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Evaluating forest management intensity on an umbrella species: Capercaillie persistence in central Europe

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ABSTRACT

Deforestation and fragmentation of forests worldwide are negatively impacting biodiversity. The capercaillie (*Tetrao urogallus*) is an endangered umbrella species of montane forests in central Europe. Despite its status, it has largely been overlooked in forest management planning in the Carpathian Mountains, a biodiversity hotspot within the European Union. Previous investigations of timber management effects on capercaillie have shown contradictory results within Europe; habitat loss and fragmentation due to intensive forest management have been implicated in population declines, while other studies have suggested neutral or positive effects. In Romania, recent changes in forest management have shifted from extensive, selective logging to intensive clearcutting; this change provides the opportunity to assess the effects of harvesting on capercaillie numbers across a full range of forest management intensities, thereby addressing discrepancies in the literature. Across the Southern and Eastern Carpathian mountains from 2009–2011, we used spring counts of capercaillie males at leks to evaluate the impact of forest management, other human activities, and habitat at two spatial scales – stand (∼2 ha) and landscape (∼300 ha). At the landscape level, the proportion of forest clearcuts and intensity of tourism had significant negative effects on the number of capercaillie males in the lek. In contrast, low intensity selective logging had a positive effect at the local stand (lek) level. Large scale (landscape level) forest clear-cutting had a negative effect on the capercaillie population – areas comprised of clearcuts of 30% reduced male lek counts by 76%. The protection of intact mature and old-growth forests, and forest management practices that emulate natural disturbance processes are recommended to support habitat of this critical umbrella species and associated biodiversity.

1. Introduction

Over the past century, global declines in mature forested area (Hansen et al., 2013) and biodiversity related to habitat loss, fragmentation, and overexploitation are causing increased concern among natural resource managers and conservationists (Wilcove et al., 1998). Large-scale clear-cutting of forested landscapes has driven the vast majority of forest species losses (Lamberson and McKelvey, 1992; Wallenius et al., 2010) and much attention has been devoted to alternative harvest strategies and associated management to retain forest species within landscapes (e.g. Franklin and Johnson, 2012). In areas such as central Europe that historically have been heavily forested but now have limited and increasingly fewer areas of old-growth forest cover (Mackey et al., 2014), identifying management impacts and alternatives is a priority. Here, we use the capercaillie, *Tetrao urogallus*, to evaluate the effects of logging old forests on mating habitat selection. The capercaille is considered an umbrella species within the region and an indicator of structurally rich forest conditions (Suter et al., 2002). Capercaillie populations in central Europe have declined rapidly in recent decades (Storch, 2007a). Identifying

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forestry practices that may aid in maintaining viable population levels of this species within forested landscapes are vital to ensure their persistence in the landscape alongside many other species commonly represented in these habitat types.

Capercaillie inhabits forests of Eurasia, and they are associated with extensive natural, old-growth or young open canopy forests, characterized by high levels of structural heterogeneity, particularly, multistoried tree layers and abundant cover of ericaceous understory shrubs (Bollmann et al., 2005; Klaus et al., 1989; Storch, 2002; Suter et al., 2002). Because capercaillie is strongly associated with open canopy forest and has a relatively large home range, it is considered an indicator species for high biodiversity and protection of its habitat will benefit other old-growth forest species as well (Pakkala et al., 2003; Suter et al., 2002).

Lek sites, where males display in spring, are particularly vulnerable to disturbance by humans and may be readily abandoned, as is common with many species of grouse with this mating system (e.g. Hess and Beck, 2012; Klaus et al., 1989). Anthropogenic activities, especially the intensification of forest management, have resulted in the significant loss and fragmentation of suitable capercaillie habitat in many parts of western and central Europe (Storch, 2007a). In many European countries, capercaillie populations are now artificially maintained using release projects, specialized habitat management measures, or predation control (Klaus, 1997; Marshall and Edwards-Jones, 1998; Siano and Klaus, 2013; Storch, 2000). Capercaillie is a red-listed species in Annex I of the EU Birds Directive in most European countries, and it is a specific designated feature of many of the Natura 2000 sites (Storch, 2007a).

One of the remaining strongholds of capercaillie populations in central Europe is the Carpathian Mountains that stretch from the Czech Republic east to Ukraine and extend to southern Romania. The Carpathian Mountains possess one of the largest areas of old-growth and natural forests in Europe with thriving populations of brown bears (*Ursus arctos*), lynx (*Lynx lynx*), grey wolves (*Canis lupus*), european bison (*Bison bonasus*) (Veen et al., 2010), and, historically, a stable and self-sustainig capercaillie population. Historic land uses, such as grazing and selective logging, maintained habitat conditions suitable for capercaillie (Hancock et al., 2011; Klaus et al., 1989). However, management practices have changed in the last few decades, with more large scale clearcuts and associated landscape fragmentation taking place, mainly due to new post-communist forest restitution laws (privatization of forest lands) and increasing accessibility by new forest roads (Knorn et al., 2012a,b).

