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# Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence

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## Summary

**1.** The Amur or Siberian tiger *Panthera tigris altaica* forms a relatively small and disjunct population of less than 600 individuals in the Russian Far East. Because tigers in this region require large territories to acquire sufficient prey, current strictly protected areas, comprising 3·4% (10 300 $km^2$) of the region, are unlikely to prevent extirpation of the subspecies in the face of expanding forestry and external demand for tiger parts.

**2.** We used resource selection function models and spatially explicit population models to analyse the distribution and predict the demographic structure of the population to identify policy options that may enhance population viability.

**3.** A resource selection function model developed from track distribution data predicted that tigers were most likely to occur in lower altitude valley bottoms with Korean pine forest and low human impacts.

**4.** The results from the spatially explicit population model suggested that current tiger distribution is highly dependent on *de facto* refugia with low human impacts but without statutory protection, and that small increases in mortality in these areas will result in range fragmentation. Although an expanded reserve network only marginally increases tiger viability under current conditions, it dramatically enhances distribution under potential future scenarios, preventing regional extirpation despite a more hostile landscape matrix.

**5.** The portion of tiger range most resistant to extirpation connects a large coastal reserve in the central portion of the region with largely unprotected watersheds to the north. A southern block of habitat is also important but more severely threatened with anthropogenic disturbances. The results suggest that preserving source habitat in these two zones and ensuring linkages are retained between blocks of habitat in the north and south will be critical to the survival of the tiger population.

**6.** *Synthesis and applications*. Conservation priorities identified in this analysis differ from those suggested by a conservation paradigm focusing only on sustaining and connecting existing protected areas that has been applied to tiger conservation in more developed landscapes with higher prey densities. An alternative paradigm that assesses population viability in a whole-landscape context and develops priorities for both protected area expansion and increasing survival rates in the landscape matrix may be more appropriate in areas where tigers and other large carnivores coexist with low-density human populations. Although landscape connectivity merits increased emphasis in conservation planning, identification of landscape linkages should be tied to broad-scale recommendations resulting from spatial viability analyses in order to prevent misdirection of resources towards protecting corridors that add little to population persistence.

*Key-words*: Amur tiger, connectivity, conservation planning, focal species, population viability analysis, resource selection functions, SEPM

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## Introduction

Conservation planners must identify and protect critical habitat for vulnerable species in the face of both a rapidly expanding human footprint and a scarcity of detailed biological data on which to base decisions. Habitat models are one tool for exploiting existing, often heterogeneous, data sets to the best advantage in the planning process. The remaining population of less than 600 Amur, or Siberian, tigers *Panthera tigris altaica* Temminck exists in a landscape that is predominantly unprotected but with relatively low human population densities (Matyushkin *et al.* 1999; Miquelle *et al.* 1999a). Therefore planners urgently need to identify areas outside the current protected area network that may be critical for the persistence of this small population. Although the Amur tiger has been the subject of long-term intensive field studies and extensive track surveys (Miquelle *et al.* 1999b, 2005b; Kerley *et al.* 2003; Goodrich *et al.* 2005a, 2005b; Miquelle, Smirnov & Goodrich 2005), little is known of the relative contribution of different areas and habitats of the region to overall population viability. However, it appears likely that the current proportion of the region within strictly protected areas (3·4%, 10 300 km$^2$) will be insufficient on its own to prevent extirpation of the subspecies in the face of expanding forestry and commercial development, external demand for tiger parts for traditional Chinese medicine, and the difficulties in preventing, or at least reducing, current levels of poaching (Miquelle *et al.* 2005a).

We used resource selection function models (RSF; Boyce & McDonald 1999) and spatially explicit population models (SEPM; Dunning *et al.* 1995) to analyse the distribution and predict the demographic structure of the Russian Far East (RFE) tiger population, in order to identify trends that may compromise viability or, conversely, offer opportunities for restoration of tiger populations and connectivity. In the first stage of analysis, we developed regional-scale static distribution models that relate geographical information system (GIS) habitat data to the occurrence probability of tiger in differing habitats. In the second stage, we incorporated these static habitat models into an SEPM, PATCH (Schumaker 1998). SEPM such as PATCH, which evaluate distribution and demography across the entire landscape, are appropriate in this situation because tigers remain widespread outside the current system of protected areas and, as a result of the large home range requirements of tigers in this region (Goodrich *et al.* 2005a), the persistence of tigers in current protected areas is dependent on maintaining connectivity and alleviating edge effects (Miquelle *et al.* 1999a). The goals of the study were to use existing data sources on regional tiger distribution and demography to provide a foundation for prioritization and land-use planning for tigers in the RFE, and to provide an example of landscape planning that might be applicable for tigers in other portions of their range, as well as for other large carnivores. Secondarily, the results may help evaluate the relative importance of direct human impacts on tiger viability (i.e. on tiger survival) vs. indirect human impacts (i.e. on tiger fecundity via prey depletion) and may provide an illuminating contrast with lessons derived from less data-intensive methods, such as least-cost path (LCP) analysis, that have been used for regional-scale tiger conservation planning in more human-dominated landscapes (Wikramanayake *et al.* 2004).

## Materials and methods

### STUDY AREA

The geographical range of Amur tigers in the RFE stretches south to north throughout the length of Primorski Krai (province) and into southern Khabarovski Krai for almost 1000 km (Fig. 1). This region, encompassing approximately 300 000 km$^2$, is bounded by China to the west, North Korea to the south and the Sea of Japan to the east. The majority of the region is represented by the Sikhote-Alin mountains, a low (500–800 m a.s.l.) mountain range that parallels the Sea of Japan from Vladivostok in the south to the mouth of the Amur River in the north.

