



Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps



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ABSTRACT

Large carnivores are declining worldwide and few examples of successful reintroductions exist, because of their large home-ranges, low reproductive rates, and penchant for human–wildlife conflict that is the main cause of their decline. Moreover, few studies assess whether habitat suitability predicted before reintroduction, a critical evaluation step, matches post-reintroduction habitat selection. We examined habitat-related factors contributing to a successful brown bear (*Ursus arctos*) reintroduction in central Europe. Starting in 1999, 10 brown bears were translocated from Slovenia to Trentino in the Italian Alps, and this population has since grown by >10%/year. First, we estimated multi-scale resource selection functions (RSF) with GPS collar data and validated models with k-folds cross validation and external VHF data. Then, we used Kappa-statistics to compare our population-scale RSF with a habitat suitability model (HSM) developed to predict potential habitat before reintroduction. Lastly, we employed least-cost path (LCP) analyses integrating our within home-range scale RSF to define movement paths. Overall, the HSM predicted post-reintroduction habitat selection well in many areas, but bears used orchards and shrubs more, and mixed/conifer forests and pastures less than expected prior to reintroduction. Finally, we identified road crossings of predicted paths between preferred habitat patches. We found two potential crossings in the Adige Valley, likely the biggest constraint for the study population to expand eastward and impeding dispersal to/from the closest bear population (Dinaric–Pindos population). Increasing awareness for key brown bear habitats and corridors, especially in potential ecological traps within cultural landscapes, will be necessary for large carnivore conservation.

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1. Introduction

Large mammalian carnivores are declining worldwide due to their high spatial requirements, low fecundity and conflict with humans (Gittleman et al., 2001; Treves and Karanth, 2003; Woodroffe, 2001). However, in some areas carnivores have increased in abundance and distribution in the last few decades in contrast to the overall worldwide trend of carnivore declines (Ripple et al., 2014). Notably, carnivore recovery in Europe differs from many other parts of the globe, such as North America,

because of much higher human population densities accompanied by increased habitat fragmentation and alteration (Chapron et al., 2014; Zedrosser et al., 2011). Thus, large carnivore conservation must be achieved in Europe where few areas can be considered wilderness (Linnell et al., 2001; Zedrosser et al., 2011). Despite this challenge, carnivores have been making a comeback, largely due to re-colonization of historical ranges following the decline of traditional agricultural activities, abandonment of mountain areas by humans, forest restoration, ungulate recolonization in the Alps and change of conservation policy in several parts of Europe (Breitenmoser, 1998). Large carnivore recovery in Europe has also been actively supported by reintroduction projects (Breitenmoser, 1998; Enserink and Vogel, 2006; Trouwborst, 2010). But, success in carnivore recovery also increases conflict between carnivores and humans (Linnell and Boitani, 2012). Overall, carnivore recovery in human-dominated landscapes poses

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one of the major challenges for conservation (Dorresteijn et al., 2014; Falcucci et al., 2009; Hayward and Somers, 2009; Stoskopf, 2012) and only few active recovery and reintroduction efforts have been successful for large carnivores, especially in Europe (Linnell et al., 2009; Stahl et al., 2001; Zedrosser et al., 2001).

Large carnivore reintroductions are often challenging because of the difficulty in assessing habitat quality and human-carnivore conflict areas especially in extirpated populations (Gusset, 2009; Hayward and Somers, 2009; Stoskopf, 2012). Therefore, a-priori science to support recovery is critical, including potential population size, distribution of habitat including prey availability, human-wildlife conflict, and population genetics (Linnell et al., 2008; Stoskopf, 2012). Perhaps the first critical step in recovery is to understand the distribution and amount of suitable carnivore habitat using predictive spatial models (Boitani et al., 1999; Guisan and Zimmermann, 2000). This process helps ensure that the initial spatial factors for carnivore declines have been identified and mitigated (Hayward and Somers, 2009). For example, if there is insufficient high suitability habitat or potentially high habitat quality is reduced due to an increased probability of human-carnivore conflicts (e.g. ecological traps; Battin, 2004) or high degree of fragmentation, recovery will be unsuccessful. Predictive habitat modeling has been used successfully to identify potential habitat for carnivores including Amur tigers (*Panthera tigris altaica*) in China (Hebblewhite et al., 2012), grizzly bears (*Ursus arctos horribilis*) in the Northern United States (Boyce and Waller, 2003), lynx (*Lynx lynx*) in central Europe (Schadt et al., 2002; Zimmermann and Breitenmoser, 2007), or identify movement corridors for large carnivore conservation (Chetkiewicz et al., 2006). Despite numerous examples of a-priori predictive modeling of potential carnivore habitat, however, there have been very few studies testing whether a-priori predictions succeeded and contributed to successful carnivore recovery following active recovery efforts.

Recovery of large carnivores in human dominated landscapes is particularly challenging, and yet will become increasingly important in the future with ongoing global carnivore declines and human population growth and expansion (Woodroffe, 2000). Western and central Europe are the most depauperated global regions for large carnivores (Dalerum et al., 2009; Ripple et al., 2014) and also the most fragmented by human landscape use (Crooks et al., 2011). The European brown bear (*U. a. arctos*) has been extirpated across most of western Europe and large parts of central Europe due to habitat loss and human persecution since the 1600s and 1700s (Swenson et al., 2000; Zedrosser et al., 2001). There have been several unsuccessful brown bear reintroductions in Europe, including 11 brown bears from Belorussia to Poland in 1938, individuals from zoo populations to Italy in the 1950s and 1960s (Clark et al., 2002), and translocations from Slovenia to Austria in the 1980s and 1990s (Güthlin et al., 2011). Among the reasons for these failures may be insufficient high quality habitat or low human tolerance, including high rates of human persecution. Another reason is that many previous reintroductions occurred in isolation, without consideration of a broader multi-scale concept for carnivore populations in Europe. More recently, the Large Carnivore Initiative for Europe (LCIE) recommended a hierarchical recovery strategy including local scale recovery of population segments that should interact to form subpopulations. However, individual subpopulations will often not be viable in isolation (Boitani et al., 1999; Kaczensky et al., 2012; Linnell et al., 2008), and also individual countries could not be able to sustain viable brown bear populations alone (Linnell et al., 2008). Consequently, several large recovery areas were identified with the ultimate goal to recover functional ecological networks of meta-populations including the Dinaric-Pindos and Alpine (Italy, Switzerland, Austria, Slovenia) population recovery areas for brown bears (Kaczensky et al., 2012). Once stable subpopulations

have been successfully recovered through reintroduction or natural dispersal, promoting subsequent expansion across regional and national borders will be key to establishment of a viable meta-population network (Boitani et al., 1999). The reintroduction of brown bears to the Autonomous Province of Trento (herein also Trentino), Italy (Duprè et al., 2000), is one potential example of successful brown bear recovery in central Europe. Between 1999 and 2002 10 brown bears from Slovenia were reintroduced to the Parco Naturale Adamello Brenta in Trentino to augment the three remaining bears that were non-reproductive (i.e., biologically extirpated; Mustoni et al., 2003). After one decade, the population reached a minimum of 40–49 bears, representing a growth rate of >10%, and expanded their distribution (Groff et al., 2013).