Habitat loss and fragmentation related to logging activities have been shown to negatively impact the reproductive success of capercaillie in boreal forests (Lakka and Kouki, 2009). Similarly, in western and central Europe, a decline of capercaillie populations also has been linked to habitat loss through fragmentation and logging (Storch, 2007a). In contrast, recent evidence from boreal forests indicates that the capercaillie is relatively tolerant to changes in forest management regimes and populations will persist in the long term, even in landscapes with large-scale clearcutting (Miettinen, 2009; Wegge and Rolstad, 2011). However, capercaillie distribution in boreal forests is continuous and not as fragmented as in other areas of Europe (Storch, 2007a), and boreal forest regeneration patterns and dynamics is different compared to temperate regions of Europe.

Given clear declines of capercaillie associated with intensification of forest management over the last two decades, the main objective of this study was to identify the most important predictors influencing capercaillie male numbers in the leks in the Southern and Eastern Carpathians. We focused on stand and landscape features surrounding lek centres where mating occurs because they are critically important for sustaining local populations (Miettinen et al., 2005; Picozzi et al., 1992; Saniga, 2003). Specifically, we were interested in how human land use, intensity of forest management, habitat fragmentation, and loss of suitable habitat affect capercaillie abundance at the display grounds. Outcomes from this study highlight threats to capercaillie and identify forest management practices compatible with conservation goals.

2. Methods

2.1. Study area

Across the Southern and Eastern Carpathians within Romanaia, we sampled forests of 11 separate mountains. The potential size of suitable habitats (mountain forests with elevation >1000 m above sea level) was estimated on 190,113 ha; total area of all studied lek centres (1 km radius around the lek centres) was 6594 ha. The climate of Romania ranges from temperate to continental, and cold winters and high precipitation are typical for mountainous areas. The mean winter temperature is −5.2 °C with mean winter precipitation of 355 mm, while mean summer temperature is 13.9 °C and summer precipitation of 1095 mm in the study area (Toader and Dumitr, 2005).

2.2. Capercaillie population in the study area

Based on hunting surveys across Romania, the total population of Capercaillie was estimated to be ~10,000 birds as of 2007 (Storch, 2007b). During our the study period, hunting of capercaillie was legal in Romania; however, since 2012, hunting of capercaillie has been prohibited, although ongoing illegal hunting may still have serious effects on capercaillie populations in some regions. The lek centres studied were located at altitudes ranging from 1320 to 1722 m above sea level. The prevalent vegetation type was Norway spruce (*Picea abies* (L.) Karst.) forest (86%), mixed European larch (*Larix decidua* Mill.)-Norway spruce forest (9.5%), and mixed Norway spruce-Silver fir (*Abies alba* Mill.)-European beech forest (*Fagus sylvatica* L.) (4.5%).

2.3. History of forest management in the study area

The capercaillie habitats in the Carpathians are mostly high elevation natural forests with old-growth characteristics, such as large amounts of dead wood, elevated root plates, and multi-cohort open canopy stands (see the Appendix). Only 9% of the lek centres occurred in areas of naturally regenerated open canopy stands (~60 years old) resulting from abandonment of grazing of montane pastures. In the past, all stands were difficult to access and forest management was predominantly selective single-tree or group logging made by the shepherds who used the surrounding mountain pastures during the summer (Huband et al., 2010). Forest management practices changed considerably in the studied area after the collapse of communism in 1989. New forest roads were built into formerly inaccessible areas and large areas of state forest were restituted to prior owners resulting in increased forest harvesting at large spatial scales (Griffiths et al., 2014; Knorn et al., 2012a,b). In addition, some forested areas were officially categorized as pastures, thus enabling owners to make large clearcuts without any control, and illegal logging has occurred during the post-communist era. Extensive clearcutting forestry has also occurred in protected areas, such as national parks. Based on remote sensing data (Landsat imagery; Table 1, Griffiths et al., 2014), in our study plots the mean percentage of clearcuts after 1990s in protected areas is higher (24.6%), compared to unprotected areas (16.4%). Based on the forest ownership

Table 1
Forest extent and losses in each study plot (*N* = 21, plot size = 314 ha) with mean values (italicized) representing subregions of the Southern and Eastern Carpathians in Romania 2009–2011. For every study plot the maximum number of capercaillie males lekking in the display ground (centre of the study plot) and maximum number of females recorded during the spring season are reported. The top portion of the table shows the values in study sites with no protection regulations while the bottom portion shows the protected study sites.

