

Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps

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Summary

1. Wolves *Canis lupus* recently recolonized the Western Alps through dispersal from the Italian Apennines, representing one of several worldwide examples of large carnivores increasing in highly human-dominated landscapes. Understanding and predicting expansion of this population is important for conservation because of its direct impact on livestock and its high level of societal opposition.

2. We built a predictive, spatially explicit, individual-based model to examine wolf population expansion in this fragmented landscape, and livestock depredation risk. We developed the model based on known demographic processes, social structure, behaviour and habitat selection of wolves collected during a 10-year intensive field study of this wolf population.

3. During model validation, our model accurately described the recolonization process within the Italian Alps, correctly predicting wolf pack locations, pack numbers and wolf population size, between 1999 and 2008.

4. We then projected packs and dispersers over the entire Italian Alps for 2013, 2018 and 2023. We predicted 25 packs (95% CI: 19–32) in 2013, 36 (23–47) in 2018 and 49 (29–68) in 2023. The South-Western Alps were the main source for wolves repopulating the Alps from 1999 to 2008. The source area for further successful dispersers will probably shift to the North-Western Alps after 2008, but the large lakes in the Central Alps will probably act as a spatial barrier slowing the wolf expansion.

5. Using the pack presence forecasts, we estimated spatially explicit wolf depredation risk on livestock, allowing tailored local and regional management actions.

6. *Synthesis and applications.* Our predictive model is novel because we follow the spatio-temporal dynamics of packs, not just population size, which have substantially different requirements and impacts on wolf–human conflicts than wandering dispersers. Our approach enables prioritization of management efforts, including minimizing livestock depredations, identifying important corridors and barriers, and locating future source populations for successful wolf recolonization of the Alps.

Key-words: adaptive management, *Canis lupus*, recolonization, SELES, social structure, spatially explicit individual-based model, wolf

Introduction

Conservation strategies for threatened and endangered species have been developed using models of varying complexities, including population models (e.g. population viability analy-

ses), landscape models (e.g. resource selection functions) and spatially explicit dynamic models [e.g. spatially explicit, individual-based model (SE-IBM)] (Shenk & Franklin 2001; Wiegand *et al.* 2004). For large carnivores, often the main factors driving small populations to extinction are contraction and modification of their habitat and increased illegal killing by humans (Ferrerias *et al.* 2001). For some, however, populations are increasing, creating controversies and challenges for

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their conservation. Wolves, for example, conflict with humans mainly through competition over livestock, a natural side-effect of wolf population expansion in Europe where the territories of carnivores and livestock husbandry often overlap (Linnell, Swenson & Anderson 2001). Hence, pressures on authorities to define control strategies are often high even when abundance is lower than a minimum viable population (Nilsson 2003). Italian wolves *Canis lupus* Linnaeus, 1758 [endangered: the Habitat Directive 92/43/CEE, the Bern Convention on the Conservation of European Wildlife and Natural Habitats (19.IX.1979) and Red list (IUCN 2001)] are of concern as they recently naturally recolonized the Western Alps after being extirpated throughout most of Western Europe during the 20th century, and their future status is uncertain. Predictive models could therefore be very important to guide conservation and management decisions, minimizing the ecological and economic costs of trial and error for endangered species. However, the conservation questions are complex and require a combination of analysis of spatial landscapes, and a knowledge of animal behaviour and population dynamics.

Population models (e.g. population viability analysis) have often been used to define conservation strategies for large carnivores (Samson 2002), including wolves, to assess extinction risk under different management strategies (Chapron *et al.* 2003), and to investigate the effects of inbreeding depression, hunting policy and catastrophic events on isolated populations in Scandinavia (Nilsson 2003). However, these models have been criticized because they inadequately represent animal behaviour (DeAngelis *et al.* 2001), and because they are often not spatially related to real landscapes (Macdonald & Rushton 2003; McIntire, Schultz & Crone 2007). For wolves, a highly social and territorial species structured in packs with a single-breeding pair, their behaviour disproportionately affects density, home-range configuration, reproduction and mortality (Mech & Boitani 2003). Social structure may inflate the importance of or amplify demographic stochasticity by restricting the number of breeding units to the number of social groups (Caro & Durant 1995; Vucetich, Peterson & Waite 1997). Yet, behavioural data have been rarely incorporated into population models (Gonzalez-Suarez & Gerber 2008).

Another type of model—the spatially explicit, geographical information system-based, landscape model—can also be very useful for species management (Adriaensen *et al.* 2003), and has been widely used in Western Europe to predict wolf distribution in areas not yet recolonized (e.g. Corsi, Duprè & Boitani 1999; Jędrzejewski *et al.* 2008). In the Italian Alps, where the landscape is human dominated and suitable habitat for carnivores is heavily fragmented by both topography and humans, the habitat can play an important role in reducing the system carrying capacity for wolves. However, social and population dynamics have never been addressed in these models, and therefore no potential feedbacks within the system have been considered (McIntire, Schultz & Crone 2007). Additionally, no pack requirements for territorial establishment have been accounted for, implying no differences between potential presence of wandering solitary wolves and established packs.