Establishment of viable populations depends on abundant, high quality habitat and also habitat connectivity to ensure movement between these habitats at different scales (Baguette et al., 2013). For large carnivores, habitat includes both forage as well as areas of reduced human activity with decreased potential for conflict and human caused mortality (Falcucci et al., 2009; Mitchell and Hebblewhite, 2012). High quality habitat supports high reproductive rates, but may pose increased risk of human-caused mortality if human-activity is also high in high quality habitat, creating attractive sinks (i.e. ecological traps; Battin, 2004). While there have been some human-caused mortalities amongst the reintroduced Trentino bear population, its high growth rate suggests that initial assessments of the sufficiency of high quality habitats were realistic. Testing whether the pre-reintroduction brown bear habitat model matched post-bear habitat selection is therefore an important question not only for this specific case study, but more generally, to support large carnivore recovery elsewhere. Next, carnivore recovery also depends on within population connectivity (e.g., among population segments; local scale) and between populations (e.g. across landscapes), especially in human-dominated landscapes (Crooks and Sanjayan 2006; Linnell et al., 2008). Despite the potential reintroduction success, expansion of this Trentino bear population has been limited to local scales and expansion to other parts of the prospective Alpine population recovery area has so far been unsuccessful. Thus, habitat connectivity remains a major concern for brown bear population persistence (Kaczensky et al., 2012; Groff et al., 2013). At larger scales connectivity will be important under the LCIE's recommended strategy to recover the European Alpine population by connecting critical areas of suitable environments through movement corridors within the human-altered matrix (Boitani et al., 1999; Kaczensky et al., 2012; Linnell et al., 2008). However, ensuring connectivity at the smallest local scale between current individual bear ranges and adjacent areas is a key prerequisite to larger-scale connectivity and expansion (Groff et al., 2013). Identifying wildlife corridors can be a difficult task, especially in the absence of sufficient animal distribution data (Chetkiewicz et al., 2006). Therefore, designation of corridors often follows simplistic assumptions of habitat suitability with little species-specific information. As a result corridors frequently fall short of their conservation promise (Chetkiewicz et al., 2006).

In this paper we aim to contribute to understanding the factors influencing this potentially successful carnivore reintroduction in Trentino by evaluating the role of habitat, both in terms of predicting potential habitat for reintroduced brown bears (the past) and also of potential habitat connectivity within this population and beyond at the local scale (the future). We focus on estimating the realized habitat selection by the recovering brown bear population using Global Positioning System (GPS) data to 1) evaluate if the current habitat selection coincides with the predicted population-scale (Meyer and Thuiller, 2006) habitat suitability prior to reintroduction, and 2) evaluate structural habitat connectivity and potential movement paths between core habitat patches

within the existing population and also for potential future expansion within Trentino. We use a resource selection function (RSF; Boyce and McDonald, 1999; Manly et al., 2002) approach to estimate resource selection by reintroduced bears and combine this RSF with least-cost path (LCP) analyses (Chetkiewicz et al., 2006) to identify and map potential movement paths both within and outside of the current range of the brown bear population in Trentino. We conclude with conservation recommendations for this Trentino population, which may be applicable to other carnivore populations in human-dominated and fragmented landscapes.

2. Materials and methods

2.1. Study area

Our study area in the central European Alps was defined by the border of the Autonomous Province of Trento in north-eastern Italy, covering approximately 6200 km². Elevations range from 65 m to >3000 m, but much of the study area is characterized by rugged, mountainous terrain. Approximately 60% of the study area is above >1000 m of altitude and only 12% below 400 m. The climate is variable ranging from mediterranean around Lake Garda to continental in the alpine river valleys to strongly alpine climates above treeline. Forests cover 65% of Trentino. The human population density is variable but averages 86/km² and the road network is denser in the south and east of the province. Most of the infrastructure (roads, railroads and towns) are concentrated at the bottom of the valleys. Especially the Adige Valley is a large basin that is divided by the motorway A22 and also contains the biggest towns. With its dense infrastructure the Adige Valley effectively divides the study area into two sections, representing the biggest obstacle to habitat connectivity for several mammal populations. The bear reintroduction area included submontane, montane and subalpine vegetation communities (Preatoni et al., 2005). The vegetation composition ranges from mixed deciduous vegetation of mainly common beech (*Fagus sylvatica*) mixed with European larch (*Larix decidua*) and pine (*Pinus spp.*) to subalpine forest communities composed of pine and spruce (*Picea spp.*). Above treeline (at about 1800 m) Krummholz stands are dominated by mountain pine (*Pinus mugo*) and open habitats comprised of alpine herbaceous species. Ungulate species inhabiting the region include (in order of abundance): roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), red deer (*Cervus elephus*), mouflon (*Ovis orientalis*), ibex (*Capra ibex*) and wild boar (*Sus scrofa*). The predator community is characterized by foxes (*Vulpes vulpes*) and reintroduced brown bears at low densities. Wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*) and the golden jackal (*Canis aureus*) frequent the area rarely (Groff et al., 2013).

2.2. Potential habitat modeling prior to brown bear reintroduction

A habitat suitability model (HSM) was developed as part of the feasibility study prior to reintroduction. The HSM was built as a function of environmental and anthropic covariates to predict habitat suitability at the population scale in the release area and the adjacent region (Duprè et al., 2000; Mustoni et al., 2003). Given the very small relict population at that time and the corresponding challenge of developing a robust habitat model (bears were not radiocollared before reintroduction), the authors developed the HSM as a sequence of several steps. A detailed description of the model can be found in Duprè et al. (2000); herein we provide a brief summary. The original model covered a larger extent than we consider here (e.g., parts of the adjacent provinces of Lombardy and South Tyrol). First, the authors broadly classified

the study area as 'suitable', 'intermediate suitable' or 'not suitable' (e.g., settlements, roads, agricultural areas including orchards, rocks and permanent snow) for bears based on landcover categories (CORINE Land Cover level III; Commission of the European Communities 1993) with information derived from literature at a resolution of 0.25 km² cells (landcover-based literature/expert model). Next, Duprè et al. (2000) summarized information on covariates related to human presence (i.e., distribution of conflict areas such as beehives, livestock, forest harvesting, road densities, population density, touristic pressure, etc.) within the same 0.25 km² grid. Additionally, signs of bear presence (e.g., sightings, feces, tracks; $n = 1\ 777$) from 1977 to 1996 were used to identify 106 cells of the 25 ha grid as 'bear presence' cells. In contrast, 106 cells without bear signs were randomly chosen. The authors then analyzed the presence of bear signs using logistic regression as a function of the aforementioned anthropogenic covariates. The resulting model (anthropogenic logistic regression model) was extrapolated over the remainder of the study area to identify areas with different levels of bear suitability in relation to anthropogenic variables. In particular, areas with $P \leq 0.5$ were considered unsuitable and areas with $P > 0.5$ were considered suitable. Finally, the baseline landcover-based model and the anthropogenic model were combined, resulting in three classification categories: (1) areas suitable for bears which included suitable/intermediate suitable landcover types according to the landcover model and $P > 0.5$ according to the anthropogenic model, (2) intermediate suitability including suitable/intermediate suitable landcover categories, but excess of human presence ($P \leq 0.5$ according to the anthropogenic model), and (3) areas that were considered unsuitable in the landcover-based model. Thus, the model by Duprè et al. (2000) represents a combination of expert- and literature-derived information as well as empirical data analyses.