Tigers are restricted to forest-covered landscapes, which includes more than 70% of Primorski and southern Khabarovski Krais (210 000 km$^2$). Typical tiger habitats are Korean pine *Pinus koraiensis* Sieb. & Zucc. broad-leaved forests. The majority of these forests have been selectively logged, and human activities, in association with fire, have resulted in conversion of many low altitude forests to secondary oak *Quercus mongolica* Fisch. and birch *Betula costata* Trautv. *Betula lanata* Regel and other birch species forests (Bogatov *et al.* 2000). Above 700–800 m, spruce *Picea ajanensis* Fisch.–fir *Abies nephrolepis* Trautv. ex Maxim. forests prevail in central Sikhote-Alin. This altitudinal transition zone to predominantly coniferous forest types decreases northwards until, at 47′20″ latitude, coniferous forests occur along the coastline.

The faunal complex of the region is also represented by a mixture of Asian and boreal life forms. The ungulate complex is represented by seven species, with red deer *Cervus elaphus* L., roe deer *Capreolus pygargus* Pallas and wild boar *Sus scrofa* L. being the most common throughout the Sikhote-Alin mountains but rare in higher altitude spruce–fir forests. Sika deer *Cervus nippon* Temminck are restricted to the southern half of the Sikhote-Alin mountains. Musk deer *Mochus moschiferus* L. and Manchurian moose *Alces alces* cameloides Milne-Edwards are associated with the conifer forests and are near the southern limits of their distribution in the central Sikhote-Alin mountains.

Detailed information on tiger ecology (estimates of survival rates, movement and territory size) were derived from radio-telemetry studies conducted in and around Sikhote-Alin biosphere zapovednik (SABZ)

**Fig. 1.** Study area for Amur tiger in the Russian Far East showing protected areas mentioned in the text (boundaries as of 2000) and tiger distribution based on the 1996 full range survey.

(Miquelle, Smirnov & Goodrich 2005), which is located in the central portion of tiger range and includes coastal and inland habitat on both slopes (east and west) of the Sikhote-Alin mountains. Survivorship was estimated using Cox proportional hazards model on 42 radio-collared tigers, and cause of mortality was derived from examination of remains in the field, pathology examinations of samples and (in the case of poaching events) information derived from local people. Home range sizes were derived from 14 and five adult resident females and males, respectively.

### DATA SOURCES

We developed RSF models of tiger distribution from data on the occurrence of tracks in snow on routes throughout the tiger range in the RFE surveyed in 1996. Standard Russian survey protocols used to estimate tiger distribution and abundance are based on two-staged track counts in winter. The entirety of tiger habitat (in 1996 134 621 km$^2$) is divided into survey units (averaging 237 km$^2$ in size in 1996; Matyushkin *et al.* 1999). A single hunter, trapper or conservation officer (all of whom spend weeks at a time in the forest) working within each unit is trained to record tiger tracks encountered over a 3-month period. At the end of this period, in mid-February, one or more survey routes (a total of 1795 in 1996) of at least 10 km are covered. Routes are placed non-randomly in survey units to maximize the probability of encountering tiger tracks. Variability in tiger track density estimates has been shown to increase with decreasing route length (Hayward *et al.* 2002), and a 10-km minimum was selected to reduce variability in tiger track density but also in acknowledgement of the logistic constraints on winter travel. The locations of tiger tracks were recorded on 1 : 100 000 maps. Although survey effort was poorly estimated in the first stage, it represents a much greater effort (multiple daily routes covered) than the second stage. Using a two-stage sampling design based on double coverage of transects within survey units within a single winter, radio-collared tigers were 'captured' 75% of the time in a single survey but 96% in double surveys (D. Miquelle, unpublished data). Thus the two-stage sampling protocol comes close to representing a true presence–absence design.

Habitat data evaluated as potential explanatory variables included both natural characteristics and human influences on the landscape. Habitat variables fell into four classes: vegetation, topographic (latitude-adjusted altitude, slope, transformed aspect (Beers, Dress & Wensel 1966), slope position), climatic (mean annual temperature and precipitation, mean January temperature and precipitation; Hijmans *et al.* 2004) and human impact (road density, interpolated population density, protected status and habitat effectiveness). Habitat effectiveness is a composite metric for relative mortality risk to large carnivores based on roads and human population (Merrill *et al.* 1999). Data layers, with the exception of climatic data (Hijmans *et al.* 2004), were compiled by TIGIS (Pacific Institute of Geography GIS Center, Vladivostok, Russia).

The scale of the input vector data layers was 1 : 500 000, while that of input raster data varied from 100 m (topographic) to 1 km (climatic). First, all data were resampled to 1 km to provide a consistent resolution. Secondly, habitat variables were evaluated at two spatial scales, that of the area within a 100-m buffer surrounding the survey routes, and a landscape scale within a 150-km$^2$ moving window around each route. The moving-window analysis was equivalent to averaging habitat values within a buffer of 7 km, the mean daily travel distance of female tigers in this region. Because moving-window metrics tend to be strongly intercorrelated over differing window sizes at larger scales, the 150-km$^2$ metrics probably also approximate those measured at the scale of a female tiger home range in the region (*c.* 400 km$^2$; Goodrich *et al.* 2005a).

A set of potential explanatory variables was developed based on field knowledge, and used to predict the probability of detecting tiger tracks on a transect (a binary response variable). We identified an optimal RSF model based on information criteria (AIC; Akaike 1973) and model interpretability and generality (Taper 2004). The form of the univariate relationship (e.g. linear or quadratic) between tiger occurrence and individual variables was first evaluated with generalized additive models (GAM; Hastie 1993). The initial 52 vegetation types were collapsed into 11 types based on dominant cover type, and then grouped into five types based on similarity of model coefficients. Stepwise analysis using AIC (Venables & Ripley 1997) was then used to identify an optimal multivariate model. We validated the RSF model by assessing how well it predicted track detection in a separate data set of tiger track locations reported during chance encounters by people active in the forest (hunters, forest guards, conservation officers, etc.) collected across the entirety of tiger habitat throughout the winter of 1996 (all-winter data set; Matyushkin *et al.* 1999).