To analyse this complex natural recolonization process and population dynamics in a fragmented landscape, and to circumvent these shortcomings, we built an SE-IBM for wolves that incorporated reproduction, age-based mortality, social structure, territoriality, juvenile dispersal, and habitat selection acting on dispersal and territory location directly within the Alps. Because our model is set in the real landscape, it is open to empirical testing and validation, and to investigate the roles of various population and landscape parameters. Moreover, the SE-IBM that we developed is a way to link individual traits and social system complexity, such as wolf pack structure, because they directly account for how population dynamics emerge from individual behaviour (Grimm & Railsback 2005). IBMs allow the effects of demographic stochasticity and the internal complexity within a population to be taken into account in a straightforward manner (Matsinos, Wolff & DeAngelis 2002), and are therefore particularly well suited for small populations (DeAngelis *et al.* 2001). Thus, we first calibrate and validate our model; then we predict the potential future wolf recolonization to guide wolf conservation and management decisions. We predict spatial absolute probabilities of future wolf packs in the Alps in the next 5, 10 and 15 years (i.e. 2013, 2018 and 2023), together with pack numbers and other population parameters. We also identify critical areas for wolf pack establishment, which will be fundamental for future sources in the wolf recolonization process of the entire Italian Alps system. Finally, we spatially predicted wolf depredation risk of livestock throughout the wolf recolonization process.

Material and methods

STUDY AREA AND THE HABITAT SUITABILITY MODEL

The study area covers the Western, Central and Eastern Alps in Italy (Fig. 1). This area is weakly connected in the south to the Apennines Mountains, the only source for the wolf population in the Alps (Fabbri *et al.* 2007). Gene flow between the Apennines and the Alps is moderate (1.25–2.50 wolves per generation; Fabbri *et al.* 2007) so we considered immigration negligible for initial purposes of our demographic submodel. The wolf population in the Alps is currently expanding in the French Alps (Marboutin & Duchamp 2005); however, we limited our analysis to the Italian side of the Alps because of data availability. In the future, as data become available, it will be important to expand the model to the entire Alps. This implies that our predictive model does not take into account the potential for immigrants (gains) or emigrants (losses) or for additional connectivity through routes not included in the area that we have modelled. Despite the trend towards more coordinated international approaches, the present Italian focus reflects present management structures. Sheep farming is widespread in the Italian Alps and livestock depredation by wolves has caused increasing conflicts over the years (Marucco *et al.* 2009a). Today, however, the wolf population is fully protected in Italy and hunting is illegal.

We used the wolf habitat suitability model for the Italian Alps (Fig. 1), developed by Marucco (2009), to explicitly represent the Alps in the SE-IBM. Marucco (2009) applied an unconditional multi-season occupancy model to estimate wolf occupancy parameters and detection probabilities (MacKenzie 2006), based on data collected

