Landscape Ecol
DOI 10.1007/s10980-014-0048-5

RESEARCH ARTICLE

Human-carnivore coexistence in a traditional rural landscape

Ine Dorresteijn · Jan Hanspach · Attila Kecskés · Hana Latková · Zsófia Mezey · Szilárd Sugár · Henrik von Wehrden · Joern Fischer

Received: 13 December 2013 / Accepted: 29 May 2014

Abstract Facilitating human-carnivore coexistence is a major conservation concern in human-dominated landscapes worldwide. Useful insights could be gained by studying and understanding the dynamics of human-carnivore coexistence in landscapes in which carnivores and humans have coexisted for a long time. We used a two-pronged approach combining ecological and social data to study coexistence of the brown bear (*Ursus arctos*) and humans in Transylvania, Romania. First, we surveyed 554 km of walking transects to estimate activity via a bear sign index, namely the proportion of anthills disturbed by bears, and used spatially explicit predictive models to test which biophysical and anthropogenic variables influenced bear activity. Second, we interviewed 86 shepherds and 359 villagers and community representatives to assess conflicts with bears and attitudes of shepherds towards bears. Our interdisciplinary study showed that bears and humans coexisted relatively peacefully despite occasional conflicts. Coexistence appeared to be facilitated by: (1) the availability of large forest blocks that are connected to the source population of bears in the Carpathian Mountains; (2) the use of traditional livestock management to minimize damage from bears; and (3) some tolerance among shepherds to occasional conflict with bears. In contrast, bear activity was unrelated to human settlements, and compensation for livestock losses did not influence people's attitudes toward bears. Our study shows that coexistence of humans and carnivores is possible, even without direct economic incentives. A key challenge for settings with a discontinuous history of human-carnivore coexistence is to reinstate both practices and attitudes that facilitate coexistence.

Keywords Carnivore conservation · Human-carnivore coexistence · Human-dominated landscapes · Eastern Europe · *Ursus arctos* · Wildlife conflicts

Electronic supplementary material The online version of this article (doi:10.1007/s10980-014-0048-5) contains supplementary material, which is available to authorized users.

I. Dorresteijn (✉) · J. Hanspach · H. von Wehrden · J. Fischer
Faculty of Sustainability, Leuphana University Lüneburg, Scharnhorststrasse 1, 21335 Lüneburg, Germany
e-mail: ine.dorresteijn@gmail.com

A. Kecskés · H. Latková · Z. Mezey · S. Sugár
"Milvus Group" Bird and Nature Protection Association, Strada Crinului 22, 540620 Târgu Mureş, Romania

H. von Wehrden
Center for Methods, Leuphana University Lüneburg, Scharnhorststrasse 1, 21335 Lüneburg, Germany

H. von Wehrden
Research Institute of Wildlife Ecology, Savoyen Strasse 1, 1160 Vienna, Austria

Published online: 11 June 2014

Introduction

Facilitating coexistence between humans and carnivores is a conservation challenge worldwide (Woodroffe et al. 2005; Treves et al. 2006; Dickman et al. 2011), because carnivores have often been extirpated locally due to conflicts with humans (Breitenmoser 1998; Woodroffe 2000). Predators are important because they exert top-down control on ecosystem processes (Estes et al. 2011; Ripple et al. 2014), and provide emotional, recreational, and cultural benefits to society (Kellert et al. 1996). Due to increasing conservation efforts (Ray 2005), some carnivore populations are growing again (Linnell et al. 2001; Enserink and Vogel 2006), but many continue to decline (Ripple et al. 2014). The two most frequently advocated strategies to counteract carnivore declines are: (i) to separate carnivores from settlements by establishing protected refuge areas (Karanth et al. 2010; Packer et al. 2013); and (ii) to promote human-carnivore coexistence in human-dominated landscapes through conflict mitigation programs (Woodroffe et al. 2005; Dickman et al. 2011).

Several studies have shown that humans and carnivores can coexist (Carter et al. 2012b; Schuette et al. 2013). However, coexistence is often hampered by human-carnivore conflicts, which can harm rural households especially (e.g. Holmern et al. 2007). Because many carnivores live in human-dominated landscapes, a key to their successful conservation is to better understand the dynamics of human-carnivore coexistence. To this end, one useful approach could be to learn from landscapes in which carnivores and humans have coexisted for a long time.

In Eastern Europe, large carnivores and humans have co-inhabited multiple-use landscapes for centuries. Romania sustains large, stable populations of the brown bear (*Ursus arctos*), wolf (*Canis lupus*) and lynx (*Lynx lynx*) (Salvatori et al. 2002), with the brown bear population being particularly large (estimated at 6,000 individuals by the IUCN). Most of Romania's bears live in the Carpathian Mountains, but many also occur in the Transylvanian foothills of the Carpathian Mountains, which harbor hundreds of villages characterized by traditional semi-subsistence agriculture. This situation is exceptional because the majority of bear populations elsewhere in Europe are confined to remote mountainous areas—and where bears do range into human-dominated landscapes, they often damage livestock, orchards and beehives (Zedrosser et al. 2001). Thus, Transylvania offers an interesting model system that may help to facilitate greater understanding of the dynamics underpinning successful coexistence of humans and carnivores.

Gathering reliable data on carnivore distribution is notoriously difficult due to their elusive nature. Especially in Romania, long-term data is scarce, and the reliability of official data collected by hunting organizations may be questionable (Salvatori et al. 2002). Therefore, we used a new, sign-based metric, namely the proportion of anthills destroyed by bears relative to the total number of anthills in an area, being fully aware of the limitations of sign-based indicators (Barea-Azcon et al. 2007; Long et al. 2007). Although the proportion of destroyed anthills may be a less accurate sign than footprints or faeces, it offers the opportunity to survey large areas in a relatively short time, which we believe more than compensates the risks of potentially higher methodological uncertainty.

