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Review articles

The impact of global climate change on the spread of parasitic nematodes

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ABSTRACT. Climate changes may influence the frequency, intensity and geographical distribution of parasites, directly affecting their dispersive stages in the environment (eggs, larvae) and, indirectly, the larvae living mainly in invertebrate intermediate hosts. In biologically diverse nematodes climate warming contributes to the increase in the range of distribution, colonization of new hosts and modification of their development cycles. This is particularly acute in the Arctic and pertains, for instance, to nematodes *Ostertagia gruehneri* and *Setaria tundra* parasitizing reindeer *Rangifer tarandus* and *Umingmakstrongylus pallikuukensis* in musk oxen (*Ovibos moschatus*). Increase in range expansion of mosquitoes Culicidae caused that nematodes of the genus *Dirofilaria*, especially *D. repens*, have been listed in autochthonous invasions even in the northern and eastern European countries. In addition, extended range of occurrence is also shown by *Ancylostoma braziliense* – a parasite of carnivores in the tropical and subtropical countries. In recent years over 20 cases of autochthonous creeping eruption (CE) caused by *cutanea larva migrans* (CLM) *A. braziliense* were detected in people in southern Europe (Italy, Spain, France, Germany).

Key words: global warming, Arctic, Trichostrongylidae, Protostrongylidae, Onchocercidae, soil-transmitted helminthiases (STHs)

Climate changes, a rise in earth's average surface temperature, in addition to pathogens and diseases, have been identified as the greatest threat to global health in the twenty-first century [1]. Most up-to-date research results show that the process of warming began in the 30s of the nineteenth century. The warming trend in recent decades has contributed to increased morbidity and mortality in many regions of the world. According to the Intergovernmental Panel on Climate Change (IPCC), predictions of climate models show that in this century the global average temperature of the earth's surface will rise by 1.1–6.4°C, while the safe level of increase is up to 2°C [2].

Climate changes may affect the frequency, intensity and geographical distribution of parasites, including helminths, directly affecting their dispersive stages in the environment (eggs, larvae) and, indirectly, larvae living particularly in invertebrate intermediate hosts (mainly insects and mollusks). In biologically diverse nematodes (geohelminths and biohelminths) climate warming contributes to increase in the range of distribution, colonization of new hosts and modification of their developmental cycles. According to Garcia-Rodrigo et al. [3], the global warming and „tropicalization of the European climate" with high temperatures and considerable humidity can promote creation of favorable conditions for dissemination of typically tropical species, such as *Ancylostoma braziliense* hookworms.

Peter Molnar, an ecologist and evolutionary biologist from Princeton University, is the author of mathematical models predicting the spread of parasites and parasitic diseases along with a rise in temperature on earth. Molnar assumed that there is equilibrium between the body size and temperature of organisms that affect metabolic processes. Known dependence of the parasite metabolism on temperature allows determining the impact of climate changes which may occur in the future. According to this method, it can be estimated how the rate of parasites development and their developmental cycles will alter with a change of climatic conditions. This pertains to parasites whose developmental stages are present in the environment or in poikilothermic hosts [4].

It is believed that larvae of nematodes present in intermediate hosts are protected by their behavioral thermoregulation, which helps them survive in extremely unfavorable temperatures. This phenomenon has been called ”the shelter effect”. The applied models suggest that climate warming in certain geographical regions, especially during the summer, may cause inhibition of development of parasites with simple life cycle and create the possibility of development for those with complex life cycle [5]. Using the models it has been demonstrated that invasiveness of diseases may increase or decrease with climate change.