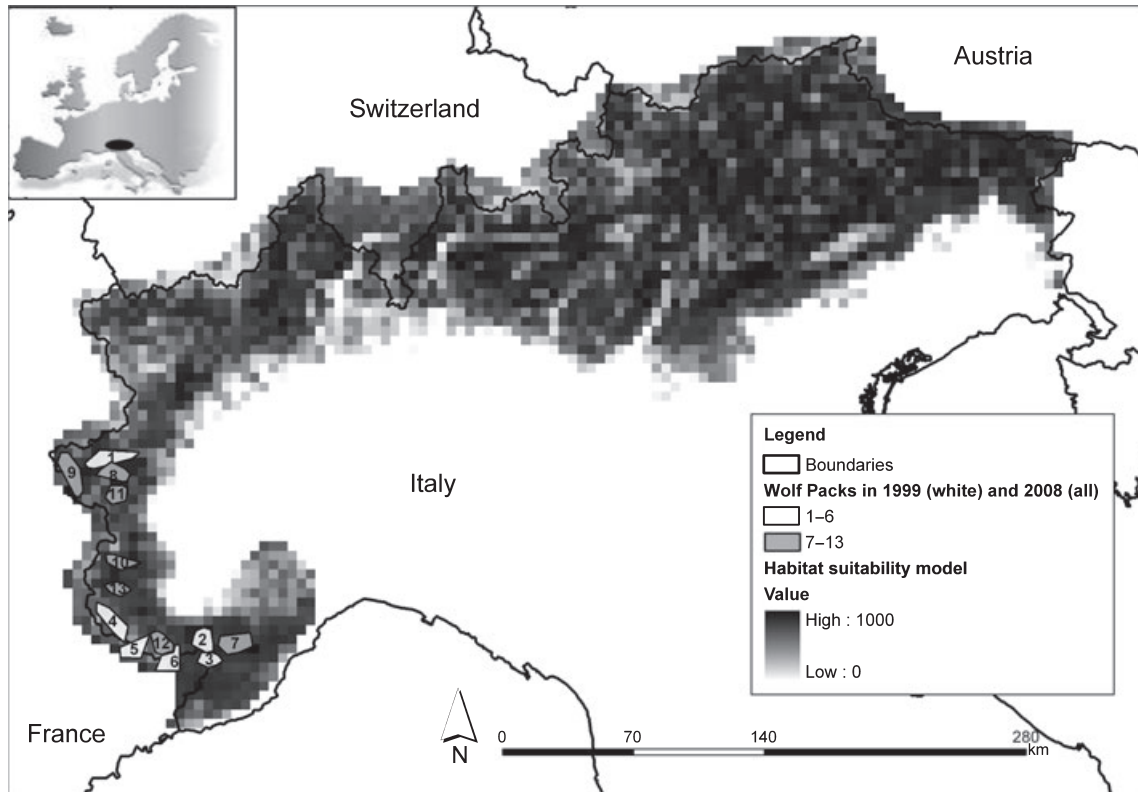


Fig. 1. Habitat suitability model for wolves in the Italian Alps, derived from Marucco (2009), and actual location of the first six packs in the South-Western Alps used as the starting state of the simulation model in 1999, and actual location of 13 pack locations in the Western Alps used as the starting state of the simulation model in 2008.

using a robust design over 5 years in the Western Italian Alps. The suitable habitat model produced had a grid structure of 25 km², and the habitat suitability values ranged from 0 to 1000 (Fig. 1). We used this habitat suitability model for both territory establishment and dispersal (see below).

THE SPATIALLY EXPLICIT, INDIVIDUAL-BASED MODEL

Model structure

We constructed the SE-IBM using the Spatially Explicit Landscape Event Simulator (SELES) (Fall & Fall 2001). SELES is a raster-based spatial modelling framework. For model structure purposes, we used a finely divided version of the habitat suitability model (1.56 km² raster cells) to allow for flexible shapes of territories. Our SE-IBM model has three main submodels: the main model for the wolf population processes that follows annual survival, reproduction and social structure formation of individual wolves (non-spatial); a dispersal submodel (spatial); and a potential territory establishment submodel (spatial). The spatial submodels are both affected by the habitat suitability map (Fig. 2) and interact with the wolf population process model. The dispersal and potential territory submodels occur on a finer time-scale, with up to 100 moves and potential territory assessments per year. The structural uncertainty (*sensu* Burgman & Possingham 2000) of the model is relatively low because the biology of wolves is well known (Mech & Boitani 2003). However, the mechanisms behind juvenile dispersal and the decision to accept a potential location as a territory are relatively unknown. This structurally uncertain component was the subject of the calibration described below.

Parameters used in model

We used two types of parameters defined by how they were estimated: (i) data-based parameters derived from an ongoing 10-year intensive wolf study in the Western Italian Alps (Marucco *et al.* 2009a,b), begun with first pack formation in the Alps (Table 1 and 2); and (ii) parameters estimated below during model calibration (Table S1). Data-based parameters were used directly in the model for model functioning (Table 1), for calibration (Table 2) or for validation (Table S2).

Reproduction, survival and pack structure

Any pack with both a male and a female breeds in a given year; however, only the breeding pair in a pack reproduces, as documented in the Alps (Marucco *et al.* 2009a). Litter size is determined by a random draw from N_{pup} (Table 1), with sex attributed randomly with equal probability. After birth, pups stay in the pack for at least 1 year; after this, young are forced to leave the pack if the pack is larger than a random draw from the maximum pack size, P_{max} (Table 1). Mortality happens every year to young, adults and dispersers at rates m_y , m_a , m_{dpm} (Table 1 and 2). Wolves older than 14 years die (A_{max}). The annual apparent adult mortality rate ($m_{\text{app,a}}$) and annual apparent juvenile mortality rate ($m_{\text{app,y}}$) were estimated from non-invasive capture-mark-recapture (CMR) analysis by Marucco *et al.* (2009b). Apparent annual mortality rates include true mortality and all losses from the study area (i.e. dispersals). As dispersal mostly happens among younger wolves (Boyd & Pletscher 1999), we assumed that the estimated apparent annual adult mortality was equal to true adult

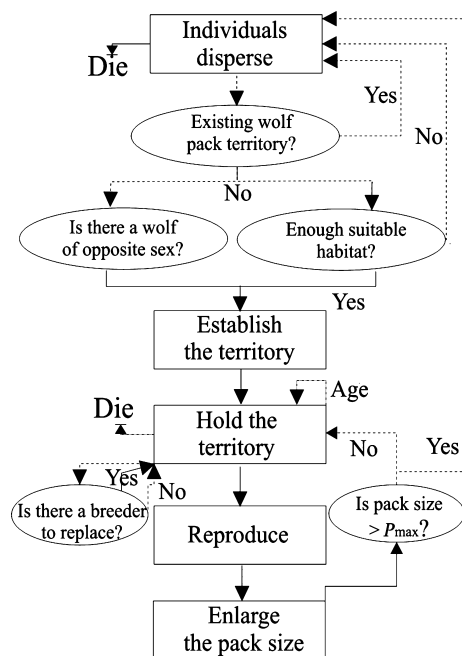


Fig. 2. Flowchart showing the way the spatially explicit, individual-based model of wolves in the Italian Alps followed the fate of individual wolves and simulated movement of dispersing wolves, home range establishment of successful dispersing wolves, mortality and reproduction for the breeding couple within a pack every year. Solid lines connecting boxes and ovals represent breeders; dashed lines represent non-breeders. Ovals represent questions and rectangles represent states or processes.

mortality. However, we could not make this assumption for juveniles. Thus, true juvenile mortality rate was estimated during the calibration phase (described below).