To understand long-term coexistence in multiple-use landscapes, both ecological and social variables are important (Treves and Karanth 2003; Treves et al. 2006; Carter et al. 2012a). Although the need for interdisciplinary work on human-wildlife coexistence has repeatedly been acknowledged (Redpath et al. 2012), few studies have combined ecological studies on habitat preferences of carnivores with social data on human-carnivore conflicts and tolerance levels towards carnivores (Glikman and Frank 2011; but see Schuette et al. 2013). The overarching goal of our study was to assess how humans and bears coexist in southern Transylvania. Our study had two specific objectives. First, we sought to understand spatial patterns of bear activity in response to anthropogenic variables, biophysical variables, as well as local connectivity between forest patches and regional connectivity to the Carpathian Mountains. Second, we examined the nature of human-bear conflicts in the region and related it to the spatial distribution of bear activity.

Methods

Study area and design

Our 7,441 km^2 study area was located within a 50 km radius around the town of Sighisoara, in the foothills of

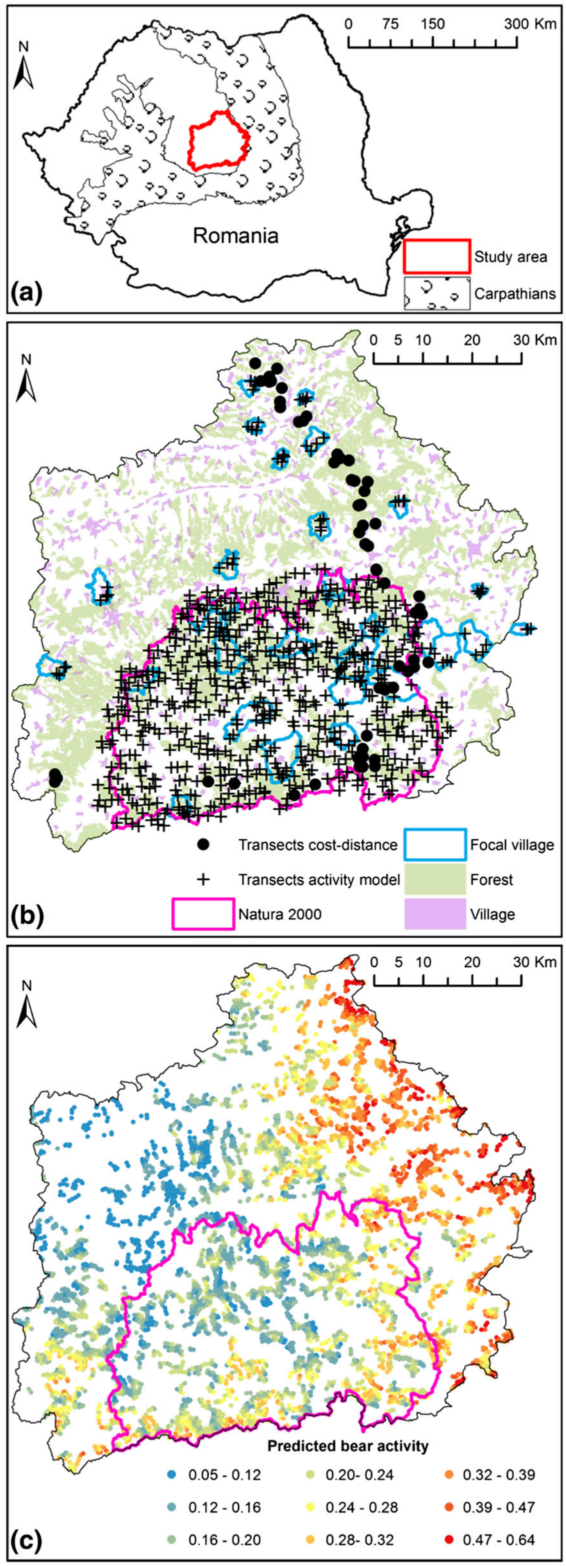

Fig. 1 Study area, study design and predicted bear activity. ▶ **a** Study area in southern Transylvania, Romania, and location of the Carpathian Mountains used for the cost-distance analysis. **b** Close-up of the study area and study design and location of the transects used for the bear activity model (n = 630) and cost-distance analysis to the Carpathian Mountains (n = 59). The focal Natura 2000 area was surveyed for bear activity in detail. The study area was surveyed at a large scale for bear activity and human-bear conflict in 30 focal villages and their surrounding land. **c** Predicted bear activity in the study area, based on generalized linear modelling. Bear activity is indicated as the predicted proportion of destroyed relative to total number of anthills

the Carpathian Mountains in southern Transylvania (Fig. 1a). Recently, one of the largest sets of non-mountainous EU protected Natura 2000 sites was established in this area (Fig. 1b). We selected transects inside and outside this focal protected area to provide data for the foundations of the brown bear management plan, and to provide reference data so the management plan can later be evaluated. A detailed description of the area is provided in Supplementary Material Text S1.

To quantify bear activity, we used the proportion of anthills destroyed by bears relative to the total number of anthills in each pasture transect. Destroyed anthills and other signs are rare in forests and therefore we walked transects on pasture adjacent to forest. Anthills are available on pastures across the entire landscape which allowed us to cover a large area in a standardized way. Ants form an important food source of protein for the brown bear (Dahle et al. 1998; Swenson et al. 1999). Ant larvae are particularly sought after by bears in spring and summer, and the incidence of destroyed anthills has been used in previous sign surveys for bear presence (Munro et al. 2006; Ciarniello et al. 2007). Anthills destroyed by bears are readily distinguishable from those destroyed by other animals (e.g. cattle) and humans because they have a characteristic "crater" dug out of the top.