Research shows that the polar region of the northern hemisphere is the area where global warming is progressing at the fastest rate in the whole world. In global terms, the average temperature rise has amounted to about 0.9°C since the beginning of the industrial revolution, while in the Arctic this figure has been twice as high [6]. In the future the rate of change, especially in northern Canada, Greenland and Siberia, can be further accelerated [2]. Therefore, the object of many parasitologists’ studies have been nematodes of ungulates, such as tundra reindeer (caribou) *Rangifer tarandus*, musk oxen (*Ovibos moschatus*) and white-tailed deer (*Odocoileus virginianus*) living in those areas. These are nematodes of the families Trichostrongylidae, Protostrongylidae and Onchocercidae, whose larvae are present in the environment or in the poikilothermic intermediate hosts. *Ostertagia gruehneri* (Trichostrongylidae, Strongylida) parasitize the tundra reindeer in the Arctic tundra of Eurasia and North America. A nematode settles in the stomach (under the mucosa of abomasum). Invasions cause lack of appetite, weight loss and slower fetal development in infected females. The life cycle of *O. gruehneri* is typical for the species of the genus *Ostertagia*. The eggs are released with feces into the environment, then larvae L1 hatch and after subsequent molting convert to L2 and L3. Invasive L3 larvae are able to migrate along the stalks of plants; infection of a host occurs *per os*. However, almost 100% of the larvae in the stomach of an animal are prevented from developing until the next year. Hypobiosis and a two-year cycle of the parasite transmission are constrained by climatic conditions.

Field and laboratory studies indicate that global warming may cause an increase in the presence of L3 in the environment by extending the vegetation period. However, short-term temperature rises in the middle of summer can split their transmission into spring and autumn periods. The increased rate of larvae development and prolonged vegetation period can alter the parasite transmission from two to one cycle per year [7].

Climate warming has the effect of prolonging the activity of poikilothermic organisms such as terrestrial gastropods which are intermediate hosts of nematodes of Protostrongylidae family. One representative of these parasites is *Parelaphostrongylus odocoilei*, dwelling in the nervous system of deer, for example, white-tailed deer in the Mackenzie Mountains in the north-western Canada. It also occurs in mountain sheep: the Thinhorn (*Ovis dalli*) and Canadian sheep (*Ovis canadensis*). Together with the temperature increase in the spring and summer months over the past 50 years, the activity period of gastropod intermediate hosts has extended, which has significantly affected the frequency of infection in sheep (up to 66 – 100%) because the peak excretion of L1 larvae by infected animals falls in the period from March to May, and the highest prevalence of L3 larvae of this nematode in gastropods is observed in August and September [8].

The consequence of unprecedented climate warming in the Canadian Arctic Archipelago is the occurrence of lung nematodes *Umingmakstrongylus pallikuukensis* (Protostrongylidae) in musk oxen on the Island of Victoria in 2008. The parasite escaped from land with animals migrating north, and four years later (2012) was recorded in the northern part of the island at a distance of several hundred kilometers from the primary focus [9]. Intermediate hosts of *U. pallikuukensis* are land slugs of the genus *Deroceras*. The threshold temperature for the development of the nematode larvae in *D. laeve* organisms is 8.5°C and in *D. reticulatum* 9.5°C [10].

One of global warming consequences is an increase in range expansion of insects, vectors of parasites, into new areas. Various types of flies, including mosquitoes (Culicidae), transfer among others microfilaria of nematodes from the family Onchocercidae. An example of territorial expansion of nematodes associated with temperature rise may be *Setaria tundra*. The species was first detected and described in reindeer (*Rangifer tarandus*) in Russia in 1928. In typical hosts it localizes in the peritoneal cavity. *S. tundra* appeared in the Scandinavian reindeer in 1973 [11]. Intensive invasions, especially in young animals, cause weakness, loss of winter pelage and peritonitis leading to death. Parasitosis causes great economic losses in breeding of these animals. Prevailing high temperatures during the summer period 2001–2003 in Finland contributed to the increase in the rate of mosquitoes development, including the genus *Aedes*, the main vectors of *S. tundra* nematodes parasitizing reindeer in the boreal region. At that time, the prevalence of the helminths accompanied by lesions in the form of peritonitis in reindeer in the province of Oulu, Finland increased from 4.9 to 42.1%. The number of animals in the herd in Kainuu (Eastern Finland) fell from 1,700 to 1,000. In 2004 a new outbreak of parasitosis located approximately 100 km to the north of Lapland was detected because in warm summer months reindeer move to the north, to wetlands conducive to the development of mosquitoes, whose peak activity in herding areas of Finland falls within the period from mid-June to the end of July. In Finland the incidence of microfilaria in mosquitoes in the tundra ranged from 0.5 to 2.5%. And *S. tundra* larvae were also found there in 39% of roe deer (*Capreolus capreolus*) and 1.4–1.8% of elks (*Alces alces*) [12].