We assumed that adult tiger survival rates are largely driven by human-related mortality factors (Kerley *et al.* 2002; Goodrich *et al.* 2005b) and therefore grouped one set of RSF model variables thought to affect tiger survival (human impact-related variables such as road density, human population and habitat effectiveness). Other variables, including habitat type and climate parameters, are likely to be more closely related to the productivity and prey biomass of an area and thus the habitat potential or productivity in the absence of human influences, which we assumed to be correlated with tiger fecundity (Carroll *et al.* 2003; Naves *et al.* 2003). The division of variables in a distribution model into mortality- and non-mortality-related is defensible for tigers and other large carnivores for which most mortality is directly caused by human persecution (Naves *et al.* 2003; Goodrich *et al.* 2005b). Prey abundance is a more proximate influence on tiger fecundity than vegetation type and other bioclimatic factors (Karanth *et al.* 2004). Therefore we compared fecundity classes derived from the RSF model with those derived from models of prey biomass developed from prey track transect data collected as auxiliary data during the course of the 1996 simultaneous surveys for tiger (Matyushkin *et al.* 1999; C. Carroll & D. Miquelle, unpublished data). Prey data were available as summarized per management unit, rather by individual survey transect. Encounter rates with tracks of the four major prey species (red deer, roe deer, Sika deer and wild boar; Miquelle *et al.* 1996) were converted to prey density by means of the Formozov equation (Stephens *et al.* 2006) using mean daily travel distances as documented from the SABZ (Stephens *et al.* 2006). In order to extrapolate prey densities across the region, we then developed linear regression models of square-root transformed prey densities using the environmental variables listed above. We produced a composite ungulate biomass index as the sum of prey abundance by species multiplied by the mean biomass of adult females of that species (Miquelle, Smirnov & Goodrich 2005) and tiger prey electivity estimates (based on data from Miquelle *et al.* 1996).

We input the GIS data produced by the RSF models and prey analysis into an SEPM, PATCH, a female-only model designed for studying territorial vertebrates (Schumaker 1998). PATCH links the survival and fecundity of individual animals to GIS data on mortality risk and habitat productivity at the scale of an individual territory (Schumaker 1998). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The different habitat types in the GIS maps are assigned weights based on the relative levels of fecundity and survival rates expected in those habitat classes. Survival and reproduction rates, derived from published field studies, are then supplied to the model as a population projection matrix

**Table 1.** Demographic parameters used in the PATCH simulations. The scaling of demographic parameters by habitat rank is shown for the adult (year 3+) age class. Cub and subadult parameters also scale by the same proportions

| Parameter | Value |
|---|---|
| Base parameters | |
| Home range size | 360 km$^2$ |
| Maximum dispersal distance | 54 km |
| Fecundity | |
| First reproduction at age | 3 |
| Maximum female young per female per year | 0·851 |
| Maximum survival (female) | |
| Cub | 0·632 |
| Year 2 | 0·747 |
| Year 3+ | 0·863 |

Scaling of parameters by habitat rank

| Adult fecundity | | Adult survival | |
|---|---|---|---|
| Rank | Value | Rank | Value |
| 1 | 0·298 | 1 | 0·345 |
| 2 | 0·383 | 2 | 0·432 |
| 3 | 0·426 | 3 | 0·518 |
| 4 | 0·468 | 4 | 0·604 |
| 5 | 0·553 | 5 | 0·647 |
| 6 | 0·596 | 6 | 0·690 |
| 7 | 0·681 | 7 | 0·734 |
| 8 | 0·723 | 8 | 0·777 |
| 9 | 0·808 | 9 | 0·820 |
| 10 | 0·851 | 10 | 0·863 |

(Table 1) (Caswell 2001). The model scales the matrix values based on the mean of the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output (Table 1). The continuous values in the RSF-derived GIS data were sliced into 10 equal-area (fecundity) or equal-interval (survival) ranked classes (Fig. 2a,b and Table 1). Habitat rankings were calibrated to demographic values by comparing the mean habitat rankings within intensive demographic study areas (i.e. over the composite home ranges of the SABZ study animals; Goodrich *et al.* 2005a) with the survival (Goodrich *et al.* 2005b) and fecundity (Kerley *et al.* 2003) rates from those same areas, as well as by comparisons with maximum and minimum demographic rates reported from long-term studies in other regions (Smith & McDougal 1991; Smith 1993). Because habitat within the SABZ population boundary showed a rank of 80% of the maximum value in the GIS fecundity model (Fig. 2b) and a rank of 95% of the maximum value in the GIS survival model (Fig. 2a), we set the maximum demographic rates in the base scenario (Table 1) as those reported for the SABZ population (Kerley *et al.* 2003; Goodrich *et al.* 2005b) divided by 0·8 and 0·95, respectively. However, we tested the sensitivity of model results to this assumption that SABZ demographic rates were exceeded in other areas of the region. Because a strong positive effect of protected area status on tiger survival and fecundity has been documented in field studies (Miquelle *et al.* 2005a) but may not be evident in regional-scale RSF models, we analysed the sensitivity of PATCH predictions to setting survival rates in strictly protected areas (zapovedniks) to the maximum ranking, and simultaneously increasing the fecundity ranking in zapovedniks by two ranks and within partially protected areas (zakazniks) by one rank.

The PATCH simulations incorporate demographic stochasticity with a random number generator. In the case of survival, a uniform random number between zero and one is selected. An individual dies if this number is greater than the scaled survival probabilities produced from the habitat rankings (Table 1). A random number is also selected to force the number of offspring in a year to take on integer values. Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements were drawn from a normal (fecundity) or beta (survival) distribution. In the scenarios incorporating environmental stochasticity, a coefficient of variation of 25% for fecundity and mortality was used. As no data were available on environmental stochasticity in the region's tiger population, this was a conservative estimate based on values used in previous population viability analyses (PVA) for large felids (Eizirik, Indrusiak & Johnson 2002).