2.3. Post-reintroduction realized habitat selection

2.3.1. Brown bear location data

We modeled realized resource selection by brown bears post reintroduction using data from 11 radio-collared animals. In particular, we used data from six bears collared in Trentino with Global Positioning System (GPS) collars (Vectronic GPS-GSM collars, Vectronic Aerospace GmbH, Berlin, Germany) between 2006 and 2012 to estimate RSFs. Of these six bears, one was a disperser from Slovenia to eastern Trentino (one male), two were reintroduced founders (two females), and three were born in the study area from founders (one female and two males). Additionally, we used data from five bears that were all reintroduced (founders; three females and two males) with Very High Frequency (VHF; MOD 505 VHF collar, Telonics) radio collars collected between 1999 and 2003 to validate the RSF model. To avoid potential effects of reintroduction on resource selection, such as exploratory movements, we excluded data before the formation of a home-range (around 6 months, usually after first denning season). VHF collared bears were triangulated from the ground twice daily (see Preatoni et al., 2005). All of the six GPS collared bears were initially radio collared because they were 'conflict' bears, that is, they used or damaged human property or were perceived as threat. The VHF bears represented 'non-conflict bears', but mostly reintroduced founders. We discuss study design implications of this difference below. The GPS-collared bears were captured either via free range darting, Aldrich snares or culvert traps (Groff et al., 2013) upon approved capture protocols (2003-DPR 357/97). For more details about the capture and reintroduction, see Mustoni et al. (2003) and Preatoni et al. (2005). GPS collars collected positions at different intervals ranging from 10 min to 1 h, which we re-sampled to a consistent 2-hour relocation schedule. The average duration bears were monitored was 397 days for both VHF and GPS collar data.

GPS collar fix-rates were high, averaging >90%, obviating the need to correct for habitat induced bias (Frair et al., 2004). We conducted RSF analyses based on annual data, but removed locations that were taken during hibernation at den sites from December to February (VHF and GPS collar data; Preatoni et al., 2005).

2.3.2. Resource selection functions at the population and within home-range scales

Resource selection is a multi-scale process (Johnson, 1980; Meyer and Thuiller, 2006) that directly links to animal movements (Nathan et al., 2008) and hence connectivity. Based on Meyer and Thuiller's (2006) update to Johnson's (1980) proposed scales of habitat selection, we estimated brown bear realized resource selection at the scale of the current Trentino population range (herein also referred to as first-order; similar to Johnson's second-order scale) and the within home-range scale (i.e., third-order selection) using a used vs. available design (Manly et al., 2002). To estimate availability at the population scale, we first used the Home Range Tools Extension (HRT; Rodgers et al., 2007) to generate annual individual 90% fixed kernel home-ranges, which we later combined to one range (sampling without replacement in case of overlapping home-ranges). We used a smoothing factor of 0.7 multiplied by the reference smoothing factor (href, Worton, 1989) for each bear, which has been suggested for large sample sizes and short-interval GPS data (Bertrand et al., 1996; Hemson et al., 2005). We also evaluated home-ranges with different smoothing factors visually to select the most biologically sensible estimate (Berger and Gese, 2007). To develop RSFs at the population scale, we treated combined individual home-ranges as used and the remainder of Trentino as available habitat and sampled both regions at a density of 50 random points/km². We then estimated the population scale RSF using logistic regression (Hosmer and Lemeshow, 2000) comparing resources of random used and random available locations to estimate the coefficients for the exponential approximation to the logistic discriminant function, which yields a relative probability of selection (Johnson et al., 2006; Lele et al., 2013).

To estimate within home-range resource selection we sampled availability within each individual bear's annual home-range (Manly et al., 2002). Within each available polygon we drew a set of random points equal in number to the sample of GPS-based used locations. We evaluated within home-range selection using Generalized linear mixed models (GLMM; Bolker et al., 2009) to account for unbalanced sample sizes between animals and non-independence of GPS locations (Gillies et al., 2006). Thus, we partitioned the total variation into a subject-specific random intercept ($\beta_0 + \gamma_{0j}$) for each individual bear (Bolker et al., 2009; Gillies et al., 2006).

We characterized brown bear habitat using environmental variables as digital maps in a geographic information system (GIS) environment, such as topography, landcover, and human disturbance similar to the original HSM model (Table A.1). We used a digital terrain model (DTM; Table A.1) to estimate elevation (m) at a 10 m resolution from which we also estimated slope (degrees) and aspect (transformed to N, E, W, S and flat) indices. Further, vector layers of linear features were used to characterize distances to human linear features (m; e.g. distances to roads; Table A.1). We subsumed the CORINE Land Cover 2006 classification into 11 categories considered to be relevant for the ecology of bears in our study area (Table A.1). Duprè et al. (2000) used very detailed anthropogenic data (e.g. densities of livestock) that were not available to build these RSFs.

Initially, all environmental variables were screened for collinearity using the Pearson's correlation coefficient threshold of $|r| > 0.6$ (Hosmer and Lemeshow, 2000). For collinear environmental variables, we retained the variable with the lower log-

likelihood, highest coefficient of determination (pseudo R^2) and lowest P -values (Boyce et al., 2002). We first conducted univariate logistic regression analysis, using a $P < 0.25$ on a Wald χ^2 -statistic as a cut-off for the inclusion in model building. To test whether coefficients were nonlinear we explored environmental variables using semi-parametric Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990), and quadratic functions (Hosmer and Lemeshow, 2000). Retained, i.e. biologically relevant, non-confounded, uncorrelated and ecologically plausible, covariates entered the pluralistic multivariate logistic regression modeling process to build a small subset of biologically sensible candidate models. We selected the top model using Akaike's information criterion (Δ AIC; Burnham and Anderson, 2002). All statistical analyses were carried out in STATA 11.0 (StataCorp LP, College Station, TX) and all GIS analyses using ArcGIS 9.3 (ESRI Redlands, CA, USA).

We mapped the per-pixel predicted values for both habitat selection models across Trentino at a 25 m resolution using the exponential function (Manly et al., 2002). In used-available designs the intercepts are meaningless and are therefore commonly dropped although they still affect the fixed effects coefficients (Gillies et al., 2006). We then used a linear stretch to re-scale RSF predicted values between 0 and 1 (Johnson et al., 2006). We confined resource values using the minimum and maximum values sampled for each model to avoid extrapolating predictions beyond the extent of sampled data. Both predictive maps of realized resource selection were initially classified into 10 categorical bins using the percentiles of predicted values for each scale of availability (Boyce et al., 2002).