Dispersal

Young wolves aged 1 and 2 years old disperse and search for their own territory if forced to leave the pack. Our dispersal data comprised 23 individual wolves with known dispersal distances (Table 2). To convert these empirical dispersal distances to a mechanistic movement process for use in the simulations (i.e. a set of rules that govern movement through the landscape), we assumed that wolf dispersal occurs by a correlated random walk (i.e. the expected direction at time t is the direction at time $t - 1$) (Turchin 1998) with two parameters: the step length (α : the number of cells a wolf moves per dispersal time step), and angular deviation (σ : the standard deviation of a wrapped normal distribution). These two parameters are estimated within the calibration phase by comparing five quantiles (0.025, 0.25, 0.5, 0.75 and 0.975) calculated from the empirical distribution of dispersal distances with the same quantiles from the simulated dispersal distances. The potential destination cell must have a habitat quality that exceeds Q_{mean} . Because step length was found to be > 1 cell (see Table S1), simulated wolves can pass 'through' any cell quality to get to the potential destination cell. As a result, low cell quality acts only as a partial barrier (i.e. 'matrix') when it is in isolation, but many contiguous low-quality cells would act as a full barrier. Furthermore, as we know that there is dispersal mortality (Marucco *et al.* 2009a), but we do not have data on its mechanisms, we assumed that the probability of mortality increases with distance and/or time travelled. Thus, we introduced a parameter for the per step dispersal mortality rate (m_{dpm}) to estimate within the calibration phase. This parameter

Table 1. Parameters estimated from data collected during an ongoing 10-year intensive study of the wolf recolonization process in the Western Italian Alps, and used for direct parameterization of the SE-IBM model

Parameters estimated from data	Code	Statistics	SD	n
Mean pack size detected in late winter*	P_{mean}	4.405	1.251	74
Mean number of pups per litter	N_{pup}	3.387	1.210	31
Maximum wolf older age	A_{max}	14		
Minimum value of total habitat suitability per wolf territory	Q_{tot}	89 288	16 655	36
Minimum value of habitat suitability per cell in the wolf territory	Q_{min}	376		36
Mean value of habitat suitability per cell in the wolf territory	Q_{mean}	840		36
Maximum territory size (km ²)*	T_{max}	404		36
Annual apparent adult mortality rate†	m_{a}	0.18	± 0.04	87
Starting number of packs in 1999*	P_{start}	6		6
Starting location of packs in 1999*	Snl	Fig. 1		6
Starting social structure of packs in 1999 (each individual)*	sss			23

*From Marucco *et al.* 2009a.

†From Marucco *et al.* 2009b.

Table 2. Parameters estimated from data collected during an ongoing 10-year intensive study of the wolf recolonization process in the Western Italian Alps, and used in the SE-IBM model for calibration of the model

Parameters	Code	Statistic	SE	n	Calibration (95% CI)
Dispersal distance quantiles (0.025–0.25–0.50–0.75–0.975)	d_{disp}	11.93–24.20–54.60–176.95–365.05		23	10.08, 36.76, 75.98, 143.16, 278.32
Apparent annual juvenile mortality rate	m_{appj}	0.76	± 0.06	87	0.76 (0.67–0.86)
Pack number in 2006	N_{pack06}	10			10 (5–17)

is a constant probability of mortality for each step, and its best value will be that found during calibration that contributes to the minimized cost function. This is a simple dispersal mortality hypothesis with no spatial component; as a result, spatially constrained mortality events (such as road mortality) will be attributed to this non-spatial mortality per step rate. Finally, in early simulation attempts, no runs produced the known long-distance dispersals when only habitat was used as all close unoccupied habitat was used first. To capture this dynamic, we introduced a behavioural transition parameter (ζ ; Table S1) to describe an initial time period (in number of steps) immediately after leaving the natal pack where the wolf will not establish a new territory, but will join a previously existing territory with a single wolf of the opposite sex, if encountered.

Territory establishment

If a dispersing wolf lands on any cell that is part of a territory of a single wolf of the opposite sex, it will join that wolf's territory and they will reproduce in the following year. To establish a new territory, every unoccupied cell that is visited by a dispersing wolf after the behavioural transition (Fig. 2) will be assessed for habitat quality following habitat suitability parameters (Q) that we derived empirically from all 36 known and mapped packs during 1999–2008. If a visited cell has a habitat quality that exceeds Q_{mean} , that cell will be the centre of a potential territory. The individual will then assess all neighbouring sufficiently good ($> Q_{\text{min}}$) unoccupied cells (up to an area of $T_{\text{max}} = 404 \text{ km}^2$), summing the habitat suitability values (each on the same, but arbitrary, relative scale of 0–1000), until a total habitat suitability, Q_{tot} , is reached. If Q_{tot} is not reached within the T_{max} area, the potential territory is abandoned. Once a territory is formed, the territory location is permanent unless mortality occurs to all the members of the pack.