Adult tigers are classified as either territorial or non-territorial (floaters). The movement of territorial individuals is governed by a site fidelity parameter, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation (tendency to continue in the direction of the last step), and attraction to higher quality habitat. However, there is no knowledge of habitat quality beyond the immediately adjacent territories. Floaters do not experience additional mortality risk because of dispersal but rather have yearly mortality rates based on the habitat class they occupy at the end of that year's dispersal path. Although simplified SEPM may be sensitive to variation in parameters such as dispersal distance and behaviour (Ruckelshaus, Hartway & Karieva 1997), PATCH results in most systems appear more sensitive to habitat ranking and demographic parameters. This is because of the presence of large patches with low extinction probability that stabilize metapopulations and reduce their sensitivity to dispersal (Carroll *et al.* 2004).

In order to evaluate the relative vulnerability of different portions of tiger range to several potential threats and policy options, we created five PATCH scenarios spanning a range from habitat degradation to restoration. These scenarios were as follows. (i) Current conditions. (ii) Increased poaching pressure in the landscape matrix (lands other than strictly or partially protected areas) as a result of relaxed enforcement or

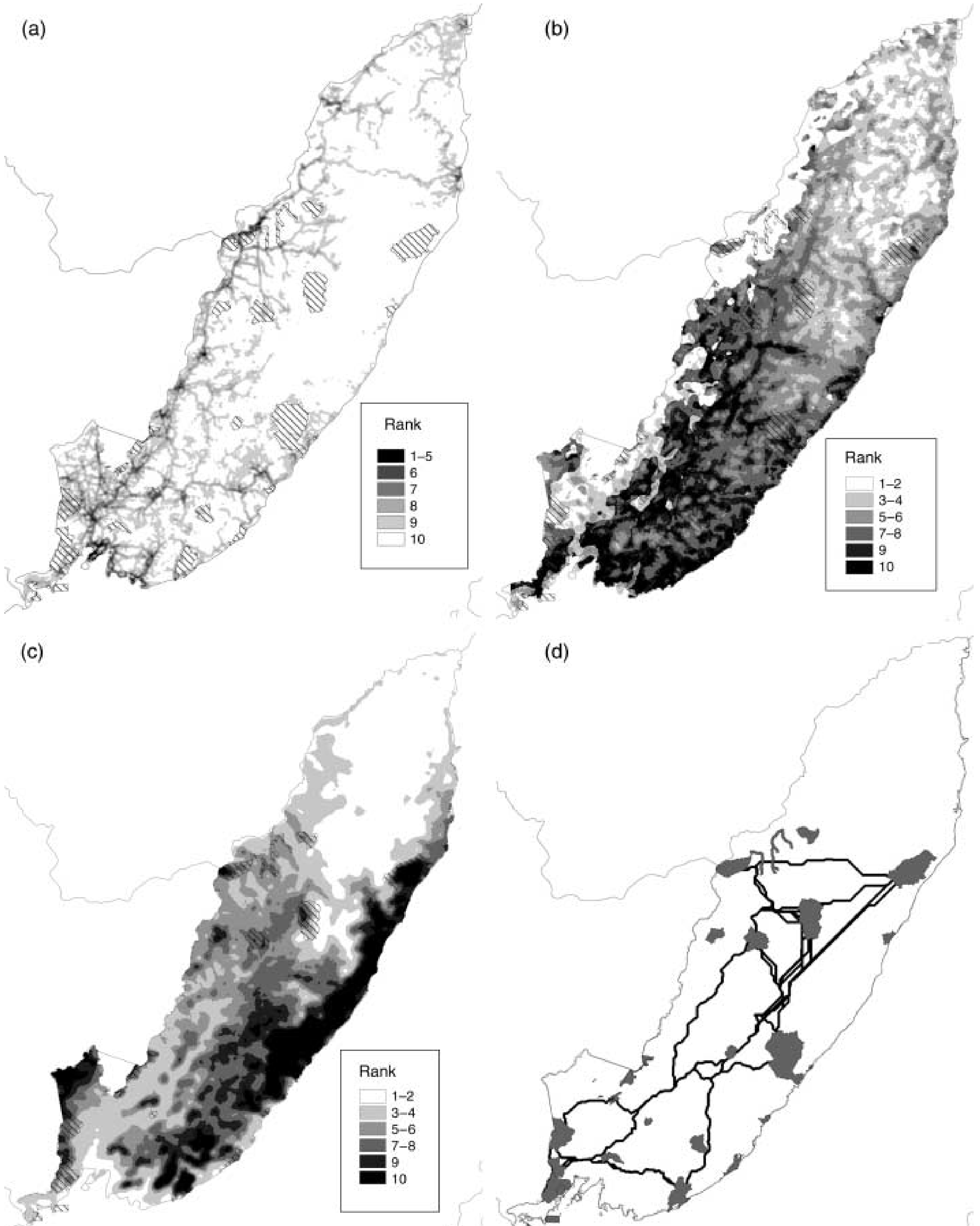

**Fig. 2.** Results from the resource selection function and least-cost path analysis for tiger in the Russian Far East. The continuous values in the resource selection function output were divided into 10 equal-area (fecundity) or equal-interval (survival) ranked classes. (a) Gradients in tiger survival rates as derived from the habitat effectiveness variable of the resource selection model. Protected areas are shown in crosshatch. (b) Gradients in tiger fecundity rates as derived from the remaining variables of the resource selection model: vegetation type, latitude-adjusted altitude and slope position. (c) Gradients in tiger fecundity rates as derived from prey biomass models developed from prey encounter rates on tiger survey transects. (d) Least-cost path network connecting major protected areas within the tiger range in the Russian Far East. The cost of paths in the network was based on the inverse of habitat effectiveness, thus paths sought to avoid roads and developed areas.

increased demand for tiger parts, expressed as a one rank decline in survival rate. (iii) Renewed logging of Korean pine *Pinus koraiensis*, a high-value timber species whose harvest is currently restricted. Logging would affect tigers primarily through increased road density. Increased logging and resultant increased road density and poaching pressure in the Korean pine forest type was expressed as a one rank decline in survival rate. (iv) Changes in management of zone 1 forests. Russian Forest Service lands are zoned into three categories, which largely dictate what types of exploitation can occur. Zone 1 forests, which are largely exempt from commercial logging, could approximate the current high value of zapovedniks as tiger habitat (Miquelle *et al.* 2005a) if road closures and increased law enforcement reduced access and poaching pressure. We set the survival rank of the larger blocks of zone 1 forests in Primorski Krai, as well as all zakazniks, to the maximum value (Table 1). This effectively increased the extent of the protected area network from its current 7·17% (21 400 km$^2$) of the region (3·44% strictly protected and 3·73% partially protected) to 13·10% (39 200 km$^2$). (v) A combination of scenarios (ii) and (iv) such that the expanded protected area network is surrounded by a more hostile landscape matrix.