Our choice of transects was guided by three design considerations. First, we sought to obtain a broad overview of bear activity in the study area. We surveyed bear activity in 30 focal villages and their surrounding land, because villages have been identified as both ecologically and socially meaningful "landscape" units (Angelstam et al. 2003). We delineated the area belonging to a given village using a cost-distance algorithm that allocated each pixel to the village with the lowest travel cost to this pixel (slope-penalized distance, implemented in ArcGIS, mean area ± SD: 20.5 ± 11.2 km^2). We randomly selected 30 villages from 448 villages in the study area, stratified to cover the full gradient in terrain ruggedness and to include Natura 2000 areas as well as unprotected areas (Fig. 1b). With few exceptions arising from logistical obstacles we surveyed four transects around each village (n = 113; described in detail below).

Second, we covered the focal conservation area (2,675 km^2) in detail to inform the new management plan. We divided the Natura 2000 area into grid cells of 2 km × 2 km (n = 759). We surveyed one transect in each grid cell with more than 15 % forest cover (n = 417), and we surveyed one transect per grid cell for 100 additional, randomly chosen cells with less than 15 % forest cover. For these two considerations, all transects were chosen to cover the full gradient of available distances to the nearest village and amount of surrounding forest cover within a radius of 1,500 m.

Third, to assess the connectivity from our study area to the assumed source population of brown bears in the Carpathian Mountains, we compared alternative cost-distance metrics to the mountains, so that the best cost-distance metric could be used in later analyses (see the section on variables used to model bear activity below). For this, we specifically surveyed 59 transects within 15–20 km from the mountains (Fig. 1b). These transects were chosen to cover a gradient from likely low cost to high cost by varying the sets of land cover types available between a given transect and the mountains.

All transects were walked once at the forest-pasture interface at approximately 10 m distance from the forest edge. Each transect was 800 m long and 6 m wide. All destroyed and undestroyed anthills within a transect were counted. We included both fresh (this year) and old (previous years but clearly visible) destroyed anthills. In total, we walked 692 transects (554 km) between April 28 and August 10, 2012. Three transects were excluded from analysis because they had no anthills. The mean number of anthills per transect was 139. All transects for the cost-distance analysis were surveyed in May and June, 2012.

Variables used to model bear activity

We used four sets of variables to explain patterns in bear activity. First, *anthropogenic disturbance* was indicated by distance to settlements. Second, the *biophysical environment* within a radius of 1,000 m from the midpoint of each transect was indicated by (i) terrain ruggedness calculated as the standard deviation of the altitude; (ii) percent pasture cover; and (iii) the shape and size of forest patches indicated by the forest edge to forest interior ratio. We did not include forest cover because it was correlated with forest edge to interior ratio ($\rho = -0.71$). Third, *local connectivity* between forest patches within the study area was indicated by betweenness centrality. Betweenness centrality is an index of how well connected a given forest patch is within the network of forest patches regardless of land-use between the different forest patches. Fourth, *connectivity to the Carpathian Mountains* (the presumed source population) was indicated by the cost-distance of each transect to the mountains. Cost-distance was based on a matrix with a resolution of 10 m × 10 m and combined distance to the mountains with weights between 1 and 10, assigned by experts to the different land uses. Detailed descriptions of these variables are provided in Supplementary Material Text S1.

We accounted for possible effects of the total number of anthills per transect and survey date (bears might be more attracted to pastures with more anthills; and the number of destroyed anthills by definition accumulates with time) by including them as variables in the model. Because the effects of number of anthills and survey date were not necessarily linear, we included their quadratic terms (e.g. the number of destroyed anthills might level off before the end of the field season if bears shift to other food sources such as fruit). Protection level was not included in the models, because the recent establishment of the Natura 2000 area has not yet resulted in different natural resource use that could affect bear activity.

Statistical modelling

All analyses were performed with the proportion of destroyed vs. total number of anthills as the response variable within generalized linear models (GLM) with a quasi-binomial error structure to account for over-dispersion. This model specification took into account that the precision of the response variable increased with an increasing total number of anthills found along a given transect (e.g. one destroyed anthill out of two total anthills is less precise information than 50 destroyed out of 100). The final GLM was obtained by using model averaging based on a tenfold cross-validation (Fielding and Bell 1997). Validation was done by relating the predicted activity (based on a model using nine tenths of the data) with the activity observed in the remaining tenth via a binomial GLM (see Table S1 for the estimates and explained deviance for each of the validation steps). We calculated the amount of deviance explained as a measure of predictive performance of each of the ten models. We averaged the parameter estimates over the 10 models, weighting the estimates from each model by its predictive performance. The averaged estimates were used to predict bear activity in forest edges bordering pastures across the entire study area, at a resolution of 800 m, equalling the transect length of the field surveys. All statistical analysis were implemented in the 'R' environment (R Core Team 2013). Further details on statistical modelling and predictive mapping are provided in Supplementary Material Text S1.