It has been demonstrated experimentally that *S. tundra* microfilaria in organisms of intermediate hosts, mostly *Aedes vexans* mosquitoes, survived for 14 days at the temperature of 21°C. In contrast, those kept at the temperature of 14.1°C did not develop for 22 days [13]. In Germany, in addition to *A. vexans*, potential vectors for microfilaria of this nematode are *Ochlerotatus sticticus*, *O. cantans* and *Anopheles claviger* [14]. *S. tundra* was also recorded in roe deer in Germany, Italy, Bulgaria and Poland. On the Polish territory it was found in deer in Lower Silesia [15], in Malopolska around Krakow [16] and in elks in the Kampinos and the Augustow Forests [17]. It must be assumed that global warming may affect the development of the parasite in intermediate hosts, and hence an increase in infection with setariosis in deer.

About 60 species of Culicidae mosquitoes may be vectors of microfilaria of *Dirofilaria repens* and *D. immitis* nematodes. The endemic area of *D. repens* occurrence in Europe is the Mediterranean region. In 2005 the nematode was found in dogs in Slovakia, later in the Czech Republic, Germany, the Netherlands, Austria, Hungary, Ukraine and in Northern Europe in Norway, which indicates the increasing incidence of occurrence of *D. repens* [18]. Recent studies in Belarus detected the presence of *D. repens* DNA in *Anopheles claviger* and *D. immitis* DNA in mosquito species of the genus *Culex* [19]. Climate changes provide the conditions for a full course of developmental cycle of the parasites involving their intermediate hosts in those areas of the world where this was not hitherto possible.

Prevalence of dirofilariasis in dogs in European countries is diverse and estimated at 9% in Spain, 1.3–22% in France, 22% in Greece and 49% in Serbia [20]. In Poland, the first cases of indigenous dirofilariasis in dogs were recorded in 2009 [21] and the first indigenous case of *D. immitis* invasion in a dog was found in Gdynia in 2012 [22]. Prevalence of microfilariasis in the dog population in Poland is estimated at 26–56%, with the central Poland considered to be endemic areas for the parasite [23]. Blood tests of sled dogs from the central Poland showed up the presence of *D. repens* DNA in 44% [24]. Microfilaria in the blood of dogs in Malopolska region were reported much less frequently – in 11.3% of animals from a shelter in Krakow [25]. By 2012, our country had recorded twenty human cases of subcutaneous dirofilariosis caused by *D. repens*. Regardless of whether subcutaneous dirofilariosis was considered autochthonous or introduced from endemic areas, most of the cases were found in the Mazovian province [26], while in Slovakia the number of dirofilariosis cases in humans was ten [27].

There is little data on the impact of climate changes on soil-transmitted helminthiases (STHs), i.e. helminthiases caused by intestinal nematodes *Ascaris lumbricoides*, *Trichuris trichiura*, *Ancylostoma duodenale* and *Necator americanus*, whose dispersive forms are present in the soil. The parasitoses are included in the WHO list of tropical diseases, especially of the poorest population [28]. It is estimated that more than 1.5 billion or 24% of the world's population are infected with helminths, whose invasive forms are present in the soil. Invasions are widespread in tropical and subtropical areas, and the largest number of the infected occurs in sub-Saharan Africa, Central and South America, China and East Asia [29]. For instance, in the population of Nigeria the prevalence of infection with a roundworm and whipworm reaches 31.7 and 19.6% respectively, and in the Republic of Congo the prevalence of hookworms is 45.9% [30]. The incidence of infection is dependent on several factors: sanitary, socio-demographic and environmental. The latter comprise the temperature of the soil surface during the day and at night, humidity and precipitation. Elevated temperatures help to increase the rate of development of larvae in the eggs of roundworms and whipworms, but exceeding the upper threshold of 37°C reduces their resilience [28]. Therefore, the parasites are rarely recorded in such regions of Africa as Chad (tropical climate) because the average temperature there exceeds 37–40°C. Also in Uganda, with mean annual temperature of 36–37°C, the prevalence reached less than 5% [31]. Whereas in Cameroon, in humid equatorial zone where the average rainfall exceeds 1500 mm per year, the incidence of infection with *A. lumbricoides* and *Trichuris trichiura* reached over 50% of patients [32]. However, torrential rains (precipitation above 1,740 mm per year) contribute to washing away eggs of the geohelminths, as research has shown in Tanzania where the prevalence of roundworms was 6.8%. It has also been demonstrated that an increase in day temperature of 1°C above 30°C will reduce the odds of *A. lumbricoides* infection by 13% [33].