Sensitivity analysis of the PATCH results involved comparison of four scenarios. (i) With (base scenario) and without environmental stochasticity. (ii) Without (base) and with enhanced fecundity and survival within strictly protected areas. (iii) With fecundity rankings derived from the tiger RSF model (base) vs. from models of prey abundance. (iv) Without (base) and with an alternate assumption that the demographic parameters documented in the SABZ population were the maximum rates shown by tigers in the region.

### IRREPLACEABILITY/VULNERABILITY ANALYSIS

We adapted an approach that sets priority areas for conservation action based on their irreplaceability and vulnerability, in order to minimize the loss of options for conservation planning during an interim period where new reserves are being achieved in some areas while habitat loss is occurring elsewhere (Pressey & Taffs 2001). An area's irreplaceability is the relative contribution it makes to reaching a conservation goal, here species persistence (Pressey & Taffs 2001). We defined irreplaceability in this context as the relative value of an area as source habitat (Carroll *et al.* 2003). Vulnerability, the likelihood that a site's conservation value will be reduced over time, is measured here as the predicted decline in demographic value (lambda) between low threat (scenario i) and high threat (scenarios ii and iii) scenarios. We created a composite metric consisting of the sum of irreplaceability and vulnerability averaged over both scenario contrasts. This took the form $Y = 2\lambda_1 - (\lambda_2 + \lambda_3)/2$, where $\lambda_i$ indicates lambda values from scenario $i$. This metric was assessed for each of the region's 32 administrative counties (Fig. 3d). Sites with high index values, and hence high irreplaceability and high vulnerability, are the highest priority sites for conservation (Pressey & Taffs 2001), and can be characterized in this context as 'threatened source habitat' (Carroll *et al.* 2003).

In order to compare priority areas suggested by a SEPM-based analysis with those suggested by a LCP-based analysis, we created a simplified corridor network between the region's seven largest protected areas. This simplified analysis served as a conceptual tool for contrasting general aspects of SEPM-based and LCP-based planning rather than as a detailed conservation plan. The cost surface was based on the inverse of the habitat effectiveness metric used in the RSF and PATCH models. Therefore the LCP algorithm (Ray 2005) sought to link protected areas by routes that minimized encounters with roads and humans. Because human-induced mortality is the primary factor affecting the ability of habitat generalist large carnivores to survive the dispersal event, it is a major input to most LCP analyses for these species (Singleton, Gaines & Lehmkuhl 2004). However, a fully developed LCP analysis would also be likely to include additional variables such as altitude and habitat type (Wikramanayake *et al.* 2004).

## Results

The optimal RSF model (model 1) included variables for vegetation type, latitude-adjusted altitude, slope position, habitat effectiveness and survey effort ($n = 1178$, d.f. = 9, AIC = 1466·94; Table 2). Based on this model, tigers were most likely to occur in lower altitude valley bottoms with Korean pine forest and low human impacts. Models at the landscape scale (150 km$^2$) performed slightly better than those at the route scale (AIC of transect-based analogue of model 1 = 1474·08). The model successfully predicted tiger distribution for the validation data set, the all-winter track data ($t = -7{\cdot}2929$, d.f. = 693, $P < 0{\cdot}0001$, two-sample $t$-test comparing predicted values on routes with and without detections).

The fecundity and survival layers derived from the vegetation-based RSF model (Fig. 2a,b) showed the strong north–south gradient in habitat productivity and human impacts in this region. The fecundity model developed from the prey abundance analysis (Fig. 2c) differed from that derived from the tiger RSF model in that protected areas and the north-eastern coastal area showed higher values in the prey-based model, and northern interior forests showed lower values.

### PATCH RESULTS

The PATCH simulations were performed using the base demographic values shown in Table 1. Sensitivity analysis of the demographic parameters suggested that model results were highly sensitive to small changes in survival rates but were less sensitive to variation in fecundity values. In base scenario (i), survival within the SABZ study population was assumed to be 95% and fecundity was assumed to be 80% of the maximum regional rate. If, however, SABZ survival rates were assumed to represent the regional maximum, the tiger distribution contracted to three isolated populations, the largest stretching northwards from SABZ to the

