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BIODIVERSITY RESEARCH

Potential impacts of oil and gas development and climate change on migratory reindeer calving grounds across the Russian Arctic

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ABSTRACT

Aim Drivers of biodiversity loss are increasingly broad in scale, requiring conservation planning to move towards range-wide assessments. This is especially challenging for migratory species, such as reindeer or caribou (*Rangifer tarandus*), which use only a small portion of their range at a given point in time, and for which some parts of their range, such as calving grounds, may be much more important than others. Our aim was to identify potential calving ground habitat of wild tundra reindeer populations throughout Russia, where scarce knowledge about seasonal reindeer habitat is an obstacle for conservation planning, and to assess possible impacts from oil and gas development and climate change.

Location Northern Eurasia.

Method We used occurrence data from known reindeer calving grounds using species distribution models to first assess calving grounds characteristics and second predict their distribution across the Russian Arctic. We then compared our calving ground map with maps of oil and gas development, and a range of climate change indicators.

Results We found areas throughout the Russian Arctic that are suitable for calving, including for some wild reindeer populations where calving ground locations are unknown. Variables relating to resource availability in spring and predator avoidance were the strongest predictors in our model. Oil and gas development affects calving grounds especially in the Barents Sea region and in south-western Siberia, whereas climate change affects calving grounds on Taymyr, Chukotka, and Kamchatka.

Main conclusions We conducted the first assessment of calving grounds of Russia's wild reindeer populations, highlighting the spatial heterogeneity of the threats that they may face. Given the potentially strong impact of oil and gas development and climate change, conservation planning should aim for designing resilient conservation networks that would allow Arctic biodiversity to freely move in time and space and thus to adapt to changing environments.

Keywords

Arctic, calving grounds, climate change, land use change, oil and gas exploitation, parturition, Russia, seasonal habitat, species distribution modelling.

INTRODUCTION

As global environmental change accelerates, conservation planning faces the challenge to move beyond protecting individual sites towards range-wide assessments (Sanderson *et al.*, 2002; Kuemmerle *et al.*, 2011; Redford *et al.*, 2011). This is particularly challenging for migratory species, which at any given point in time use only a fraction of their total range (Berger, 2004; Mueller *et al.*, 2011; Singh & Milner-Gulland, 2011). However, not all parts of their ranges are

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equally important for migratory species' populations (e.g. growth, survival or reproductive success). Because inadequate knowledge of seasonal habitat use can result in protected areas that do not actually protect the full range of species (Singh & Milner-Gulland, 2011; Taillon *et al.*, 2012), identifying critical habitat, such as migratory stopover, breeding or nesting sites, is crucial for effective conservation planning (Berger, 2004; Martin *et al.*, 2007; Bolger *et al.*, 2008). Species distribution models are powerful tools to map species' ranges, but have so far mainly been used to map entire ranges (Zurell *et al.*, 2009; Franklin, 2010) rather than the most critical parts of a given species' range.

Reindeer or caribou (*Rangifer tarandus*[1]) play a central role in Arctic food webs, shapes the region's plant communities (Bergerud, 1988; Baskin & Danell, 2003) and is a cornerstone of the livelihoods of circumpolar indigenous cultures (Baskin, 2009; Forbes *et al.*, 2009). Wild reindeer conduct one of the last large-scale migrations of large mammals in the Northern Hemisphere (Baskin & Danell, 2003). Every spring, reindeer migrate from wintering ranges in the taiga or boreal forest to calving grounds and then on to summer ranges in the tundra, before returning to their winter ranges in fall. During calving, female reindeer of a population are highly concentrated (Gunn *et al.*, 2012), and calf mortality strongly depend on environmental conditions during the calving season (Baskin, 1983; Skogland, 1989; Griffith *et al.*, 2002). Thus, although calving grounds are only occupied for a few weeks, the availability and quality of calving grounds critically impact reindeer reproductive success and calf survival and thus ultimately population viability (WWF, 2012). Unfortunately, calving ground characteristics are not well understood although forage availability, predator–prey relations, landscape composition or anthropogenic influence all influence calving ground selection (e.g. Baskin, 1983; White *et al.*, 1987; Skogland, 1989; Barten *et al.*, 2001; Post *et al.*, 2003; Gunn *et al.*, 2012). Likewise, the location and area of calving grounds remains unclear for many reindeer populations (Baskin & Miller, 2007; Gunn *et al.*, 2012).

Reindeer are also an archetypical example of a species affected by global environmental change throughout its range. Climate change affects Arctic ecosystems strongly via changing temperature, precipitation regimes and vegetation patterns (Anisimov & Nelson, 1997; Sturm *et al.*, 2001; Rinke & Dethloff, 2008). These changes can impact reindeer populations in both positive and negative ways (Baskin *et al.*, 2008; Joly *et al.*, 2011). Warming can result in higher resource availability in summer and increased reproductive success (Griffith *et al.*, 2002). However, climate change can also lead to reduced reproductive success when parturition and vegetation green-up are decoupled (Post & Forchhammer, 2008), to increased frequency of icing events which can trigger mass mortality (Bartsch *et al.*, 2010; Hansen *et al.*, 2011) and to higher insect harassment in summer which can lower survival rates in the following winter (Skogland, 1989; Baskin, 2009; Witter *et al.*, 2012).

The Arctic is also rich in oil and gas deposits. Already more than 400 terrestrial oil and gas fields have been developed, mainly in western Siberia and northern Alaska (Gautier *et al.*, 2009). Vast unexplored reserves exist, particularly in Russia (Gautier *et al.*, 2009), and interest in these deposits is rising as many occur in relative proximity to major markets such as the European Union. Yet, even small-scale, low-intensity anthropogenic disturbances can strongly affect Arctic vegetation and wildlife (Forbes, 1999; Pelley, 2001), including reindeer populations, due to habitat fragmentation and increasing human disturbance (Nellemann & Cameron, 1996; Kumpula *et al.*, 2011). Moreover, although reindeer populations can adapt well to some extent to human disturbance, behavioural studies suggest reindeer are most sensitive to human disturbance during late winter and the calving season (Dyer *et al.*, 2001; Kumpula *et al.*, 2007; Anttonen *et al.*, 2011).

Information about reindeer calving grounds and how they are potentially threatened by climate change and oil and gas development is particularly scarce in Russia, which is unfortunate, because Russia contains the largest portion of reindeer's range and the status of wild migratory reindeer in Russia is highly uncertain. Many wild reindeer populations in Russia have declined recently (Syroechkovskii, 1999; Baskin & Miller, 2007; Baskin, 2009). Official estimates of wild reindeer numbers (939,000 in 2010, MNREP, 2011) are largely driven by the Taymyr population (400,000–1,000,000 animals), whereas the other 95 populations number on average only 3900 reindeer, and at least 66 populations are under imminent threat of extirpation (Syroechkovskii, 1999; Baskin & Miller, 2007). The reasons for these declines are likely manifold. While hunting of wild reindeer has for long been an important part of subsistence economies in Russia (Baskin, 1998, 2000), heavy poaching occurred after the collapse of the Soviet Union due to weaker nature protection and economic hardships. Moreover, oil exploration and gas exploration have been booming in Russia, triggering environmental pollution, an inflow of non-native workers, which often engage heavily in hunting and fishing, and infrastructure development that fragments habitats (Forbes, 1999; Baskin, 2009; Kumpula *et al.*, 2011). Finally, climate change will lead to warming and vegetation changes (Russell & Gunn, 2010; WWF, 2012) and is likely already impacting reindeer populations in Russia (Baskin *et al.*, 2008; Forbes *et al.*, 2011), although these impacts are not fully understood. Preserving wild and semi-domestic reindeer populations, and the key role reindeer play in the socio-ecological systems of Russia's north, thus urgently requires a better understanding of how these threats may affect reindeer populations.