To assess the predictive capabilities of RSF models, we conducted 5-fold cross validation (internal validation) using the Spearman rank (r_s) test statistic to compare the frequency of the predicted values of the test data set within one of 10 bins to the bin's respective RSF score rank following Boyce et al. (2002). A more robust form of validation is, however, testing the ability of models to predict external data that were not used in the model development (Fielding and Bell, 1997). To understand if habitat selection from conflict bears (GPS data used to build the RSF models) differed significantly from habitat selection of non-conflict bears, we used bear VHF location data that were completely withheld from the model training data set. We sampled use and availability for VHF data in the same manner as for GPS data and intersected used and available locations with the spatial extrapolations of the population- and within home-range-scale resource selection models. We again used Spearman rank correlations of the relative frequencies of brown bear use within 10 ordinal, categorical ranks (Boyce et al., 2002).

2.4. Comparison of realized habitat selection with predicted habitat suitability prior to reintroduction

To test the hypothesis that the realized brown bear habitat selection matches predicted habitat selection prior to reintroduction, we used the spatial predictions of the first-order RSF and compared it with the HSM developed by Duprè et al. (2000) before bears were translocated. First, we clipped both models to the extent in which they overlapped, approximating the western half of Trentino (3358 km²). The HSM was classified into three suitability categories based on a combination of their landcover model and the anthropogenic model by Duprè et al. (2000). To compare our RSF model of realized habitat selection to the HSM we re-classified the RSF model's predictive values into three ordinal, categorical bins of equal area based on the percentiles of predicted values of availability (Boyce et al., 2002). We compared the habitat quality rank of the predicted HSM with the RSF model by generating 10,000 random points and intersecting these points with both models. Spatial discrepancies were assessed using a weighted

Kappa statistic (Monserud and Leemans, 1992) with the standard weighting option. The Kappa index value indicates the difference between the observed agreement and the amount of agreement that would occur by chance, where a value of 1 reflects perfect agreement and a value of 0 suggests that the amount of agreement is approximately equal to what one would expect by chance. Finally, we subtracted the HSM from the RSF model and mapped the difference between ranks in each cell to visually inspect areas of high discrepancy (Polfus et al., 2014). We also subtracted the values of the HSM from the RSF models for all 10,000 random locations and assessed the difference in ranks by landcover class to understand for which landcover classes the HSM diverged from the RSF.

2.5. Modeling structural brown bear habitat connectivity

We modeled structural brown bear habitat connectivity incorporating the likelihood that habitat patches are suitable for brown bears and the movement probability between those patches using the spatial prediction of the within home-range scale RSF combined with least-cost path analysis (Chetkiewicz and Boyce, 2009). First, we identified habitat source patches with the highest probabilities of suitability based on the three highest ranked of the 10 RSF bins. We converted the RSF raster surface into polygons. Based on the frequency distribution of all patch area sizes, we only used the patches that fell into the highest 95th percentile. Thereby we excluded all patches of high quality habitat that were approximately $\leq 0.5 \text{ km}^2$. By setting this threshold, we aimed to specify a minimum area of suitable habitat (i.e., core habitat), although we acknowledge that this threshold is subjective (Beier et al., 2008). We used the center of each of these selected habitat patches as potential source and destination points for LCP modeling. Next, we used the inverse of the within home-range scale RSF to estimate a movement cost surface (Chetkiewicz and Boyce, 2009). Pixels with lower RSF ranks were assumed to associate with a higher resistance and in contrast, values with higher RSF ranks were assumed to have lower probabilities of resistance. We used 'cost distance' and 'cost path' functions in ArcGIS 9.3 to then calculate the distance and cost between all pairwise combinations of source/destination points in high quality habitat patches.

Connectivity itself is challenging to define and can be measured in multiple ways (Crooks and Sanjayan, 2006). Here, we conducted several analyses to rank the potential importance of paths and identify areas for increased road conflict once all LCPs were modeled. First, we identified all potential paths outside of high RSF value patches that therefore could potentially aid structural connectivity between core habitat patches. Second, we assessed overlap of individual paths with other paths between patches (i.e., putative path density). Finally, due to the growing concern for brown bear road mortality we then identified crossing areas along three types of roads, i.e., motorways (A22), local highways and secondary local roads, where our putative paths crossed. We did this by projecting a 1 km grid over the path segments outside of core habitat patches and counted the number of paths that fell within each cell. Thus, by summarizing the number of paths within the 1 km grid across our study area we derived a measure of structural landscape permeability, both overall, and next also for each road crossing.

3. Results

3.1. Pre-reintroduction potential habitat model

The landcover-based model classified mixed and deciduous forests as high bear suitability and all agricultural and urban areas as

unsuitable. The anthropogenic model suggested that bear sign data coincided negatively with higher tourism pressure and positively with areas with elevated cattle densities. Bear presence data were not statistically related to road density or human density. The combination of the landcover-based and anthropogenic model (Duprè et al., 2000) is shown in Fig. 1a and indicates that high suitability habitat tended to be distributed away from valley bottoms and at intermediate elevations. Unsuitable habitat comprised mountain top and urban areas, while intermediate suitability included habitat surrounding human settlements at lower elevations. See Duprè et al. (2000) for more details.

3.2. Population and within home-range scale resource selection functions

At the scale of the current population range, bears selected areas at mid elevations (quadratic relationship) of approximately 1100 m and avoided flat areas (Fig. 1b, Table 1). Bear ranges were placed away from main roads by selecting intermediate distances to main roads of approximately 2 500 m. Bear ranges tended to occur more in areas with a greater proportion of wetland and shrub complexes, orchards and deciduous forests, but were negatively associated with cultivated lands. All other landcover variables were subsumed in the intercept. The population scale model had very high predictive capacity with an average r_s of 0.999 ($P < 0.0001$) for the internal k-folds cross validation. Population-scale resource selection by external, independent non-conflict VHF bears was also well predicted by this model, with an r_s of 0.964 ($P < 0.0001$).

At the within home-range scale, bears selected higher elevations compared to the population scale (approximately 1450 m, Fig. 2a, Table 1). Based on our top mixed-effects logistic regression model, bears also selected habitats within their home-ranges far from bike trails (about 5000 m), potentially indicating avoidance of human recreation. Further, bears selected northern aspects, mixed forests and shrub landcover types. In contrast, bears avoided cultivated lands, human dominated areas and water. Also the within home-range scale RSF validated very well with an average r_s of 0.987 ($P < 0.0001$). Similarly to the population-scale RSF, also the predictive accuracy for bear VHF data with the within home-range scale RSF was excellent with an r_s of 0.977 ($P < 0.0001$).