Investigation of the impact of temperature on the development of *Ascaris suum* eggs conducted in Korea [34] has shown that the lower thermal limit is 5°C, and at 37°C embryos in an egg develop more rapidly than at 25°C. In this country there has been a high percentage (17.6%) of infected pigs and the authors suggest that global warming can result in acceleration of developmental rate of invasive roundworm eggs and an increase in contagion with these geohelminths.

To a lesser extent, high temperatures and lack of rainfall affect the hookworm larvae, whose stage L3 is endowed with the ability to migrate to places more humid, which determines their survival. The human hookworms *A. duodenale* and *N. americanus* require slightly different conditions for their development. At the temperature of 15–25°C 90% of *A. duodenale* eggs are capable of further development, while for *N. americanus* the range is 20–35°C. *A. duodenale* eggs are less sensitive to drying and may preserve resilience in more arid and colder areas outside the range of hookworms [28]. It has been shown that *A. duodenale* occurs in areas where *N. americanus* L3 larvae cannot survive during the winter months. In Central Africa, hookworms have upper threshold survival of larvae within 40–47°C. Hookworm adaptation to adverse environmental conditions is arrested larvae development in the human body. *A. duodenale* infections in some regions of West Africa increase after the rainy season; at earlier time L3 larvae are dormant in the host [35].

One species of hookworm occurring endemically in tropical and subtropical countries, mainly on the islands of the Caribbean, is *Ancylostoma braziliense*. This parasite of dogs, cats and other carnivores may in the form of *cutaneous larva migrans* (CLM) cause creeping eruption (CE) in humans. In Europe, numerous cases of CE have been reported in people who visited the tropical and subtropical countries. In Poland, these were patients after returning from Thailand and Madagascar. [36] However, in southern Europe (Italy, Spain, France and Germany) more than 20 cases of autochthonous CE have been found in recent years [3].

The complexity of the parasite-host system and interaction between parasites co-occurring in the host cause that not always climate changes and an increase in temperature contribute to the growth of infections with nematodes, whose larvae develop in the soil. The impact of climate change on free-living stages of two nematode species of the family Trichostrongylidae (*Graphidium strigosum* and *Trichostrongylus retortaeformis*) parasitizing the European rabbit *Oryctolagus cuniculus* was studied in Scotland [37]. These were 23-year field and laboratory studies inspired by observations of the increase in intensity of *G. strigosum* invasion with rising mean air temperature throughout 30 years, and remaining at a similar level or even reduced prevalence of *T. retortaeformis* [38]. *G. strigosum* species locates mainly in the stomach and *T. retortaeformis* in the small intestine of the host. The prepatent period for *G. strigosum* is 42–44 days, and for *T. retortaeformis* 12–13 days [37].

Between 1980 and 2002, the mean air temperature at the site of research increased by 1°C. High temperatures were mainly recorded in summer months (July and August). Laboratory tests were conducted in climate chambers. With the temperature rising, rapid hatching of larvae from eggs of both nematode species followed in the laboratory together with an increase in L3 larvae survival on pasture, thus augmenting the risk of host contamination. However, hatching and survival of L3 larvae were more effective for the species *T. retortaeformis*. Nonetheless, during various seasons of the year in two decades of research a positive relationship between the intensity of infection in rabbits and temperature was observed only for *G. strumosum*. Earlier studies [39] indicate that *T. retortaeformis* shows seasonal immune resistance acquired with host age. During experimental infections in rabbits with two nematode species it was found that the intensity of *G. strumosum* invasion in co-invasion was higher than in single infection, and in the case of *T. retortaeformis* not significant differences were observed [40].

