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Increases in extreme heat stress in domesticated livestock species during the twenty-first century

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Abstract

Anthropogenic climate change is expected to have major impacts on domesticated livestock, including increased heat stress in animals in both intensive and extensive livestock systems. We estimate the changes in the number of extreme heat stress days per year for animals raised outdoors that can be expected in the major domesticated animal species (cattle, sheep, goats, poultry, and pigs) across the globe during this century. We used the temperature humidity index as a proxy for heat stress, calculated using temperature and relative humidity data collated from an ensemble of CMIP6 climate model output for mid and end century. We estimate changes in the proportions of different livestock species that may be at increased risk of extreme heat stress under two contrasting greenhouse gas emission scenarios. Results are discussed in relation to changes in the suitability of different climate conditions for domesticated livestock during the current century. We find that by end century, extreme heat stress risk is projected to increase for all livestock species in many parts of the tropics and some of the temperate zones, and to become climatically more widespread, compared to 2000. Although adaptation options exist for both intensive and extensive livestock production systems, the increasing pervasiveness of extreme heat stress risk in the future will seriously challenge the viability of outdoor livestock keeping, particularly in the lower latitudes in lower and middle-income countries where the costs of adaptation may be challenging to address.

KEYWORDS

cattle, chickens, CMIP6, goats, pigs, sheep, suitability, temperature humidity index

1 | INTRODUCTION

Heat stress in domesticated livestock arises when environmental conditions challenge the animal's thermoregulatory mechanisms. These conditions result from combinations of temperature, humidity, solar radiation, and wind speed beyond the ability of an animal to thermoregulate (Silanikove, 2000). The effects of heat stress include

reduced productivity, reduced animal welfare, reduced fertility, increased susceptibility to disease, and in extreme cases increased mortality (Godde et al., 2021), and affect all domesticated species.

The ways in which a specific animal will respond to heat stress, and the point at which production losses begin to occur, vary widely (Hammami et al., 2013). They depend on factors such as species, breed, age, genetic potential, physiological status, nutritional

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status, animal size, and previous exposure, with high-yielding individuals and breeds the most susceptible (Godde et al., 2021). For example, dairy cows are generally more susceptible than beef cattle, and temperate *Bos taurus* breeds tend to be more susceptible than tropically adapted *Bos indicus* cattle and their crosses (Polsky & von Keyserlingk, 2017). Within the dairy breeds, Holsteins are less heat tolerant than other breeds such as Jersey and Brown Swiss, in that they have a higher core temperature, are larger and thus have a lower skin surface to mass ratio (Polsky & von Keyserlingk, 2017), have thicker coats, and higher yield potential (Galán et al., 2018). In general, increases in the productive capacity of domestic animals, partially driven by increased selection pressure for animals with higher productivity, can compromise thermal acclimation and plasticity; this is a serious issue in view of the escalating demand for livestock products in lower and middle-income countries (LMICs), steadily increasing temperatures, and the investments that are likely to be required for domestic livestock to adapt to new thermal environments (Collier & Gebremedhin, 2015).

The increased seriousness of the heat stress issue as a result of anthropogenic greenhouse gas emissions in the present century has been underlined in recent literature (see, e.g., Hempel et al., 2019; Rahimi et al., 2021; Rashamol et al., 2019; Sejian et al., 2018). Increases of 1.5°C and above may exceed limits for normal thermoregulation of poultry (broiler and layer chickens), pigs, and cattle and could result in persistent heat stress for these animals in a range of different environments (Dunn et al., 2014; Lallo et al., 2018; Rahimi et al., 2021; Ranjitkar et al., 2020). In Brazil, high ambient temperatures (29–35°C) reduced average daily weight gain in growing-finishing pigs by nearly 10% and feed intake by nearly 14% compared with a thermoneutral environment (18–25°C; da Fonseca de Oliveira et al., 2019). Compared with cattle, the direct effects of higher temperatures on sheep and goats may be less severe, though goats are better able to cope with multiple stressors than sheep (Sejian et al., 2018). In LMICs, indigenous poultry contribute significantly to the livelihoods of many households, including via modest improvements in nutritional outcomes of children in the household (de Bruyn et al., 2018). Indigenous poultry are often assumed to be hardy and well adapted to stressful environments, but there is little information about their performance under warmer climates or about possible interactions with other production challenges (Nyoni et al., 2019).

We present new information on projected increases in extreme heat stress in five of the major domesticated animal species (cattle, sheep, goats, poultry, and pigs) during the present century, using the temperature humidity index (THI) as a proxy for heat stress, calculated using daily temperature and relative humidity data collated from an ensemble of bias-corrected and downscaled CMIP6 climate model output for mid and end century under two contrasting greenhouse gas emission scenarios. Results are presented in relation to changes in the proportion of animals affected in future and changes in the suitability of different environmental conditions for domesticated livestock. For future livestock production systems, a range of adaptation options exist. We conclude with some comments as to their limits in intensive and extensive production systems and some

critical knowledge gaps. These gaps include more nuanced information on the impacts of heat stress on the productivity of different species and breeds, and how livestock producers in different contexts may be able to adapt.