CALIBRATION PHASE

There were five unknown parameters in our model (Table S1). We repeatedly simulated the recolonization process until 2006 (7 years) with numerous (10 000), biologically plausible combinations of these parameters and picked the best combination that minimized a model-fitting cost function. The details of the calibration procedure are outlined in Appendix S1.

VALIDATION PHASE

We validated our model using data that were not used for model calibration (Table S2). We simulated 10 000 replicates until 2008 (9 years), 2 years past our calibration phase, to test our model predictions. First, at the individual level, we used the known fate and territory establishment history of all wolves that died from the initial 23 wolves ($n = 16$). Secondly, at the population level, we compared simulated annual growth rate with a genetic CMR estimate (Marucco *et al.* 2009b). Thirdly, we assessed the wolf population size estimate in 2008 obtained using results from genetic analysis on scat samples and snow-tracking data (Marucco *et al.* 2009a). Fourthly, we did a spatial cross-validation test used commonly in the resource selection function literature (Boyce *et al.* 2002). Fifthly, to contrast the strength of this model with non-dynamic approaches, we calculated and compared the binomial likelihood of the data given each of three hypotheses of pack presence: complete spatial randomness, a habitat-only hypothesis and our SE-IBM. The SE-IBM creates absolute probabilities as an output and can be used directly in the likelihood. For the habitat-only model, we calculated the expected absolute probability

of use for each cell as the ratio of the true number of cells used ('population size'; 992) to number of cells available (44 592) multiplied by the relative probability obtained in the habitat suitability map. This approach makes the unrealistic assumption that cells are the unit of habitat selection (i.e. not groups of cells); however, given that our habitat suitability map is stationary across the entire region (i.e. there were high quality cells everywhere), we anticipate that this simple test will be approximately equal to the much more complex optimization procedure of placing packs in the best clusters of cells. For complete spatial randomness, the procedure was the same, except without multiplying by relative habitat suitability. Finally, we spatially cross-validated the forecast 2008 depredation risk map with the wolf depredation events documented in 2008 in the Italian Alps.

WOLF RECOLONIZATION PREDICTIONS AND DEPREDATION RISK ANALYSIS

We ran 10 000 replicate simulations (with parameters in Tables 1 and S1) to predict the future pack locations, pack numbers and population size for years 2013, 2018 and 2023. We used the 2008 locations of the 13 known packs (Fig. 1) and pack structures (i.e. numbers, sexes, ages of each individual) as the starting state of the simulation model. Absolute probability maps of wolf pack presence were obtained by averaging all replicate raster maps of pack presence (1 for pack present, 0 for absent). To forecast relative depredation risk (low, medium, high), we assumed that every non-rocky open pasture could be used by livestock during the summer and we multiplied these with the probability map forecasts of wolf pack presence, assuming that an increased number of settled packs in an area increase the depredation risk (Kaarinen, Luoto & Kojola 2009).

Results

MODEL CALIBRATION AND VALIDATION

From the model calibration procedure, we were able to find parameter combinations (Table S1) that fit perfectly for the non-spatial parameters; the spatial dispersal distance quantiles had an average 21% deviation between simulated values and data (Table 2).

Our five validation tests showed good support for the model. First, the ages at death for the 14 known individuals all fell within the 95% confidence intervals of the predicted ones from the best model scenario (Fig. S1). Moreover, of these known-fate individuals in the data, only three successfully dispersed and established new packs, consistent with model predictions. Secondly and thirdly, our predicted mean wolf population growth rate and population size were both very close to the estimated means from data, and these estimates fell within the 95% simulation intervals (Table S2). Fourthly, the spatial validation of the absolute probability forecast of wolf pack distribution in 2008 with the pack presence data for 2008 gave a highly significant ($P < < 0.0001$) Spearman-rank coefficient ($r_s = 0.969$), indicating high consistency with the independent data. This correlation would have been higher; however, the model equally predicted 0 wolves in the least suitable 4 of the 10 classes, and was thus penalized. Fifthly, AIC comparisons of the three models (complete spatial randomness, habitat-only and the current model) indicated unambiguous, large support

for the SE-IBM (best: SE-IBM, $\Delta\text{AIC} = 0$; second: habitat-only, $\Delta\text{AIC} = 3256$; third: CSR, $\Delta\text{AIC} = 15\,536$). Finally, the validation of the 2008 depredation risk map for the Italian Alps gave a highly significant test ($P < < 0.0001$), showing high consistency between independent data on 2008 wolf depredation events ($n = 109$) and simulations.