The relationship between climate change and the acquisition of parasites by the host is important, but successful infection ultimately depends on the interaction between these organisms [37].

References

[1] Patz J.A., Campbell-Lendrum D., Holloway T., Foley J.A. 2005. Impact of regional climate change on human health. *Nature* 438: 310-317. doi:10.1038/nature04188

[2] Costello A., Abbas M., Allen A., Ball S., Bell S., Bellamy R., Friel S., Groce N., Johnson A., Kett M., Lee M., Levy C., Maslin M., McCoy D., McGuire B., Montgomery H., Napier D., Pagel C., Patel J., de Oliveira J.A.P., Redclift N., Rees H., Rogger D., Scott J., Stephenson J., Twigg J., Wolff J., Patterson C. 2009. Managing the health effects of climate change. *The Lancet* 373: 1693-1733. http://dx.doi.org/10.1016/s0140-6736(09)60935-1

[3] Garcia-Rodrigo C.G., Romero F.T., Olivo C.Z. 2017. Cutaneous larva migrans, welcome to a warmer Europe. *Journal of the European Academy of Derma - tology and Venereology* 31: e33-e35. doi:10.1111/jdv.13621

[4] Kelly M. 2013. How will climate change affect parasites and their animals hosts? Research News Features, University of Princeton, USA.

[5] Molnár P.K., Dobson A.P., Kutz S. J. 2013. Gimme shelter – the relative sensitivity of parasitic nematodes with direct and indirect life cycles to climate change. *Global Change Biology* 19: 3291-3305. doi:10.1111/gcb.12303

[6] Sobolewski M. 2014. Globalne wyzwania w Arktyce [Global challenges in the Arctic region]. *Infos* 2: 1-4 (in Polish with summary in English).

[7] Hoar B.M., Ruckstuhl K., Kutz S. 2012. Development and availability of the free-living stages of *Ostertagia gruehneri*, an abomasal parasite of barrenground caribou (*Rangifer tarandus groenlandicus*), on the Canadian tundra. *Parasitology* 139: 1093-1100. https://doi.org/10.1017/s003118201200042x

[8] Jenkins E.J., Veitch A.M., Kutz S.J., Hoberg E.P., Polley L. 2006. Climate change and the epidemiology of protostrongylid nematodes in northern ecosystems: *Parelaphostrongylus odocoilei* and *Protostrongylus stilesi* in Dall's sheep (*Ovis d. dalli*). *Parasitology* 132: 387-401. https://doi.org/10.1017/S0031182005009145

[9] Kutz S.J., Checkley S., Verocai G.G., Dumond M., Hoberg E.P., Peacock R., Wu J.P., Orsel K., Seegers K,. Warren A.L., Abrams A. 2013. Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. *Global Change Biology* 19: 3254-3262. doi:10.1111/gcb.12315

[10] Kutz S.J., Hoberg E.P., Polley L. 2001. *Umingmakstrongylus pallikuukensis* (Nematoda: Protostrongylidae) in gastropods: larval morphology, morphometrics, and development rates. *Journal of Parasitology* 87: 527-535. doi:10.1645/0022-3395 (2001)087[0527:upnpig]2.0.co;2

[11] Laaksonen S., Kuusela J., Nikander S., Nylund M., Oksanen A. 2007. Outbreak of parasitic peritonitis in reindeer in Finland. *Veterinary Record* 160: 835-841. doi:10.1136/vr.160.24.835

[12] Laaksonen S., Solismaa M., Kortet R., Kuusela J., Oksanen A. 2009. Vectors and transmission dynamics for *Setaria tundra* (Filarioidea: Onchocercidae), a parasite of reindeer in Finland. *Parasites and Vectors* 2: 3. doi:10.1186/1756-3305-2-3

[13] Laaksonen S., Pusenius J., Kumpula J., Venäläinen A., Kortlet R., Oksanen A., Hoberg E. 2010. Climate change promotes the emergence of serious disease outbrakes of filarioid nematodes. *EcoHealth* 7: 7-13. doi:10.1007/s10393-010-0308-z