2 | METHODS

2.1 | Heat stress

There are several methods for assessing the risk of heat stress in animals. These include the use of indices that combine ambient temperature and relative humidity measurements to estimate the thermal (dis)comfort of animals, and methods that involve estimating the temperature as actually experienced by the animal (Herbut et al., 2018). Several different metrics have been proposed and compared to study heat stress effects over time periods of weeks and months (see, e.g., Dikmen & Hansen, 2009; Hammami et al., 2013; Herbut et al., 2018). The THI is the most widely used index, with much of the literature based on the equation of Thom (1959):

$$\text{THI} = 0.8 \times T + ((\text{RH}/100) \times (T - 14.3)) + 46.4, \quad (1)$$

where T is the dry bulb air temperature (°C) and RH is the relative air humidity (%). The algebraically equivalent equation given by NRC (1971) is:

$$\text{THI} = (1.8 \times T + 32) - (0.55 - 0.0055 \times \text{RH}) \times (1.8 \times T - 26.8). \quad (2)$$

These two forms are numerically equivalent other than for some rounding differences in the coefficients. Various extensions and modifications to the basic THI equation have been used. For example, St-Pierre et al. (2003) provided equations for production losses from cattle, pigs, and poultry (including mortality), using modifications to the basic THI formula that accounted for diurnal duration of heat stress and cumulative heat load. Gaughan et al. (2008) proposed a heat load index (HLI), which is more sophisticated than THI as it takes account of wind speed and solar radiation.

Thermoneutral thresholds are usually determined by physiological responses, such as changes to the animal's respiration rate and body temperature, rather than changes to behavior (e.g., Galán et al., 2018), and are dependent on other factors such as geographic location and type of animal (Jeelani et al., 2019). As such, a wide range of thresholds have been published in the literature. For dairy cattle, Pinto et al. (2020) cite a range of THI from 60 to 72 as the threshold for milk yield losses, while the review of Wang et al. (2018) tabulates "THI thresholds of alert" of between 60 and 78.2 for Holstein cattle across the United States and Europe, calculated using Equation (2) above. Similarly, Xin and Harmon (1998) reported different THI thresholds for pigs, cattle, and laying hens, and Gaughan et al. (2010) reported substantial differences in thresholds of the HLI, based on a wide range of different cattle breeds and management. Clearly, the context of the animal's situation matters considerably.

For purposes of a global study such as this, there is strong justification from the literature for using Equations (1) or (2) above for the five major livestock species (Table 1). THI thresholds for different levels of heat stress for the different livestock species are shown in Table 1. There are also clear breed differences in these thresholds, but there is only very limited literature on THI differences in heat stress thresholds in different breeds of livestock. For example, Valente et al. (2015) showed that dry matter intake of *Bos indicus* bulls was not affected up to a THI value of 81.5, for example, suggesting a THI threshold for extreme stress in such cattle of 94. In another study, McManus et al. (2016) estimated THI thresholds, equivalent to the onset of “moderate heat stress” in Table 1, for 12 breeds of sheep (mostly European and Australasian) under Brazilian conditions; these ranged from 69 to 74.

Given the considerable uncertainties in THI thresholds by breed, we disaggregated global animal numbers based on temperate and tropical zones (defined for the purposes of this analysis as shown in Figure S1), and then empirically estimated THI thresholds for extreme heat stress for the latter regions, as described below.

2.2 | Weather and climate data

For climate data, downscaled climate projections from an ensemble of the bias-adjusted, statistically downscaled outputs from five CMIP6 global climate models (MRI-ESM2-0, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL, GFDL-ESM4) were utilized. These data were from the ISIMIP3b simulation round (<https://www.isimip.org>), at a spatial resolution of 0.5° latitude–longitude. We assembled data for current and future time slices as projected in response to a lower and a higher greenhouse gas emission scenario (SSP1-2.6, based on SSP 1 and RCP 2.6; and SSP5-8.5, based on SSP5 and RCP 8.5; Lange, 2019, 2020) to simulate a wide range of feasible future environmental

conditions. We used daily data for years centered in 2000 (which we took as the baseline climate year), 2050, and 2090, for the following variables: daily average temperature and daily average relative humidity. These data were at a spatial resolution of 0.5° latitude–longitude. Because of projected increases in the intensity and duration of heat waves during the current century (IPCC, 2018), we estimated the THI on a daily basis. This allowed us to identify areas where the risk of extreme heat stress is projected to increase, to the extent that suitability for outside livestock production may not be viable in the future.

2.3 | Livestock numbers and distribution

We used the livestock density data layers of Gilbert et al. (2018) for cattle, sheep, goats, pigs, and chickens. These are for 2010, herd numbers at national level matching FAOSTAT country-level data for that year. Global animal numbers amounted to 1.43 billion cattle, 0.93 billion goats, 1.1 billion sheep, 0.96 billion pigs, and 20.1 billion chickens (FAO, 2021). Livestock systems are highly dynamic, and both extensive and intensive livestock production systems can be expected to change significantly in the coming decades in response to drivers such as the changing demand for animal source foods of different types and the effects of climate change, for example (Rust, 2019). In view of the difficulties involved in projecting livestock system changes into the future, we decided to keep livestock numbers constant for the purposes of the analysis reported here.