WOLF PREDICTIONS AND DEPREDATION RISK

Assuming unchanging habitat, mortality rate and protected status, the number of wolf packs and the wolf population size is predicted to increase from 2008 through the next 15 years on the Italian Alps range (Figs 3 and 4). After the 15 years of simulation from 2008, the Ligurian-Maritime Alps (i.e. the South-Western Alps) reached a high density level and probably attained saturation point (Fig. 4). Our simulations showed this region to be the main source for dispersing wolves repopulating the Alps from 1999 to 2008 (consistent with Fabbri *et al.* 2007; Marucco *et al.* 2009a). This source of dispersing wolves will shift to the Cozie Alps (i.e. the North-Western Alps) in subsequent years until 2018 (Fig. 4). By 2023, this recolonizing source will continue to move eastward to the Graie Alps, west of the lakes close to Switzerland (Fig. 4), allowing the recolonization of the Eastern part of the Alps, currently too far away for effective recolonization. With the same spatial trend, the depredation risk will increase over the Alps from West to East together with wolf expansion (Fig. 4). However, the trend of

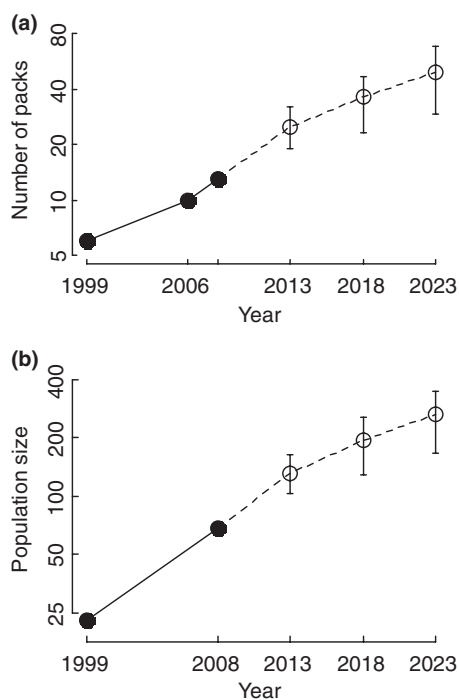


Fig. 3. Estimated (filled circles and solid lines; input data used in this study) and simulated (open circles and dashed lines) mean number of wolf packs with 95% confidence intervals (a) and mean wolf population size with 95% confidence intervals (b) through 2023 based on 100 replicate simulations of the spatially explicit, individual-based model of the wolf recolonization process over the Italian Alps. Simulations started with known packs and wolves in 2008.

the amount of pastures at low, medium and high risk of depredation is different, with increases in only low- and high-risk pastures, probably due to the trend in wolf recolonization (Figs 4 and 5).

Discussion

Our predictive model is one of the first attempts to produce year-specific spatial and temporal predictions of the natural recolonization of wolves in the Alps. The model enables conservation efforts to be prioritized in different areas, including measures to prevent livestock depredations before wolves move into high-risk areas in a given year. This ability to project the spatial and temporal expansion of small populations is critical to management and conservation (Carroll *et al.* 2003) and has been carried out for other carnivores species in Europe (Kramer-Schadt *et al.* 2004; Wiegand *et al.* 2004).

Dispersing wolves will travel through unfavourable areas, but pack establishment success is restricted to large expanses of higher-quality habitats (Mladenoff *et al.* 1995) and is dependent on pair establishment (Hurford, Hebblewhite & Lewis 2006). Therefore, in any wolf landscape analysis, it is fundamental to distinguish between predictions of wolf pack establishment (important in the context of wolf-human conflict such as livestock depredations) and of general wolf presence, which includes data on dispersing animals (data that our model produced, but is not shown here). Pack number estimates and location are the most useful information to describe wolf population expansion, especially for management purposes (Mech & Boitani 2003). Moreover, in the Italian Alps, where the landscape is human dominated and suitable habitat is heavily fragmented, habitat constraints on wolf pack establishment can reduce the carrying capacity for wolves. Carroll *et al.* (2003), in a modelling analysis for planning a wolf reintroduction programme in North America, suggested that social carnivores may be more vulnerable to environmental stochasticity and landscape fragmentation than their vagility and fecundity would suggest. Hurford, Hebblewhite & Lewis (2006) suggested that a reduced probability of finding wolf mates at low density (Allee effects) may slow recolonization rates and the establishment of new breeding pairs. Kojola *et al.* (2009) demonstrated that dispersing wolves in Finland, also capable of long-distance movements, do not reach the isolated small population resident on the Scandinavian peninsula because of barriers and human exploitation. Our study demonstrates that dispersing animals will continue to range long distances across the Alps, but pack establishment and the associated predation risks to livestock will lag far behind.