1985–1990		1990–2010		1990–2010	1990–2010	Conservation status	Male numbers	Female numbers
Clearcut (ha)	Forest (ha)	Clearcut (ha)	Forest (ha)	Clearcut (%)	Average forest loss			
0	314.1	12.96	301.14	−4.1	16.40%	No protected	7	5
0	239.85	6.3	234.54	−1.7			4	2
0	240.57	33.21	207.36	−10.6			2	2
3.06	304.65	178.47	129.24	−55.8			2	0
0	135.09	9.27	125.82	−3			3	1
0	283.32	45.81	238.23	−14.4			1	2
1.89	267.93	6.48	263.34	−1.5			3	3
1.26	291.42	108.18	184.5	−34			1	1
4.95	253.62	75.51	183.06	−22.5			1	1
1.24	*258.95*	*52.91*	*207.47*	*−16.4*				
21.78	165.69	19.62	167.85	0.7	21.14%	Protected	3	1
0	303.03	135.72	167.31	−43.2			4	2
9	237.42	3.6	242.82	1.7			1	1
1.44	281.34	123.57	159.21	−38.9			3	1
0	266.85	225.81	41.85	−71.6			1	1
0	212.22	119.97	92.61	−38.1			1	2
8.19	224.19	77.04	155.34	−21.9			2	1
0	277.65	5.67	272.88	−1.5			2	1
61.47	200.34	3.06	258.75	18.6			2	3
7.02	130.23	51.39	85.86	−14.1			2	1
17.01	297.36	132.48	181.89	−36.8			6	8
1.08	258.03	27.99	231.12	−8.6			9	4
10.58	*237.86*	*77.16*	*171.46*	*−21.14*				

data (Abrudan, 2012) in our study plots, 43% were private and 57% owned by state. For the whole of Romania (as of early 2013), over 4.4 million hectares of state, public, and private forest lands were administered by state and experimental forest districts, with a further 1.7 million hectares of forest land administered by private forest districts (Marinchescu et al., 2014). It is evident that changes in ownership have resulted in changes in forest management and structure across multiple scales (Griffiths et al., 2014; Knorn et al., 2012a,b)

2.4. Data sampling

2.4.1. Study design

Clearcutting has been widely documented to lead to local extirpation of capercaillie (Storch, 2007b). Our objective was not to document population declines, but rather to identify forest practices that would permit persistence of capercaillie. Therefore, we sampled forest conditions representing a range of no harvest to partial harvest within the known range of capercaillie. Using capercaillie distribution and density maps provided by the Forest Research and Management Institute of Romania (ICAS), localities with the highest capercaillie densities across 11 mountain ranges were intensively surveyd in a 1 km radius area (314 ha), which was considered to be the average territorial area used by capercaillie males during the lekking period (Storch, 1995). We identified 21 lek centres in Făgăraș (*n* = 4), Rodnei (*n* = 4), Harghita (*n* = 3), Maramureş (*n* = 3) Piatra Craiului (*n* = 1), Bucegi (*n* = 1), Diham (*n* = 1), Prisciu (*n* = 1), Hâşmaş (*n* = 1), Călimani (*n* = 1), and Piatra Mare (*n* = 1) (Fig. 1.).

2.4.2. Data collection

Capercaillie males gather in lek centres to display and compete for females; within display grounds, males establish display territories spaced ~50 m apart. Counting of males at lek centres is a widely used technique across many species of grouse to monitor population trends (Miettinen et al., 2005; Picozzi et al., 1992; Saniga, 2003). During the daytime period, they remain within a radius of approximately 1 km of the lek centre (Storch, 1995). Plot locations, defined by lek centres, were determined by the position of the alpha capercaillie male; GPS coordinates recorded after birds finished displaying during each visit. These lek centres are usually located in the same sites annually and may be used for several decades (Klaus et al., 1989). Lek surveys were conducted from March to May during 2009–2011 with two visits per season; the maximum counts were used in the analyses. Surveys were performed from 03:00 to 09:00, and all observed or heard capercaillie males were recorded. During the day we returned to look for signs and display stances, which helped to clarify the capercaillie male numbers in the leks.

2.4.3. Environmental data and scale consideration

To understand drivers of capercaillie abundance we collected data on three principal types of data: habitat, forest management, and human activity, excluding forest management activities (Table A1). Data were restricted to stand scale and landscape scale; stand scale measurements were defined as an 80 m radius circular plot (2.1 ha), and landscape scale as a 1 km radius area (314 ha) to evaluate broader scales impacts, such as forest management and intensity of tourism. Landscape scale considerations were also defined by distance based variables for habitat or human activity variables (e.g. distance to the closest building, water spring, etc.).

