

ARCTIC

VOL. 72, NO. 1 (MARCH 2019) P. 28–42

<https://doi.org/10.14430/arctic67916>

Assessment of Climatic Conditions for Siberian Reindeer Herding on the Basis of Heat Balance Modelling

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(Received 2 February 2018; accepted in revised form 11 September 2018)

ABSTRACT. The purpose of the research is to assess suitable climatic conditions for traditional herding of reindeer by Indigenous people in different areas of Siberia. A computer simulation model allowed us to calculate reindeer's heat balance according to a number of meteorological indices; it was used to assess climatic conditions in 70 localities. To show the impact of climatic conditions on reindeer's well-being, we introduce the notion of the thermal comfort index (K_t). The best environmental conditions for reindeer are in the areas where K_t takes the highest values in winter and the lowest ones in summer. We showed the results of the reindeer heat balance computer simulation on two maps visualising the average K_t values in summer and in winter. Finally, using official statistics, we calculated the number of reindeer per 100 km² in areas with different types of traditional reindeer herding. The territories with the largest domesticated reindeer populations per 100 km² in the two major tundra reindeer breeding areas (Samoed and Chukchi-Koriak types of reindeer herding) are located in the regions with the relatively low value of K_t in summer and high in winter. In the taiga, K_t is relatively high in summer, and reindeer herding (Tungus and Saian types) is developed mostly in highlands, where the summer K_t is lower than in flatlands because of the vertical temperature gradient. The results obtained prove that thermal conditions are extremely important for traditional reindeer herding.

Key words: reindeer herding; reindeer population; climate; heat balance; simulation model; Indigenous people; Russian North; Siberia

RÉSUMÉ. L'objectif de cette recherche consiste à évaluer les conditions climatiques convenables à l'élevage traditionnel des rennes par les peuples indigènes de différentes régions de la Sibérie. Au moyen d'un modèle de simulation informatisé, nous avons calculé le bilan thermique des rennes en fonction de plusieurs indices météorologiques. Nous avons évalué les conditions climatiques de 70 localités. Pour illustrer les incidences des conditions climatiques sur le bien-être des rennes, nous avons introduit la notion de l'indice du confort thermique (K_t). Pour le renne, les meilleures conditions environnementales sont celles pour lesquelles K_t a les plus grandes valeurs en hiver, et les moins grandes valeurs en été. Nous avons illustré les résultats de la simulation informatisée du bilan thermique du renne sur deux cartes permettant de visualiser les valeurs K_t moyennes de l'été et de l'hiver. Pour terminer, à l'aide de statistiques officielles, nous avons calculé le nombre de rennes par 100 km² dans des zones ayant différents types d'élevage traditionnel de rennes. Les territoires comptant les plus grandes populations de rennes domestiqués par tranche de 100 km² dans les deux grands secteurs de reproduction de la toundra (les types d'élevage Samoed et Chukchi-Koriak) se situent dans les régions où la valeur K_t est relativement basse l'été et élevée en hiver. Dans la taïga, le K_t est relativement élevé pendant l'été, et l'élevage des rennes (de types Tungus et Saïan) est surtout développé dans les hautes terres, où la valeur K_t d'été est moins élevée que dans les plaines en raison du gradient thermique vertical. Les résultats obtenus prouvent que les conditions thermiques jouent un très grand rôle dans l'élevage traditionnel des rennes.

Mots clés : élevage des rennes; population de rennes; climat; bilan thermique; modèle de simulation; peuples indigènes; nord de la Russie; Sibérie

Traduit pour la revue *Arctic* par Nicole Giguère.

Цель исследования состоит в оценке климатических условий для традиционного оленеводства коренных народов в разных областях Сибири. Использование имитационной компьютерной модели позволило по ряду метеорологических показателей рассчитать значения теплового баланса северного оленя для 70 географических пунктов. Чтобы отразить влияние климатических условий на организм оленя, мы ввели понятие коэффициент теплового комфорта (K_t). Самые благоприятные для северного оленя условия там, где K_t принимает наиболее высокие значения зимой и самые низкие значения летом. Мы отразили результаты компьютерного моделирования теплового

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баланса оленя на двух картах, отражающих средние значения K_t в летний и зимний периоды. Для интерпретации результатов мы рассчитали количество оленей на 100 км² в ареалах с различными типами традиционного оленеводства, используя данные официальной статистики. Оказалось, что в двух крупнейших областях тундрового оленеводства (самоедский и чукотско-корякский типы оленеводства) территории, с наибольшим числом домашних оленей на 100 км², расположены в районах с относительно низкими значениями K_t летом и высокими зимой. В тайге (в ареалах тунгусского и саянского типов оленеводства) значения K_t летом сравнительно велики. Оленеводство здесь развивается в основном в районах, где есть высокие горы и из-за вертикального градиента температуры значения K_t летом понижены. Полученные результаты подтверждают значимость температурных условий для традиционного оленеводства.

Ключевые слова: северное оленеводство; популяции северного оленя; климат; тепловой баланс; имитационная модель; коренные народы; Север России; Сибирь

INTRODUCTION

Wild and domesticated *Rangifer* (*Rangifer tarandus* L.) is an important species in the circumpolar Arctic, providing sustenance for Indigenous and settler societies. It is the key species in Arctic ecosystems (Forbes et al., 2009; Nyman Larsen et al., 2010; Meltofte, 2013). As the effects of climate change in the Arctic become increasingly visible, interest has grown in documenting the impact of these effects on the well-being of domesticated and wild reindeer populations and reindeer herders' strategies in Eurasia in general (Maynard et al., 2010; Uboni et al., 2016) and in northern Europe (Weladji and Holand, 2006; Moen, 2008; Rees et al., 2008; Reinert et al., 2008; Oskal et al., 2009; Magga et al., 2011; Pape and Löffler, 2012; Turunen et al., 2016). Some of this work has focused specifically on Russia (Forbes and Stammer, 2009; Klovov, 2012; Forbes et al., 2016).

The impact of climatic factors on *Rangifer* can be either direct or indirect. Direct impact involves the effect on the heat balance of the animal's body, whereas indirect impact has to do with the impact on the reindeer's habitat (for example, the state of the vegetation cover and the availability of pastures, the intensity of summer mosquitoes, the formation of ice crusts on the snow, and the development of epizootics associated with weather conditions). In this paper we will concern ourselves only with the direct effects of climatic factors, which determine the areas with favourable conditions for *Rangifer*. Indirect climate impacts can narrow this area, but they cannot expand it.

Much of the literature focuses on measuring the indirect effect of climate change on reindeer husbandry. Several studies have examined the climate impact on grazing pastures (Turunen et al., 2009; Forbes et al., 2010; Macias-Fauria et al., 2012) and the cumulative effect of climate change and industrial development, in an attempt to determine which of them is most harmful for reindeer herding societies (Walker et al., 2011; Kumpula et al., 2012; Degteva and Nellemann, 2013; Forbes, 2013).

A more recent comprehensive study (Uboni et al., 2016) assessed the climate impact on 14 Eurasian populations of wild and domesticated reindeer on the basis of regression modelling of the relation between population growth rates and climate indices (the North Atlantic Oscillation, the

Arctic Oscillation, and the North Pacific Index), and of Pearson correlation coefficients of growth rates between pairs of reindeer populations. The authors analysed trends in population dynamics, investigated the synchrony among population growth rates, and assessed climate effects on population growth rates. They revealed that most of the synchrony in reindeer population dynamics did not seem to be explained by the climate indices that were considered. In a few reindeer populations the climate indices explained growth rates, but the patterns were not linked to the synchrony among populations (Uboni et al., 2016: Tables 1, 2, and S3).