We predicted that in the next 15 years, from 2009 to 2023, the wolf pack density will increase in the Western Alps where probabilities of finding a mate will increase. In the Eastern part of the Alps, wolf densities will remain very low due to low probabilities of finding a mate, even with long-distance dispersals. These will increase the depredation risk in the Western Alps, because of high pack density, whereas in the Eastern Alps, the depredation risk will be lower (Figs 4 and 5). Nevertheless, the importance of packs as sources for colonizers will

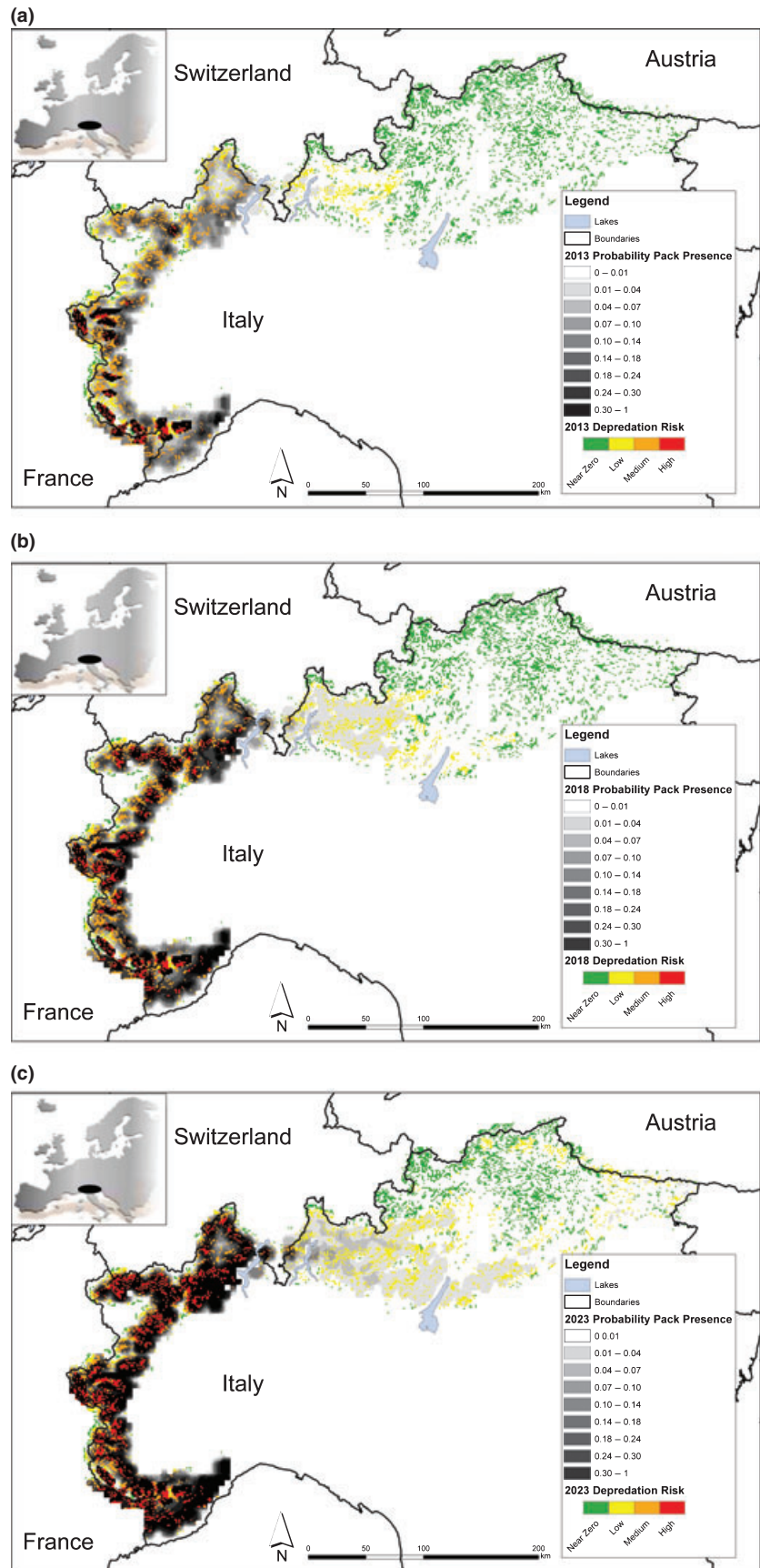


Fig. 4. Absolute probability maps which predict wolf pack locations and depredation risk in 2013 (a), 2018 (b) and 2023 (c) from the SE-IBM of the wolf recolonization process over the Italian Alps, with a starting scenario from 2008 over the next 5, 10 and 15 years, after 10 000 simulations. Note: uneven legend for plotting clarity.

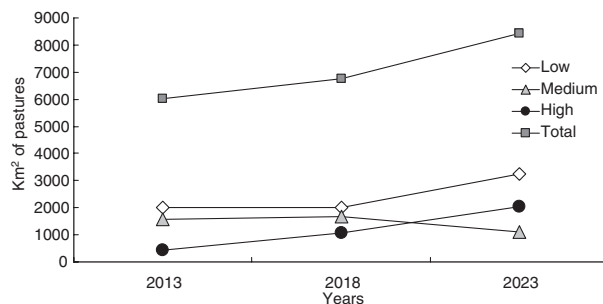


Fig. 5. Forecast area of pasture that is predicted to have low, medium and high levels of depredation risk in the Italian Alps.

shift from west to east during this time period. Finally, in the Central Alps, the large lakes, in combination with high human density nearby, will be likely to slow the trend for wolf expansion in the Eastern Alps. Although these predictions, in their qualitative form, are possible without this simulation approach, the particular time sequence, the role of given packs, and the quantitative estimates of the barriers and the assessments of local and regional risks are not.