[14] Czajka C., Becker N., Poppert S., Jöst H., Schmidt-Chanasit J., Krüger A. 2012. Molecular detection of *Setaria tundra* (Nematoda: Filarioidea) and an unidentified filarial species in mosquitoes in Germany. *Parasites and Vectors* 5: 14. doi:10.1186/1756-3305-5-14

[15] Bednarski M., Piasecki T., Bednarska M., Sołtysiak Z. 2010. Invasion of *Setaria tundra* in roe deer (*Ca - preolus capreolus*) – case report. *Acta Scientiarum Polonorum, Medicina Veterinaria* 9: 21-25.

[16] Kowal J., Kornaś S., Nosal P., Basiaga M., Lesiak M. 2013. *Setaria tundra* in roe deer (*Capreolus capreolus*) – new findings in Poland. *Annals of Parasitology* 59: 179-182.

[17] Kuligowska I., Demiaszkiewicz A.W., Rumiński A. 2015. Przypadek nietypowej lokalizacji nicieni *Setaria tundra* u sarny (*Capreolus capreolus*) The non-typical location of nematodes *Setaria tundra* in roe deer (*Capreolus capreolus*) – a case report]. *Życie Weterynaryjne* 90: 599-601 (in Polish with summary in English).

[18] Sapierzyński R., Wojtczak M. 2014. Dirofilarioza podskórna u psów [Subcutaneous dirofilariasis in dogs]. *Życie Weterynaryjne* 89: 478-483 (in Polish with summary in English).

[19] Şuleşco T., Volkova T., Yashkova S., Tomazatos A., von Thien H., Lühken R. 2016. Detection of *Dirofilaria repens* and *Dirofilaria immitis* DNA in mosquitoes from Belarus. *Parasitology Research* 115: 3535-3541. doi:10.1007/s00436-016-5118-y

[20] Tarello W. 2011. Clinical aspects of dermatitis associated with *Dirofilaria repens* in pets: a review of 100 canine and 31 feline cases (1990–2010) and a