Here, our goals were to assess, for the first time, the characteristics and the spatial distribution of wild migratory reindeer calving grounds throughout the Russian Arctic, as well as identify their potential threats due to oil and gas

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[1] Hereafter, the term reindeer is used to refer to *Rangifer tarandus*, including both Eurasian reindeer and North American caribou.

development and climate change. We used species distribution models based on a comprehensive set of known reindeer calving grounds to address the following research questions:

1. What characterizes migratory reindeer calving grounds of wild populations in Russia?

2. What is the spatial distribution of areas suitable for wild reindeer calving across the Russian Arctic?

3. Which wild reindeer calving grounds face potential threats from land use and climate change?

METHODS

Calving ground occurrence data

We analysed the areas of all known wild reindeer calving grounds. Wild reindeer populations use the same calving grounds every year in spring for a few weeks (Skogland, 1989; Couturier *et al.*, 1990). However, the exact area used within a calving ground and the location of this area may vary from year to year (Schaefer *et al.*, 2000; Hinkes *et al.*, 2005; Gunn *et al.*, 2012; Taillon *et al.*, 2012) and calving grounds can differ substantially in size among populations (Taillon *et al.*, 2012). Here, we refer to calving ground as the total area within the range of a wild reindeer population that is used for calving over longer time periods (i.e. decades). Our calving ground definition therefore includes year-to-year variation in actual calving area and location, and we did not map the area used for calving in a particular year.

Maps of calving grounds exist for some wild reindeer populations, including those on Taymyr (Kuksov, 1981; Kolpashchikov, 2000), in the Lena River delta, and in Yakutia (Safronov *et al.*, 1999). For other populations, descriptions of calving ground locations were available from the literature (Baskin & Miller, 2007), from researchers and local experts (V. I. Fil, V. I. Mosolov, L. A. Kolpashchikov, pers. comm.), as well as our own experience of several decades of field research on reindeer populations in Russia. For all these populations, we digitized calving grounds using topographic maps at a scale of 1:200,000 as a reference. We generally digitized calving ground ranges conservatively (i.e. only clearly documented areas), and we excluded uncertain ranges. Generally, calving ground maps and descriptions referred to the total area utilized for calving over time, whereas year-to-year variations were only available for the Taymyr population. In total, we digitized 24 calving grounds of wild reindeer populations (18 based on scientific reports and 6 based on expert knowledge; out of a total of 50 documented reindeer populations in our study region). In addition, we included information on the calving grounds of 27 semi-domestic reindeer populations which were digitized in the same way as those for wild populations. These semi-domestic reindeer populations occur in regions where wild reindeer populations were extirpated or severely decimated in the past (e.g. Chukotka and Yamal Peninsula). The reindeer calving grounds in our dataset had average sizes of 6750 km² (standard deviation: 11,330 km²) and 1850 km² (1060 km²), respectively, for wild and semi-domestic populations. To analyse reindeer calving ground characteristics and to map calving ground suitability (see below), we randomly selected up to 25 locations within each calving ground with a 15 km minimum distance between points to minimize pseudoreplication (our analyses was carried out using a 10 × 10 km² grid, see below). In total, we used 406 calving ground occurrence points (339 points from wild reindeer populations and 67 points from semi-domestic populations; the calving grounds of 12 wild and all semi-domestic populations were too small to harbour 25 points, and fewer points were used for these populations). See Appendix S1 in Supporting Information for a detailed description of the calving ground data.

Predictor variables and rationale

Our study region included Russia north of 60° latitude plus Kamchatka. We excluded the portion of Chukotka east of the datum shift (as no reindeer populations occur there) and west of 50°E longitude (because of a lack of calving ground occurrence data).

We gathered five groups of predictors (Table 1), which influence reindeer calving ground selection (e.g. Baskin, 1983; White *et al.*, 1987; Skogland, 1989; Post *et al.*, 2003; Baskin & Miller, 2007; Gunn *et al.*, 2012): (a) resource availability in spring (17 candidate variables), (b) resource availability in summer (11), (c) predator avoidance (3), (d) anthropogenic disturbance (2) and (e) landscape composition (4). We aggregated all predictors to ten-km grid cells (using cubic convolution for continuous variables and a majority rule for categorical variables). All spatial layers were transformed to the Albers equal-area conic projection. A detailed rational and description of these predictor variables as well as data sources are provided in Appendix S2 in Supporting Information.

Predicting calving grounds

To assess the spatial distribution of calving ground suitability, we used two nonparametric algorithms and averaged their results. Averaging results from multiple models often yields more robust predictions than single models (Araújo & New, 2007). Specifically, we used two nonparametric algorithms: maximum entropy modelling (Maxent) and boosted regression trees (BRTs). Maximum entropy modelling (Phillips *et al.*, 2006) approximate species' distributions by deriving a probability distribution, while respecting constraints inferred from environmental variables. Regularization parameters prevent overfitting (Elith *et al.* (2011). To fit maximum entropy models, we used Maxent (v3.3.3, http://www.cs.princeton.edu/~schapire/maxent/), using default regularization and only quadratic and hinge features to avoid overfitting. Boosted regression trees (Elith *et al.*, 2008) fit many single decision tree models that are then combined for prediction. Overfitting is avoided through regularization, that is, by jointly optimizing the final number of trees, their learning

Table 1 Summary of predictor variables used for mapping reindeer calving grounds across Russia. A detailed rational and description of these variables, including full data sources, time periods covered, pre-processing steps and references, is provided in Appendix S1. All variables were ultimately aggregated to 10 $\times$ 10 km^2 grid cells.

Predictor group	Rational	Proxy variable used	Spatial scale	Data type	Data source
Resource availability in spring	Lichen and herbaceous vegetation cover during calving are important because female reindeer and their newborns can only travel over moderate distances after parturition (Baskin & Miller, 2007).	Fractional bare ground and herbaceous vegetation cover	500 $\times$ 500 m^2 grid cells	Continuous	MODIS Vegetation Continuous Field Product
		Weekly average snow cover	500 $\times$ 500 m^2 grid cells	Continuous	MODIS daily snow cover product
		May and June temperature	1 $\times$ 1 km^2 grid cells	Continuous	WorldClim database
		Slope and southerners index	1 $\times$ 1 km^2 grid cells	Continuous	Topographic maps
Resource availability in summer	Female reindeer select calving grounds that green-up shortly after parturition, allowing them to follow the green-up frontier (Post *et al.*, 2003; Baskin, 2009).	Median and standard deviation vegetation index values (NDVI) for 16-day periods	500 $\times$ 500 m^2 grid cells	Continuous	MODIS NDVI product
	Calving grounds are also often within or close to productive summer grounds characterized by high vegetation productivity (White *et al.*, 1987).	Mean temperature of the warmest quarter and maximum temperature of the warmest month	1 $\times$ 1 km^2 grid cells	Continuous	WorldClim database
Predictor avoidance	Female reindeer select for open ground and away from the tree line because predators are more numerous in the forest zone (Baskin, 1983; Skogland, 1989; Heard & Williams, 1992).	Distance to the taiga-tundra boundary	10 $\times$ 10 km^2 grid cells	Continuous	Tree line from the Circumpolar Arctic Vegetation Map
		Fractional tree cover	500 $\times$ 500 m^2 grid cells	Continuous	MODIS Vegetation Continuous Field Product
		Elevation	1 $\times$ 1 km^2 grid cells	Continuous	Topographic maps
Anthropogenic disturbance	Human presence often affects reindeer populations negatively (e.g. poaching, traffic).	Human population density	1 $\times$ 1 km^2 grid cells	Continuous	LandScan 2007 database
		Road density	10 $\times$ 10 km^2 grid cells	Continuous	Topographic maps
Landscape composition	Female reindeer select for more diverse landscapes with complex topography, often close to water bodies (Baskin & Miller, 2007)	Dominant land cover type	500 $\times$ 500 m^2 grid cells	Categorical	GlobCover
		Diversity of land cover types	500 $\times$ 500 m^2 grid cells	Continuous	GlobCover
		Distance to water bodies	10 $\times$ 10 km^2 grid cells	Continuous	GlobCover
		Dominant vegetation type	10 $\times$ 10 km^2 grid cells	Categorical	Map of Russian vegetation zones

rate (or shrinkage) and complexity (Elith *et al.* (2008). We fitted BRT models in R using the gbm package (http://cran.r-project.org/web/packages/gbm/), using a bag fraction of 50%.

Some of the predictor variables (e.g. different climate variables) were correlated (Pearson's $r > 0.85$, based on a sample of 10,000 random locations), which does not impair Maxent or BRT model performance, but can hinder the interpretation of variable importance. We fitted alternative models for correlated variables, retaining the variable yielding higher overall performance as measured by the mean area under the curve (AUC) value of the receiver operating characteristics curve and fivefold cross-validation using validation data not used for model building (Phillips *et al.*, 2006; Elith *et al.*, 2011). For both algorithms, we used a logit link function to convert predictions into a calving ground suitability index ranging from zero to one. The final prediction map of the contemporary distribution of areas suitable for reindeer calving across the Russian Arctic was calculated as the geometric mean of the two respective predictions. Variable importance was assessed by calculating variable drop contributions in Maxent (i.e. model performance loss when randomly permuting values of a variable on presence and background data) and the relative variable importance in BRT (i.e. the number of times a variable is selected for splitting the data, weighted by the model improvement resulting from each split).