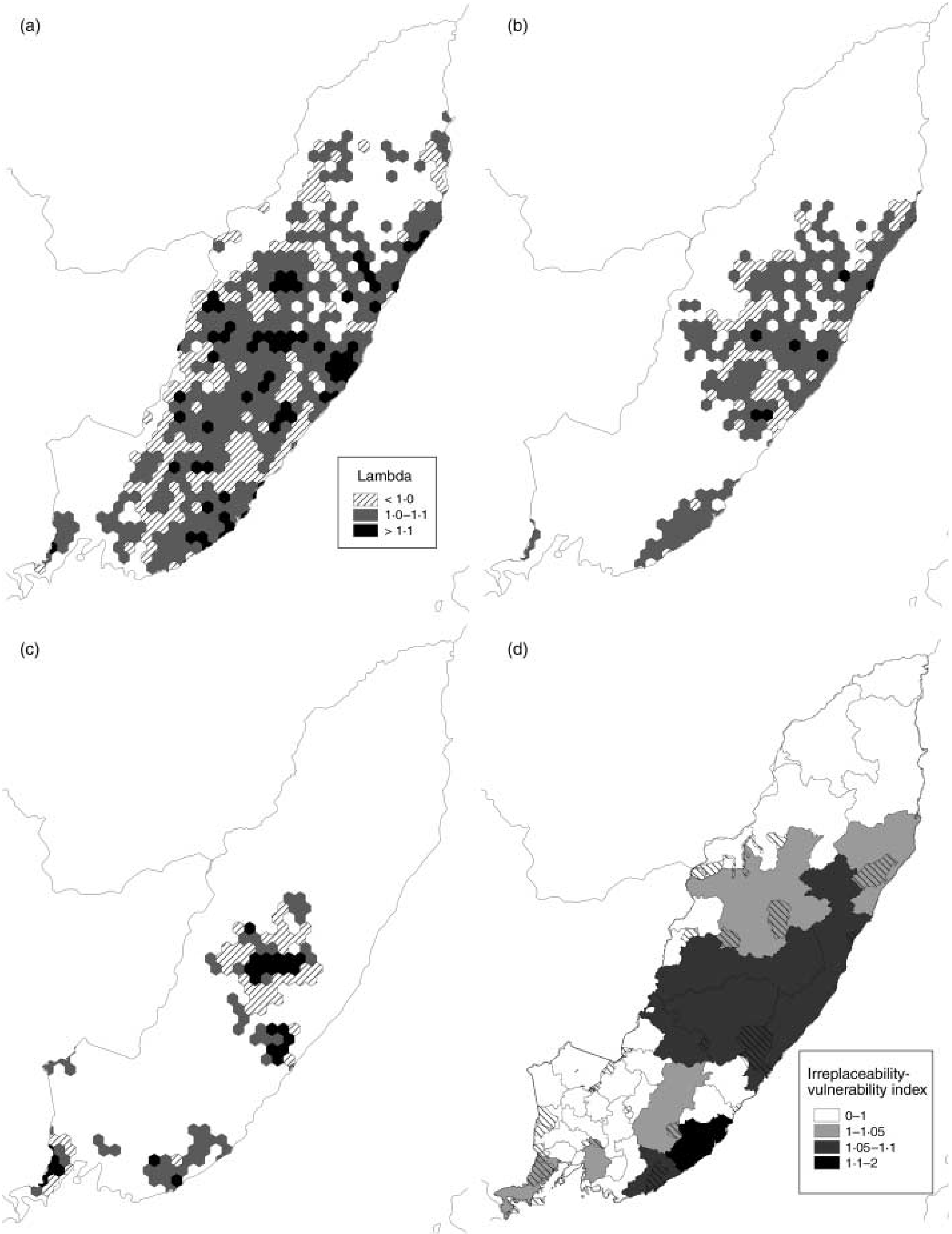

**Fig. 3.** Results from a spatially explicit population model of the demography and distribution of Amur tiger. (a) PATCH results from scenario (i) (current conditions). Predicted lambda values for areas with greater than 50% predicted occupancy in Fig. 2a–c are shown as in the legend. Areas with less than 50% predicted occupancy are shown in white. (b) PATCH results from scenario (iii) (increased logging of Korean pine). (c) PATCH results from scenario (v) (expanded protected area system embedded in a landscape matrix experiencing higher poaching pressure). (d) Irreplaceability–vulnerability index values for administrative units within the tiger range in the Russian Far East. The irreplaceability–vulnerability index is derived by comparison of PATCH results from scenario (i) (low threat) with those from scenarios (ii) and (iii) (high threat).

Bikin River. Alternately, if SABZ fecundity rates were assumed to represent the regional maximum, the distribution was similarly fragmented but the three populations, especially the northernmost, were more extensive. Only by assuming that both SABZ survival and fecundity rates were exceeded elsewhere in the region (base scenario i; Fig. 3a) did results approximate the current tiger distribution as documented from

**Table 2.** Optimal model resulting from the resource selection function analysis of tiger snow transect data

| Variable | Coefficient | SE | $t$ | $P$ (Wald test) |
|---|---|---|---|---|
| Vegetation-based model | | | | |
| Transect length (km) | 0·0614 | 0·0080 | 7·6483 | < 0·0001 |
| Vegetation type | | | | |
| Oak | 1·6005 | 0·6726 | 2·3797 | 0·0173 |
| Korean pine | 2·1776 | 0·6636 | 3·2815 | 0·0010 |
| Spruce | 1·8749 | 0·6967 | 2·6912 | 0·0071 |
| Other forest | 1·7008 | 0·6957 | 2·4448 | 0·0145 |
| Latitude-adjusted altitude | –0·0011 | 0·0003 | –4·3623 | < 0·0001 |
| Slope position | –0·0397 | 0·0132 | –3·0027 | 0·0027 |
| Habitat effectiveness | 7·7631 | 1·7805 | 4·3602 | < 0·0001 |

**Table 3.** Mean percentage of the Russian Far East study region occupied by tigers in the alternate PATCH model scenarios (Fig. 2). Scenarios designated 'no ES' were simulated without environmental stochasticity. Scenarios with 'protected areas adjustment' had survival and fecundity rates increased within strictly protected areas to assess sensitivity to alternate assumptions regarding habitat quality in those areas

| Scenario | Base | No ES | Protected areas adjustment |
|---|---|---|---|
| 1 | 55·38 | 60·94 | 59·37 |
| 2 | 2·92 | 3·52 | 6·85 |
| 3 | 30·69 | 36·73 | 38·93 |
| 4 | 63·02 | 66·24 | 64·20 |
| 5 | 17·57 | 19·86 | 19·95 |
| Prey-based | 43·58 | 47·33 | 45·91 |

the 1996 survey data (Fig. 1), which is relatively continuous throughout Primorski and southern Khabarovski Krais. Under this base scenario, a relatively continuous zone of source habitat through the interior and coastal portions of Primorski and southern Khabarovski Krais was bisected by sink habitat along the main access road to the coastal portion of central Primorski. Vulnerable areas appeared to exist to the south of the highway (Lazovski and Ussuriski zapovedniks). In addition to the two large habitat blocks created by this division, isolated populations were predicted in the southern extreme of the region along the Chinese border (Fig. 3a). Scenario (ii) (increased poaching) caused general extirpation of the regional population, with a remnant refugia centred in SABZ (Table 3). Scenario (iii) (increased road building in Korean pine zones) resulted in fragmentation of the tiger range into a large block north of the coastal access road, a smaller central coastal block anchored by Lazovski zapovednik and Vasilkovski zakaznik, and small isolated populations along the southern border (Fig. 3b). Scenario (iv) (an expanded zapovednik system under current conditions) produced results similar to that of scenario (i) but with strengthened populations along the southern border (Table 3). Scenario (v) (an expanded protected area system with increased poaching in matrix) showed, in contrast to scenario (ii), continued occupation of the northern, central and Chinese border habitat blocks, although reduced in size compared with scenarios (i) and (iii) (Fig. 3c and Table 3).