2.4.4. Habitat measurements

Habitat characteristics were measured in the lek centres during the summer months. We used an extensive list of site characteristics to evaluate possible lek centre preferences in the under-researched part of the species distribution in Southern and Eastern Carpathians. The variables recorded included topography, surface type, main canopy characteristics, understorey, ground vegetation, dead wood, soil, habitat use by large herbivores, human land use, type of forest management, and the landscape; for a complete listing, see Table A1.

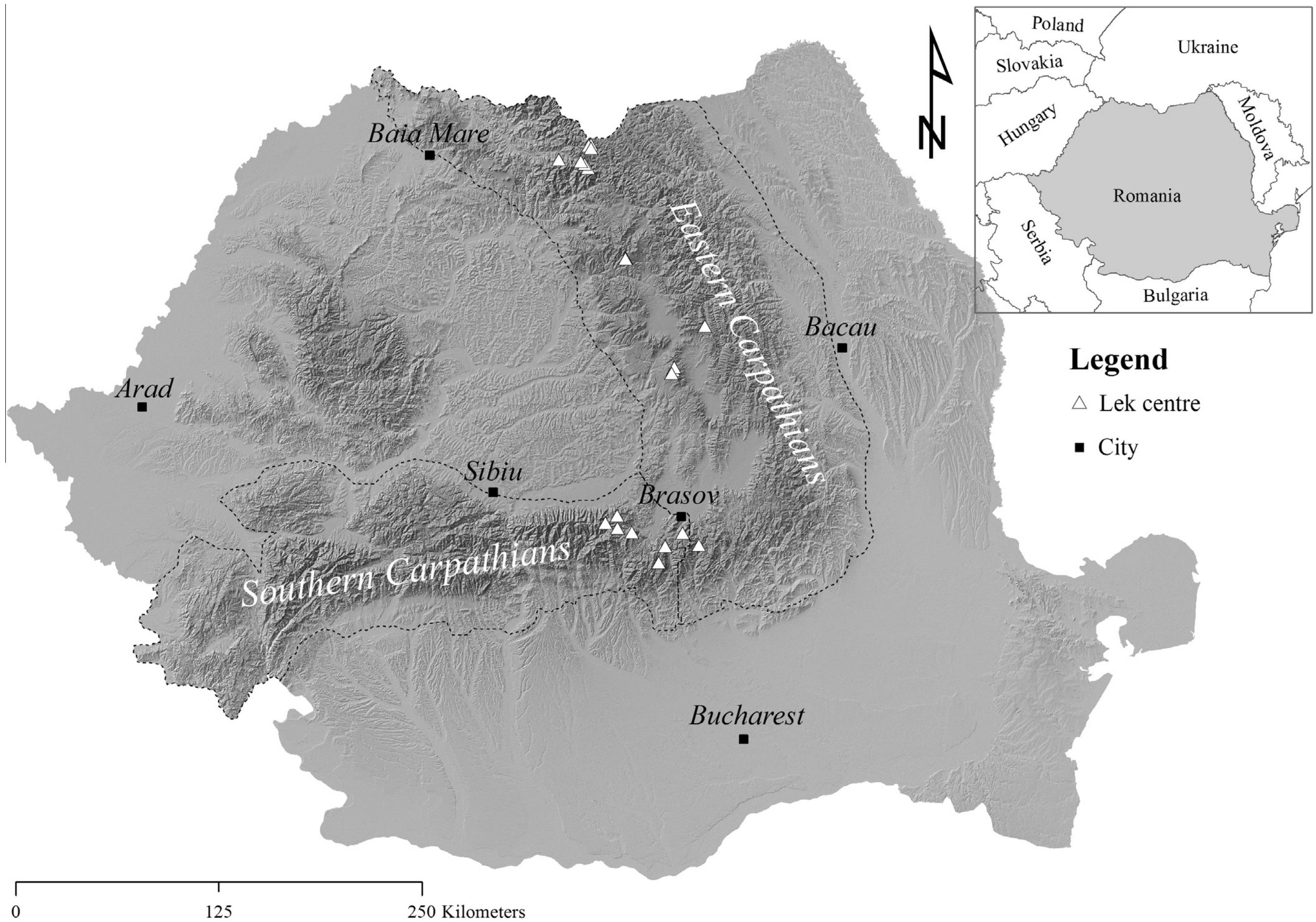

Fig. 1. Locations of the studied lek centres.