Despite these advances, little work has been done on the direct climatic impact to understand how animals themselves experience temperature differentials in combination with other climatic factors; how this, in turn, influences their use of territory; and how these changes affect their well-being. A number of Canadian zoologists have used computer simulations to model the caribou energy balance in North America (Russell, 1976; White et al., 2014). Russell (1976) proposed a model that simulated an individual female caribou and used decision-based modelling of caribou feeding cycles. This allowed researchers to determine the energetic consequences of insect harassment combined with foraging strategies. And the results of Canadian researchers concerning the modelling of *Rangifer* energy and protein balance were summarized in an important review article (White et al., 2013).

Our research uses similar approaches to focus on an important subspecies of *Rangifer*—the large populations of domestically kept *Rangifer* held by traditional reindeer-herding societies in Siberia. Using the knowledge of Indigenous herders, we also expand the computer simulation model to reflect the reindeers' own experience of body heat balance. The model presented here is based on the algorithms created by the Saint Petersburg Institute for Informatics and Automation of the Russian Academy of Sciences (Mikhailov, 2012, 2013). This model was designed to derive the value of the heat balance of the *Rangifer*'s body by combining environmental factors such as air temperature, wind speed, and solar radiation. The simulation was based on the concept of critical thermal environments (Moen, 1968), according to which thermoregulation is defined as an animal's ability to



FIG.1. Map of geographical names used in the text.

regulate body temperature despite large variations in environmental conditions.

The simulation hinges upon the definition of a thermoneutral zone, which is defined as a set of environmental conditions where reindeer's heat balance is maintained by the work of the thermoregulation physiological system (Parker and Robbins, 1985; Parker and Gillingham, 1990). In extremely cold conditions beyond the range of the thermoneutral zone, animals have to burn fat reserves accumulated over the summer. In extremely hot conditions beyond the range of the thermoneutral zone, they will cease feeding and stop accumulating fat. The simulation allows one to specify the upper and lower boundaries at which overheating or hypothermia occurs for adult *Rangifer* or calves through the use of meteorological data (Mikhailov and Pestereva, 2013; Makeev et al., 2014).

It is well known that reindeer are well adapted to cold but tolerate heat rather poorly. Across Siberia they prefer cool, windy, and rainy summers and moderately warm, low-wind weather in winter, with a relatively shallow snow cover (Baskin, 2009). Our computer simulations allow us to expand and refine these qualitative characteristics.

We hypothesize that reindeer's well-being is connected with the state of the thermoregulation system, which depends on climatic factors: air temperature, wind speed,

solar radiation, cloud cover, precipitation, and air humidity. The principal aim of our study has been to reveal the territories that are most favourable for domesticated reindeer populations, according to their meteorological parameters. These favourable weather conditions are strongly associated with the optimal thermoneutral zone. To compare different areas, we calculated a special index, which we called "the thermal comfort index" (K_t). At the upper limit of the thermoneutral zone, $K_t = 1$, and $K_t = 0$ at its lower limit; $K_t > 1$ can lead to overheating, and $K_t < 0$, to hypothermia. In the course of the study, we had to deal with a number of issues:

- a) to adapt the existing heat balance model created for the Taimyr wild reindeer population (Mikhailov, 2012, 2013; Mikhailov and Pestereva, 2013; Makeev et al., 2014; Mikhailov et al., 2016) to domestic reindeer populations in different regions of Russia (Fig. 1).
- b) to reveal the critical periods of the year when environmental conditions can cross the boundaries of the reindeer's thermoneutral zone;
- c) to calculate the thermal comfort index (K_t) for different regions of Siberia and northwestern Russia with developed reindeer husbandry;

- d) to put K_i on bioclimatic maps; and
- e) to interpret the results of the research.

METHODS AND MATERIALS

The simulating model we used in our research (Mikhailov, 2012, 2013; Mikhailov and Pestereva, 2013; Makeev et al., 2014) was based on the following biological concepts. The stability of body temperature in variable environmental conditions is the result of a balance between heat production and heat loss. This balance is maintained by the thermoregulation system of reindeer, which includes physiological and chemical regulation subsystems. The physiological subsystem regulates the heat loss of the organism, and the chemical subsystem regulates heat production.

The physiological thermoregulation mechanism includes piloerection (thickness change) of fur, redistribution of blood flow near the body surface, perspiration, and adaptive changes in the respiratory system. The subsystems' effectiveness was described by Sokolov and Kushnir (1997) and Cuyler and Øritsland (2002) on the basis of experimental data. As a result of piloerection, fur cover thickness and its thermal resistance can almost double; the coefficient of thermal insulation of body tissue increases by 100%, and of the lower extremities by almost 10 times. The role of perspiration in the thermoregulation of reindeer is minor; it does not exceed 10%. In winter, when the air temperature drops from 0°C to -40°C, heat transfer with breathing decreases by 40%; in summer, when the temperature rises from 0°C to +20°C, heat transfer increases almost threefold.

At a high air temperature (approximately above +20°C), the physiological thermoregulatory system cannot provide reindeer's heat balance. Overheating is avoided through a decrease in the level of metabolism and, accordingly, the heat production of the animal's body. Nutritional activity is limited to the night hours; energy costs for grazing, digestion, and accumulation of nutrient reserves (mostly by fat accumulation) are reduced. In winter, in extremely cold weather the physiological thermoregulation system cannot support the reindeer's thermal balance. In these conditions the animals have to expend the energy accumulated in summer exclusively for sustaining heat balance (Sokolov and Kushnir, 1997). Thus, within the thermoneutral zone, heat balance is sustained by regulating the body's heat loss, and beyond this zone, by regulating an animal's heat production.

The thermal processes in the animal's body obey thermodynamics laws and can be described with the equations of mathematical physics. The complexity of biological systems, however—the large number of factors that influence them and the difficulty of obtaining the required experimental data—calls for significant simplification of real processes and a transition from classical mathematical models to computer simulations.

Our model envisioned the reindeer body as divided into compartments (Winkel, 2016). The model simulated the redistribution of heat between the compartments as a result of the physiological thermoregulation mechanisms of the reindeer. Considering the variability of the body temperature of warm-blooded animals, one can distinguish the internal part of the body with a relatively constant temperature, whose changes do not exceed a tenth of a degree (the “core”), from the external parts of the body (the “shell” or “envelope”), whose temperature can vary from units to tens of degrees. The compartment model, then, consists of two layers. The first is the core; the second includes the compartments of the shell: the head, neck, upper and lower limbs. The source of heat production in the model is the core; the temperature is assumed to be constant. The shell provides thermal insulation for the core; heat transfer occurs through the thermal conductivity of the coat and through heat loss from respiration. This structure is related to the variable thermal characteristics of different parts of the reindeer's body and the presence of information necessary for the adjustment of the model. Thermal balance components are interconnected and together define the animal's thermal condition.

Radiation and thermal balance are described by the following equation:

$$Q + R F + P F - E_b - F E_p - F E_d = T_i,$$

where Q is body heat production, R is the radiation thermal balance of the skin surface, F is the skin surface area, P is heat exchange between skin surface and fur and external air due to fur air permeability, E_b is heat loss from breathing, E_p is heat loss from perspiration, E_d is heat loss due to passive diffusion of water from skin surface, and T_i is the thermal imbalance causing body temperature change.

The model works as follows. First, heat production is calculated depending on the morpho-physiological characteristics of the animal and its activity (walking, snow-breaking, pasturing, rest). Then, the parameters of the physiological system of thermoregulation (thermal resistance of the wool cover and of the tissue envelope, and other) are selected in such a way as to ensure equality ($T_i = 0$) or minimize ($|T_i| \rightarrow \min$) the difference between heat production and heat loss under given weather conditions. Within the thermoneutral zone, the balance between heat production and heat loss can always be achieved by changing the parameters of physiological thermoregulation, and the model changes heat release so that it is equal to heat production ($T_i = 0$). Outside the thermoneutral zone, the possibilities of physiological thermoregulation are no longer sufficient, and the value of heat production must be increased or decreased to minimize the imbalance. Heat production increase ($T_i > 0$) means that a reindeer is spending its fat reserves. Heat production decrease ($T_i < 0$) means that a reindeer is forced to reduce (or even completely stop) its motor and feeding activities.