Analysing potential climate change and human disturbance effects on calving grounds

To analyse potential threats to calving grounds, we compared calving ground suitability to indicators of human disturbance and climate change. Regarding human disturbance, we first compared our calving ground suitability map to a global geospatial database of all current and potential future oil and gas concessions (IHS, 2013). This database captures all known oil and gas fields and the development status of all concessions, distinguishing between open areas, bidding blocks, contract blocks and whether a concession is active or historical. Open areas are designated for future oil and gas exploration, and bidding blocks are areas open for leases. Contract blocks are areas where companies have signed contracts to explore, drill or produce. The database also contains information on oil and gas pipelines (current and planned; below- and aboveground).

Second, we overlaid our calving ground suitability with maps of changes in night-time lights. Yearly maps of night-time lights from the Operational Linescan System (OLS) sensors of the Defense Meteorological Satellite Program (DMSP) satellites for 1993–2009 are a good proxy of human presence and industrial activity (Chen & Nordhaus, 2011). We used the stable night-time light product (version 4, http://www.ngdc.noaa.gov/dmsp/), calculated three-year averages for the focal years 1993 (i.e. 1992–1994) and 2008 (i.e. 2007–2009) and derived changes in night-time lights between these focal years. This time period was characterized by drastic changes in economic activity and rural population in Russia (Ioffe *et al.*, 2004; Forbes *et al.*, 2009; Kumpula *et al.*, 2011).

Climate and related vegetation changes may affect reindeer populations in both negative and positive ways (Sharma *et al.*, 2009; Joly *et al.*, 2011; WWF, 2012). To assess potential climate change effects on calving grounds, we analysed two climate measures: (1) precipitation below 0.5 °C (average precipitation in March, April and May at temperatures <0.5 °C) and (2) summer temperature (average temperature of June, July and August). Changes in winter precipitation can lead to more frequent freeze-over-thaw events, and ice rains, as well as deeper snow, all of which can increase reindeer mortality (Forchhammer *et al.*, 2002; Sharma *et al.*, 2009; Stien *et al.*, 2010, 2012; Hansen *et al.*, 2011). Changing summer temperature (i.e. warmer and longer summers) may result in higher vegetation productivity, but also the decoupling of parturition and vegetation green-up, and lower reproductive success (Post & Forchhammer, 2008), plus increasing insect harassment (Skogland, 1989; Weladji & Holand, 2006; Witter *et al.*, 2012). Both climate indicators were averaged from the outputs of three climate models (ECHAM5, HadCM3 and NCAR-CCSM3) from the 4th IPCC Assessment Report. Climate indicators were calculated for 2100 (using a baseline period of 1980–2009) under the A2 (more divided world, continuously rising population and consumption) and B1 (more integrated, ecologically friendly world) emission scenarios (Grubler *et al.*, 2007).

To assess potential future changes in vegetation, we applied the biosphere model LPJmL (version 3.5), which simulates composition, production and dynamics of nine natural vegetation plant functional types (PFTs) (Sitch *et al.*, 2003; Thonicke *et al.*, 2010). Applying LPJmL to the same climate data, time horizon, and scenarios as for the climate indicators, we derived two vegetation change indicators (i) woody vegetation cover and (ii) woody biomass. These indicators capture both shrub encroachment and a potential northward shift of the tree line, both of which may lead to increasing predation or decreasing pasture area (Baskin *et al.*, 2008; Sharma *et al.*, 2009) and thus ultimately to increasing reindeer mortality.

RESULTS

Reindeer calving grounds in the Russian Arctic were characterized by relatively high herbaceous cover (mean = 65%, standard deviation = 15%), moderate snow cover after mid-May (>2 days of snow cover in our case), relatively flat terrain (mean = 1.4%, standard deviation = 1.9%) and south-facing slopes (average southerners index = 76, Fig. 1). Vegetation productivity at calving sites rapidly increased after mid-May (Julian days 145–161, Fig. 1), peaking in June and July (NDVI > 0.6), with little intra-annual variation (standard deviation always <0.13). Calving grounds generally had little or no tree cover (mean 8%, standard deviation 15%), were located at intermediate altitude (mainly 50–350 m

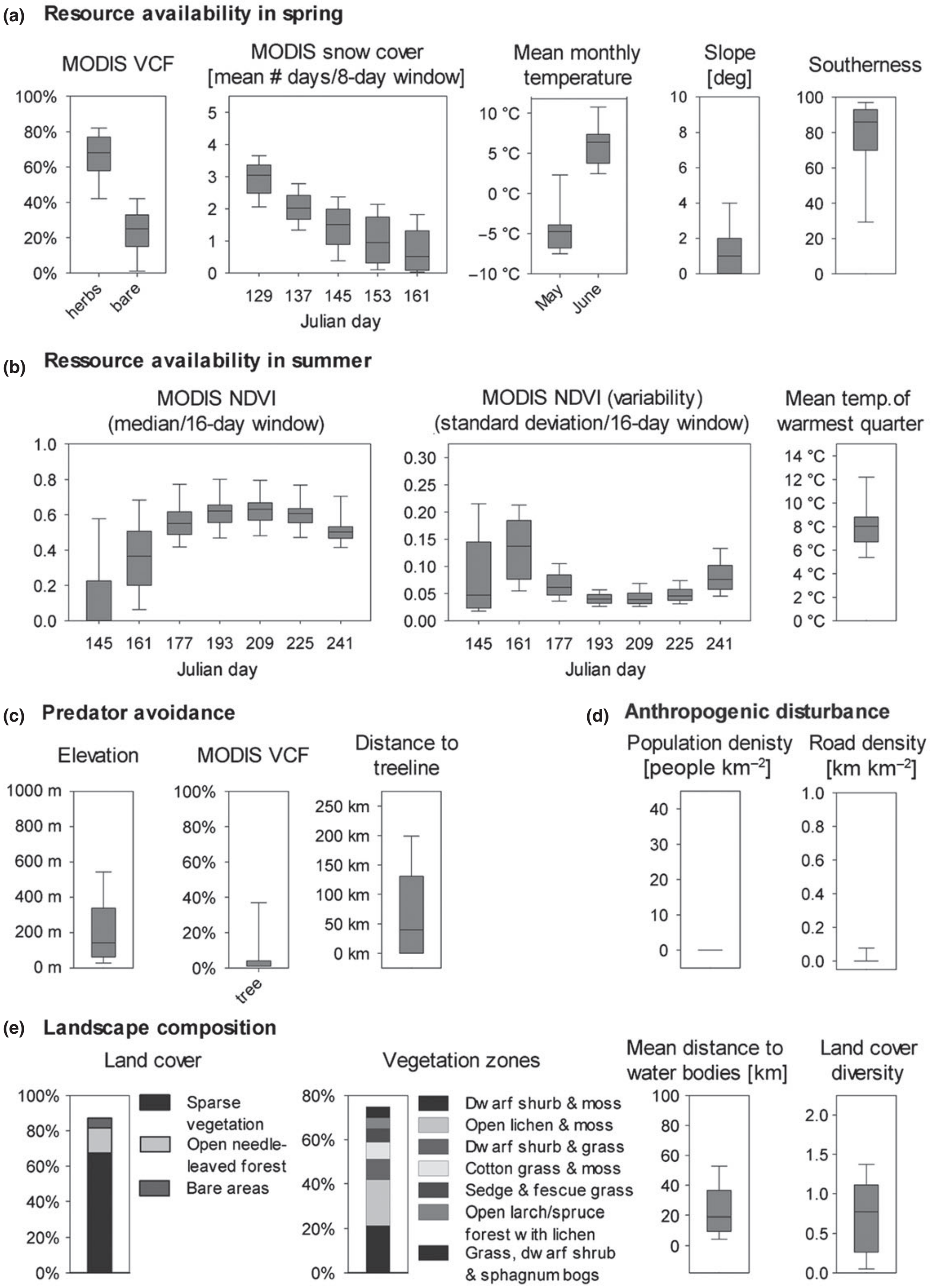

Figure 1 Characteristics of known reindeer calving grounds in Russia according to factors characterizing (a) resource availability in spring, (b) resource availability in summer, (c) predator avoidance, (d) anthropogenic disturbance and (e) landscape composition. For details on the calving ground data and descriptive variables see Materials and Methods. For categorical variables (land cover and vegetation zone), only classes containing more than 5% of the calving ground points are shown. (Acronyms: MODIS, Moderate Resolution Imaging Spectroradiometer; NDVI, normalized difference vegetation index; VCF, vegetation continuous field product, °C, degree Celsius, deg, degree). Box plots show the median (straight line), the 25th and 75th percentile (lower and upper box edge, respectively) and 10th and 90th percentile (lower and upper whiskers, respectively. Julian day references (regular years): 129 (9 May), 145 (May 25), 161 (10 June), 209 (28 July) and 241 (29 August).

above sea level), afar from the taiga/tundra tree line (median = 40 km, standard deviation = 90 km), and generally in regions with very low human pressure (average population density <0.05, Fig. 1).