2.4.5. Forest management

Forest management activities were evaluated at the stand and landscape levels. At the stand scale, selective logging intensity was measured based on percent canopy removal and presence of forest roads within 80 m plot radius (2.1 ha). At the landscape scale, clearcut estimates were based on the proportion of the 1 km radius (314 ha) plot area that was clearcut within the previous five years (since 2005) and larger than one ha. A detailed list of variables and an explanation of variable scales are provided in Table A1 and Table 2, respectively.

2.4.6. Impact of (non-logging) human activity

To evaluate human land use intensity, activities were defined based on maps and direct enquiries of local and regional experts (administrators of national and natural parks, forestry administrators, and local shepherds), similar to Rösner et al. (2013). Every activity was classified on a scale from 0 to 5 to define intensity, with '0' being the least intensive and '5' being the most intensive (Table 2). The tourist activity was evaluated for the peak tourist period that included weekends during the winter/spring period; it was based on the number of tourists who visited the 314 ha plot.

Table 2
Detailed description of the scales of measured variables.

	0	1	2	3	4	5
Intensity of tourism (314 ha plot)	No tourism	<10 person/day	10–50 people/day	50–100 people/day	100–150 people/day	>150 people/day
Selective logging intensity (2.1 ha plot)	Non-managed forest	Presence of a forest road, no cuttings in the lek centre	Cuttings in the lek centre <1%	Cuttings 1–15%	Cuttings 15–30%	Cuttings >30%
Intensity of grazing (314 ha plot)	No grazing	Grazing of <15 standard livestock units irregularly	Grazing of 15–150 livestock units irregularly	Grazing <15 livestock units regularly	Grazing of 15–150 livestock units regularly	More than 150 livestock units
Intensity of hunting (314 ha plot)	No hunting	Legal hunting of 1 capercaillie per 15 years	Legal hunting of 1 capercaillie per 10 years	Legal hunting of 1 capercaillie per 5 years	Legal hunting of more than 1 capercaillie per 5 years	Illegal hunting
Spatial distribution of vegetation clustering (ID) (2.1 ha plot)	Homogenic matrix	Obscure clusters	Small clear clusters	Large clear clusters	Small orientated clusters	Large orientated clusters

The number of tourists was based on information from administrators of national and natural parks and tourist centre administrators (e.g. ski-lift companies, mountain cottages owners). Distance-based variables, such as distance to the closest buildings, and distance to closest road, were also used to evaluate human activity and presence.

2.5. Statistical analyses

Because a large numbers of explanatory variables were measured for a relatively small sample size ($n = 21$), the number of explanatory variables was reduced prior to analyses to avoid problems with collinearity (Dormann et al., 2013). Principal component analysis (PCA) on correlation matrices of landscape characteristics (12 variables), the cover of individual species in the tree layer (7 variables), the shrub layer (11 variables), and the herb layer (27 variables) was used to reduce the dimensionality. The broken stick model was used to identify the number of non-trivial principal components (Jackson, 1993). This selection process resulted in one principal component (PC) for the landscape characteristics, two PCs for the tree layer, two PCs for the shrub layer, and four PCs for the herb layer (see Table A2).

The relationships between capercaillie numbers and environmental characteristics were analysed using generalized linear models (GLM; McCullagh and Nelder, 1989). In addition to the latent variables described above, the remaining variables (see Tables A1 and A2) were then combined to form a list of candidate predictors. An exhaustive best-subset regression procedure was employed in search of the most parsimonious model (McLeod and Xu, 2009). Poisson distribution and logarithmic link-function were used within GLMs to relate numbers of males in the lek centres with the predictors. The Bayesian information criterion (BIC) was used for model selection. Due to the limiting number of degrees of freedom, only those models with a maximum of 5 explanatory variables were considered in the analyses. Parameters of the final model were tested using likelihood ratio tests (Crawley, 2007), and the model fit was assessed using McFadden's (pseudo) determination coefficient (McFadden, 1973). Standardized regression coefficients were calculated to facilitate direct comparisons across significant predictors, regardless of differences in the scale of the predictors. The relative importance of explanatory variables on capercaillie abundance was assessed by variation partitioning (Borcard et al., 1992). The deviance explained by each variable was expressed as a percentage of the total variation, represented by the deviance of a null model. Partial regression plots and effect plots were constructed to depict partial relationships in the final model (Fox, 2001). Partial regression plots allowed us to visualize the effect of each predictor after adjusting for all the other predictors in the final model. Effect plots display fit for each partial relationship while the other predictors are fixed at mean values. All analyses were performed in R (R Development Core Team 2010) using the *bestglm* (McLeod and Xu, 2011) and *vegan* (Oksanen et al., 2011) packages.