3.3. Comparison of realized habitat selection with predicted habitat suitability prior to reintroduction

The comparison between the predictive pre-reintroduction HSM and the realized population-scale RSF resulted in a Kappa statistic of 0.382 (SE = 0.008, $P < 0.0001$), indicating overall poor, but close to fair, agreement according to Monserud and Leemans (1992). The assessment of spatial similarities and discrepancies between the population-scale RSF and the HSM indicated very high rates of agreement (a difference of 0 habitat ranks) in rocks and ice (agreement for 80% of the random locations), cultivated areas (agreement for 78% of the random locations) and human landcover types (agreement for 68% of the random locations; Fig. 1c, Table 2). Minor spatial discrepancies (i.e., ± 1 habitat rank) were observed mainly in wetlands (36% of all random locations) and deciduous vegetation (36% of all random locations; Table 2). High spatial discrepancies (± 2 habitat ranks) resulted mainly from the HSM predicting much lower suitability of orchards (predominantly in the northeastern portion of the study area; Fig. 1c), where 46% of the intersected locations predicted a higher habitat selection (RSF) than the HSM suggested (Table 2). Also, for 17% of the locations falling into shrublands the habitat suitability was predicted to be lower than the RSF suggested.

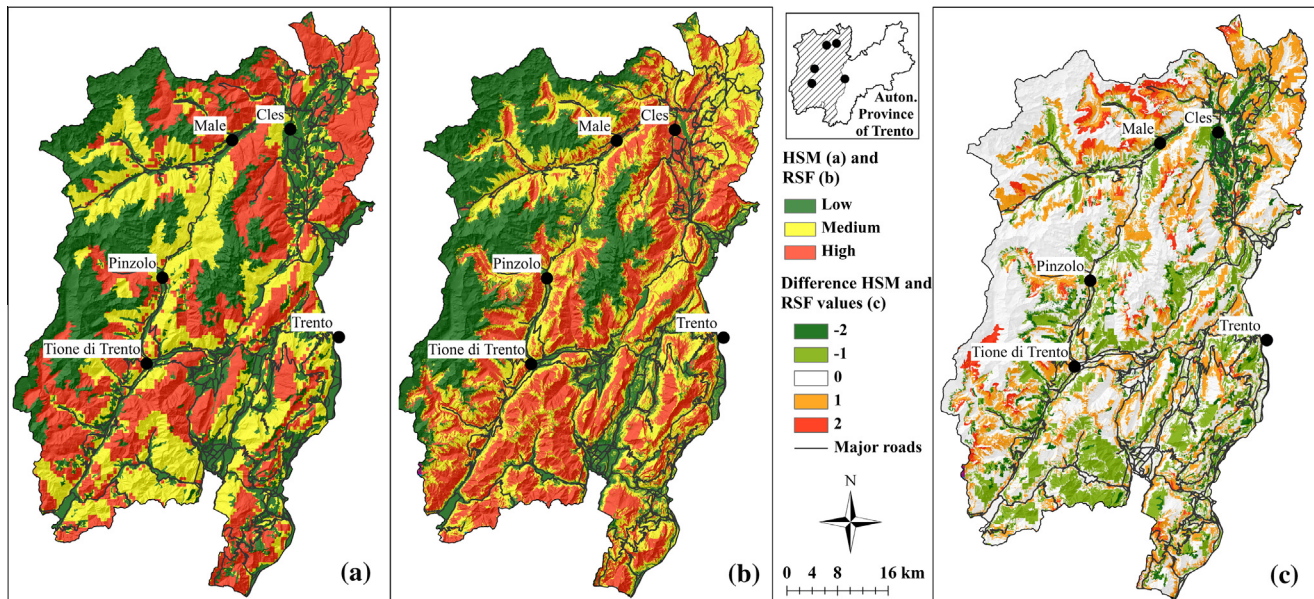


Fig. 1. Comparison between the predictive habitat suitability model (HSM; a) built by Duprè et al. (2000) showing three classes of brown bear habitat suitability in part of the Autonomous Province of Trento, Italy, and the estimated resource selection at the current population scale modeled with a resource selection function (RSF; b) using GPS data of six brown bears and validated with very high frequency (VHF) data of five brown bears. The RSF model was reclassified into three habitat bins to facilitate comparison to the HSM. Panel c) shows spatial discrepancies between the HSM and the RSF model. Warm colors indicate areas where the HSM predicted high brown bear suitability and the RSF model predicted low probability of brown bear use. Cold colors indicate places where the RSF predicted high probability of use and the HSM model predicted low bear suitability prior to reintroduction. The differences range from -2 habitat ranks ($HSM < RSF$) to $+2$ habitat ranks ($HSM > RSF$). White areas indicate perfect agreement between both models ($HSM = RSF$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Selection coefficients (β), standard errors (SE) and P -values from (a) the most parsimonious logistic regression model describing brown bear resource selection at the population scale and (b) the most parsimonious generalized linear mixed model with a random intercept describing bear resource selection at the within home-range scale in the Autonomous Province of Trento, Italy. Global position collar data were collected from 2006 and 2012. Conifer was the reference category for landcover types.

Covariates	β -Coefficient	SE	P -value
<i>(a) Population scale</i>			
Elevation (100 m)	0.149	0.0025	<0.001
Elevation ² (100 m)	$-6.93E-05$	$8.45E-07$	<0.001
Slope	0.008	0.0003	<0.001
Flat (aspect)	-0.693	0.0239	<0.001
East (aspect)	0.126	0.0073	<0.001
Distance main roads (100 m)	0.0280	0.0006	<0.001
Distance main roads ² (100 m)	$-4.23E-06$	$9.29E-8$	<0.001
Shrub	0.612	0.0158	<0.001
Deciduous	0.152	0.0101	<0.001
Cultivated (without orchard)	-0.283	0.0263	<0.001
Orchard	0.600	0.0189	<0.001
Wetland	0.865	0.1093	<0.001
Model intercept	-1.284	0.0181	<0.001
<i>(b) Within home-range scale</i>			
Elevation (100 m)	0.807	0.0289	<0.001
Elevation ² (100 m)	$-2.82E-04$	$9.58E-06$	<0.001
North (aspect)	0.288	0.0364	<0.001
Distance to bike trails (100 m)	$4.68E-02$	$2.82E-03$	<0.001
Distance to bike trails ² (100 m)	$-4.7E-06$	$2.63E-07$	<0.001
Urban	-0.232	0.1850	0.209
Mixed	0.154	0.0613	0.012
Cultivated (without orchards)	-0.420	0.2227	0.059
Water	-0.696	0.2456	0.005
Shrub	0.392	0.0565	<0.001
Model intercept	-6.225	0.5087	<0.001

3.4. Modeling structural brown bear habitat connectivity

We identified 87 core habitat patches from the within home-range scale RSF with an average size of 12.33 km² ha (Fig. 2a). In Fig. 2a we show the concentrations of putative bear paths and in

Fig. 2b where the putative bear paths crossed roads. In general, we found a range of 0–86 LCPs/km² and categories of path densities were ranked as low (0–14), medium (15–51) and high (52–86) path density. Our analysis of densities between putative paths and roads resulted in a total of 492 potential crossings (Fig. 2b). In total, 75% of these identified road crossings were on main roads, 22% on local roads and 2% of these crossings were on the major motorway A22 in the center of Trentino. About 50% of all road crossings had a density of 15–51 overlapping paths and 24% had a density of 52–86 overlapping paths. We consider road crossings with the highest densities as most important in terms of risk for traffic collisions. For example, for the major motorway A22 we identified two such ‘hotspots’ with a high density of putative bear path crossings, one located in the northern part of the provincial motorway segment one in the south. Other potentially important road crossings were found, e.g. in the center of the province at provincial roads connecting northern and southern habitat patches.

