A Practical Information Theoretic Approach. Springer-Verlag, New York.
Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304.
Chapron, G., Kaczensky, P., Linnell, J.D.C., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216), 1517–1519.
Dobrowolska, D., 2008. Growth and development of silver fir (*Abies alba* Mill.) regeneration and restoration of the species in the Karkonosze Mountains. J. For. Sci. 54, 398–408.
Elling, W., Dittmar, C., Pfaffelmoser, K., Rötzer, T., 2009. Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. For. Ecol. Manage. 257, 1175–1187.
Flowers, R., Kanaskie, A., McWilliams, M., 2012. Aerial Survey of Tree Mortality in Northwest OR. Oregon Department of Forestry (Memorandum).
Fruziński, B., 2002. Gospodarka łowiecka. Wydawnictwo Łowiec Polski, Warszawa (in Polish).
Gill, R.M.A., 1992. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65 (2), 145–169.
Giusti, G.A., 1990. Black bear feeding on second growth redwoods: a critical assessment. In: Davis, L.R., Marsh, R.E. (Eds.), Proceedings of the Fourteenth Vertebrate Pest Conference, Sacramento, Calif, 6–8 March 1990. University of California, Davis, pp. 214–217.
Green, G.I., Mattson, D.J., 2003. Tree rubbing by Yellowstone grizzly bears (*Ursus arctos*). Wildl. Biol. 9, 1–9.
Grissino-Mayer, H.D., 2001. Research report evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57 (2), 205–221.
Hauck, M., Zimmermann, J., Jacob, M., Dulamsuren, C., Bade, C., Ahrends, B., Leuschner, C., 2012. Rapid recovery of stem increment in Norway spruce at reduced SO_2 levels in the Harz Mountains, Germany. Environ. Pollut. 164, 132–141.
Hegland, S.J., Lilleeng, M.S., Moe, S.R., 2013. Old-growth forest floor richness increases with red deer herbivory intensity. For. Ecol. Manage. 310, 267–274.
Heinze, E., Boch, S., Fischer, M., Hessenmöller, D., Klenk, B., Müller, J., Prati, D., Schulze, E.D., Seele, C., Socher, S., Halle, S., 2011. Habitat use of large ungulates in northeastern Germany in relation to forest management. For. Ecol. Manage. 261, 288–296.
Hell, P., Slamecka, J., 1999. Medved v slovensky Karpatoch a vo svete. PaRPRESS, Bratislava, Slovakia (in Slovakian).
Holmes, R.L., 1986. Quality control of crossdating and measuring users manual for computer program COFECHA. In: Adams, R.K., Fritts, H.C. (Eds.), Tree-rings Chronol. West. North Am. California, East. Oregon North. Gt. Basin. Chronol. Ser. 6. Univ. Arizona, Tucson, pp. 41–49.

Hörnberg, S., 2001. Changes in population density of moose (*Alces alces*) and damage to forests in Sweden. For. Ecol. Manage. 149, 141–151.

Ionescu, O., 2002. Bear Status and Management in Carpathians. Forest Research and Management Planning Institute (ICAS), Bucharest, Romania.

Jakubiec, Z., 2001. Niedźwiedź brunatny *Ursus arctos* L. w polskiej części Karpat. Stud. Nat. 47 (in Polish).

Jakubiec, Z., 2010. Niedźwiedź brunatny *Ursus arctos* (Linneus 1758). In: Makomaska-Juchiewicz, M. (Ed.), Monitoring gatunków zwierząt. Przewodnik metodyczny. Część I. Główny Inspektorat Ochrony Środowiska, Warszawa (in Polish).

Jakubiec, Z., Borusiewicz, B., Gwiazdowicz, D.J., Wuczyński, A., 1993. Uszkodzenia drzew przez niedźwiedzia brunatnego (*Ursus arctos* L.) w Bieszczadach. Rocz. AR w Poznaniu 255, 81–86 (in Polish).

Jędrzejewski, W., Sidorovicz, V., 2010. Sztuka tropienia zwierząt. Zakład Badania Ssaków PAN, Białowieża (in Polish).