3. Results

Active capercaillie leks were not found within recent clearcuts and they were not detected where clearcutting exceeded 62% of the surrounding landscape (314 ha) (Fig. A1). Almost all lek centres were situated in forests with old-growth characteristics and limited anthropogenic influence (see Table A1). Only two lek centres were situated in younger forests, but these were in fact abandoned pastures and not clearcut areas. The average forest cover in the 314 ha plot was 187 ha (60%), with a range between 79 ha (25%) and 301 ha (96%); the remaining areas were covered by mountain pastures or clearcuts. The average number of capercaillie males counted in the lek centres was 2.9 (SD = 2.15), and the average number of females was 2 (SD = 1.8) (see Table 1.)

The best model to explain the number of male capercaillie at lek centres contained three variables: the proportion of clearcuts at the landscape scale and intensity of tourism negatively influenced male capercaillie numbers, but selective logging intensity at the stand scale had a positive effect (Table 3). The overall model significantly explained 62.8% of the deviance ($\chi^2_{(3)} = 17.27$, $p < 0.001$), and partial regression plots indicated the model provided a reasonable fit to the data (Fig. 2a–c). Based on standardized regression coefficients, the effect size of landscape scale clearcuts was largest. Variation partitioning indicated that >37% of the deviance in male numbers could be explained by the proportion of clearcuts; holding the effect of other variables constant, clearcuts of 30% reduced male lek counts by more than four times (Fig. 2d). The deviance attributable to tourism and selective logging intensity amounted to 31% and 20%, respectively. Differences between no (0) and intensive (5) tourism and selective logging indicated a 4.4-fold decrease and a 3.7-fold increase in male lek counts, respectively, when other factors were held constant (Fig. 2e–f).

4. Discussion

Of all the studied variables, three anthropogenic factors had the highest influence on capercaillie numbers: the proportion of clearcuts, intensity of tourism, and selective logging. Romania has experienced massive socio-economic and institutional change over the past 25 years (Knorn et al., 2012a,b) that has impacted ownership and human land use, such as forestry and tourism. Negative effects of emerging land use (increased forest exploitation and tourism) were evident, while historic forest practices were positively related to capercaillie numbers. The average capercaillie male numbers per lek were similar to numbers detected in other regions, where long term declining population trends were detected (e.g. Zawadzki and Zawadzka, 2012; Saniga, 2012).

4.1. Capercaillie and forest harvesting

The effects of forest harvesting on capercaillies depend on the intensity and extent of harvesting practices (Klaus, 1991). The selective logging intensity in the lek centres had a positive effect on capercaillie male numbers. In dense managed stands, selective logging reduces canopy cover in a manner similar to small-scale natural disturbance processes, which makes the forest canopy more open and increases structural heterogeneity of the stand (Broome et al., 2014; MacMillan and Marshall, 2004). Multistoried tree layers with gaps and abundant cover of ericaceous understory shrubs may improve summer forage and cover from predators for capercaillies. Although our results did not show a significant relationship between number of capercaillie males and bilberry cover, the capercaillie habitats typically contained extensive patches of bilberry; based on other studies, we do know

Table 3
Parameters of the final GLM model showing relationships between the number of capercaillie males in the lek centres and the proportion of clearcuts, intensity of tourism, and intensity of forest management. Standardized regression coefficients (β), regression coefficients (b), standard errors (se), test statistics (χ) and probabilities (p) are displayed.

Parameter	β	b	Se	χ	p
Intercept		2.036	0.187	44.54	<0.001
Proportion of clearcuts	−0.41	−0.048	0.009	14.32	<0.001
Intensity of tourism	−0.22	−0.296	0.071	9.86	0.002
Selective logging intensity	0.24	0.262	0.083	5.35	0.021