4. Discussion

The positive population growth of the reintroduced brown bears to Trentino indicates that the a-priori modeling of potential habitat correctly predicted sufficient high quality habitat for reintroduction. Prior to reintroduction, brown bears were expected to select deciduous and mixed forest cover and avoid human activity including agricultural lands, rock and ice, and select mid to high elevations (Duprè et al., 2000; Mustoni et al., 2003). Insights from the HSM closely matched other regional analyses of habitat selection in central and western European bear populations, where habitat is both a function of food resources (e.g., productive land-cover types), but more importantly, security from high human-caused mortality (Boitani et al., 1999; Falcucci et al., 2009; Gütthlin et al., 2011; Wiegand et al., 2004). For example, over a larger area including all of the east-central Alps, both Boitani et al.

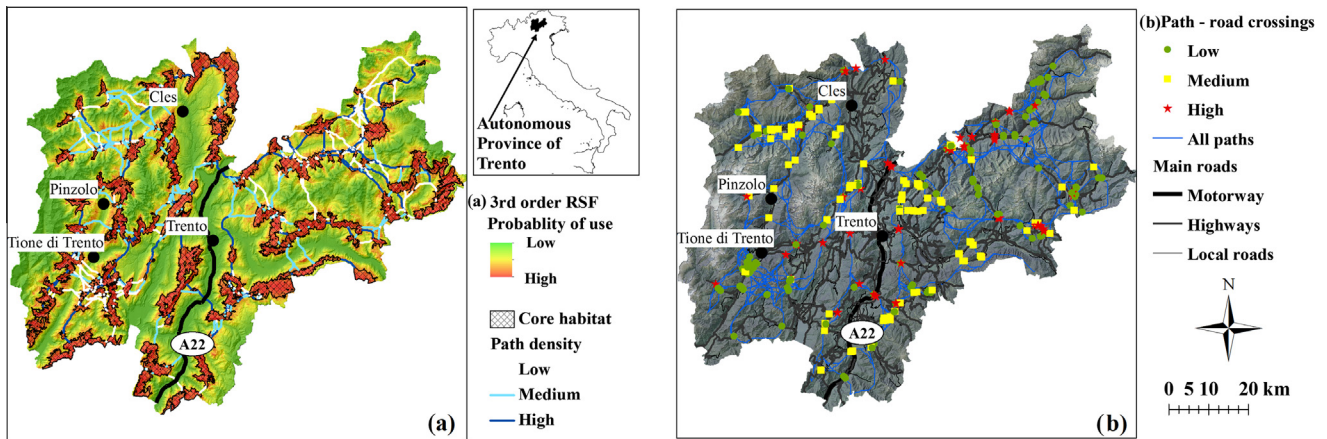


Fig. 2. Predicted paths facilitating brown bear movements between core habitat patches generated by least-cost path (LCP) analysis of a habitat surface empirically defined by a within home-range scale resource selection function (RSF) in the Autonomous Province of Trento, Italy. Panel (a) shows the amount of overlap (three categories) between all generated paths connecting core habitat patches defined as the highest three of 10 habitat bins of the RSF. Panel (b) shows all possible predicted paths crossing roads and the amount of overlap of paths at these crossings.

Table 2

Rank differences (−2 to +2) between the predictive habitat suitability model (HSM) and the current population-scale resource selection function (RSF) model for brown bears in the Autonomous Province of Trento, Italy, at 10,000 random locations intersected with both raster layers by landcover category. Negative values indicate locations where the RSF predicted a higher probability of use while the HSM model predicted lower bear suitability. In contrast, positive values indicate that the HSM predicted high bear suitability, but the RSF predicted a lower probability of use.

Rank difference	HSM < RSF		HSM = RSF	HSM > RSF	
	−2	−1	0	+1	+2
Rocks & ice	0.02	0.08	0.80	0.07	0.03
Urban	0.02	0.20	0.68	0.11	0.00
Cultivated	0.00	0.02	0.78	0.17	0.02
Conifer	0.02	0.20	0.45	0.29	0.03
Deciduous	0.05	0.36	0.47	0.11	0.01
Mixed	0.01	0.23	0.47	0.28	0.00
Orchards	0.46	0.21	0.32	0.01	0.00
Pastures	0.03	0.21	0.41	0.23	0.12
Shrub	0.17	0.25	0.51	0.04	0.02
Wetland	0.09	0.36	0.36	0.09	0.09
Water	0.01	0.08	0.74	0.13	0.04

(1999) and G uthlin et al. (2011) found that brown bears were associated with forest cover, higher elevations, avoided roads and human activity, and were found in deciduous forest types more often. From studies with more detailed demographic monitoring in both Europe (Bischof et al., 2009; Falcucci et al., 2009) and North America (Johnson et al., 2004; Nielsen et al., 2006), we know that a combination of productive habitats with low risk of human-caused mortality are critical components of high-quality brown bear habitat. Overall, the generally close match between predicted habitat suitability before and after reintroduction by both reintroduced bears and animals born in the study area, supports our conclusion that the Trentino study area contains high habitat suitability that contributed to both high adult survival and reproduction, and continued growth and expansion of this reintroduced population. However, while reproductive rates may be high due to sufficient high quality habitat, large carnivore populations often experience increased human-caused mortality rates due to, e.g. road collisions or poaching, and management of such attractive sinks will be key for long term population viability (Liberg et al., 2011; Wiegand et al., 2004).

Few studies have assessed the performance of carnivore habitat models developed prior to reintroduction or recovery. One of the reasons is that many potential carnivore reintroductions may not

be realized and consequently these prior evaluations are often theoretical academic exercises. For example, post re-introduction evaluation of habitat models predicting potential habitat of wolves and lynx in Britain (Wilson, 2004) or cougars (*Puma concolor*) to the northeastern United States (Laundre, 2013) may never occur because of public opposition to reintroductions in these landscapes, low overall habitat suitability identified by such a-priori habitat modeling, or lack of policy or administrative support. However, while several successful realized carnivore reintroductions followed a-priori habitat modeling (Schadt et al., 2002; Zimmermann, 2004), there have been few examples of post-reintroduction evaluation of the success of habitat models predicting carnivore habitat distribution following recovery. The best example of evaluation of carnivore habitat following recovery occurred in a naturally recovering population of gray wolves in the Great Lakes region of the USA. Mladenoff et al. (1995) built a-priori predictive models of wolf distribution based on wolf data from nearby Minnesota and Michigan to predict the distribution of recovering wolves in Wisconsin. Then, following wolf recovery in Wisconsin through natural dispersal, Mladenoff et al. (1999) showed that their model closely predicted post-recovery habitat of wolves 10-years later. This textbook example, like our case study, shows that carnivore habitat can be predicted quite accurately at landscape scales.