TABLE 1. List of the meteorological factors used for the simulation.

Meteorological factors	Units
Air temperature	°C
Wind velocity	m/sec
Humidity	%
Amount of clouds	point
Precipitation	mm/m ²
Solar radiation on horizontal surface	kcal/m ² hr
Scattered radiation	kcal/m ² hr
Sun angle	degree

The model simulated five thermoregulation mechanisms: 1) hair piloerection, 2) change in the thermal resistance of “envelope” tissues, 3) change in heat loss with breathing, 4) changes in feeding activity, and 5) changes in heat production.

The weather data for the heat balance model included a set of variables characterizing (Table 1): air temperature, wind speed, cloud cover, air humidity, and direct and diffuse solar radiation.

We used monthly average data for 2001–10 obtained from meteorological databases (NASA Surface Meteorology and Solar Energy, Database MERRA2, <https://disc.sci.gsfc.nasa.gov/datasets> and the International Data Center [RIHMI-WDC] <http://meteo.ru>).

The input data included body mass; skin thermal insulation; tissue insulation; energy consumption for digestion, absorption, transport and assimilation of nutrients; and energy consumption for production (e.g., fat formation).

The model is implemented in the environment of MATLAB. To set and verify the model we used the results of field observations and experiments published by Moote (1955) Segal’ (1980), Sokolov and Kushnir (1986, 1997), Ovsov (1991), Cuyler (1992), and Cuyler and Øritsland (2002). For identification, we used data of field experiments and the results of computer calculations on the amount of heat production, the thermal characteristics of the coat and tissue membranes, and skin temperature of different parts

of the animal’s body. As an example, Table 2 compares the data of experiments (Sokolov and Kushnir, 1997) and our model calculations of reindeer skin temperature depending on air temperature. Table 3 shows the results of the model estimation of the lower critical temperature for reindeer (adult males and females) as a function of wind speed.

To link the results of simulation to the reindeer’s well-being, the model calculated the *thermal comfort index* (K_t). We suggested that the model can mimic the reindeer’s thermoregulatory system to indicate the animal’s level of comfort with the heat. In this case, the normalized factor of the thermoregulatory system state can be used as the K_t index. It takes the value of 1 at the overheating limit and the value of 0 at the supercooling limit. According to our hypothesis, the weather conditions most favourable for thermoregulation systems and most comfortable for reindeer correspond to the average K_t values ($0.4 < K_t < 0.6$) equidistant from the limits of the thermoneutral zone. Beyond the thermoneutral zone the relative value of non-compensated thermal energy (Ti/Q) is added to K_t values at the limit of the zone. Thus in summer, K_t will be more than 1 in the overheating zone; in winter in the supercooling zone, K_t will take negative values. The magnitude of the K_t index deviation from the boundary values (0 and 1) determines the level of an animal’s thermal discomfort. If the index drops below zero ($K_t < 0$), it implies that an animal is forced to spend nutrients (burn calories) to maintain a stable heat balance. When the value of K_t is greater than 1, the reindeer experience overheating. Thus, the best weather conditions for reindeer herding are in the areas where the K_t coefficient takes the highest values in winter and the lowest values in summer.

Figures 2 and 3 show examples of favourable and unfavourable thermal conditions for reindeer. In the northern part of Taimyr Peninsula (Taimyr Lake) and in the northwestern part of Iakutia (Olenek) in winter (from November to April), thermal conditions for reindeer calves are unfavourable due to over-cooling, and there are no domesticated reindeer wintering in these areas (Fig. 1). In the central part of Iamal-Nenets Autonomous Okrug

TABLE 2. Reindeer skin temperature depending on air temperature calculated from the model/experimenters’ data (Sokolov and Kushnir, 1986).

Reindeer body parts	Air temperature, °C			
	+3°	–20°	–30°	–40°
Body side	36.7°/36.6°	36.3°/36.3°	36.2°/36.2°	36.1°/36.0°
Upper limbs	36.3°/36.2°	35.4°/35.6°	35.1°/35.0°	34.9°/35.0°
Lower limbs	31.3°/30.6°	21.7°/21.7°	15.6°/13.1°	9.1°/9.3°

TABLE 3. Lower critical temperature for reindeer as a function of wind speed. (The critical temperature is the temperature at which the reindeer’s physiological subsystem of thermoregulation is insufficient.)

Reindeer mass, kg	Wind speed, m/sec				
	0	5	10	15	20
130 (male)	–62°	–41°	–33°	–27°	–20°
80 (female)	–53°	–38°	–29°	–24°	–17°

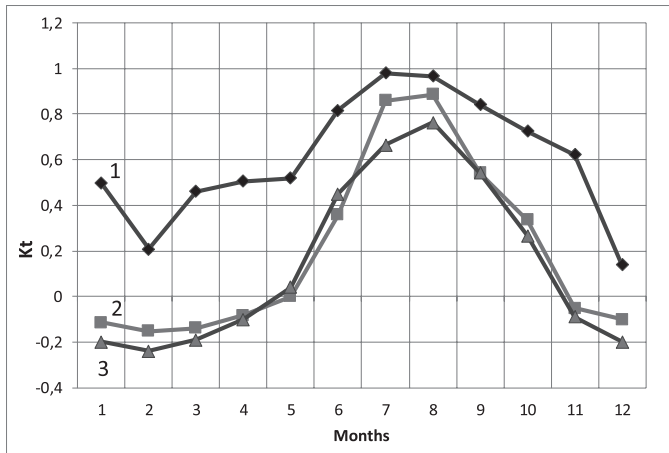


FIG. 2. Examples of annual dynamics of the thermal comfort index (K_t) for calves in resting lying down position. 1 – Nadym (the central part of Iamal-Nenets Autonomous Okrug); 2 – Olenek (northwestern Yakutia); and 3 – Taimyr Lake (northern part of Taimyr Peninsula). Calves are most sensitive to supercooling. When $K_t < 0$ (Taimyr Lake and Olenek from November to April), thermal conditions for reindeer herding are unfavourable. There are no domesticated reindeer wintering in these areas. In the region of Nadym, thermal conditions are favorable ($K_t < 0$ throughout the winter), and many domesticated reindeer herds use this area for wintering.

(Nadym), winter thermal conditions are favourable ($K_t < 0$ throughout the winter), and many domesticated reindeer herds use this area for winter pasturing.

During the summer, unfavourable time ($K_t > 1$) is noted in Chara (the southern part of Yakutia) from June to August, and in Kanevka (the central part of Kola Peninsula) in July and August. In Maresale (the main area of summer reindeer pastures on the Iamal Peninsula) $K_t < 1$ throughout the summer (Fig. 3).

Our study included five steps. First, we adapted the existing heat balance models to domestic reindeer populations. There is a difference between heat balance models of wild and domesticated *Rangifer*. On a physical level, heat balance models examine differences in animals' mass, as well as in calving dates, which are significantly different for domesticated and wild reindeer. In general, the body mass of a domesticated reindeer is less than that of a wild *Rangifer*, and then those values will differ according to the regional breed of domesticated reindeer. Rut and calving dates, as well as seasonal migration routes of domestic reindeer, are often adjusted or regulated by herders. Several Indigenous herding traditions select breeding does for either earlier or later calving dates depending on local geographic conditions. Similarly, migration routes may vary depending on local herders' strategies of keeping reindeer for meat or for transport (Klokov and Mikhailov, 2015). Heat balance parameters differ significantly depending on the age and sex of the animal and its behavioural type. Therefore, we developed values for three age groups (calves, mature stags, and mature does) as well as for four different types of animal activity: moving, feeding, resting standing, and resting lying down. Finally, we calculated different heat balance models for the three most commonly cited reindeer herding traditions: Samoed (the Nenets and the