Our modelling approach predicted wild reindeer calving grounds well, with an average cross-validated AUC value of 0.932 (Maxent = 0.906; BRTs = 0.958) and a standard error of 0.03 (0.01; 0.01). The final model included 22 predictor variables, and out of these variables, 13 had a relative contribution higher than in a null model (4.55%, i.e., 100%/22 variables, Fig. 2). Spring resources together accounted for a relative contribution of 47% (cumulative contribution, average of both algorithms), followed by summer resources (21%), predator avoidance (19%), landscape composition (12%) and human disturbance variables (<1%). Response functions were mainly hump-shaped (e.g. snow cover, distance to tree line) or linearly increasing (e.g. mean NDVI variables) (Fig. 2).

Our best model predicted widespread areas suitable for wild reindeer calving across the Russian Arctic (Fig. 3). Potential calving grounds were especially widespread in the northern Urals, western Siberia (southern Yamal Peninsula, Gydansky Upland and the Tazovsky Peninsula), Taymyr, western Yakutia (e.g. Pronchishcheva Kryazh Ridge, Kystyk Plateau and the Lena River delta) and Chukotka (e.g. Elgygytgyn Lake Area). In other regions, suitable calving ground areas were more concentrated such as on Kamchatka (e.g. Kronotsko-Zhupanovskaya region), in Yakutia (e.g. Muksunikha-Tas and Uryung-Khastakh hills) and on Wrangel Island (Fig. 3). Our model did predict areas suitable for calving for many populations that were not represented in our sample of training locations, for example for populations in the Shchuchya, Enisey and Angara catchments, in southwestern Siberia and in the Amguema catchment in Chukotka. However, for a few populations, our model made no prediction, particularly in central Siberia.

Overlaying our reindeer calving ground map with areas of oil and gas development highlighted several at-risk calving grounds (Fig. 4). Ongoing oil and gas development was mainly clustered in western and central Siberia and frequently in calving grounds there, especially on Yamal (Shchuchya River population), and Tazovsky and Gydansky peninsulas (Nadym–Pur river and Pur–Taz river populations) (Fig. 4). Much oil and gas development also occurs in the Khanty-Mansiysk area, in close proximity to the Konda – Sos'va River and the Yugan River populations. Western Siberian calving grounds also overlapped with many undeveloped oil and gas fields (especially in the Nenets, Yamalo-Nenets and Khanty-Mansi Autonomous Okrugs). In addition, substantial overlap occurred in the Siberian Plateau (e.g. Enisey River population and Angara River populations). Pipelines connected to oil and gas exploitation fragmented in particular calving grounds in western Siberia (e.g. Tazovsky Peninsula, Konda – Sos'va River population, Fig. 4).

Trends in DMSP night-time lights for the Russian Arctic revealed several hotspots of human activity, especially in the eastern part of Nenetsky Okrug and in southern parts of Yamal-Nenets Okrug and Khanty-Mansi Okrug, where large-scale oil extraction and gas flaring occurs (Fig. 5). Human activities were high, for example, for the populations in the

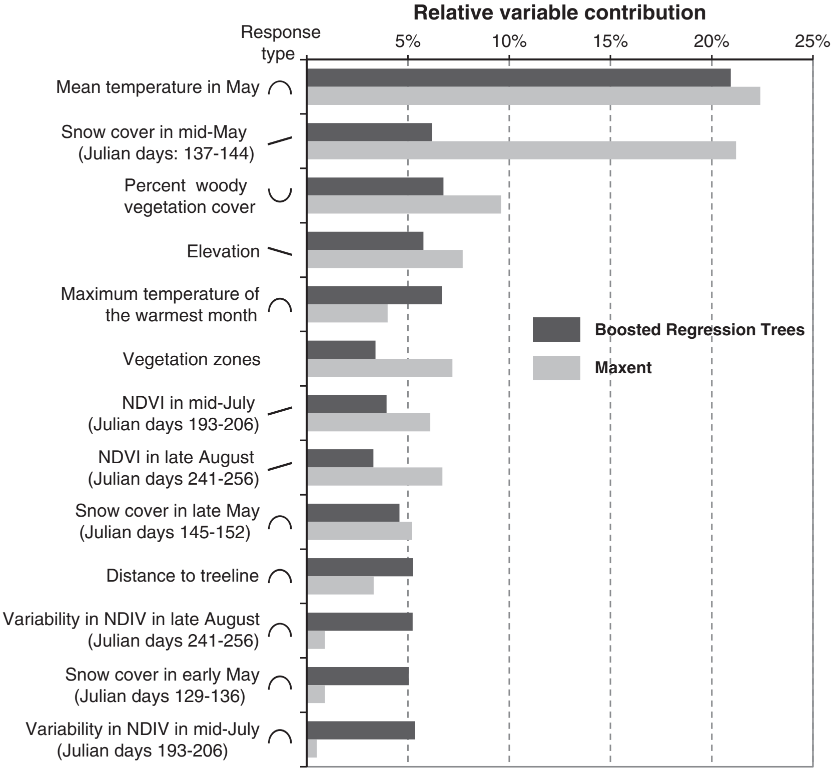

Figure 2 Relative contributions and response type of predictor variables of the Maxent (light grey bars) and boosted regression tree (dark grey bars) models.