The addition of environmental stochasticity to the PATCH simulations had relatively small effects on model results under current conditions (scenario i) because the large, single interconnected population provided a buffer from chance fluctuations. Environmental stochasticity caused the greatest impact where distribution was relatively fragmented (e.g. scenario iii), as a large proportion of the range in these scenarios consisted of sink habitat surrounding small isolated source areas (Table 3). Increasing survival and fecundity rates within protected areas also had the greatest effect in scenario (iii), resulting in expansion of the southern edge of the northern habitat block and increased viability in the central and border populations (Table 3). Overall, changes associated with increased demographic rates within protected areas were not pronounced (Table 3), as these areas generally already had high survival rates as a result of low road and human population densities. Alternative PATCH scenarios in which fecundity was based on prey models resulted in less occupied ranges in the interior mountains and overestimation of tiger distribution along the northern coastal region.

### IRREPLACEABILITY AND VULNERABILITY ANALYSIS

Areas with high irreplaceability and vulnerability in both scenario contrasts included the southern coast near Vasilkovski zakaznik and Lazovski zapovednik and, to a lesser degree, the central portion of tiger range from SABZ eastwards along the Iman and Bikin rivers (Fig. 3d). The simplified LCP network identified multiple corridor options connecting SABZ northwards to zakazniks on the border of Khabarovski Krai, as well as more circumscribed corridors extending from these areas to protected areas in southern Primorski Krai (Fig. 2d).

## Discussion

Abiotic factors such as climate and resulting gradients in productivity are typical limiting factors for carnivores at their northern range boundaries (Ferguson & McLoughlin 2000). For the Amur tiger, prey productivity and distribution is limited to the north by such abiotic factors, while to the south high human impacts have fragmented formerly continuous ranges and isolated the Russian population as a range fragment containing less than 600 individuals. Although the national strategy for conservation of Amur tigers calls for a zoning process to identify and protect tiger habitat (SCRFPE 1996), and there exist survey data over the entire range of tigers (Matyushkin *et al.* 1999) as well as detailed ecological data (Miquelle, Smirnov & Goodrich 2005), much uncertainty remains concerning how best to identify critical tiger habitat. Despite their complexity, modelling techniques such as SEPM that link survivorship and fecundity to landscape parameters provide a means of exploiting existing data to the best advantage in the planning process.

### VALUE OF RESOURCE SELECTION FUNCTION MODELS

The RSF modelling results are useful in interpreting biological limiting factors to tiger distribution as well as for predicting tiger distribution in areas not surveyed. Earlier distribution analyses based solely on the degree of range overlap suggested only weak associations between tiger distribution and Korean pine forests (Miquelle *et al.* 1999b), while the RSF modelling, which relied on finer-scale presence–absence and vegetation data, suggests a stronger relationship between the two. While tiger distribution is by no means restricted to Korean pine forests, remaining forest tracts of this type are often high-quality habitat for key prey species (red deer and wild boar). The RSF model also confirmed earlier assessments (Miquelle *et al.* 1999b) that riverine forests are favoured in winter; prey densities are often higher in these habitats and valley bottoms often provide easy travel corridors for tigers as well (Matyushkin *et al.* 1999). Although the snow transects used in the analysis had a minimum length of 10 km, the wide variation in transect length above this threshold caused survey effort (length of transect) to be included in the final RSF model.

The high significance of habitat effectiveness in our RSF results suggests that tiger distribution is strongly limited by human impacts, which can be approximated by surrogates such as road density and human population density. Our results suggest that the most productive habitat in the RFE is also the most impacted by humans. Therefore tigers, which must persist in an intermediate zone with sufficient productivity yet low human presence, may be vulnerable to small increases in human-caused mortality. Surprisingly, protected area status, as distinct from human impact factors, was not a significant explanatory variable in the RSF models, perhaps because of the small size of most protected areas in comparison with mean territory size for tigers in the RFE. Other analyses using long-term intensive monitoring data have found tiger track density and cub density to be significantly higher within protected areas than within paired control areas (Miquelle *et al.* 2005a). These contrasting results may be the result of the lower spatial and temporal sampling intensity in the 1996 survey data vs. the monitoring data set.

Comparison of the fecundity estimates derived from the tiger RSF model with those derived from prey abundance models suggests that estimates of fecundity and survival derived from carnivore distribution may be superior to more direct estimates based on prey density if, as is the case here, prey encounter data are of poorer quality than presence–absence data for the focal large carnivore species. However, given that carnivore distribution and densities are clearly linked to prey distribution and abundance (Carbone & Gittleman 2002; Miquelle *et al.* 2005b), improved regional prey abundance data would none the less be valuable.

### VALUE OF SPATIALLY EXPLICIT POPULATION MODELS

Because low prey densities force tigers to retain large territories to ensure adequate prey availability (Miquelle, Smirnov & Goodrich 2005), conservation of Amur tigers requires a vast, intact forest ecosystem (Miquelle *et al.* 1999a). Because of these large area requirements, the tiger may be an appropriate umbrella species for biodiversity conservation planning in the region (Miquelle *et al.* 1999a; Bogatov *et al.* 2000; Sergio *et al.* 2006). A spatially explicit population model such as PATCH, by allowing assessment of the demographic effects of habitat changes in the landscape as a whole, provides an effective tool for analysing threats in this landscape context. The PATCH results (Fig. 3), in addition to reproducing the information on tiger distribution found in the transect data and RSF models, add insights on the location of source and sink habitat and on the existence of a threshold of range fragmentation and collapse with small increases in mortality. The strong effect of adult survival on population viability is consistent with other population viability analyses of large carnivores and other relatively long-lived mammals (Kenney *et al.* 1995). However, recent research from the Indian subcontinent has placed more emphasis on prey density as a key determinant of tiger abundance (Karanth *et al.* 2004). This contrast in emphasis may arise from the contrasting landscape context for tiger conservation in India, where most tigers occur within reserves, highly fragmented landscapes do not allow dispersal, and reproduction is higher than needed to ensure population persistence within reserves, at least over the short term.