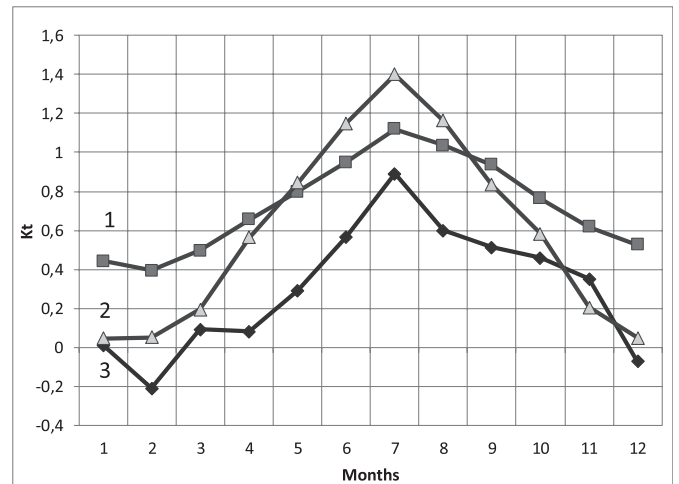


FIG. 3. Examples of annual dynamics of the thermal comfort index (K_t) for mature reindeer in resting standing position. 1 – Kanevka (central part of Kola Peninsula, Murmansk Area); 2 – Chara (southern part of Yakutia); and 3 – Maresale (western part of Iamal Peninsula). Mature reindeer are most sensitive to overheating ($K_t > 1$). Unfavourable periods for reindeer herding are June–August in Chara and July–August in Kanevka. The west coast of the Iamal Peninsula (Maresale) has optimal conditions for reindeer grazing in summer ($K_t < 1$ throughout the summer).

Komi-Izhem reindeer herding in northwestern Russia), Chukchi-Koriak (in northeastern Russia), and Tungus and Saian in the Siberian taiga between the Enissei River and the Pacific Ocean (Vasilevich and Levin, 1951; Klokov, 2007). We further distinguished three ecological types of reindeer husbandry: tundra types, lowland taiga types, and highland taiga types (Klokov, 2007). Table 4 records the differences in reindeer body mass and terms of calving period in different regions of Russia according to the data of Mukhachev and Laishev (2002).

Secondly, we developed daily averages over an entire year for a reindeer's body heat balance by using the data from 45 weather stations located in areas with different climate conditions and reindeer herding types. This calculation was designed to reveal the critical periods of the year when weather conditions are unfavourable for reindeer; that is, when their physiological subsystem of thermoregulation is insufficient. We detected two severe periods that are likely to move reindeer out of their thermoneutral zone (Figs. 2 and 3). The first one is between December and February, when calves are most likely to experience cold stress. The second one is between July and August, when mature reindeer are most likely to experience heat stress. The success of the rut in autumn, and hence the success of calving next spring, depended very much on the physical condition of does. We made further calculations using the data from a larger number of weather stations, but only with regard to the limiting months (January–February and July–August).

Thirdly, we calculated the thermal comfort index (K_t) using the data received from 70 weather stations located in areas with different types of reindeer herding (Fig. 4). Those were all the stations for which weather data were available on the website www.meteo.ru/english/index.php. We used

TABLE 4. Parameters used for heat balance simulation in different regions of Russia: reindeer body mass and time of calving period (according to Mukhachev and Laishev, 2002).

Regions	Mature stag body mass, kg	Average time of calving period
Tundra of the European North, Yamalo-Nenets Autonomous Okrug, and Taimyr	119	beginning of June
Taiga of the European North and Western Siberia	119	beginning of June
Tundra of Yakutia	126	mid May
Taiga of Yakutia, Evenkia, Eastern Siberia	142	mid May
Tundra of the Far East	103	beginning of May
Taiga of the Far East	142	beginning of May

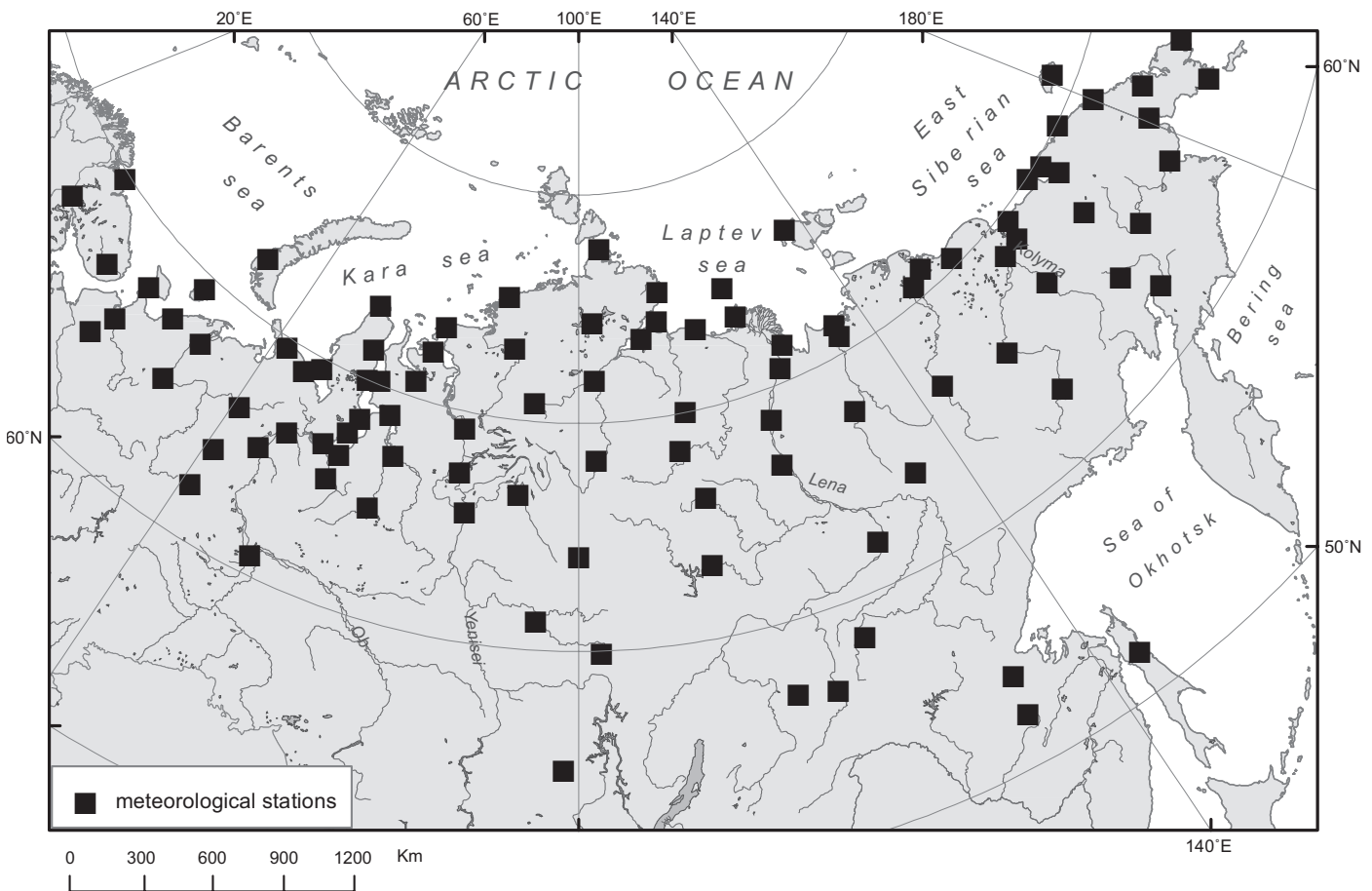


FIG. 4. Location of weather stations used in the simulation modelling.

the parameters (Table 4) for each region. Then we combined all the data into two data arrays, one for the summer and another for the winter, to present the K_t value on the maps. With the above data we placed the thermal comfort index onto geographical maps. We used isolines with an interval 0.1 to build the maps in ArcGIS using a standard GRID model, after which the isolines obtained were smoothed using the smooth-line 500 km method. We represented the final results on the two maps reflecting average K_t values for the summer (K_{ts}) and winter (K_{tw}) periods.