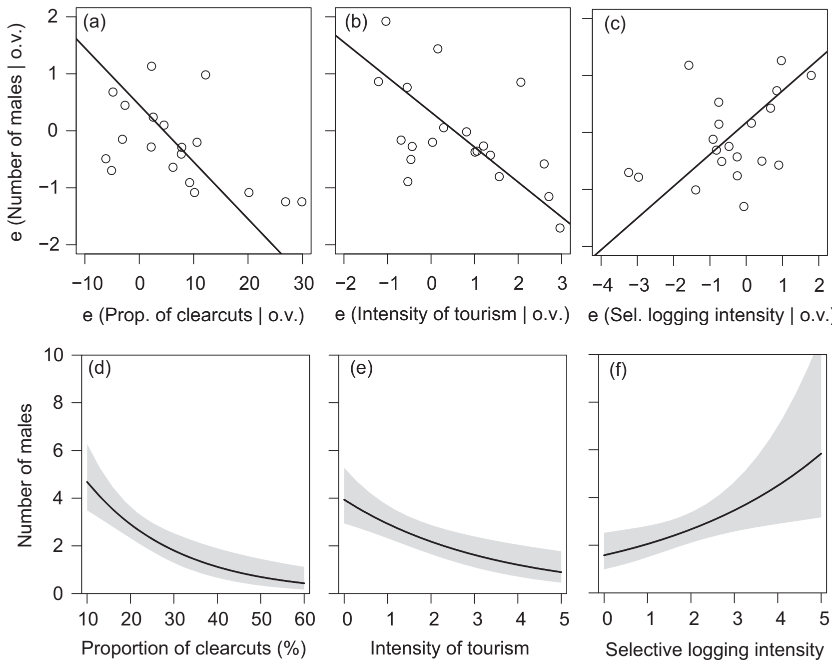

Fig. 2. Partial regression plots (a, b, c) and effect plots (d, e, f) demonstrating the multivariate relationship between number of males in the lek centres and the proportion of clearcuts (a, d), intensity of tourism (b, e) and selective logging intensity (c, f). Lines represent partial regression slopes (a, b, c) and partial fitted relationships holding the other variables (o.v.) constant at their means (d, e, f). Ninety-five percent confidence intervals are shown in grey.

that bilberry is an important habitat component (eg. Wegge and Rolstad, 2011; Hancock et al., 2011; Storch, 2002, 1993).

At the landscape scale, the proportion of clearcuts surrounding the lek centres had an exponential negative effect on capercaillie numbers (Fig. 2d), as suitable habitats are lost and fragmented by clearcuts. The relationship between habitat fragmentation and extinction has been demonstrated to be highly non-linear (Fahrig, 2003), thus, the presence of clearcuts also has broader implications to population and metapopulation dynamics throughout the region.

Our results are in contrast with the findings of studies conducted in the boreal zone (Miettinen, 2009; Wegge and Rolstad, 2011); they observed that capercaillie were tolerant to clearcutting across the landscape because capercaillie were also able to use open canopy middle-aged plantations (>30 years old) with bilberry ground cover. The findings of these studies cannot necessarily be applied to central Europe or the Southern and Eastern Carpathians, which are all outside the boreal zone. Capercaillie distribution in central Europe is very fragmented compared to the boreal zone; capercaillie persist here in patchy populations embedded in a mountainous landscape (Storch, 2007a). In fragmented conditions of central Europe it is very difficult to maintain viable capercaillie populations, which require ca. 250 km^2 and an estimated 470 interacting capercaillie individuals (Grimm and Storch, 2000). Inter-patch dispersal is very important for the persistence of capercaillie, thus, high habitat connectivity is important for metapopulation dynamics. In the Carpathians, suitable capercaillie habitats are a mere small 'habitat band' of coniferous dominated forest situated between mountaintops and the deciduous forests of lower altitudes. In case of intensive clearcutting, alternative forest nearby which represents suitable capercaillie habitat is thereby naturally limited. When stepping stones are lost and habitat connectivity is disrupted by clearcuts on large spatial scales, as in this study, migration of individuals between populations could be severely limited and population persistence may be threatened because small isolated populations are unlikely to survive (Segelbacher et al., 2003). These factors has lead to extinction debt in other small and isolated metapopulations (Pullin, 2002). In addition, the typical management practices in central Europe do not enable creation of open canopy forest structure suitable as capercaillie habitat (Bollmann et al., 2005). Plantation establishment after clearcutting is mandatory in central Europe; the result is very dense forest canopies with very little ground vegetation, particularly critical bilberry cover (*Vaccinium myrtillus* L.), which provides food for adults, invertebrates for chicks, and hiding and thermal cover (Hancock et al., 2011; Storch, 1993).

The negative landscape level effect of large clearcuts on capercaillie numbers was significant and outweighed the positive effects of selective logging intensity. These clearcuts cover large areas and might almost completely remove the narrow spruce forest vegetation belt in some areas. Unlike smaller clearcut patch harvesting that creates fine grain forest fragmentation that may be suitable for capercaillie in the boreal forests (Sirkiä et al., 2011), large clearcuts cause long-term loss of habitat with no alternative options of suitable habitats in the surrounding forests where the birds could migrate. Increased harvesting using clearcuts practices are largely related to restitution laws implemented after the collapse of communism in 1989; forest harvesting increased sharply in two waves around 1995 and 2005 (Knorn et al., 2012a). Clearcuts recorded in our study (younger than 5 years) in the capercaillie habitats coincide with the second wave of harvesting after 2005. The area of suitable habitats is declining and becoming more fragmented as a result of large-scale clearcuts in the Carpathians, with little differentiation in forest management practices between protected or non protected areas (Knorn et al., 2012a).