Kanaskie, A., Chetock, J., Irwin, G., Overhusler, D., 1990. Black Bear Damage to Forest Trees in Northwest Oregon, 1988–1989. Oregon Department of Forestry, Salem.

Khoyetskyy, P., 2013. Dynamika liczebności niedźwiedzia brunatnego w Karpatach Wschodnich. Forest Res. Pap. 74 (2), 111–116 (in Polish).

Kimball, B.A., Nolte, D.L., Engeman, R.M., Johnston, J.J., Stermitz, F.R., 1998a. Chemically mediated foraging preference of black bears (*Ursus americanus*). J. Mammal. 79, 448–456.

Kimball, B.A., Turnblom, E.C., Nolte, D.L., Griffin, D.L., Engeman, R.M., 1998b. Effects of thinning and nitrogen fertilization on sugar and terpenes in Douglas-fir vascular tissues: implications for black bear foraging. For. Sci. 44 (4), 599–602.

Kindberg, J., Ericsson, G., Swenson, J.E., 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. Biol. Conserv. 142, 159–165.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C., Taberlet, P., 2011. Estimating population size and trends of the Swedish brown bear (*Ursus arctos*) population. Wildl. Biol. 17, 114–123.

Knight, R.R., Blanchard, B.M., Eberhardt, L.L., 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildl. Soc. Bull. 23, 245–248.

Kojola, I., Laitala, H.M., 2000. Changes in the structure of an increasing brown bear population with distance from core areas: another example of presaturation female dispersal? Ann. Zool. Fenn. 37, 59–64.

Koreň, M., Find'o, S., Skuban, M., Kajba, M., 2011. Habitat suitability modelling from non-point data: the case study of brown bear habitat in Slovakia. Ecol. Inform. 6, 296–302.

Kraft, G., 1884. Beiträge Zur Lehre Von Den Durchforstungen, Schlagstellungen Und Lichtungshieben [WWW Document]. Klindworth, Hann. <http://www.bookcity.pl/A19571685/Beitrage_Zur_Lehre_Von_Den_Durchforstungen_Schlagstellungen_Und_Lichtungshieben/Gustav_Kraft> (accessed 5.7.14).

Krameko, 2010. Plan ochrony Bieszczadzkiego Parku Narodowego. Operat ochrony ekosystemów leśnych, Kraków (in Polish).

Krapinec, K., Majnarić, D., Jovanović, D., Kovač, I., Medarić, I., 2011a. Prvi rezultati istraživanja šumskih šteta koje čini smeđi medvjed (*Ursus arctos*) u šumama obične jele (*Abies alba*) u Hrvatskoj. Croat. J. For. Eng. 32, 259–269.

Krapinec, K., Majnarić, D., Tomac, A., Kalčić, D., 2011b. Braunbärschäden in Kroatiens Waldbeständen. Beitr Jagd & Wild 36, 63–73.

Krzysik, F., 1975. Nauka o drewnie. PWN, Warszawa (in Polish).

Kunovac, S., Bašič, M., Skrobo, N., Ličanin, S., 2008. Brown bear (*Ursus arctos* L.) damages at forest stands in Central Bosnia Canton. Works Facul. For. Univ. Sarajevo 1, 79–90.

Leśnictwo, 2013. Główny Urząd Statystyczny, Warszawa (in Polish).

Linnell, J.D.C., Salvatori, V., Boitani, L., 2008. Guidelines for Population Level Management Plans for Large Carnivores in Europe. A Large Carnivore Initiative for Europe Report Prepared for the European Commission.

Lowell, E.C., Dykstra, D., McFadden, G., 2010. Effects of bear damage on Douglas-fir lumber recovery. West. J. Appl. For. 25 (2), 73–80.

Manly, B.F.J., Miller, P., Cook, L., 1972. Analysis of a selective predation experiment. Am. Nat. 106, 719–736.

Manning, J.L., Baltzer, J.L., 2011. Impacts of black bear baiting on Acadian forest dynamics – an indirect edge effect? For. Ecol. Manage. 262, 838–844.