Human-bear conflicts

Human-bear conflicts were assessed using questionnaires in the same 30 villages targeted for bear transects (Fig. 1b). We used a detailed questionnaire for shepherds that addressed attacks on livestock, attitudes towards bears, and the current compensation scheme; and a shorter one for villagers that addressed the types of damage caused by bears. To assess attitudes among different stakeholder groups relevant to coexistence dynamics, we used the same short questionnaire for mayors, hunters and local councillors. These groups are in charge of compensation payments after carnivore damage, and we therefore included several questions regarding compensation (questionnaires are available as Supplementary Material Text S2–4). We aimed to interview approximately three shepherds (on average a village had between one and four shepherds), ten villagers, one mayor and one hunter or councillor per village, but not everyone was available in all villages. Ultimately, we obtained questionnaires from 86 shepherds (73 sheep-herders, 13 cow-herders), 302 villagers, 22 mayors or vice-mayors, 20 local councillors and 15 hunters (for ethical considerations see Supplementary Material Text S1).

We expected a significant relationship between bear activity and perceived number of conflicts (e.g. higher bear activity could increase bear-related impacts), as well as livestock management (e.g. proactive measures prevent attacks by bears). To test for a possible relationship between bear activity and conflicts, we first averaged predicted bear activity within the land associated with each village. We then calculated Spearman rank correlations between average predicted bear activity and: (i) the mean number of bear attacks on sheep in the last 3 years; and (ii) perceived damage to orchards, crops and beehives. For the latter we used the proportion of local people who stated that bears caused damage to local orchards, crops or beehives. To assess whether certain herding techniques were more or less prone to attacks we used Spearman rank correlations between number of bear attacks on sheep and (i) the number of sheep in the herd; (ii) the number of sheep per guarding dog; (iii) total number of dogs, and (iv) the number of sheep per shepherd.

Results

Predictive model of bear activity

Bear activity was recorded in 52 % of the 630 transects. Cost-distance to the Carpathian Mountains had the largest effect on bear activity (Table 1), which decreased with increasing cost-distance. Biophysical variables also were strongly related to bear activity (Table 1). Bear activity was highest in rugged terrain, near large forest patches with a low edge to interior ratio, and in areas with low pasture cover. The effects of distance to the village and local connectivity between forest patches were weak and not significant (Table 1; Table S1).

Predicted bear activity showed a gradient with proximity to the Carpathian Mountains but was otherwise relatively homogenous throughout the region (Fig. 1c). We found no obvious hotspots for bear activity inside the focal Natura 2000 area, but noted that predicted bear activity was particularly high just north-east of (i.e. outside) the focal Natura 2000 area.

Human-bear conflicts

Predicted bear activity did not correlate with the average number of bear attacks on sheep reported by shepherds ($n = 73$, $rho = -0.1$, $p = 0.61$). However,

Table 1 Model-averaged coefficient estimates (weighted mean ± weighted SE) of the bear activity model

Variable	Estimate ± SE	Number of times significant in the ten separate models	
		$P < 0.05$	$P < 0.01$
(Intercept)	−1.66 ± 0.099	10	10
Number of anthills	0.04 ± 0.113	0	0
Number of anthills^2	−0.29 ± 0.072	10	10
Time	0.58 ± 0.073	10	10
Time^2	−0.24 ± 0.069	10	9
Distance to village	0.02 ± 0.069	0	0
Ruggedness	0.17 ± 0.059	10	7
Pasture cover	−0.15 ± 0.069	8	3
Forest edge:forest area	−0.17 ± 0.065	10	5
Betweenness centrality	0.04 ± 0.076	0	0
Cost-distance to Carpathian Mountains	−0.34 ± 0.069	10	10

Ten separate models were initially calculated, and then a tenfold cross-validation procedure was used. The ten models were largely consistent in terms of which variables were significantly related to the response

predicted bear activity was positively related to the damage perceived by local villagers to orchards ($n = 302$, $rho = 0.61$, $p < 0.001$) and fields ($n = 302$, $rho = 0.5$, $p = 0.004$), but not to beehives ($n = 302$, $rho = 0.03$, $p = 0.86$). All participants, except one, stated that bear attacks on humans happened rarely or never.

The median herd size of sheep was 500, the median number of sheep per dog (typically including one herding dog and several guarding dogs per herd) was 88, and the median number of sheep per shepherd was 400. Of 34 described attacks in 23 villages, 56 % occurred at night, 79 % in pastures, and 61 % in shrubby places. In 69 % of cases, less than three sheep were killed. Among the shepherds who had suffered attacks, there was no correlation between the number of attacks and the number of sheep per shepherd ($rho = 0.13$, $p = 0.45$), the number of sheep per dog ($rho = 0.29$, $p = 0.11$), the total number of dogs ($rho = 0.18$, $p = 0.11$), or the total number of sheep ($rho = 0.34$, $p = 0.052$). Many shepherds mentioned that having good dogs was the most important to avoid sheep predation (pers. comm.).

The majority of shepherds perceived bear populations to be increasing over the past decade, regardless of how many attacks they had suffered (Fig. 2a). However, shepherds who had suffered more bear attacks perceived more strongly that bear attacks had increased over the past decade (Fig. 2b). Despite these trends, approximately 50 % of shepherds had neutral or positive feelings towards bears (Fig. 2c). The percentage of shepherds who strongly disliked bears was higher for shepherds who had suffered more attacks (Fig. 2c). Only six of 86 shepherds indicated that their feelings towards bears had changed over the past decade. Over 50 % of shepherds did not support immediate killing of bears after attacks on livestock (indicated by "no" and "depends"). Shepherds who answered "depends" supported the killing of a bear if livestock losses occurred repeatedly by the same bear. Support for immediate killing (indicated by "yes") was slightly higher among shepherds who had suffered attacks than among those who had not (Fig. 2d).