4.2. Capercaillie and tourism

The negative effect of intensive tourism (e.g. ski resorts) on capercaillie and other bird populations has been reported in many regions (e.g. Moss et al., 2014; Rösner et al., 2013; Thiel et al., 2011). Human disturbance may influence metapopulation dynamics and contribute to genetic impoverishment in small populations (Moss et al., 2014). For example, collisions with ski-lift cables may increase capercaillie mortality. Intensive tourism can negatively influence brood success because it increases levels of the stress hormone corticosterone, which influences reproduction and survival (Thiel et al., 2011). Also, areas frequented by people have increased carrying capacity for a family of avian predators – the *Corvidae*; ravens, crows and jays favour human inhabited areas (Storch and Leidenberger, 2003). Recent increased use of snowmobiles and off-road vehicles concentrated near tourist recreation areas may have the most negative effects, as they may cause serious yearlong disturbances to the capercaillie in many regions. To offset the effects of tourism on capercaillie populations, sufficiently large habitat patches that provide good hiding cover and buffers from touristic areas and roads should be established and maintained (Newsome and Moore, 2012). Increased use of selective harvesting can help to achieve this. Further, by planting dense vegetation bordering frequented tourist paths, the probability of people leaving marked trails and disturbing capercaillies would be reduced (Coppes and Braunisch, 2013).

4.3. Old growth forests as refuge

Old-growth forests are the primary habitats for capercaillies (Klaus et al., 1989) and it was shown already for the Carpathians as the main capercaillie habitat type (Saniga, 2003). The habitat characteristics of most of the studied lek centres were typical of old-growth forests – large amounts of dead wood, elevated root plates, multi-cohort open canopy stands, etc. (Table A1). The structure of these forests is a result of natural disturbance regimes characterized by windthrows and bark beetle outbreaks, which are usually infrequent, moderate- to high-severity disturbances that influence forest structure across all spatial scales – tree, stand, and landscape (Svoboda et al., 2014; Trotsiuk et al., 2014). These disturbances create canopy gaps and forest edges of different sizes (Fraver and White, 2005), which provides suitable habitats for capercaillie. These types of stands are currently just a small fraction of the landscape in central Europe (Wesolowski, 2005), thus, they play a key role for the preservation of capercaillie populations and many other species in the Carpathians. There has been a clear trend in the large-scale destruction of mountain spruce forests, including old-growth and natural forests across the whole Carpathian region over the past few decades (Griffiths et al., 2014; Knorn et al., 2012a,b; Kuemmerle et al., 2009, 2007), and the natural mountain forest community is endangered. The long-term survival of the species is therefore reliant on the viability of core areas to serve as refuges.

5. Conclusions and implications for forest management

Our study indicates that extensive human land use, such as low intensity selection harvesting, can have positive effects on capercaillie, but large-scale clearcutting and intensive tourism can also have very negative effects. Measures to conserve the umbrella species capercaillie will benefit a wide range of other forest species and better preserve a wide range of ecosystem functions and services (Balvanera et al., 2006; Suter et al., 2002). Our results indicate that even protected areas do not ensure the protection of threatened species and their habitats in the Carpathian region (Table 1). This can only be changed if the priority in protected areas is the conservation of biodiversity and prioritization of non-extractive ecosystem services rather than timber production as in typical commercial forests.

Conservation and forest management goals should be based on a multi-scale approach. Commercial forest management in relevant areas should be modified to emulate natural disturbance processes across multiple scales. With single-tree selection, group selection, conversion of spruce to mixed species, increasing large snag densities, and creating a multi-layered canopy at the stand level, foresters can accelerate the development of suitable natural forest habitats (Franklin et al., 2002). Sufficient areas (cca 250 km^2) of quality habitat are necessary foundations for viable capercaillie populations (Grimm and Storch, 2000), thus, management planning for viable populations should be in accordance with broader relationships at the landscape scale to ensure a sufficiently-sized mosaic of suitable habitats and connectivity between habitat patches (Graf et al., 2009; Segelbacher et al., 2003). To ensure the long-term survival of capercaillie populations in the Carpathians, it is necessary to conduct further assessments of the suitability of existing capercaillie habitats (e.g. create a habitat suitability model) and identify the optimal extent of suitable habitat and its connectivity (Braunisch and Suchant, 2008). The habitat suitability model should be adapted regionally, because species – habitat relationships may differ between regions, due to different site conditions, vegetation types, and successional processes (Graf et al., 2005), as exemplified by differences in capercaillie habitat use in Norway and central Europe. Management at the landscape scale should include the protection of old-growth forests, the restriction of fragmentation and large-scale deforestation, to ensure a more ecologically sustainable forestry model in central Europe.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.07.001.

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