Marszałek, E., 2011. Gospodarka leśna w karpackiej części Regionalnej Dyrekcji Lasów Państwowych w Krośnie i jej wpływ na ochronę przyrody. Rocz. Bieszcz. 19, 59–75 (in Polish).

Matthews, S.M., 2002. Population Attributes of Black Bear in Relation with Douglas-fir Damage on the Hoopa Valley Reservation, California (Master Thesis).

Meyer-Holzapfel, M., 1968. Zur Bedeutung verschiedener Holz-und Laubarten für den Braunbären. Zool. Gart. 36, 12–33.

Noble, W.O., Meslow, E.C., 1998. Spring foraging and forest damage by black bears in the central coast ranges of Oregon. Ursus 10, 293–298.

Nolte, D.L., Dykzeul, M., 2002. Wildlife impacts on forest resources. In: Clark, L. (Ed.), Human Conflicts with Wildlife: Economic Considerations. US Dep. Agric., Animal Plant Health Inspection Ser., Fort Collins, Colorado, USA, pp. 163–168.

Nolte, D.L., Kimball, B.A., Ziegltrum, G.J., 1998. The impact of timber management on the photochemicals associated with black bear damage. In: Bakerand, R.O., Crabb, A.C. (Eds.), Proceedings of the Eighteenth Vertebrate Pest Conference, Costa Mesa, Calif., 2–5 March 1998. University of California, Davis, pp. 111–117.

Okarma, H., Tomek, A., 2008. Łowiectwo. Wydawnictwo Edukacyjno-Naukowe H_2O, Kraków, pp. 319 (in Polish).

Pirga, B., 2014. Monitoring zwierząt drapieżnych zachodzących na obszar Bieszczadzkiego Parku Narodowego w sezonach 2012/2013 oraz 2013/2014. Raport techniczny (in Polish).

Poelker, R.J., Hartwell, H.D., 1973. Black bear of Washington. Biol. Bull. 14, 180 (Olympia, WA: Wash. State Game Dept).

Radwan, M.A., 1969. Chemical composition of the sapwood of four tree species in relation to feeding by the black bear. For. Sci. 15, 11–16.

R Development Core Team, 2015. R: A language and environment for statistical computing. http://www. R-project.org. Vienna: R Foundation for Statistical Computing.

Rigg, R., Adamec, M., 2007. Status, Ecology and Management of the Brown Bear (*Ursus arctos*) in Slovakia. Slovak Wildlife Society, Liptovský Hrádok.

Sato, Y., Kamiishi, C., Tokaji, T., Mori, M., Koizumi, S., Kobayashi, K., Itoh, T., Sonohara, W., Takada, M.B., Urata, T., 2013. Selection of rub trees by brown bears (*Ursus arctos*) in Hokkaido, Japan. Acta Theriol. 59 (1), 129–137.

Selva, N., Zwijacz-Kozica, T., Sergiel, A., Olszańska, A., Zięba, F., 2011. Management Plan for the Brown Bear (*Ursus arctos*) in Poland. University of Live Sciences, Warsaw.

Solberg, K.H., Bellemain, E., Drageset, O.M., Taberlet, P., Swenson, J.E., 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biol. Conserv. 128, 158–168.

StatSoft, Inc., 2014. STATISTICA (Data Analysis Software System). Version 12 [computer program]. <http://www.statsoft.com/>.

Sullivan, T.P., 1993. Feeding damage by bears in managed forests of western hemlock-western red cedar in mid coastal British Columbia. Can. J. For. Res. 23, 49–54.

Sullivan, T.P., 2009. Bear Damage and Free-growing Stands in the Golden TSA. Forest Investment Account 2008–09. Annual Report. Louisiana-Pacific Canada Ltd.

Sutherland, W.J., Newton, I., Green, R.E., 2004. Bird Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford.

Ševčenko, L., Škvirâ, M., 2009. Vedmìd Burij. In: Akìmova, Ì.A. (Ed.), Červona kniga Ukraïni. Tvarinnij svìt. Globalkonsalting, Kiïv, p. 537.