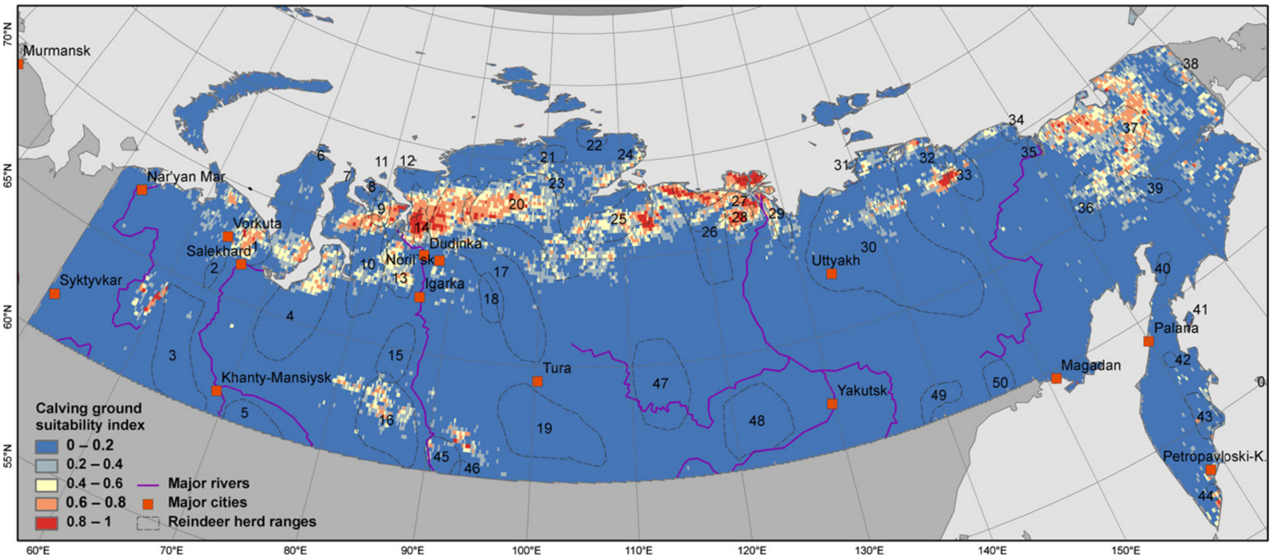

Figure 3 Reindeer calving ground suitability in Russia (1 = highest suitability). Areas suitable for reindeer calving were predicted by an average of two species distribution models based on the locations of all known calving grounds and a suite of environmental and human disturbance variables. Wild reindeer population ranges are 1: Shchuchya River, 2: Shuryshkarskiy Lake, 3: Konda and Sos'va rivers, 4: Nadym–Pur rivers, 5: Yugan River, 6: Belyi Island, 7: Yavay Peninsula, 8: Mamonta Peninsula, 9: Gydan Peninsula, 10: Pur–Taz rivers, 11: Sibiryakov Island, 12: Chichagov Shore, 13: western Taymyr, 14: Agapa River, 15: Turukhan River, 16: Taz River headwaters, 17: Pura River, 18: Putoran Mountains, 19: Middle Siberian, 20: Dudypta River, 21: Nizhnya Taymyra River, 22: Faddey River, 23: Taymyr Lake, 24: Mariya Pronchishcheva Bog, 25: Popigay River, 26: Lena and Olenek rivers, 27: Bulun River, 28: Kystyk Uplands, 29: Lena River Delta, 30: Yana and Indigirka rivers, 31: Novosibirsky River, 32: Indigirka River, 33: Sudrunskaya, 34: Galgavam River, 35: Kolyma River, 36: Omolon River, 37: Elgygytgyn Lake, 38: Amguema River, 39: Mine River, 40: Parapolsky Lowlands, 41: Karaginsky Island, 42: Elovka-Uka River, 43: Kronotsko-Zhupanovskaya, 44: southern Kamchatka, 45: Enisey River, 46: Angara River, 47: western Yakutian, 48: Lena and Vilyuy rivers, 49: Yudoma River and 50: Kava River (Source: Baskin & Miller, 2007). This figure is available in colour online at http://wileyonlinelibrary.com.

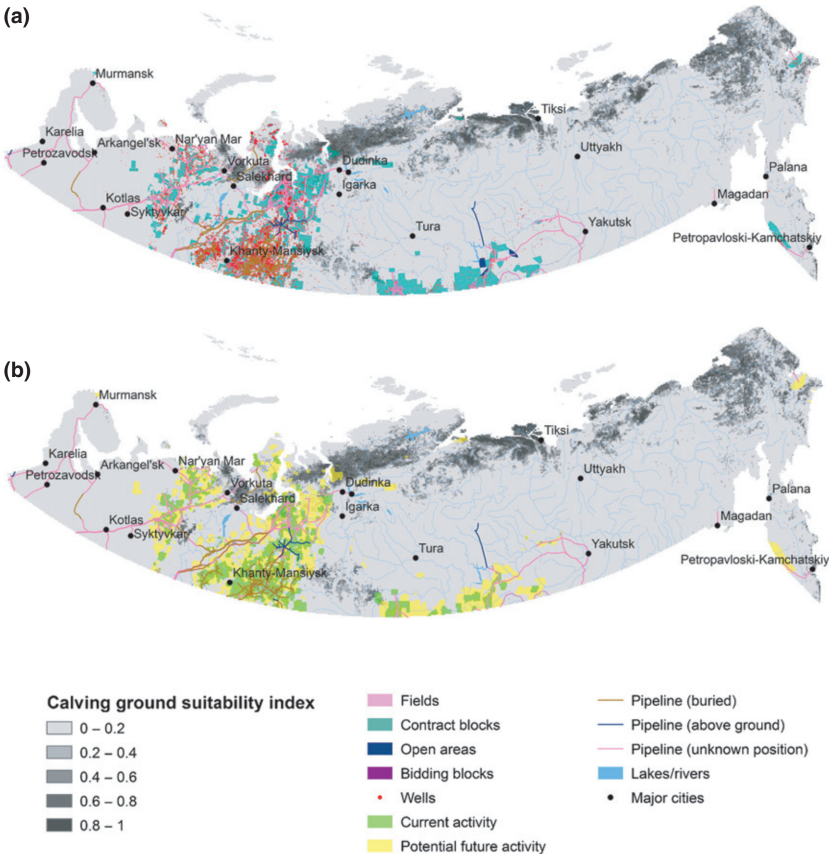

Figure 4 Overlap of oil and gas development with areas suitable for reindeer calving. (a) Oil and gas fields, wells, open areas, bidding blocks and contract blocks. (b) Current and potential future oil and gas development. This figure is available in colour online at http://wileyonlinelibrary.com.

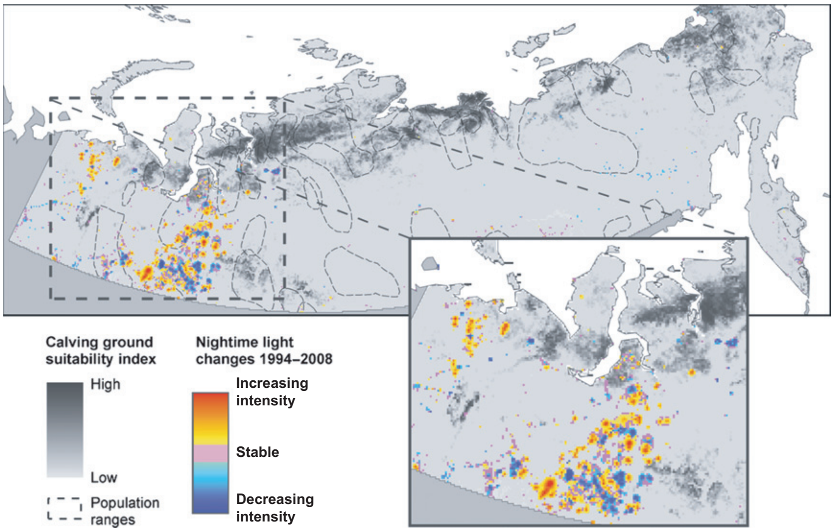

Figure 5 Changes in night-time lights between 1993 and 2008 in relation to areas suitable for reindeer calving across the Russian Arctic. Night-time lights were measured by the DMSP OLS sensors. Each time period represents the average of three consecutive years (i.e. 1993 = average of 1992/93/94). Only changes exceeding ±5 digital numbers (8 bit data) are shown. This figure is available in colour online at http://wileyonlinelibrary.com.

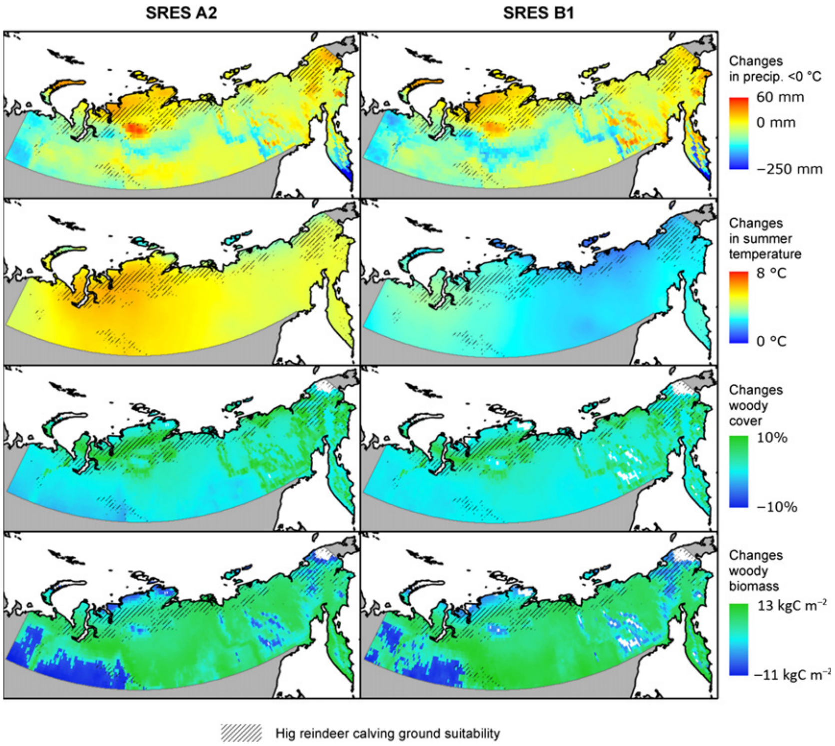

Figure 6 Projected changes in average spring precipitation at temperatures <0.5 °C (in March, April and May), average summer temperatures (in June, July and August), woody vegetation cover and woody plant biomass until 2100 and for two climate scenarios (SRES A2 and B1). Future climate parameters were derived by averaging projections from three global climate models. Future vegetation change was calculated using the dynamic global vegetation model LPJ-GUESS (see Methods for details). Hatched areas denote areas suitable for reindeer calving. (We used the 10th percentile of the distribution of suitability values within confirmed calving grounds as threshold here. Note that this threshold was only chosen for visualization purposes, other thresholds may be equally plausible.). This figure is available in colour online at http://wileyonlinelibrary.com.