For large carnivore reintroductions, however, evaluations commonly focus on behavioral, movement, genetic, or demographic aspects following reintroduction (De Barba et al., 2010; Devineau et al., 2010; Gusset, 2009; Preatoni et al., 2005). The few evaluations of post-release habitat selection that exist are often purely qualitative or descriptive (Breitenmoser et al., 2001; Hayward and Somers, 2009). One example is a controversial review of the Florida panther (*P.c. coryi*) recovery plan (Beier et al., 2006; Gross, 2005), where an expert review team revealed a systematic failure of the pre-reintroduction habitat model used to guide and evaluate recovery efforts. This rare case of quantitative assessment revealed that the original pre-reintroduction model made unrealistic assumptions that Florida panthers would not use non-forested habitats, treated roads as permanent barriers, and as such, underestimated potential habitats for Florida panthers. They concluded that quantitative scientific evaluation of the underlying habitat models for carnivore recovery was lacking. We were unable to find other examples of a quantitative comparison of pre- and post-reintroduction habitat selection or use by a large carnivore, suggesting that this may be a common weakness in carnivore

reintroductions (Hayward and Somers, 2009). In this respect, the Trentino brown bear example provides a valuable case study, especially as carnivore recovery programs will likely gain of considerable global importance in the future (Ripple et al., 2014).

While every model remains a testable hypothesis (Garshelis, 2000), we often learn the most from models when they fail. In this case study, we found overall broad agreement visually (Fig. 2c) and to a lesser degree statistically by the Kappa statistic between the a-priori HSM and the post-reintroduction RSF at the population scale. There was broad agreement in the avoidance of brown bears for cultivated areas (without orchards) and human settlements (Mustoni et al., 2003; Table 2). However, the pre- and post-reintroduction models showed disagreement in areas where reintroduced brown bears used orchards, shrublands, and rocky areas more and some forested areas less than expected based on the HSM. In other words, some of the 'most suitable habitats' in the HSM were used by bears less than predicted and some 'unsuitable habitats' (e.g., rocks and ice, orchards) were instead used more than predicted prior to reintroduction. Further, some areas defined as 'limited suitability' by the HSM (suitable habitat, but elevated anthropogenic disturbance) were used more than expected by the HSM. Duprè et al. (2000) explicitly expected this intermediate suitability category to be important once high suitability habitat became saturated. However, Duprè et al. (2000) also noted that in these areas, which may be suitable in terms of forage, but with high anthropogenic impact, human-bear conflicts are more likely to be expected. The biggest differences between models were in the northern part of the study area (Fig. 1c). For example, areas in the northeastern study area were dominated by orchard land-cover types, which the bear RSF showed more frequent selection for than expected. Thus, this selection for more orchards than expected is important because of the increased potential for human-wildlife conflict. The strength of selection for orchards is especially substantial because it was averaged across the entire year, when it would be expected to be much higher during late summer and fall, when the large plantations of apple trees bear fruits. Human conflict with black bears (*U. americanus*) in Montana, USA, increased in proximity to orchards during the fall in human dominated landscapes (Merkle et al., 2013). The strong selection we found for brown bear home-ranges to contain orchards poses a potentially underappreciated risk factor for continued conservation of this population in the future. However, at the within home-range scale, bears used orchards in proportion to availability at the temporal resolution of the entire year. Further analyses of seasonal resource selection and movements may help identify orchard-specific bear-human conflict mitigation strategies (Merkle et al., 2013). Regardless of spatial and temporal scale, important differences in use of orchards pre- and post-bear reintroduction suggest that future work could focus on potential mitigation for human-bear conflict (Merkle et al., 2011, 2013). In contrast, in the north-central part of the study area, rich in heavily forested areas, the bear RSF showed less frequent selection than predicted by the HSM. The underutilization of this area could potentially be because of the over-importance attributed to coniferous forests in the HSM model, or because connectivity to these areas is limited.

These differences could be ecologically important, or potentially due to methodological differences. First, pre-reintroduction, bear habitat selection was assessed at a population scale by comparing bear use to availability within a 1700 km² area defined by signs of presence of the remnant individuals of the local population. However, post-reintroduction, brown bears ranged over a wider area (Duprè et al., 2000; Mustoni et al., 2003) of almost 3000 km², thus changing the scale of availability. Previous studies identifying brown bear habitat in the Alps used a variety of methods and scales (Güthlin et al., 2011), but results from different

models were broadly similar. We therefore conclude that our sampling approach was robust to the scale used pre- and post-reintroduction. More ecologically important could be differences between remnant and reintroduced bears, in terms of acquaintance to humans. The HSM was built using all bear observations over a 20-year period prior to the bear reintroduction. These bears consisted of three non-reproductive, senescent individuals (Mustoni et al., 2003). Consequently, prior to reintroduction Trentino bears may have selected only areas away from humans seeking security in contrast to translocated animals from Slovenia that were more accustomed to coexist with humans, potentially leading to the differences in selection we observed. Indeed, we developed habitat models with several GPS collared bears that were, in part, radio-collared because of their conflict status with humans. Hence differences pre- and post-reintroduction could be potentially because of behavioral differences of conflict bears. However, since we failed to find any differences between GPS (conflict) and VHF collared (non-conflict) bears based on external data validation (Boyce et al., 2002), we conclude that any potential differences in habitat selection between the HSM and the RSF did not arise because of our sample. Moreover, habitat selection, and in particular response to anthropic variables and diet, are known to differ as a function of age and sex class as a result of interspecific avoidance and differences in life-histories (Elfström et al., 2014). For example, differences in habitat use by reproductive female bears, which seek more secure habitat, could also drive differences pre- and post-reintroduction as well (Mueller et al., 2004; Waller and Servheen, 2005). While we did not have sufficient data to test for between-sex and -age class differences our conclusions still appear robust at the population-level in comparison to previous bear habitat models. Finally, our modest sample size of 11 radio-collared bears could be argued to limit our results. However, this sample represented a significant proportion of a total population size that grew from 10 to approximately 48 (including adults and subadults of both sexes) during the monitoring period. Specifically, when VHF data were collected the bear population comprised about 10 bears and thus, we sampled 50% of the population at that time. We used GPS data from six bears between 2006 and 2012 and therefore sampled 15–27% of the population during that time period, because the population size was estimated to range between 22 and 40 bears during that time (Groff et al., 2013).

One of the key motivations for recovering the Italian Alps brown bear population with the core range in Trentino was to facilitate the establishment of the larger Alpine population comprised of Austrian, Swiss and Friuli-Slovenian population segments in the future (Mustoni et al., 2003; Linnell et al., 2008). Population growth has naturally led to an expansion of the bear population in Trentino, bears from the founder group have dispersed up to 163 km (De Barba et al., 2010) and offspring from this study population dispersed even further into previously unoccupied habitat in Austria and Germany (e.g., 'Bruno the bear', Rosen and Bath, 2009) as well as Switzerland and the Dinaric-Pindos population (Groff et al., 2013). Yet, connectivity remains a concern at multiple spatial scales (Linnell et al., 2008). For example, because dispersal is generally lower in female compared to male brown bears (Zedrosser et al., 2007), we might expect to observe female dispersal not until habitat in the range of this Trentino population becomes saturated. Also, while several bears dispersed, likely many of them experienced human caused mortality and no to little emigration of genes from this population must be assumed (Groff et al., 2013). Moreover, transboundary movements of bears like Bruno have revealed interagency inconsistencies in addressing bear-human conflicts that will likely need to be addressed before achieving long term (meta-) population viability (Rosen and Bath, 2009). Thus, despite managing demographic threats to recovery, such as human-caused mortality, ensuring habitat connectivity

both within the Trentino population and between the Slovenian population and potentially also in the future in Austria and Switzerland will be important (Linnell, 2013).