Ninety-three percent of shepherds found compensation for damage to livestock important. However, 92 % of shepherds agreed that compensation should be received only if appropriate measures were taken by herders to protect livestock from carnivores. Interestingly, 90 % of shepherds were unaware of the (officially) existing compensation scheme. This finding, however, should be interpreted cautiously because two shepherds indicated they had tried to receive compensation, but were of the impression that no current compensation scheme was active. In stark contrast, 85 % of mayors, hunters and local councillors thought the compensation scheme was readily accessible; but only 43 % of mayors, hunter and councillors believed that the majority of the community was aware of the scheme.

Discussion

There is growing recognition of the need to conserve large carnivores outside protected areas (e.g. Athreya et al. 2013; Schuette et al. 2013), however, insights from human-dominated landscapes are still limited (e.g. Ghosal et al. 2013). Our approach drawing on both ecological and social data suggests an apparent balance between humans and bears in southern Transylvania. The main factors contributing to this appeared to be: (i) the availability of large forest blocks connected to

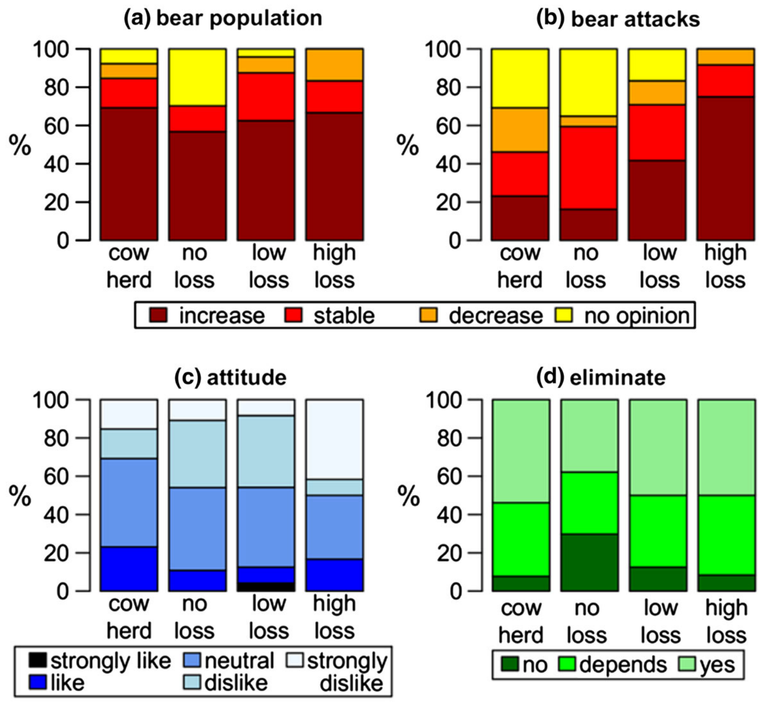

Fig. 2 Perceptions of shepherds regarding the brown bear. **a** trend in bear populations over the last decade; **b** trend in attacks of bears on livestock over the last decade; **c** attitudes towards bears; and **d** immediate elimination of bears after attacks on livestock. Cow herd = cow herders; no loss = shepherd with no attacks by bears in the past 3 years; low loss = shepherd with fewer than ten attacks by bears in the past 3 years; high loss = shepherds with ten or more attacks by bears in the past 3 years

the presumed source population of bears in the Carpathian Mountains; (ii) the use of traditional livestock husbandry techniques to minimize damage from bears; and (iii) some tolerance among shepherds to occasional conflict with bears. Unlike elsewhere, avoidance of human settlements by bears (Posillico et al. 2004; Preatoni et al. 2005; Nellemann et al. 2007) and financial incentives (Maclennan et al. 2009; Banerjee et al. 2013) appeared to play negligible roles in facilitating human-bear coexistence.

Explaining coexistence

The Carpathian Mountains support the largest extant populations of the brown bear in Europe (excluding Russia, Zedrosser et al. 2001). Consistent with this, the most important predictor of bear activity was proximity to the Carpathians. Higher bear activity was also found in rugged areas and near large blocks of forest, which is most likely related to better shelter and den sites in rough terrain, and potentially a wider variety of food resources (Nellemann et al. 2007; May et al. 2008; Güthlin et al. 2011). Local connectivity between forest patches, however, was unrelated to bear activity, suggesting that forest patches are well-connected throughout the region. Indeed, forest cover in our study area was close to the presumed 30 % threshold below which the effects of habitat loss may be exacerbated by isolation effects (Andrén 1994). Alternatively, local connectivity may be related to shrub cover which was not accounted for in our analyses, and this may partly explain the lack of statistical significance of local connectivity. In contrast to other studies (Posillico et al. 2004; Preatoni et al. 2005; Nellemann et al. 2007), bears were not affected by distance to human settlements. This may be because, at present, vehicle traffic does not increase strongly near settlements, and major agricultural machinery is also relatively uncommon, although agricultural intensification is likely in the future (Mikulcak et al. 2013). In addition, human presence *per se* may not deter bears because local people are not a major threat, given that bears are protected by law and hunting is prohibited. Finally, retaliation killing is probably uncommon in the study area, though better knowledge on this would be useful to more fully understand human-bear coexistence.

Interestingly, observed bear activity was not related to the frequency of attacks on sheep, but was negatively related to perceived damage to orchards and fields. Unlike sheep, fields and orchards are often guarded less carefully and most lack (effective) fences, suggesting that the livestock husbandry techniques used by shepherds may effectively prevent bear attacks. The use of guarding dogs and nightly confinement appears to reduce livestock attacks worldwide (Gehring et al. 2010; Rigg et al. 2011). Indeed, most of the reported bear attacks occurred on the pasture, and not in the well-guarded sheepfolds. Similar to observations in the Romanian mountains (Mertens and Schneider 2005), we found no relationship between the frequency of bear attacks and the number of sheep per dog. This is surprising, given the shepherds' emphasis on the importance of good guarding dogs. The lack of a relationship between attacks and the number of dogs could arise from: (i) the use of an appropriately large number of dogs by the majority of shepherds; (ii) our sample size being too small to detect a significant relationship; or (iii) our model for bear activity only explaining bear distribution in spring and summer, while bear attacks occurred year-round.