Shuryshkarskiy district, in the Konda, and Sos'va catchments, in the Shchuchya catchment, and on Tazovsky (Fig. 5). According to our calving ground suitability map, some south-central Siberian calving grounds also appeared to be affected by human development (Fig. 5). In contrast, we did not find major increases in night-time lights for on Taymyr, in the Yana-Indigirka region, in Chukotka or in Kamchatka.

Several calving grounds of wild reindeer in Russia will likely be strongly affected by climate change (Fig. 6). The amount of spring precipitation at temperatures below 0.5 °C, a proxy for both snow depth and the risk of freeze-over events, was projected to decline in European Russia and southern Siberia. In contrast, precipitation at freezing temperatures was projected to increase markedly in calving grounds in north-central Siberia (especially on Taymyr), Chukotka and along Kamchatka's eastern coast (Figs 6 and 3). Summer temperatures will likely increase across all reindeer calving grounds study region, especially in western Siberia. In terms of future vegetation transformations, LPJmL projected substantial tree line advances into reindeer calving grounds on the Gydan and Taymyr peninsulas, in the Pronchishcheva Kryazh Ridge, the Arctic shore of Yakutia (e.g. the Kava River and Indigirka River populations), and on Chukotka. Woody plant biomass was projected to increase substantially across much of the study region, including most areas suitable for calving (Fig. 6).

DISCUSSION

Identifying crucial habitat within the ranges of wide-ranging, migratory species is critical for efficient conservation planning. Calving grounds are key habitats for reindeer populations and reindeer conservation. Conservation planning urgently needs better information on the characteristics, spatial distribution and potential threats to calving grounds, especially in Russia (Baskin & Miller, 2007). Analysing occurrence data from all known Russian calving grounds of wild reindeer populations, we showed that resource availability and proxy variables linked to predator avoidance play key roles in determining reindeer calving grounds. Our analyses provide the first map of wild reindeer calving ground suitability across Siberia, revealing vast areas suitable for wild reindeer calving, including for populations where calving grounds have so far not been documented. Our assessment also highlights the substantial and spatially heterogeneous effects of potential climate change and oil and gas development on reindeer populations, underpinning the need for region-wide conservation planning to safeguard and restore reindeer populations in Russia.

Our analyses showed that wild reindeer populations in Russia select calving grounds based on environmental conditions that are highly dynamic in both space and time. High calving ground suitability was most strongly related to resource availability in spring (Fig. 2). Calving grounds commonly had abundant open ground (i.e. not covered by snow) in early spring (Fig. 1) and high vegetation productivity in late spring. This further corroborates that female reindeer mainly select calving sites that provide forage (i.e. lichen or herbaceous vegetation) after calving. The high importance of the weekly snow cover and biweekly NDVI variables, as well as the hump-shaped response of the temperature variables, suggested that female reindeer critically select calving sites at the snow melt frontier (Figs 1 and 2). Also important were elevation and landscape openness (e.g. distance to tree line, fraction of woody vegetation, elevation), factors reflecting proxy variables for predator avoidance. In contrast, topography and human disturbance were less important in our continental-scale assessment, although we caution that these factors may well be vital for understanding calving ground selection of individual populations or at finer spatial scales.

Suitable reindeer calving grounds were relatively widespread across the Russian tundra. One explanation for this is that the area actually used for calving in a given year within a population's calving ground is often small and variable among years, for example due to snow or forage conditions (Schaefer *et al.*, 2000; Hinkes *et al.*, 2005). The reindeer populations of Taymyr, Russia's largest wild population, for which we identified the most extensive calving grounds, indeed show substantial interannual variation in their calving sites (Kuksov, 1981; Kolpashchikov, 2000), similar to some North American populations (Gunn *et al.*, 2012). Yet, the large areas of suitable calving grounds that we found also suggest that many contemporary populations are potentially the relicts of larger, historic reindeer populations which are now absent due to overhunting, competition with semi-domestic reindeer, or environmental change (e.g. in north-eastern European Russia, western Siberia or Chukotka). For example, south-western Taymyr harboured a large population until 40 years ago, and the Omolon River population on Chukotka once numbered several hundred thousand animals (Chernyavsky, 1984). Our calving ground suitability map thus provide new insights into the likely locations of the calving grounds of contemporary populations for which calving ground data are not available (e.g. northern Ural, Gydan and Tazovsky peninsulas, headwaters of Nadym and Taz rivers, Anabar Uplands in Yakutia, Chukotka), as well as probable locations for the calving grounds of severely decimated or extirpated populations. This is important information for conservation planners seeking to restore these populations and their important ecological roles.

Several reindeer calving grounds overlapped or occurred in close proximity to current or potential future oil and gas development. This is concerning in at least three ways. First, oil and gas development is often connected to substantial development roads and pipelines, which can fragment the ranges of reindeer populations (Nellemann & Cameron, 1996; Kumpula *et al.*, 2011). Such fragmentation can result in overgrazing in the remaining habitat or inhibits migrations (Forbes *et al.*, 2009). For example, the Nadym–Pur river and Pur–Taz river populations declined strongly since 1960, and our calving ground map suggests that infrastructure development established a barrier between the population's calving and wintering grounds (Fig. 3). Likewise, we found large, but currently unused calving areas close to the Norilsk industrial zone in Taymyr, where the Messoyakha-Norilsk pipeline separated calving and summer grounds in 1969, leading to population collapse (Yakushkin *et al.*, 1970). Second, oil and gas development results in noise, pollution and traffic, which negatively affects reindeer populations (Johnson *et al.*, 2005). Finally, oil and gas development often results in an inflow of workers with little understanding of Arctic ecosystems, potentially causing high poaching rates and environmental degradation (Vilchek & Bykova, 1992; Forbes *et al.*, 2009).

Whereas oil and gas development impacts were concentrated in western Siberia, climate change will affect wild reindeer calving grounds across the Russian Arctic – both positively and negatively. For example, several suitable calving areas will likely experience warming in the future (Fig. 6), potentially resulting in earlier green-up and increased calf survival (Griffith *et al.*, 2002), but also a decoupling of parturition and vegetation green-up and decreasing reproductive success (Forchhammer *et al.*, 2002).

Increasing winter precipitation, especially on Taymyr and Chukotka, may result in deeper snow and a higher frequency of ice crusts, and freeze-over rain events, both of which can contribute to dramatic declines of survival and recruitment in reindeer populations (i.e. population crashes of up to 99%, Tews *et al.*, 2007; Stien *et al.*, 2010; Hansen *et al.*, 2011). Furthermore, we found landscape openness to be a main characteristic of calving ground selection, yet many calving grounds face an advancing tree line and increasing woody vegetation density (Fig. 6), which may increase predation risk. The capacity of many reindeer populations to adapt to changing climate and vegetation patterns (e.g. via shifting calving grounds north) is likely limited, especially where calving areas are already close to the northern shoreline (Fig. 3). We caution though that causal effects of climate change on reindeer populations remain unclear and our broad-scale assessment of potential climate change impacts cannot replace more fine-scale, population-based assessments of possible climate effects on Russia's reindeer populations.