Finally, in order to interpret the results, we compared the maps of the thermal comfort indexes (K_{ts} and K_{tw}) with the statistical data representing the domesticated reindeer population distribution across the administrative districts in Russia.

RESULTS

The maps of K_{tw} and K_{ts} isolines built on the basis of the simulation results allowed us to detect the zones with both favourable and unfavourable climatic conditions for winter and summer (Figs. 5 and 6). According to our hypothesis, the best environmental conditions for reindeer herding are in the areas where the coefficient K_t takes the highest values in winter and the lowest values in summer: ($\max K_{tw}$) and ($\min K_{ts}$). Poor thermal conditions for reindeer herding exist in the areas with either the lowest K_t in winter or the highest K_t in summer: ($\min K_{tw}$) or ($\max K_{ts}$).

In winter, areas with low K_{tw} values are unfavourable for reindeer herding. The simulation showed that the region with the worst conditions was the northern part of

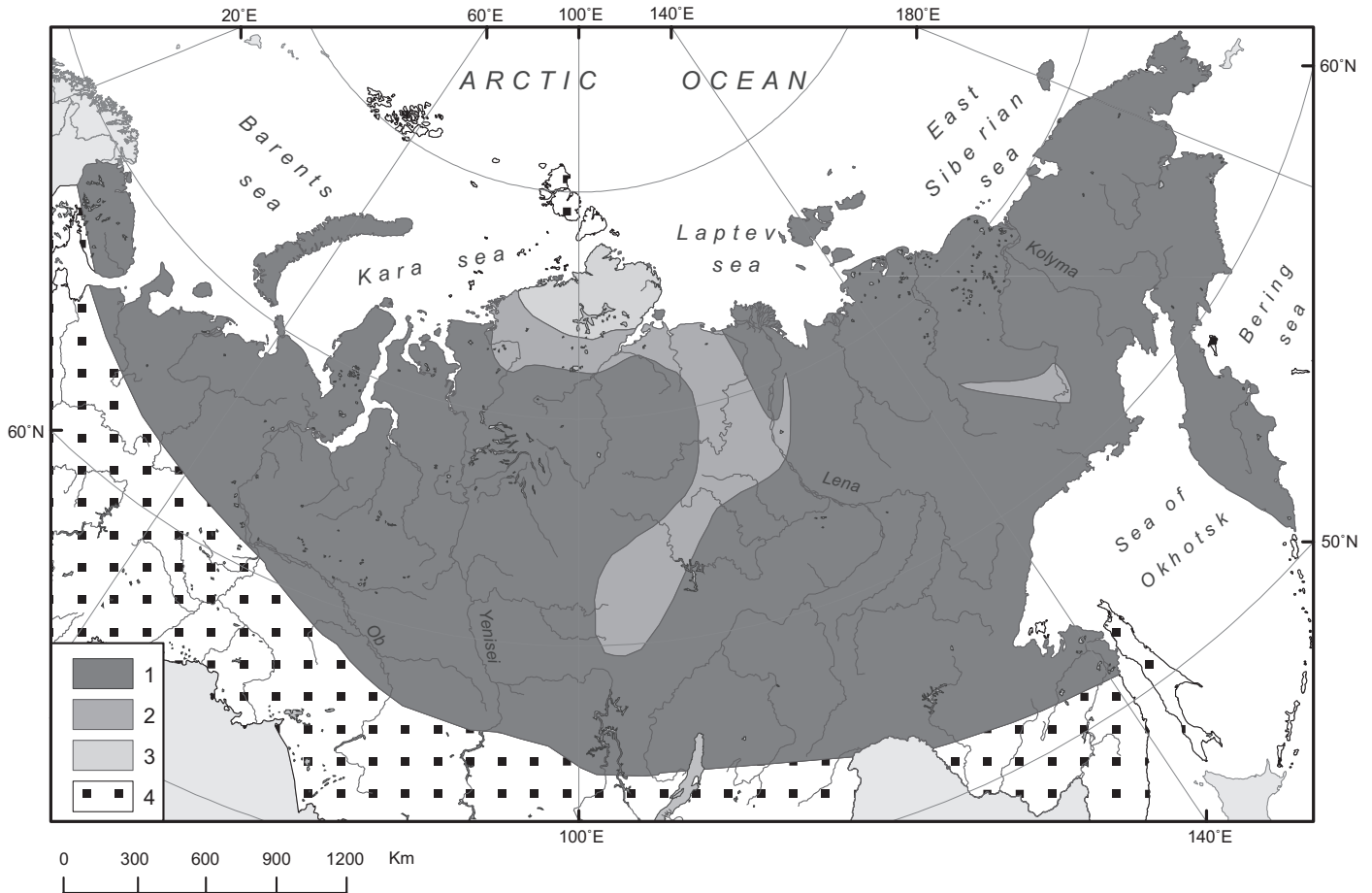


FIG. 5. Summary of domesticated reindeer heat balance intensity (K_{tw}) estimates during the winter limiting period (December–February). 1 – territories without winter hypothermia risk ($0.2 < K_{tw}$); 2 – territories with significant winter hypothermia risk ($0.1 < K_{tw} < 0.2$); 3 – territories with the high winter hypothermia risk ($K_{tw} < 0.1$); and 4 – territory without reindeer herding (no calculations made).

the Taimyr Peninsula (Fig. 1). In this area the climate is extremely severe and reindeer herding has never been developed. It should be noted that wild reindeer, which are somewhat better adapted to cold, hibernated in small groups even there (Makeev et al., 2014). In the southern part of Taimyr and in the western part of Yakutia, the value of K_{tw} is also low and we can assume that reindeer herding there is associated with a relatively high risk of hypothermia during winter. Winter climatic conditions in the rest of the Siberian tundra and taiga were favourable for reindeer husbandry.

Thus, we can identify two comparatively small areas with unfavourable winter conditions for reindeer herding: the area with extremely severe winters in northern Taimyr and the areas with the risk of hypothermia in southern Taimyr and western Yakutia (Fig. 5).

The best summer conditions for reindeer herding (min K_{ts}) are on the coast of the Arctic Ocean; they are worse in the south, as the values of the coefficient K_{ts} regularly increase in a southerly direction (Fig. 6). This pattern was disrupted on the Pacific coast, where the K_{ts} values were less than in the continental areas, and therefore the conditions for reindeer herding were better. Exceptions were also the mountain regions (the Ural Mountains, and

mountains in Yakutia and the southern part of Siberia), where K_{ts} was lower than on the plains.

The simulation results allowed us to identify the regions with optimal climatic conditions for the three main traditional types of reindeer herding.

The Samoed Reindeer Herding Area

In Iamal-Nenets Autonomous Okrug, tundra thermal conditions were most favourable both in summer and in winter. The best summer conditions were in the northern and central parts of the Iamal Peninsula. In terms of the combination of summer and winter thermal conditions, the northern Iamal-Nenets Autonomous Okrug can be divided into three parts. In the forest tundra and the northern taiga, thermal conditions were optimal for wintering, but less favourable for summer grazing. On most of the Iamal Peninsula, thermal conditions were optimal in summer and quite favourable in winter. In all other tundra areas, thermal conditions, both in summer and in winter, were less optimal, but favourable enough in general.

In the European part of Russia in the tundra, winter conditions were optimal, but in the forest tundra we observed a little overheating in all areas in the summer.