The lack of a relationship between bear activity and frequency of attacks further suggests that local conditions may be more important than actual carnivore densities in determining rates of attack (Kaczensky 1999; Rigg et al. 2011). This supports the notion that human-carnivore coexistence is possible, but knowledge of local conditions is necessary for effective, proactive conflict management. In our case, relevant local conditions may include the quality of guarding dogs and vigilance of shepherds, but also the prevalence of woody vegetation in pastures. Because local conditions can, in principle, be managed, our findings indicate opportunities for proactive conflict mitigation.

Public attitudes towards carnivores are typically most positive in areas without carnivores (Kellert et al. 1996), or where people and carnivores have coexisted for a long time (Boitani 1995). The long-term coexistence of bears and shepherds may have led to the acceptance of occasional livestock loss by some shepherds, however, as observed elsewhere (Kaczensky et al. 2004), shepherds that were affected by bears were also less tolerant to livestock loss. Tolerance could be further enhanced via compensation measures (Dickman et al. 2011) or the availability of lethal measures to local authorities to take care of occasional 'problem bears' (Lescureux and Linnell 2010). At present, coexistence was not artificially upheld by economic incentives, suggesting that in the absence of effective payment schemes, relatively cheap traditional, non-lethal methods can help facilitate coexistence. Thus, the key to successful human-bear coexistence could lie in limiting livestock losses to levels that are acceptable to a large proportion of the shepherd community, while also establishing an understanding between local authorities and people that authorities will increase efforts to prevent damage by bears. Developing such an understanding might be a difficult challenge in Romania, where trust between local people and authorities is low due to historical suppression, corruption and poverty (Hartel et al. 2014).

Local management priorities

To facilitate the ongoing coexistence of bears and humans in southern Transylvania, conservation measures should aim to maintain or improve: (i) connectivity between the foothills and the Carpathian Mountains; (ii) availability of large forest blocks; and (iii) acceptance of occasional losses to bears within the rural population. Maintaining regional connectivity and large forest blocks could be challenging because of increasing pressure on forests from illegal logging activities (Knorn et al. 2012), and because of new major highways planned to cut through the study area. Highways can negatively impact bear populations by causing habitat fragmentation and increasing the risk of collisions with vehicles (Kaczensky et al. 2003; Karamanlidis et al. 2012). Wildlife crossing structures could partly counteract these impacts, but research is needed to identify suitable locations for such structures (Clevenger and Waltho 2001). Furthermore, there is the danger that conservation efforts will focus on the protected Natura 2000 area, which does not extend all the way to the Carpathian Mountains, and does not capture all of the most important areas for the brown bear (Fig. 1c). While we recognize that additional protected Natura 2000 areas exist beyond our focal Natura 2000 area, major gaps in connectivity to the Carpathians remain.

Compensation payments are often used to increase tolerance levels of people negatively affected by carnivores (Dickman et al. 2011). In Romania, damage caused by protected species should be compensated through the central public authority for environmental protection (law 407/2006). Yet, most shepherds indicated they found compensation payments important but did not know about the existence of the compensation scheme. Many officials dealing with compensation thought the scheme was still relatively unknown, but overall, despite a complicated application process (Mertens and Promberger 2001), they believed that the scheme was readily accessible. This suggests that the compensation payments need to be more transparent and accessible to local people. Importantly, monetary compensation is not the only plausible policy option. Proactive payments for preventive measures may be more successful in improving conditions for coexistence (Swenson and Andrén 2005), and subsidizing electric fences along forest edges and around sheepfolds could help reduce sheep predation. Moreover, given widespread mistrust in authorities, bottom-up compensation payments organized by local groups could be more effective. For example, contributions to a local livestock insurance program (Mishra et al. 2003) or replacements of lost livestock from a communal compensation herd may be worth considering.

Limitations

The proportion of destroyed anthills to total anthills turned out to be a low-cost and pragmatic, but evidently useful, index of bear activity. However, this metric has several limitations. First, bear use of anthills in a given pasture might be influenced by overall levels of anthill availability and by other pasture characteristics. Our large sample size and stratification of transects should minimize systematic biases caused by general pasture characteristics, and the availability of anthills was accounted for in the model. Therefore, we are confident that our indicator measured actual bear activity rather than bear exploitation of anthills. Second, ant larvae are a seasonal food source, and thus, other variables may explain bear distribution patterns in other seasons. The seasonal nature of our surveys could partly explain the lack of a correlation between bear activity and self-reported attacks of bears on sheep, which occurred year round. That said, we did find significant correlations between bear activity and perceived damage to orchards and fields, suggesting a certain level of cross-validation of methods—by definition, it is highly unlikely that a statistical significant correlation between our activity index and perceived damage would have arisen by chance if there was in fact no relationship between these two variables. Third, our data on damage caused by bears was based on the perceptions of shepherds and local people, and was not validated by official damage reports. Interview data therefore should be interpreted with care. While these limitations should be kept in mind, we do not believe they fundamentally undermine the validity of our overall findings.

Future research and conclusion

Although coexistence of humans and carnivores is a socially desired goal in many landscapes around the world, most research takes place in protected areas with few people (Ghosal et al. 2013). Our interdisciplinary approach demonstrated the usefulness of combining ecological and social data to highlight conservation priorities in carnivore conservation. Arguably, framing carnivore conservation in a social-ecological context would also be useful in other human-dominated landscapes.