LIMITATIONS OF MODELLING APPROACH

Although we can provide probabilities of pack establishment, we will underestimate the impact of stochastic events. For example, our model predicts that there is a low (but not zero) probability that wolves will establish reproductive packs east of the large lakes in the Central Alps by 2013. If in reality a pack does form there in say 2013, or if two long-distance dispersers establish a new pack, it may dramatically change the predictions for the next 10 years. For example, an isolated Scandinavian population of grey wolves, found by only two individuals, was recovered by the arrival of a single immigrant that suddenly resulted in exponential population growth (Vila *et al.* 2003). For these types of events, it is important to have simulation as part of an ongoing, adaptive management strategy, where rare events can be immediately incorporated into the model and re-projected.

Our model did not include any new migrants to or from the Italian Alps, including to or from the Apennines (the nearest population to the south), France (contiguous with the present distribution of wolves in the Italian Alps) or Slovenia (the closest population to the east that is currently expanding). For the current forecasts, we feel that the consequences of these assumptions are minimal. Current estimates suggest that 1.25–2.5 wolves per generation (i.e. 4 years) emigrate from the Apennines (Fabbri *et al.* 2007) but genetic data (Marucco *et al.* 2009a) indicate that all new packs since 1999, except one, came from packs identified and used in our model. Thus, there were no relevant immigrants from other sources. As the population increases and expands, however, it will become more important to also expand the model to the entire Alps ecosystem. Hence, the predictions are maybe conservative, because Switzerland and Austria might increase the area available for recolonization in the north of the lakes. Although, Switzerland has shown to not be highly tolerant to the presence of wolves,

hence the model might reflect reality anyway. Currently, although this impact is possibly low in the model, it may partly explain why our mean population size predictions were slightly (i.e. 4 wolves) below the actual number. As we further develop this model to incorporate genetic factors, the impact of immigrants from the Apennines and Slovenia will become more important as they will provide new alleles, which will be important when forecasting effective population size.

FUTURE CONSERVATION ISSUES AND MANAGEMENT IMPLICATIONS

Validation of models and their structure is important when they are a basis for management decisions (Grimm *et al.* 2005). Our validation used data that were withheld during model development and calibration, and we obtained sufficiently accurate fits for the wolf recolonization of the Italian Alps. Therefore, we have tentative confidence in our model as a decision support tool for implementing efforts to prevent livestock depredations. This potential 'early warning system' might be very useful because newly arrived wolves tend to have a greater impact on livestock than wolves that have been settled for several years (Linnell, Swenson & Anderson 2001; Marucco *et al.* 2009a), because shepherds learn how to implement preventive measures, promoting healthy coexistence. Thus, temporally specific predictions of wolf packs (not just individual presence) and high depredation risk can optimize preventive efforts by initiating management at an appropriate time before wolf pack establishment, promoting wolf–human coexistence and acceptance.

The wolf population in the Alps is likely to increase from the West to the East barring changes in its protected status. The high dispersal capability of wolves allows for long-distance dispersal (Boyd & Pletscher 1999) and potential observations of solitary individuals, but this will not necessarily indicate pack recolonization. At the same time, wolf pack density will increase in the Western Alps, increasing the importance of new sources of mortality, such as road kill and an increase in intra-species competition (Mech & Boitani 2003). Moreover, poaching can have an important impact on the population (Marucco *et al.* 2009a), and it will be important to evaluate the effects of different poaching levels on the future of the alpine wolf population. Falcucci *et al.* (2009) developed a spatial model based on presence and mortality data for the Apennine brown bear *Ursus arctos marsicanus* to identify attractive sink-like areas, important to define area-specific management interventions. These aspects should be incorporated in the future development of this model because they are key components of wolf population dynamics.

We predicted that the North-Central Alps, west of the lakes close to Switzerland, will be a source area important for effective wolf recolonization of the Eastern Alps. This area will be likely to have a high depredation risk within the next 15 years, hence preventive measures to limit livestock depredation should be promoted before wolf recolonization. At the same time, it will be important to restore or preserve a possible corridor near these large lakes to allow connectivity to the Eastern

Alps, a successful strategy for large carnivores in North America (e.g. Duke *et al.* 2001). These and other results and recommendations derived from this model can assist in wolf conservation and, in the future, can also help to determine the influence that land use and further human development may have on the spatial expansion and connectivity of the wolf population in the Alps.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Age of death of known wolves from real data and simulations.

Table S1. Parameters estimated during calibration phase

Table S2. Documented parameters used for validation of the model

Appendix S1. Calibration of the model.

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