Śmietana, W., Matosiuk, M., Czajkowska, M., Ratkiewicz, M., Rutkowski, R., Buś-Kicman, M., Jakimiuk, S., 2014. Ocena rozmieszczenia i liczebności niedźwiedzia brunatnego *Ursus arctos* (L.) we wschodniej części polskich Karpat. Rocz. Bieszcz. 22, 289–301 (in Polish).

Vasiliauskas, R., 2001. Damage to trees due to forestry operations and its pathological significance in temperate forests: a literature review. Forestry 74 (4), 319–336.

Vospernik, S., 2006. Probability of bark stripping damage by red deer (*Cervus elaphus*) in Austria. Silva Fenn. 40 (4), 589–601.

Watanabe, H., 1980. Damage to conifers by the Japanese black bear. Int. Conf. Bear Res. Manage. 4, 67–70.

Watanabe, H., Noborio, J., Nimura, K., Wada, S., 1970. Damage to cryptomeria by wildbears in the Ashu Experimental Forest of Kyoto University. Bull. Kyoto Univ. For. 41, 1–25.

Wertz, B., Wilczyński, S., Muter, E., 2014. Dendrochronologiczna ocena przyrostu grubości jodły pospolitej (*Abies alba* Mill.) w Polskich Karpatach. Studia i Materiały CEPL w Rogowie R. 16. 40(3), 88–98 (in Polish).

Wiegand, T., Naves, J., Stephan, T., Fernandez, A., 1997. Assessing the risk of extinction for the brown bears (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecol. Monogr. 68, 539–570.

Winnicki, T., Zemanek, B., 2009. Przyroda Bieszczadzkiego Parku Narodowego. Bieszczadzki Park Narodowy, Ustrzyki Dolne, pp. 176 (in Polish).

Witmer, G.W., Nolte, D.L., Stewart, W.B., 2000. Integrated pest management of black bear reforestation damage. In: Salmon, T.P., Crabb, A.C. (Eds.), Proceedings of the Nineteenth Vertebrate Pest Conference, San Diego, Calif., 6–9 March 2000. University of California, Davis, pp. 228–235.

Yamada, A., Fujioka, M., 2010. Features of planted cypress trees vulnerable to damage by Japanese black bears. Ursus 21 (1), 72–80.

Zawada, J., 2001. Incremental symptoms in revitalization of Silver fir in the forests of Carpathian and Sudeten Mts and their silvicultural consequences. Pr. IBL, A 3 (922), 79–101.

Zedrosser, A., Swenson, J.E., 2005. Do brown bear litter sizes reported by the public reflect litter sizes obtained by scientific methods? Wildl. Soc. Bull. 33, 1352–1356.

Ziegltrum, G.J., Nolte, D.L., 2001. Black bear forest damage in Washington State, USA: economic, ecological, social aspects. Ursus 12, 169–172.

Ziegltrum, G.J., 2005. Annual Report. Animal Damage Control Program. Washington Forest Protection Association, Olympia, Washington, USA.

Ziegltrum, G.J., 2006. Cost-effectiveness of the black bear supplemental feeding program in Western Washington. Wildl. Soc. Bull. 34 (2), 375–379.

Zyśk-Gorczyńska, E., Jakubiec, Z., 2010. Żerowanie niedźwiedzia brunatnego (*Ursus arctos*) na jodłach w polskiej części Karpat. Chrońmy Przyr. Ojcz. 66 (1), 71–75 (in Polish).

Zyśk-Gorczyńska, E., Jakubiec, Z., 2014. Ranienie drzew przez niedźwiedzia brunatnego (*Ursus arctos*) w Bieszczadach. Sylwan 158 (5), 377–382 (in Polish).

Zyśk-Gorczyńska, E., Jakubiec, Z., Wuczyński, A., 2015. Brown bears (*Ursus arctos*) as ecological engineers: the prospective role of trees damaged by bears in forest ecosystems. Can. J. Zool. 93, 133–141.