Our study indicates that coexistence of humans and carnivores is possible, even without direct economic incentives. Continuous coexistence with large carnivores appears to foster the development of management tools and attitudes that effectively reduce conflicts. Nevertheless, this shared history of relationships between humans and bears has been eroded in many regions worldwide. Thus, a key challenge for settings with a broken history of human-carnivore co-occurrence is to reinstate both practices and attitudes that facilitate coexistence. While a history of continuous coexistence cannot be re-created in places where carnivores have been extirpated, it is noteworthy that in areas were carnivores are slowly re-colonizing landscapes, initially negative attitudes can become more neutral as people once again become accustomed to living with carnivores (Majić and Bath 2010).

Although our study indicates that coexistence is possible, the functional mechanisms facilitating this remain poorly understood. One recently discussed mechanism is that of behavioural adjustment on behalf of the carnivores, who may adjust temporal activity patterns (Martin et al. 2010; Carter et al. 2012b). Our study suggests that "behavioural" mechanisms on behalf of people—that is, social mechanisms—also deserve more attention. Social mechanisms underpinning human-carnivore coexistence are acknowledged by several authors (e.g. Carter et al. 2012a; Athreya et al. 2013), but still remain poorly accounted for in many studies on human-carnivore conflicts, as well as in many mitigation programs (Dickman 2010; Glikman and Frank 2011). Future research should investigate the drivers of human attitudes towards carnivores, which may vary substantially in relation to the behaviour and ecology of the species in question, the prevalence of traditional ecological knowledge, dominant cultural values and beliefs, differences in social equity and distribution of carnivore impacts, and political context (Dickman 2010; Lescureux and Linnell 2010).

Acknowledgments We thank Z. Aczél-Fridrich, R. Bigonneau, M. Brix, K. Delille, L. A. Dénes, A. Fletcher, T. Fülöp, F. Helissandre, C. Klein, I. Kósa, A. Krieg, C. Moga, N. Moraru, M. Roellig, B. Scheele, J. Schultner, A. Szapanyos, L. Teixeira, and J. Tinnemans for field efforts and data entry. We thank the shepherds and local people, and O. Bodin for advice on connectivity analyses. We thank two anonymous reviewers and the handling editor for constructive suggestions on a previous draft of this manuscript. The project was funded by a grant of the International Association for Bear Research and Management to ID and a SofjaKovalevskaja Award by the Alexander von Humboldt Foundation to JF. Part of the data collection was supported by the European Regional Development Fund (ERDF) through Sectorial Operational Plan—Environment (POS Mediu) under the project "For nature and local communities—the basis for a Natura 2000 integrated management in the Hârtibaciu—Târnava Mare—Olt area".

References

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. Oikos 71(3):355–366

Angelstam P, Boresjö-Bronge L, Mikusiński G, Sporrong U, Wästfelt A (2003) Assessing village authenticity with satellite images: a method to identify intact cultural landscapes in Europe. AMBIO 32(8):594–604

Athreya V, Odden M, Linnell JDC, Krishnaswamy J, Karanth U (2013) Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLoS One 8(3):e57872. doi:10.1371/journal.pone.0057872

Banerjee K, Jhala YV, Chauhan KS, Dave CV (2013) Living with lions: the economics of coexistence in the Gir forests, India. PLoS One 8(1):e49457. doi:10.1371/journal.pone.0049457

Barea-Azcon JM, Virgos E, Ballesteros-Duperon E, Moleon M, Chirosa M (2007) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodivers Conserv 16(4):1213–1230

Boitani L (1995) Ecological and cultural diversities in the evolution of wolf-human relationships. In: Carbyn LN, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Alberta, pp 3–11

Breitenmoser U (1998) Large predators in the Alps: the fall and rise of man's competitors. Biol Conserv 83(3):279–289

Carter NH, Riley SJ, Liu J (2012a) Utility of a psychological framework for carnivore conservation. Oryx 46(04):525–535

Carter NH, Shrestha BK, Karki JB, Pradhan NMB, Liu J (2012b) Coexistence between wildlife and humans at fine spatial scales. Proc Natl Acad Sci 109(38):15360–15365

Ciarniello LM, Boyce MS, Heard DC, Seip DR (2007) Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. J Wildl Manag 71(5):1446–1457

Clevenger AP, Waltho N (2001) Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conserv Biol 14(1):47–56

Core Team R (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Dahle B, Sørensen OJ, Wedul EH, Swenson JE, Sandegren F (1998) The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. Wildl Biol 4(3):147–158

Dickman AJ (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Anim Conserv 13(5):458–466

Dickman AJ, Macdonald EA, Macdonald DW (2011) A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. Proc Natl Acad Sci USA 108(34):13937–13944

Enserink M, Vogel G (2006) Wildlife conservation—the carnivore comeback. Science 314(5800):746–749

Estes JA, Terborgh J, Brashares JS et al (2011) Trophic downgrading of planet earth. Science 333(6040):301–306

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24(1):38–49

Gehring TM, VerCauteren KC, Landry J-M (2010) Livestock protection dogs in the 21st century: is an ancient tool relevant to modern conservation challenges? Bioscience 60(4):299–308

Ghosal S, Athreya V, Linnell JC, Vedeld P (2013) An ontological crisis? A review of large felid conservation in India. Biodivers Conserv 22(11):2665–2681

Glikman JA, Frank B (2011) Human dimensions of wildlife in Europe: the Italian way. Hum Dimens Wildl 16(5):368–377