report of a new case imported from Italy to Dubai. *Journal of Parasitology Research* 2011. doi:10.1155/2011/578385.
[21] Demiaszkiewicz A.W., Polańczyk G., Pyziel A.M., Kuligowska I., Lachowicz J. 2009. Pierwsze ogniska dirofilariozy psów wywołanej przez *Dirofilaria repens* Railliet et Henry, 1911 w centralnej Polsce [The first foci of dirofilariosis of dogs evoked by *Dirofilaria repens* Railliet et Henry, 1911 in central Poland]. *Wiadomości Parazytologiczne* 55: 367-370 (in Polish with summary in English).
[22] Świątalska A., Demiaszkiewicz A.W. 2012. Pierwszy w Polsce rodzimy przypadek inwazji nicieni *Dirofilaria immitis* u psa [First autochthonous case of *Dirofilaria immitis* invasion in dog in Poland]. *Życie Weterynaryjne* 87: 685-686 (in Polish with summary in English).
[23] Demiaszkiewicz A.W., Polańczyk G., Osińska B., Pyziel A.M., Kuligowska I., Lachowicz J., Sikorski A. 2014. The prevalence and distribution of *Dirofilaria repens* in dogs in the Mazovian Province of Central-Eastern Poland. *Annals of Agricultural and Environmental Medicine* 21: 701-704.
[24] Bajer A., Mierzejewska E.J., Rodo A., Bednarska M., Kowalec M., Welc-Falęciak R. 2014. The risk of vector-borne infection in sled dogs associated with existing and new endemic areas in Poland. Part 1. A population study on sled dogs during racing season. *Veterinary Parasitology* 202: 276-286. http://dx.doi.org/10.1016/j.vetpar.2013.12.033
[25] Wróblewska P., Wilczyńska M., Zaleśny G. 2016. The evaluation of dirofilariosis among shelter dogs in Kraków. *Annals of Parasitology* 62 (suppl): 140.
[26] Cielecka D., Żarnowska-Prymek H., Masny A., Salamatin R., Wesołowska M., Gołąb E. 2012. Human dirofilariosis in Poland: the first cases of autochthonous infections with *Dirofilaria repens*. *Annals of Agricultural and Environmental Medicine* 19: 445-450.
[27] Miterpáková M., Iglódyová A., Čabanová V., Antolová D. 2016. Canine and human dirofilariosis in Slovakia (2005-2015). *Annals of Parasitology* 62 (suppl): 30.
[28] Weaver H.J., Hawdon J.M., Hoberg E.P. 2010. Soil-transmitted helminthiases: implications of climate change and human behavior. *Trends in Parasitology* 26: 574-581. http://dx.doi.org/10.1016/j.pt.2010.06. 009
[29] WHO. 2016. Soil transmitted helminth infections. In: Media Centre. Fact sheet. (updated March 2016). http://www.who.int/mediacentre/factsheets /fs366/en/
[30] Hotez P.J., Kamath A. 2009. Neglected tropical diseases in Sub-Saharan Africa: review of their prevalence, distribution, and disease burden. *Plos Neglected Tropical Diseases* 3: e412. doi:10.1371/journal.pntd.0000412
[31] Brooker S., Kabatereine N.B., Tukahebwa E.M., Kazibwe F. 2004. Spatial analysis of the distribution of intestinal nematode infections in Uganda. *Epidemiology and Infection* 132: 1065-1071. https://doi.org/10.1017/S09502688 04003024
[32] Brooker S. Beasley M., Ndinaromtan M., Madjiouroum E.B., Baboguel M., Djenguinabe E., Hay S.I., Bundy D.A.P. 2002. Use of remote sensing and a geographical information system in a national helminth control programme in Chad. *Bulletin of World Health Organization* 80: 783-789.
[33] Schüle S.A., Clowes P., Kroidl I., Kowuor D.O., Nsojo A., Mangu C., Riess H., Geldmacher C., Laubender R.P., Mhina S., Maboko L., Löscher T., Hoelscher M., Saathoff E. 2014. *Ascaris lumbricoides* infection and its relation to environmental factors in the Mbeya Region of Tanzania, a cross-sectional, population-based study. *PLos ONE* 9: e92032. doi:10.1371/journal.pone.0092032
[34] Kim M.K., Pyo K.H., Hwang Y.S., Ki Hwan, Park K.H., Hwang I.G., Chai J.Y., Shin E.H. 2012. Effect of temperature on embryonation of *Ascaris suum* eggs in an environmental chamber. *Korean Journal of Parasitology* 50: 239-242. https://doi.org/10.3347/kjp.2012.50.3.239
[35] Brooker S., Bethony J., Hotez P.J. 2004. Human hookworm infection in the 21st Century. *Advances in Parasitology* 58: 197-288. http://dx.doi.org/10.1016/s0065-308x(04)58004-1
[36] Kacprzak E., Silny W. 2004. Zespół larwy wędrującej skórnej u turystów powracających z krajów strefy klimatu ciepłego [Cutaneous larva migrans syndrome in travelers returning from warm climate countries]. *Postępy Dermatologii i Alergologii* 21: 24-29 (in Polish with summary in English).
[37] Hernandez A.D., Poole A., Cattadori I.M. 2013. Climate changes influence free-living stages of soil-transmitted parasites of European rabbits. *Global Change Biology* 19: 1028-1042. doi:10.1111/gcb.12106
[38] Harvell D., Altizer S., Cattadori I.M., Harrington L., Weil E. 2009. Climate change and wildlife diseases: when does the host matter the most? *Ecology* 90: 912-920. doi:10.1890/08-0616.1
[39] Cornell S.J., Bjornstad O.N., Cattadori I.M., Boag B., Hudson P.J. 2008. Seasonality, cohort-dependence and the development of immunity in a natural host-nematode system. *Proceedings of the Royal Society of London B* 275: 511-518. doi:10.1098/rspb.2007.1415
[40] Murphy L., Pathak A.K., Cattadori I.M. 2013. A co-infection with two gastrointestinal nematodes alters host immune responses and only partially parasite dynamics. *Parasite Immunology* 35: 421-432. doi:10.1111/pim.12045

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