SEPM may provide important benefits over other methods, such as LCP, that primarily focus on assessing the level of landscape connectivity between protected areas (Wikramanayake *et al.* 2004). Although, in common with the PATCH results, our simplified LCP did identify the region stretching north-west from SABZ as an important corridor, it failed to identify the importance of the coastal highway in fracturing tiger distribution and the resultant vulnerability of the coastal protected areas to the south of SABZ (Fig. 3d). This highlights two major contrasts between LCP and SEPM models. First, a LCP-based approach assumes that tiger populations exist as islands in a sea of humanity, and that these island-like 'sources' of dispersers are known a priori and fixed. While this approach may have merit in human-dominated landscapes, it has the potential to exclude suitable habitat outside protected areas from the conservation plan if it does not represent the least-cost path between core areas. Such an approach may lead to the abandonment of habitat that could increase the effective size of core areas. Secondly, unlike a static model such as a LCP or RSF, a dynamic model such as a SEPM can evaluate the relative vulnerability of priority areas to novel future scenarios and thus identify which policy changes offer most hope or risk to regional population viability. When these broad insights into regional population structure have set the initial context for land-use planning and identified critical areas both within and outside the current reserve system, LCP or other corridor analyses may play a secondary role in identifying the most effective linkage habitat.

### CONSERVATION IMPLICATIONS

The sensitivity of the PATCH results to small variations in demographic parameters, particularly survival rates, suggests that either (i) the viability of the regional population is currently maintained by areas with higher survival and fecundity than that documented within the only long-term demographic study area (SABZ), or (ii) the regional population is in decline. Over a 38-year span (1966–2003) indices of tiger abundance in SABZ suggest a positive growth rate (lambda = 1·05) but growth rates have slowed over the course of the intensive ecological studies (1992 to present; Miquelle, Smirnov & Goodrich 2005) and there is evidence that, during the first part of these studies, the SABZ population was suffering very high mortality rates (Smirnov & Miquelle 2005). Given that recent survey data suggest that the regional population appears stable (Miquelle, Smirnov & Goodrich 2005), it seems likely that higher survival and/or fecundity exists in other parts of the tiger range in the RFE.

Comparisons of the results from alternate PATCH scenarios (Fig. 3a–c) reinforce the conclusion that the RFE tiger population is vulnerable to small increases in mortality rates. Because RFE tigers have the largest recorded home ranges for the species (Miquelle *et al.* 1999a; Goodrich *et al.* 2005a) and a low percentage (3·4%) of the region lies within strictly protected areas, current tiger distribution is highly dependent on *de facto* refugia with low human impacts but without statutory protection. Based on the PATCH results, the portion of tiger range most robust to threat of extirpation connects the SABZ with the Iman and Bikin watersheds to the north (Fig. 3b,c). Designation of this region as an IUCN World Heritage Site is an indication of its importance to conservation in the RFE. The recent designation of a large zakaznik in the Bikin headwaters has the potential to enhance tiger conservation in this area. In scenarios with even higher mortality rates (scenario ii), the tiger distribution shrinks to encompass only the SABZ itself, as it is the largest protected area with relatively high productivity. Despite their higher productivity, more isolated southern protected areas appear more vulnerable than the SABZ. A zone of high human impact along a main coastal access road that bisects tiger habitat could fracture the tiger range and accentuate vulnerability in this southern habitat block. Similarly, the much smaller and more isolated south-west border tiger population is also highly vulnerable (Fig. 3d).

Despite the small proportion of this region currently within protected areas, it none the less plays a critical role in retaining tiger viability, and this role is likely to increase as human pressures mount and the landscape matrix becomes less benign. Although the potential effect of an expanded zapovednik network only marginally increases tiger viability under current conditions (scenario iv), it dramatically enhances distribution under potential future scenarios (scenario v; Fig. 3c), and prevents regional extirpation despite a more hostile landscape matrix. Thus both protected area expansion and efforts to decrease tiger mortality in the landscape matrix will be critical components for ensuring the presence of tigers in such landscapes (Kerley *et al.* 2002; Miquelle *et al.* 2005a). The SEPM model results suggest preserving source habitat in areas of highest irreplaceability and vulnerability (Fig. 2d), for example in the zone connecting the Bikin, Iman and SABZ, as well as ensuring linkages across the coastal access road to prevent loss of the population to the south. This differs from recommendations produced by a model such as LCP based primarily on evaluating connectivity between existing protected areas. Because of the paucity of protected areas within *de facto* refugia such as the Iman watershed, a LCP-based analysis would probably overlook such areas.

This contrast in methodologies is paralleled by a broader contrast in conservation paradigms between regions such as the RFE and Myanmar, where tigers still (or could potentially) inhabit much of the landscape matrix and where unprotected lands still play a critical role in biodiversity conservation, and regions such as much of the Indian subcontinent where human population density outside protected areas effectively excludes use by large carnivores (Thapar 1999). Rather than devaluing the importance of protected areas, our results suggest that their role and vulnerability should be analysed in a whole-landscape context. Landscape connectivity merits increased emphasis in conservation planning, as mortality of dispersing individuals as a result of roads and other landscape barriers may have a significant impact on metapopulation viability (Kramer-Schadt *et al.* 2004). However, identification of landscape linkages should be tied to the broad-scale recommendations resulting from spatial PVA in order to prevent misdirection of resources towards protecting corridors that add little to population persistence.

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