Our calving ground suitability model yielded a high goodness-of-fit and plausible calving ground patterns. Yet, several shortcomings need to be discussed. First, detailed calving ground data were only available for a few Russian wild reindeer populations, and our suitability map was relatively coarse to reflect that uncertainty. Systematic population monitoring based on GPS collars, though common in North America, is still in its infancy in Russia. Second, we used calving ground data from both wild and semi-domestic populations to predict calving grounds of wild reindeer populations in Russia. Our main reason for doing so was that wild reindeer populations in some areas in the Russian Arctic (e.g. European Russia, Chukotka) have been severely decimated or extirpated. Calving ground locations from contemporary wild reindeer populations may thus not fully represent areas suitable for calving. Semi-domestic reindeer are guided by herders. The location of high-quality calving grounds is an important part of traditional knowledge and often coincides with the calving grounds of historic wild reindeer. Traditional knowledge is thus a vital source of information given the paucity of data on calving sites of Russia's wild reindeer populations, especially where wild populations have been severely decimated. Important differences between wild and semi-domestic reindeer exist, for example concerning diets or energetics (Klein, 1980; Syroechkovskii, 1999; Baskin & Danell, 2003), yet reindeer are in an early stage of domestication and still exhibiting most features of the ecology and behaviour of wild reindeer. Despite these arguments for utilizing semi-domestic calving ground locations to proxy wild reindeer calving grounds, and the similarity of calving grounds maps from models with and without semi-domestic calving locations (see Appendix S4 in the Supporting Information), we cannot fully rule out bias. Third, the importance of some predictor variables may be underestimated due to their coarse resolution (e.g. slope) or because underlying variables were unavailable and we had to rely on proxy variables instead (e.g. bare ground, snow cover and NDVI variables instead of a more direct measure of lichen cover). Fourth, we used a comprehensive database of oil and gas development, but other industrial activities (e.g. mining) may also affect reindeer populations in negative ways. Fifth, our goal was to identify which calving grounds may be affected by climate change, not a full assessment of climate change impacts on reindeer ecology, behaviour or population dynamics in Russia. The latter would require analysing a wider range of climate parameters at finer spatial and temporal scale, which was beyond the scope of our study. Likewise, some of the variables we used can only indirectly proxy potential climate change impact (e.g. precipitation at temperatures around and below 0 °C in spring to proxy freeze-over events) and improved proxy variables may become available as the complexity and reliability of regional climate models improves. Finally, we focused on Arctic reindeer populations because we had no information on the calving grounds of the small reindeer populations in southern Siberian and Yakutia exists (e.g. Sayan and Altai mountains, East Siberian ridges). Our model did not identify these calving grounds, suggesting these populations are ecologically different, and need to be studied in order to protect them.

Several conservation management implications arise from our work. New protected areas for Russia's wild reindeer populations are currently discussed, and our calving ground map provides guidance as to where protection is important (e.g. the small and isolated calving grounds on Kamchatka and in the northern Urals). Oil and gas development is a major threat, but careful management can lessen these threats considerably (Haskell & Ballard, 2008). Russian energy enterprises are increasingly interested in the conservation of Arctic reindeer. Minimizing oil and gas development impact should include avoiding range fragmentation (e.g. less road development, burying pipelines), minimizing poaching, both via education of workers and better law enforcement, and strengthening environmental institutions. Finally, considering climate change, conservation planning should aim to minimize range fragmentation in order to allow wild and semi-domestic reindeer populations to roam freely and to adapt to changing environments (Forbes *et al.*, 2009).

Managing for the survival of migratory species is challenging, in part because they only use a small portion of their range at a given point in time, and some parts of their range may be much more important than others (Berger, 2004; Singh & Milner-Gulland, 2011). Identifying key elements within migratory species' ranges, such as breeding sites, stopover sites or calving grounds, is thus important for efficient conservation. Our assessment provides the first map of calving grounds of Russia's wild reindeer populations and highlights the spatial heterogeneity of challenges that these populations may face. This underlines the need for improved monitoring of Russia's reindeer populations and their seasonal habitat use patterns. Reindeer conservation needs to move beyond protecting individual sites towards region-wide conservation planning to safeguard and restore wild reindeer populations in Russia and elsewhere.

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REFERENCES

Anisimov, O.A. & Nelson, F.E. (1997) Permafrost zonation and climate change in the northern hemisphere: results from transient general circulation models. *Climatic Change*, **35**, 241–258.

Anttonen, M., Kumpula, J. & Colpaert, A. (2011) Range selection by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in relation to infrastructure and human activity in the boreal forest environment, Northern Finland. *Arctic*, **64**, 1–14.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42–47.

Barten, N.L., Bowyer, R.T. & Jenkins, K.J. (2001) Habitat use by female caribou: tradeoffs associated with parturition. *Journal of Wildlife Management*, **65**, 77–92.

Bartsch, A., Kumpula, T., Forbes, B.C. & Stammler, F. (2010) Detection of snow surface thawing and refreezing using QuikSCAT: implications for reindeer herding. *Ecological Applications*, **20**, 2346–2358.

Baskin, L.M. (1983) The causes of reindeer mortality. *Acta Zoologica Fennica*, **175**, 133–134.

Baskin, L.M. (1998) Hunting of game mammals in the Soviet Union. *Conservation of biological resources* (ed. by E.J. Milner-Gulland and R. Mace), pp. 331–348. Blackwell Science, London.

Baskin, L.M. (2000) Reindeer husbandry/hunting in Russia in the past, present, and future. *Polar Research*, **19**, 23–29.

Baskin, L.M. (2009) *Reindeer. Managing behavior and populations. Reindeer husbandry and hunting*. KMK Publications, Moscow.

Baskin, L.M. & Danell, K. (2003) Reindeer - Rangifer tarandus. *Ecology of Ungulates. A handbook of species in Eastern Europe and Northern and Central Asia* (ed. by L.M. Baskin and K. Danell), pp. 127–155. Springer, Berlin.

Baskin, L.M. & Miller, F.L. (2007) Populations of wild and feral reindeer in Siberia and Far East of Russia. *Rangifer*, **27**, 227–241.

Baskin, L.M., Sylven, M. & Jungius, H. (2008) Global warming impact on reindeer populations. *Vozdeistvie izmeneniya klimata na rossiyskuyu arcticu: analiz i puti resheniya problemy*. (ed. by A.O. Kokorin, D.V. Karelin and A.B. Stetsenko), p. 20. WWF Russia, Moscow.

Berger, J. (2004) The last mile: How to sustain long-distance migration in mammals. *Conservation Biology*, **18**, 320–331.

Bergerud, A.T. (1988) Caribou, wolves and man. *Trends in Ecology & Evolution*, **3**, 68–72.

Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**, 63–77.

Chen, X. & Nordhaus, W.D. (2011) Using luminosity data as a proxy for economic statistics. *Proceedings of the National Academy of Sciences*, **108**, 8589–8594.

Chernyavsky, F.B. (1984) *Mammals of extreme north-east of Siberia*. Nauka publ, Moscow.

Couturier, S., Brunelle, J., Vandal, D. & St-Martin, G. (1990) Changes in the population dynamics of the George River caribou herd, 1976–87. *Arctic*, **43**, 9–20.

Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S. (2001) Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management*, **65**, 531–542.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Forbes, B.C. (1999) Land use and climate change on the Yamal Peninsula of north-west Siberia: some ecological and socio-economic implications. *Polar Research*, **18**, 367–373.

Forbes, B.C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A. & KaarlejÃ¤rvi, E. (2009) High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences USA*, **106**, 22041–22048.

Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2011) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542–1554.

Forchhammer, M.C., Post, E., Stenseth, N.C. & Boertmann, D.M. (2002) Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology*, **44**, 113–120.

Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.

Gautier, D.L., Bird, K.J., Charpentier, R.R., Grantz, A., Houseknecht, D.W., Klett, T.R., Moore, T.E., Pitman, J.K., Schenk, C.J., Schuenemeyer, J.H., Sorensen, K., Tennyson, M.E., Valin, Z.C. & Wandrey, C.J. (2009) Assessment of undiscovered oil and gas in the Arctic. *Science*, **324**, 1175–1179.

Griffith, B., Douglas, D.C., Walsh, N.E., Young, D.D., McCabe, T.R., Russell, D.E., White, R.G., Cameron, R.D. & Whitten, K.R. (2002) The Porcupine caribou herd. *Arctic Refuge coastal plain terrestrial wildlife research summaries, Biological Science Report USGS/BRD BSR-2002-0001* (ed. by D.C. Douglas, P.E. Reynolds and E.B. Rhode), pp. 8–37.

U. S. Geological Survey, Biological Resources Division, Anchorage, USA.

Grubler, A., O'Neill, B., Riahi, K., Chirkov, V., Goujon, A., Kolp, P., Prommer, I., Scherbov, S. & Slentoe, E. (2007) Regional, national, and spatially explicit scenarios of demographic and economic change based on SRES. *Technological Forecasting and Social Change*, **74**, 980–1029.

Gunn, A., Poole, K.G. & Nishi, J.S. (2012) A conceptual model for migratory tundra caribou to explain and predict why shifts in spatial fidelity of breeding cows to their calving grounds are infrequent. *Rangifer*, **20**, 259–267.

Hansen, B.B., Aanes, R., Herfindal, I., Kohler, J. & Sæther, B.-E. (2011) Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology*, **92**, 1917–1923.

Haskell, S.P. & Ballard, W.B. (2008) Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **86**, 627–637.