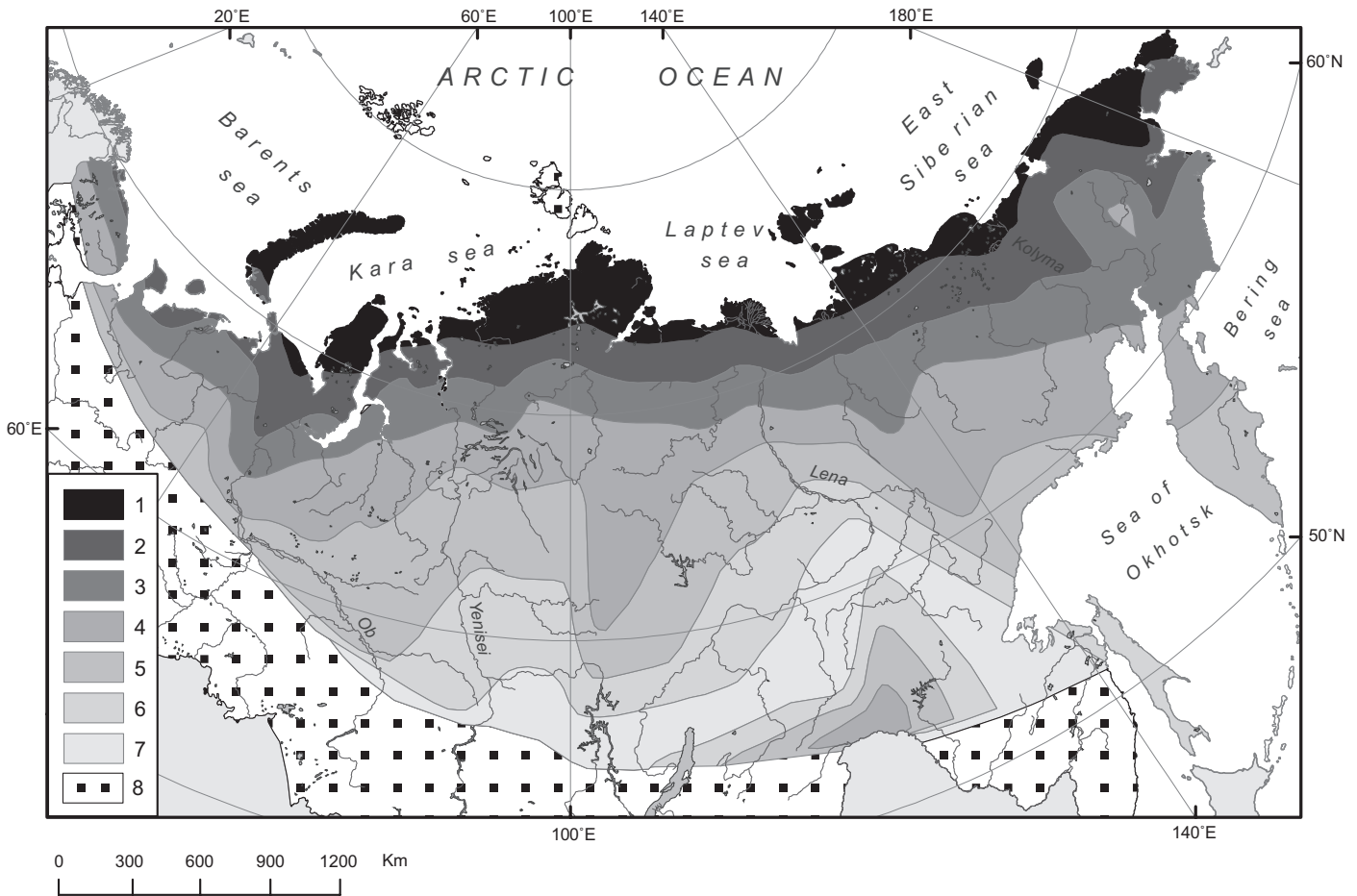


FIG. 6. Summary of domesticated reindeer heat balance intensity (K_{ts}) estimates during the summer limiting period (July to August). The most favourable conditions (suitable for commercial large-scale reindeer herding) are shaded areas 1 ($K_{ts} < 1.0$) and 2 ($1.0 < K_{ts} < 1.05$). Relatively favourable conditions (suitable for limited-scale commercial reindeer herding) are shaded areas 3 ($1.05 < K_{ts} < 1.10$) and 4 ($1.10 < K_{ts} < 1.15$). Fairly unfavourable conditions (suitable for breeding small herds mostly in the highlands) are shaded areas 5 ($1.15 < K_{ts} < 1.20$) and 6 ($1.20 < K_{ts} < 1.25$). Unfavourable conditions (impossible to breed reindeer in summer unless special techniques are employed) are shaded areas 7 ($1.25 < K_{ts}$) and 8 (territory without reindeer herding, so no calculations made).

Summer thermal conditions were best on Kolguev Island and along the northern coast of the Nenets Autonomous Okrug, but were somewhat less favourable along the northern coast of the Kola Peninsula and in the continental, interior tundra of the Nenets Okrug.

The Chukchi-Koriak Reindeer Herding Area

In the tundra of northeastern Russia, thermal conditions were favourable for reindeer both in summer and winter. The best summer conditions were in the northern coastal tundra of the Chukchi Autonomous Okrug. Relatively favourable thermal conditions both in summer and in winter have been noted as well in the neighbouring Chukotka districts in northeastern Yakutia and in the north of the Magadan area.

The Tungus and Saian Reindeer Herding Areas

The best summer thermal conditions were noted in the taiga of the central and eastern part of Siberia (including Yakutia), first along its northern periphery (i.e., closer to

the tundra boundary), and second in the highland areas of the Trans-Baikal, southern Yakutia and Amur regions. Unfavourable winters (with a risk of hypothermia for calves) were characteristic primarily of the northwestern regions of Yakutia and eastern Evenkia. To the east, the risk of hypothermia gradually decreased.

Comparing the bioclimatic maps of the thermal comfort index with the statistical data demonstrated that the territories with a large reindeer population most often overlapped with areas with favourable thermal conditions. We counted the number of reindeer per 100 km² of the administrative districts occupied by Samoedic and Chukchi-Koriak reindeer herding on the basis of state statistical data. In areas where reindeer herding had a continuous distribution, the number of deer per unit area was positively correlated with the K_{ts} values (Tables 5 and 6).

Thus, more than 90% of the reindeer in the Samoedic tundra area are concentrated in the regions with relatively low K_{ts} values (Table 5). The highest density of reindeer (215.5 head per 100 km²) is on the Iamal Peninsula, where the thermal comfort index is close to optimum (i.e., min K_{ts} and max K_{tw}).

TABLE 5. Number of reindeer per 100 km² in regions with different K_{ts} values in the Samoed reindeer herding area.

K_{ts} values	Districts	# of reindeer as of 31 December 2016 (1986)	Area, km ²	# of reindeer per 100 km ²
$K_{ts} < 1.0$	Iamal district of the Yamal-Nenets Autonomous Okrug	256 700 (151 500)	119 121	215.5 (127.2)
$1.0 < K_{ts} < 1.05$	Priural'skiy and Tazov'skiy districts of the Yamal-Nenets Autonomous Okrug, the Nenets Autonomous Okrug, Lovozerskiy district of the Murmansk Area, and Taimyr'skiy district of the Krasnoyarsk Territory (the western part, located on the left bank of the Enissei River)	855 700 (574 800)	591 650	144.6 (97.2)
$1.05 < K_{ts} < 1.10$	Shuryshkarskiy and Nadym'skiy districts of the Yamal-Nenets Autonomous Okrug	57 100 (63 900)	154 532	36.9 (41.4)
$1.10 < K_{ts} < 1.15$	Purov'skiy district of the Yamal-Nenets Autonomous Okrug	28 700 (33 800)	108 797	26.4 (31.1)

TABLE 6. Number of reindeer per 100 km² in regions with different K_{ts} values in the Chukchi-Koriak reindeer herding area.