Previous studies identified potential movement corridors between prospective future subpopulations at larger scales across landscapes (Boitani et al., 1999; G uthlin et al., 2011; Lyon et al., 1985). In this paper we focused on identifying structural connectivity within Trentino, recognizing that habitat connectivity is multi-scale, and that in human-dominated landscapes permeability at the smaller scales is an important component of local habitat quality (Chetkiewicz et al., 2006). While this Trentino population experienced several bear-vehicle collisions and mortalities (22 collisions since reintroduction with at least three deaths), our movement paths suggested that structural connectivity was generally high within the western portion of our study area, the original reintroduction site, and also where relative bear densities were the highest (Groff et al., 2013). Specifically, we found that paths were more concentrated with higher overlapping densities in the central and north-eastern parts of Trentino, an area currently mostly unoccupied by bears. The high concentration of paths in these regions may be partly explained by the overall lower densities of predicted high quality habitat by the RSF. In contrast, south-western Trentino has comparatively more high quality habitat as well as higher connectivity. Most importantly though, connectivity across the main Adige Valley to eastern Trentino was reduced to 2 or 3 main potential crossing sites of the main motorway, the A22, one of the primary north-south transportation routes in central Europe. Moreover, suitable habitats were generally more distant from each other in the northern part of our study area (Fig. 2), decreasing connectivity due to increased movement costs through less ideal habitats in this region (Boitani et al., 1999). Our LCP model suggests that active mitigation measures to increase habitat connectivity in potential corridors and potentially address highway-vehicle collision risk would be a valuable conservation strategy to enhance survival and recovery (Sawaya et al., 2013). Given that gene flow has been low with two founder males producing all first generation offspring and also cases of mother-to-son reproductions have been recorded (Groff et al., 2013), increasing functional connectivity would be especially crucial at this stage of the population growth, especially if further translocations are not considered. Even low levels of immigration, e.g. of individuals from the eastern Alps which would have to cross the Adige Valley, resulting in successful reproduction with resident bears would have the potential to prevent the loss of polymorphism and heterozygosity (Mills and Allendorf, 1996). Lastly, like many studies, our connectivity analysis assumed that movement probability was a function of habitat quality (Chetkiewicz and Boyce, 2009). However, bears may not necessarily move through the optimal paths connecting two habitat patches that were identified using LCP analyses, especially without a-priori knowledge of the area. Therefore our putative movement paths remain testable models, but are a relative measure for comparing connectivity between different habitat patches.

Our results are consistent with the conclusion based on demographic monitoring that many large carnivore populations are not 'habitat' limited in the classic sense of habitat being defined by biophysical functional traits (Gaillard et al., 2010). Instead, several recent studies demonstrate that ultimately, carnivore habitat quality depends on the reduction of human-caused mortality (Falcucci et al., 2009; Johnson et al., 2004; Mitchell and Hebblewhite, 2012; Nielsen et al., 2006). While this bear population increased since reintroduction, also conflict potential between bears and humans increased (Groff et al., 2013) due to, e.g. livestock and crop damages or close encounters of humans with more habituated bears. However, the number of 'damage' incidents (predation on livestock, attacks to beehives or crops) is not necessarily related to

the bear population size per se, because only few individuals caused the most of the economic damage (Groff et al., 2013). Indeed, the economic impact of each bear is much lower than what envisioned in the pre-reintroduction study, i.e. one third (about 8 000 euro/bear/year vs. 26,000  /bear/year in the worst case scenario of Dupr e et al. (2000). Regardless, the success of the reintroduction over the last decade also corresponded to a decrease in human acceptance towards reintroduced bears, including the first instances of illegal poaching (Groff et al., 2013). As the number of humans continues to grow, interactions with bears will persist as an important management and conservation issue (Woodroffe, 2000). Understanding the ecological fundamentals prior to recovery actions is critical, and in our case study of the Trentino bear reintroduction, it seems that successful identification of bear habitat prior to reintroduction contributed to its success. However, ultimately the success of carnivore reintroduction depends on human social carrying capacity, especially in rural landscapes in which carnivore recovery could ecologically be feasible, but where social acceptability is low (Linnell et al., 2001; Treves and Karanth, 2003). Addressing social conflicts as well as continuing to work on mitigating bear-human conflict and addressing functional bear habitat connectivity within this Trentino population and beyond will be required to establish a viable greater Alpine brown bear population and a meta-population network in the future.

5. Conclusions

Human-carnivore coexistence poses a major challenge to carnivore recovery worldwide, but is especially important in human-dominated population ranges as in Europe (Chapron et al., 2014; Dorresteijn et al., 2014; Zedrosser et al., 2001). The apparent early success of the Trentino brown bear reintroduction appears to at least be partially due to the predictive accuracy of the pre-reintroduction brown bear potential habitat model. This speaks to the importance of this crucial step for all large carnivore reintroductions. We found potentially important differences between the pre-reintroduction brown bear HSM and our population scale RSF in terms of how brown bears used orchard habitats. In particular, post-reintroduction, brown bears used orchards at large spatial scales more than expected prior to reintroduction, which could pose a potential risk to bear recovery especially if it increases bear-human conflict potential. We now know that for many carnivores, human activity and especially agricultural land use may create attractive (sink) habitats in which, however, fitness may be reduced (Northrup et al., 2012). This highlights the importance of a niche-based definition of habitat that includes both resources and mortality sources in the definition of habitat for large carnivores. Regardless, although a potential decline has been noted in 2013 (Groff et al., 2013), this bear population has overall grown and expanded and is now the only population with potential to support the establishment of a larger prospective Alpine population in Europe (Kaczensky et al., 2012). However, connectivity supporting local population expansion will be important for future persistence (Boitani et al., 1999). Our LCP modeling demonstrated that areas with high quality habitat, low in human activity and high in mixed forests and shrublands at intermediate elevations will potentially facilitate connectivity. However, for population expansion to eastern Trentino and potentially connectivity to the Slovenian portions of the Dinaric-Pindos population, the most important barrier will be the Adige Valley with the A22 motorway. Given uncertainty about the best way to measure connectivity, it will be important to validate our movement paths and to assess habitat permeability and potential barriers directly with field-based methods through, e.g. genetic monitoring or confirmed road crossings (Proctor et al., 2012). Thus, regardless of the apparent

reintroduction success to date, the long-term viability of the Trentino population and its future expansion will likely depend on mitigating bear-human conflicts.

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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.biocon.2015.02.034>.

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