Heard, D.C. & Williams, T.M. (1992) Distribution of wolf dens on migratory caribou range in the Northwest Territories. *Canadian Journal of Zoology*, **70**, 1504–1510.

Hinkes, M.T., Collins, G.H., Van Daele, L.J., Kovach, S.D., Aderman, A.R., Woolington, J.D. & Seavoy, R.J. (2005) Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *Journal of Wildlife Management*, **69**, 1147–1162.

IHS (2013) *International Exploration and Production Database (IRIS21)*. Available at: http://www.ihs.com/products/oil-gas-information/data-access/geophysical-surveys/ (accessed 10 April 2013).

Ioffe, G., Nefedova, T. & Zaslavsky, I. (2004) From spatial continuity to fragmentation: the case of Russian farming. *Annals of the Association of American Geographers*, **94**, 913–943.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A. & Mulders, R. (2005) Cumulative effects of human development on Arctic wildlife. *Wildlife Monographs*, **160**, 1–36.

Joly, K., Klein, D.R., Verbyla, D.L., Rupp, T.S. & Chapin, F.S. (2011) Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography*, **34**, 345–352.

Klein, D.R. (1980) Conflicts between domestic reindeer and their wild counterparts: a review of Eurasian and North American experience. *Arctic*, **33**, 739–756.

Kolpashchikov, L.A. (2000) *Taymyr population of wild reindeer. Biological foundations of management and sustainable use of resources*. In, p. 282. Nauchno-Issledovatel'skiy Institute Krainego Severa, Norilsk.

Kuemmerle, T., Radeloff, V.C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Bashta, A.-T., Chikurova, E., Parnikoza, I., Baskin, L., Angelstam, P. & Waller, D.M. (2011) Predicting potential European bison habitat across its former range. *Ecological Applications*, **21**, 830–843.

Kuksov, V.A. (1981) Distribution of wild reindeer in Taymyr during the calving season. *Ekologiya I khozyaistvennoe ispolzovanie nazrmnoy fauny Eniseyskogo Severa* (ed. by A.I. Solomakha), pp. 3–13. Sibirskoe Otdelenie VASKHNIL, Novosibirsk.

Kumpula, J., Colpaert, A. & Anttonen, M. (2007) Does forest harvesting and linear infrastructure change the usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*)? *Annales Zoologici Fennici*, **44**, 161–178.

Kumpula, T., Pajunen, A., Kaarlejärvi, E., Forbes, B.C. & Stammler, F. (2011) Land use and land cover change in Arctic Russia: ecological and social implications of industrial development. *Global Environmental Change*, **21**, 550–562.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. (2007) Optimal conservation of migratory species. *PLoS ONE*, **2**, e751.

MNREP (2011) *Hunting and hunting resources of the Russian Federation*. Special Issue 2011. In, p. 331. Ministry of Natural Resources and Environmental Protection of the Russian Federation, Moscow.

Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, ., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., DeStefano, S., Calabrese, J.M. & Fagan, W.F. (2011) How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, **20**, 683–694.

Nellemann, C. & Cameron, R.D. (1996) Effects of petroleum development on terrain preferences of calving caribou. *Arctic*, **49**, 23–28.

Pelley, J. (2001) Will drilling for oil disrupt the Arctic national wildlife refuge? *Environmental Science & Technology*, **35**, 240A–247A.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Post, E. & Forchhammer, M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 2369–2375.

Post, E., Bøving, P.S., Pedersen, C. & MacArthur, M.A. (2003) Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology*, **81**, 1709–1714.

Redford, K.H., Amato, G., Baillie, J., Beldomenico, P., Bennett, E.L., Clum, N., Cook, R., Fonseca, G., Hedges, S., Launay, F., Lieberman, S., Mace, G.M., Murayama, A., Putnam, A., Robinson, J.G., Rosenbaum, H., Sanderson, E.W., Stuart, S.N., Thomas, P. & Thorbjarnarson, J. (2011) What does it mean to successfully conserve a (Vertebrate) species? *BioScience*, **61**, 39–48.

Rinke, A. & Dethloff, K. (2008) Simulated circum-Arctic climate changes by the end of the 21st century. *Global and Planetary Change*, **62**, 173–186.

Russell, D.E. & Gunn, A. (2010) Wild reindeer and caribou. In: *Arctic biodiversity trends 2010*(ed. C.O.a.F.a.F. Caff). Arctic Council, Akureyri, Iceland.

Safronov, V.M., Reshetnikov, I.S. & Akhremenko, A.K. (1999) *Reindeer of Yakutia. Ecology, morphology and use*. Nauka, Novosibirsk.

Sanderson, E.W., Redford, K.H., Chetkiewicz, C.L.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G. & Taber, A.B. (2002) Planning to save a species: the Jaguar as a model. *Conservation Biology*, **16**, 58–72.

Schaefer, J.A., Bergman, C.M. & Luttich, S.N. (2000) Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*, **15**, 731–739.

Sharma, S., Couturier, S. & Steeve, D. C.(2009) Impacts of climate change on the seasonal distribution of migratory caribou. *Global Change Biology*, **15**, 2549–2562.

Singh, N.J. & Milner-Gulland, E.J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. *Journal of Applied Ecology*, **48**, 35–46.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Skogland, T. (1989) *Comparative social organization of wild reindeer in relation to food, mates, and predator avoidance*. Paul Parey Publications, Berlin.

Stien, A., Loe, L.E., Mysterud, A., Severinsen, T., Kohler, J. & Langvatn, R. (2010) Icing events trigger range displacement in a high-arctic ungulate. *Ecology*, **91**, 915–920.

Stien, A., Ims, R.A., Albon, S.D., Fuglei, E., Irvine, R.J., Ropstad, E., Halvorsen, O., Langvatn, R., Loe, L.E., Veiberg, V. & Yoccoz, N.G. (2012) Congruent responses to weather variability in high arctic herbivores. *Biology Letters*, **8**, 1002–1005.

Sturm, M., Racine, C. & Tape, K. (2001) Climate change: increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.

Syroechkovskii, E.E. (1999) Wild and semi-domesticated reindeer in Russia: status, population dynamics and trends under the present social and economic conditions. *Rangifer*, **20**, 113–126.

Taillon, J., Festa-Bianchet, M. & Côté, S.D. (2012) Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biological Conservation*, **147**, 163–173.

Tews, J., Ferguson, M.A.D. & Fahrig, L. (2007) Potential net effects of climate change on high Arctic Peary caribou: lessons from a spatially explicit simulation model. *Ecological Modelling*, **207**, 85–98.

Thonicke, K., Spessa, A., Prentice, I.C., Harrison, S.P., Dong, L. & Carmona-Moreno, C. (2010) The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model. *Biogeosciences*, **7**, 1991–2011.

Vilchek, G.E. & Bykova, O.Y. (1992) The origin of regional ecological problems within the northern Tyumen Oblast, Russia. *Arctic and Alpine Research*, **24**, 99–107.

Weladji, R.B. & Holand, Ø. (2006) Influences of large-scale climatic variability on reindeer population dynamics: implications for reindeer husbandry in Norway. *Climate Research*, **32**, 119–127.

White, R.G., Holleman, D.F., Hubbert, M.E. & Staaland, H. (1987) Herbivores in cold climates. *The nutrition of herbivores* (ed.by J.B. Hacker and J.H. Tennouth), pp. 465–486. Academic Press, Sydney.

Witter, L.A., Johnson, C.J., Croft, B., Gunn, A. & Poirier, L. (2012) Gauging climate change effects at local scales: weather-based indices to monitor insect harassment in caribou. *Ecological Applications*, **22**, 1838–1851.

WWF (2012) *Conservation plan for circum-arctic migratory tundra caribou and wild reindeer*. Available at: http://assets.wwf.ca/downloads/wwf_caribou_strategy_for_review.pdf (accessed 18 February 2012).

Yakushkin, G.D., Michurin, L.N., Pavlo, v.B.M. & Zyryanov, V.A. (1970) Numbers and migrations of wild reindeer in Taymyr. Proceedings of IX Game Biologists Congress in Moscow, pp. 335-338.

Zurell, D., Jeltsch, F., Dormann, C.F. & Schroder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32**, 733–744.

SUPPORTING INFORMATION

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

Appendix S1 Summary of calving ground data.

Appendix S2 Description of predictor variables.

Appendix S3 Variables included in the final model.

Appendix S4 Model comparison with and without semi-domestic populations.

BIOSKETCH

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