K_{ts} values	Districts	# of reindeer as of 31 December 2016 (1986)	Area, km ²	# of reindeer per 100 km ²
$K_{ts} < 1.0$	Iultinskiy district of the Chukotka Autonomous Okrug	46 100 (87 900)	134 600	34.2 (65.3)
$1.0 < K_{ts} < 1.05$	Chukotskiy, Providenskiy and Chaun'skiy districts of the Chukotka Autonomous Okrug	38 100 (81 100)	116 220	32.8 (69.8)
$1.05 < K_{ts} < 1.10$	Anadyr'skiy and Bilibinskiy districts of the Chukotka Autonomous Okrug, Penzhinskiy and Oliytorskiy districts of the Kamchatka Territory	89 000 (430 800)	651 038	13.7 (66.2)
$1.10 < K_{ts} < 1.15$	Karaginskiy and Tigil'skiy districts of the Kamchatka Territory	13 700 (42 800)	104 125	13.1 (41.1)

There are many fewer reindeer in the Chukchi-Koriak reindeer herding area than in the Samoed area. Most reindeer graze in the northern coastal tundra and the tundra along the shore of the Pacific Ocean, where there is a good combination of K_{ts} and K_{tw} . In the northern part of Kamchatka, as well as in the central and western part of Chukotka, where the K_{ts} values are higher, the number of reindeer per 100 km² is lower (Table 6).

There was no obvious correlation between the number of reindeer per 100 km² and K_{ts} values in the area of Tungus and Saian reindeer herding, where herders choose only the most favourable areas for pasture. In this area the domesticated reindeer population was never large, since deer were bred here not to produce meat, but mainly for transport. Most reindeer were located in the mountainous regions of eastern Yakutia, where the K_{ts} values were more favourable. At the same time, in the western and central parts of Yakutia where winters are especially severe (the K_{tw} values are too low), reindeer herding is undeveloped.

In most taiga regions of eastern Siberia, the development of reindeer herding depends on the possibility of driving the animals to the highlands in the summer months. Average daily temperatures drop by approximately 0.6°C for each 1000 m of relative height. In addition, the move from forest landscapes to highland tundra meant a strengthening of the wind, which was equivalent to an additional drop in temperature of 2–3°C. Therefore, driving a domesticated reindeer herd to an elevation in the highlands of approximately 1500 m was equivalent to its migration several hundred kilometres north. Thus, in the Saian foothills, K_{ts} was greater than 1.3 (calculated according to

data from the Nizhneudinsk weather station at 54°54'N, 99°01' E), which was obviously quite unfavourable for herding. However, in the Saian highlands, the Tofa people in summer keep reindeer herds at elevations between 1500 and 2000 m where, according to our estimates, K_{ts} was around 1.15.

It should be noted that improving the heat balance is not the only reason for moving reindeer to windy places. Open spaces help to reduce insect harassment, in addition to providing preferred forage.

DISCUSSION

The best-known authors of fundamental works on *Rangifer* in Russia (Syroechkovski, 1986, 1995, 2000; Baskin, 2005, 2009; Baskin and Miller, 2007) considered the influence of several drivers on the geographic distribution and dynamics of *Rangifer* populations, including fodder resources (pastures), impact of predators, diseases, and competition between populations of domestic and wild reindeer. They also paid close attention to the impact of hunting on wild reindeer populations and to the particularities of domesticated reindeer herding in different regions. They scarcely considered climatic factors.

Two Arctic Council reports (Jernsletten and Klovov, 2002; Ulvevadet and Klovov, 2004) intended to provide a systematic review of *Rangifer* management all over the circumpolar region, including Russia, devoted only a few short paragraphs to climatic drivers. Special research with a focus on climate influence on Yamal reindeer husbandry

appeared in the 2000s (Rees et al., 2008; Stammler, 2008; Forbes and Stammler, 2009; Forbes et al., 2009; Forbes, 2013). These works focused on the impact of climate change on the socio-ecological systems of the traditional Nenets reindeer herding and responses of herders' communities. The direct influence of climatic drivers on reindeer has not been studied.

Regional officials argue that the main natural factor influencing productivity and sustainability of reindeer herding is the availability of forage resources and pastures. This was true during the Soviet period, when 94% of reindeer pasture resources were used (Klokov, 2007). However, this claim does not explain why, over the past decades in the vast territories of Siberia, with substantial forage resources, the domesticated reindeer population declined or stayed at a low level, and it grew significantly only in the tundra of the Iamal-Nenets Autonomous Okrug (Klokov, 2007, 2011, 2012)—that is, in the region with a lack of pastures, but apparently the most favourable thermal conditions for reindeer herding.

The computer simulation helped us to explain better the patterns of spatial distribution of domesticated reindeer in the Russian North. The simulation demonstrated that summer heat balance conditions played a major role in the success of traditional nomadism. During hot summers (with high K_{ts} values), reindeer are unable to accumulate sufficient nutrients before winter periods, even if there are enough forage plants on the pasture. After a bad summer and high energy consumption in winter (due to low temperatures, strong wind, deep snow, etc.), there is a high risk of animals' death, and emaciated females are unable to have healthy offspring the following spring.

Reindeer herders in Nyda village (southern part of Iamal-Nenets Autonomous Okrug, 66°37' N, 72°54' E) remembered the hot summer of 1979 with numerous blood-sucking insects: "It was hot and there was no wind, the calves had no blood remaining in them, does escaped from mosquitoes in herders' tents, 200 calves from our herd died, i.e., about 20% of all young calves." The summer of 1990 was reported as another extremely hot one. "Everything was dry, the reindeer went into the lakes, they ate little, lost mass; the calves were weak." Herders from Antipaiyta village (69°06' N, 76°52' E) said that the summer of 1990 was the hottest one in their area: "the temperature reached 35°C–36°C, the shallow lakes ran dry and the rivers became shallow." The summers of 1997 and 2005 were also exceptionally hot: "the lakes ran dry, the ground cracked" (Makeev et al., 2014:55).

In the Siberian taiga, summer temperatures are significantly higher than in the tundra, and the herders traditionally use various techniques to improve thermal conditions and help animals sustain their heat balance. Thus, in the eastern part of Siberia, because of the permafrost, there are overflow ice formations on certain rivers where ice cover stays for the whole summer. Herders often keep their reindeer in these places. In the western Siberian taiga, herders keep reindeer in open windy

swamps in summer. As demonstrated by modelling, a wind speed increase from 0 to 4–5 m/sec significantly increased the heat expenditure required for the reindeer to maintain balanced thermoregulation. By moving the herds to a windy area, the herders could mitigate the negative effect of high summer temperatures. At the same time, the wind protects reindeer from insects. In many taiga regions, herders build special sheds to protect reindeer from the sun.

Our work examines the dependence between bioclimatic parameters (K_t) and seasonal migration of domesticated reindeer. However, research on the Taimyr wild reindeer population (Mikhailov and Pestereva, 2013; Makeev et al., 2014; Mikhailov et al., 2016) showed that the pattern of seasonal migration allowed wild reindeer to stay in the areas with conditions most favourable for maintaining a stable heat balance.

We analysed the correlation between seasonal migration of domesticated reindeer herds and K_t on the Iamal Peninsula (Klokov and Mikhailov, 2015). It turned out that domesticated reindeer herds were distributed across the territory according to the most favourable bioclimatic conditions. It is quite probable that the climatic characteristics of a locality were embedded in the traditional knowledge of the herders, who choose for large herds the territories that best suit the reindeer's heat balance and stick to them even when forage resources are depleted. It should be noted that during the Soviet period, administrative decisions changed traditional land-use patterns of reindeer herders in many regions, which made the use of thermally optimal areas impossible. This history could have been one of the reasons the actual spatial distribution of domesticated reindeer populations does not always correspond to the climatic optimum.

Heat balance is not the only climatic factor that has a strong impact on reindeer herding. In some areas, especially the coastal territories, economic success relies heavily on another ecological factor, which in this environment could be considered a limiting condition. This is the risk of grazing lands icing over—the formation of an ice crust inside a mass of snow or on the ground (Bartsch et al., 2010; Tyler, 2010; Vikhamar-Schuler et al., 2013). This risk is greatest when winter temperatures fluctuate around zero, which is favourable weather from the point of view of heat balance. Therefore, we should not expect heat balance modelling for coastal regions to generate results that would match the actual geographic distribution of the herds. The analysis of reindeer population dynamics in various districts of Chukotka has demonstrated that in areas where favourable thermal conditions are combined with a high risk of ice crust formation, the reindeer population in some periods could be large. It was unstable, however, because of the mass mortality of the animals in unfavourable years (Klokov and Khrushchev, 2004).