Güthlin D, Knauer F, Kneib T et al (2011) Estimating habitat suitability and potential population size for brown bears in the Eastern Alps. Biol Conserv 144(5):1733–1741

Hartel T, Fischer J, Câmpeanu C, Milcu AI, Hanspach J, Fazey I (2014) The importance of ecosystem services for rural inhabitants in a changing cultural landscape in Romania. Ecol Soc 19(2):42

Holmern T, Nyahongo J, Røskaft E (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol Conserv 135(4):518–526

Kaczensky P (1999) Large carnivore depredation on livestock in Europe. Ursus 11:59–71

Kaczensky P, Knauer F, Krze B, Jonozovic M, Adamic M, Gossow H (2003) The impact of high speed, high volume traffic axes on brown bears in Slovenia. Biol Conserv 111(2):191–204

Kaczensky P, Blazic M, Gossow H (2004) Public attitudes towards brown bears (*Ursus arctos*) in Slovenia. Biol Conserv 118(5):661–674

Karamanlidis AA, Straka M, Drosopoulou E et al (2012) Genetic diversity, structure, and size of an endangered brown bear population threatened by highway construction in the Pindos Mountains, Greece. Eur J Wildl Res 58(3):511–522

Karanth KK, Nichols JD, Karanth KU, Hines JE, Christensen NL (2010) The shrinking ark: patterns of large mammal extinctions in India. Proc R Soc B 277(1690):1971–1979

Kellert SR, Black M, Rush CR, Bath AJ (1996) Human culture and large carnivore conservation in North America. Conserv Biol 10(4):977–990

Knorn J, Kuemmerle T, Radeloff VC et al (2012) Forest restitution and protected area effectiveness in post-socialist Romania. Biol Conserv 146(1):204–212

Lescureux N, Linnell JD (2010) Knowledge and perceptions of Macedonian hunters and herders: the influence of species specific ecology of bears, wolves, and lynx. Hum Ecol 38(3):389–399

Linnell JDC, Swenson JE, Anderson R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Anim Conserv 4(4):345–349

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS (2007) Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. J Wildl Manag 71(6):2018–2025

Maclennan SD, Groom RJ, Macdonald DW, Frank LG (2009) Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biol Conserv 142(11):2419–2427

Majić A, Bath AJ (2010) Changes in attitudes toward wolves in Croatia. Biol Conserv 143(1):255–260

Martin JMJ, Basille MBM, Bram Van Moorter B et al (2010) Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). Can J Zool 88(9):875–883

May R, Van Dijk J, Wabakken P et al (2008) Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. J Appl Ecol 45(5):1382–1391

Mertens A, Promberger C (2001) Economic aspects of large carnivore-livestock conflicts in Romania. Ursus 12:173–180

Mertens A, Schneider H (2005) What is wrong with Romanian livestock guarding dogs? A discussion. Carniv Damage Prev News 9:9–14

Mikulcak F, Newig J, Milcu AI, Hartel T, Fischer J (2013) Integrating rural development and biodiversity conservation in Central Romania. Environ Conserv 40(1):1–9

Mishra C, Allen P, McCarthy T, Madhusudan M, Bayarjargal A, Prins HH (2003) The role of incentive programs in conserving the snow leopard. Conserv Biol 17(6):1512–1520

Munro RHM, Nielsen S, Price M, Stenhouse G, Boyce M (2006) Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. J Mamm 87(6):1112–1121

Nellemann C, Støen O-G, Kindberg J et al (2007) Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biol Conserv 138(1–2):157–165

Packer C, Loveridge A, Canney S et al (2013) Conserving large carnivores: dollars and fence. Ecol Lett 16(5):635–641

Posillico M, Meriggi A, Pagnin E, Lovari S, Russo L (2004) A habitat model for brown bear conservation and land use planning in the central Apennines. Biol Conserv 118(2):141–150

Preatoni D, Mustoni A, Martinoli A et al (2005) Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. Acta Oecologica 28(3):189–197

Ray JC (2005) Large carnivores and the conservation of biodiversity. Island Press, Washington DC

Redpath SM, Young J, Evely A et al (2012) Understanding and managing conservation conflicts. Trends Ecol Evol 28(2):100–109

Rigg R, Findo S, Wechselberger M, Gorman ML, Sillero-Zubiri C, Macdonald DW (2011) Mitigating carnivore-livestock conflict in Europe: lessons from Slovakia. Oryx 45(2):272–280

Ripple WJ, Estes JA, Beschta RL et al (2014) Status and ecological effects of the world's largest carnivores. Science 343(6167):1241484

Salvatori V, Okarma H, Ionescu O, Dovhanych Y, Find'o S, Boitani L (2002) Hunting legislation in the Carpathian Mountains: implications for the conservation and management of large carnivores. Wildl Biol 8(1):3–10

Schuette P, Creel S, Christianson D (2013) Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. Biol Conserv 157:148–154

Swenson J, Andrén H (2005) A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife, conflict or co-existence?. Cambridge University Press, Cambridge, pp 323–339

Swenson JE, Jansson A, Riig R, Sandegren F (1999) Bears and ants: myrmecophagy by brown bears in central Scandinavia. Can J Zool 77(4):551–561

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv Biol 17(6):1491–1499

Treves A, Wallace RB, Naughton-Treves L, Morales A (2006) Co-managing human-wildlife conflicts: a review. Hum Dimens Wildl 11(6):383–396

Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. Anim Conserv 3(02):165–173

Woodroffe R, Thirgood S, Rabinowitz A (2005) People and wildlife, conflict or co-existence?. Cambridge University Press, Cambridge

Zedrosser A, Dahle B, Swenson JE, Gerstl N (2001) Status and management of the brown bear in Europe. Ursus 12:9–20