Stammler (2008) gave an example of how dangerous the ice crust can be for reindeer herding. When he was accompanying a group of reindeer herders in the Iamal Peninsula during a 200 km trip in the early winter

of 2006–07, the weather conditions were extremely unfavourable. In October 2006 severe frost set in, and on 6 November it rained for 12 hours. After the rain, the temperature dropped to -40°C , which led to the formation of an ice crust on the snow. The snow cover was fairly thick, and it took great effort for the reindeer to break the crust and get at the forage. If the crust had formed on the surface of the ground, the animals would not have been able to reach the forage. The reindeer herders had to decide where else to go. After some discussion, they decided to cross the Ob, as the pastures on its southern bank had suffered less damage. The other option was to migrate to the north and spend the winter in the northern tundra, free from the ice crust. Several months later, in February 2007, it rained again in the southern part of the Yamal Peninsula, and an ice crust formed. During the spring migration, all herds that had spent the winter in the forest tundra had to cross huge territories covered by the ice crust, and up to 30% of the livestock died. In addition to these challenges, in the autumn of 2007 the Ieri-Yakha froze up very late, which delayed the migration to the south, and the herds arrived much later than usual. According to Stammeler (2008), Yamal reindeer herders still remember one winter during World War II when the pastures in the north of the peninsula were covered with a thick ice crust.

Thus, although the use of the reindeer thermal balance model together with the data received from the herders themselves has led to interesting results, it does not explain the impact of climatic conditions on reindeer herding during the winter when the temperature fluctuates around zero. To explain how reindeer breeding depends on a year-round climate cycle, it is necessary to create several models to simulate the impact of several weather conditions.

Socio-economic conditions exert a considerable impact on the dynamics of the domesticated reindeer population in Russia, which often obscured the impact of the climate (Klokov, 2012; Uboni et al. 2016). The effects are mainly related to broader economic reform. The greatest changes in both the total number of domesticated reindeer in Russia and their spatial distribution were caused by collectivization in the 1930s and post-Soviet market reforms of the 1990s. In addition, in some regions the spatial distribution of reindeer changed significantly because of land management reorganizations in Soviet times (Klokov, 2011, 2012).

The system of economic management in the USSR significantly influenced the reindeer population. The plan called for an increase in the number of livestock, even in the areas where the local conditions did not favour this increase. Therefore, we cannot expect the distribution of the reindeer population over the territory of the USSR to correspond to climatic conditions. The transition to a market economy in most regions was accompanied by a decrease in the number of reindeer. This decrease can be explained not only by the general deterioration of economic conditions (e.g., a shrinking venison market and rising prices for fuel), but also by the fact that after the fall of the Soviet system, reindeer stock might simply be returning to

its “normal” level, corresponding to the local environment (Klokov, 2016). Most often this was a lower level. However, in the tundra of Yamal-Nenets Autonomous Okrug, after the administrative restrictions imposed by the Soviet land-use planning system had been removed, reindeer herders actually increased the number of livestock over the feeding capacity of pastures, which led to overgrazing.

After the transition economic processes caused by post-Soviet market reforms, we can expect that the location of the domesticated reindeer population will be now more in line with climatic conditions than the locations of reindeer in Soviet times. For this reason, we used the official statistics for the last years to compare the K_{II} values with the density of the reindeer population (see above), and this comparison showed a correlation. Certainly, we should not consider this correlation as proof that the heat balance conditions are the main factor determining the geographical distribution of the reindeer population. The distribution of reindeer livestock results from the overlapping of many drivers besides the climatic ones. The most important of them are food resources, industrial destruction of pastures, predators, labour force (nomadic herders’ families), access to markets, regional legislation, regulation, and management (see general reviews of these drivers in Jernsletten and Klokov, 2002; Ulvavadet and Klokov, 2004; Klokov, 2007).

The model offers possibilities for predicting the effects of climate change on reindeer herding. The heat balance model can predict possible changes in areas favourable for domesticated reindeer herding in the future. The calculations should be carried out on the basis of data obtained using global climate models. As Uboni et al. (2016) pointed out, however, in Russia the impact of social and economic factors on reindeer husbandry is often so strong that it overshadows the impact of climate drivers. On the other hand, it is obvious that the aggravation of climatic conditions can accelerate the degradation of reindeer husbandry or slow its development.

Heat balance simulation makes it possible to take into account the influence of only one of the climatic drivers on the population of domesticated reindeer. It will not predict all possible effects of climate change on reindeer herding. As Uboni et al. (2016) have shown, the effect of climate change on reindeer populations in different regions with different conditions is rarely synchronous, but often multidirectional, which may be for several reasons. First, climatic impact might have been overridden by other factors (predators, disease, changes in human habitats); second, different populations can react to the same climatic driver in different ways; third, the local weather can affect the population more strongly than climatic indicators (Uboni et al., 2016).

We would add to these observations that climate change can affect the population in several opposite ways. The general warming can be associated with a decrease in average summer temperatures—summers can get cooler, wetter, and windier, which is generally favourable for reindeer. The heat balance model can predict this effect.

On the other hand, winters can be warmer, which can cause fluctuations in winter temperatures around 0°C, and this will increase the risk of ice crust formation. The model of heat balance does not take this driver into account. To explain how reindeer herding depends on climate in a year-round cycle, it is necessary to create several models, each focusing on a specific way in which reindeer are most vulnerable to negative weather conditions.

CONCLUSION

Mapping the computer simulation of heat balance made it possible to identify the areas with optimal thermal conditions and favourable zones for traditional reindeer herding. The geographic distribution of the domesticated reindeer population—taking into account differences in traditional types of reindeer herding—is connected with bioclimatic zones. The territories with the largest domesticated reindeer populations per 100 km² in the two major tundra nomadism areas (the Samoed and the Chukchi-Koriak) are located in the regions with relatively low K_{ts} values and relatively high K_{tw} values, that is, where cool and windy summers are not accompanied by severe winters. In the taiga areas of Siberia, thermal conditions were rather unfavourable. Herders use special techniques to protect reindeer from overheating. Reindeer herding is developed chiefly in the region with highlands, where the thermal conditions in summer pastures are more favourable than on the taiga flatlands. On the whole, our modelling showed that over most of the territory, summer conditions limit the development of traditional reindeer herding to a greater extent than winter conditions.

The results obtained may be considered a proof of the working hypothesis about the significant importance of thermal conditions for reindeer herding. Successful large-scale commercial herding with significant profits is developed only in the regions where the thermal conditions are close to optimal. An example of this could be the Iamal Nenets tundra nomadism area. In the territories where thermal conditions are less comfortable for reindeer, large herd development would be much more labour intensive.

No doubt the climate is not the sole factor affecting traditional reindeer herding. However, the mapping of bioclimatic fields on the basis of computer-modelling data contributes to a better understanding of the sustainability and success of traditional indigenous nomadism in some areas and the decline of these practices in other Siberian regions. This methodology might also be used for making projections about the effect of global climate change on traditional reindeer herding.

ACKNOWLEDGEMENTS

The study was performed with the financial support of the Russian Foundation of Basic Research (grants number

15-06-041-95 and 16-08-00510), the Russian Academy of Sciences (project number 0073-2019-0004), and the European Research Council project “Arctic Domus: Humans and Animals across the North” (AdG 295458). Dr. Evgeniy Aleksandrov assisted in obtaining, ordering, and preparing weather data, and Dr. Evgeniy Shpikerman developed GIS and bioclimatic maps. The authors express their gratitude to Professor David Anderson and Dr. Dmitriy Arzyutov for their assistance in preparing this manuscript for publication.

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