2.4 | Empirical estimation of extreme heat stress thresholds for temperate and tropical livestock

Although there is plenty of evidence that livestock breeds vary in their heat stress tolerance, there is little detailed information on

TABLE 1 Selected studies that use some form of the Thom (1959) equation for the temperature humidity index (THI) to estimate heat stress in animals, and the threshold values used

Species	Onset of heat stress level			References
	Moderate	High	Extreme	
General	70	75	80	Thom (1959)
General	72	78	90	Fuquay (1981)
Cattle–dairy	72	79	89	Moran (2005); Dunn et al. (2014); Ranjitkar et al. (2020); Rahimi et al. (2021); Pinto et al. (2020)
Cattle–general	72	79	90	Xin & Harmon (1998)
Cattle–beef	72	82	94	Valente et al. (2015)
Goats	70	79	89	Serradilla et al. (2018)
Sheep	72	78	90	McManus et al. (2016); Beldadj Slimen et al. (2019)
Pigs	75	79	84	Xin & Harmon (1998); Lallo et al. (2018); Mutua et al. (2020)
Poultry–broilers	74	79	84	Oliveira et al. (2019)
Poultry–layers	71	76	82	Du et al. (2020); Xin and Harmon (1998)
Poultry–general	73	81	85	Moraes et al. (2008)

Note: Moraes et al. (2008) used five different categories for poultry—light and moderate discomfort were merged here.

differences in THI thresholds for species other than cattle; even the information for cattle is limited. We thus combined information on the current location of cattle and breed stress tolerance to develop a method to estimate plausible higher tolerance levels for sheep, goats, pigs, and poultry.

Several studies agree on a THI value of 89 as being the onset of extreme heat stress in several breeds of cattle in temperate regions (Table 1). For current conditions (1991–2010), we calculated pixel-specific THI values across the globe and then calculated the number of days per year on which this threshold was exceeded for cattle in the temperate zones identified in Figure S1, using the cattle distribution data layer of Gilbert et al. (2018). Nearly 10% of cattle in the temperate zones are located in places with one or more days each year with a THI value >89 (Table 2). The average number of extreme heat stress days per year in this population of cattle is 10.4 across all temperate subregions; several regions have zero days per year. We then calculated the number of days of extreme heat stress per year for the tropical cattle population, using a range of integer THI thresholds. At a THI threshold of 94, nearly 7% of the tropical cattle population experiences one or more days of extreme heat stress per year. This proportion increased to 14% at a THI threshold of 93 and decreased to 4% at a THI threshold of 95. We thus used a THI threshold of 94 for tropical cattle in subsequent analysis. This threshold for extreme heat stress onset is in accord with the estimate for a *Bos indicus* breed in the study of Valente et al. (2015). In the analysis of thresholds presented below, we made no distinction between dairy and beef cattle, although there are differences in the effects of heat stress on dairy and beef animals, due to some differences in the mechanisms involved as well as differences in levels of production (St-Pierre et al., 2003).

We repeated this process of estimating THI thresholds for the separate temperate and tropical populations of goats, sheep, pigs, and poultry. Results are shown in Table 2. Extreme heat stress onset at a THI value of 89 (calculated as above, at the integer THI value giving as near to 10% of the population as possible) applies across the temperate zone for all species except for sheep, for whom onset was estimated to occur at THI threshold of 86. There was some variation in onset threshold for the tropical animals: 94 for cattle and goats, 93 for sheep, and 92 for pigs and poultry.

TABLE 2 The THI thresholds for “extreme heat stress” above which approximately 10% of livestock numbers in the tropical and temperate zones, as defined in Figure S1, are currently located

Species	THI threshold		Population share, %	
	Temperate	Tropical	Temperate	Tropical
Cattle	89	94	9.7	6.8
Goats	89	94	10.3	8.5
Sheep	86	93	12.5	8.0
Pigs	89	92	8.5	12.5
Poultry	89	92	12.4	11.3

2.5 | Changes in the suitability niches of domesticated livestock

Following Xu et al. (2020), who investigated the future of the human climate niche, we summarized how livestock suitability niches might change in the future because of increasing extreme heat stress by plotting the current distribution of animals against mean annual temperature (MAT) and mean annual precipitation (MAP) for current (2000) and future conditions.

3 | RESULTS

Results of the analysis were aggregated to the IPCC land subregions (Iturbide et al., 2020); see Figure S1.

3.1 | Changes in the proportion of animals potentially exposed to extreme heat stress

The projected change in the number of days per year of extreme heat stress and the total number of animals affected are shown in Table 3, for the five livestock species under SSP1-2.6 and SSP5-8.5 in 2050 and 2090, compared to 2000. The proportion of animals affected in temperate and tropical regions is shown in Table 4. For example, some 8% of the global cattle herd is in areas with 8 days per year of extreme heat stress in 2000, or 9.7% of the temperate cattle herd and 6.8% of the tropical cattle herd. The number of days per year of extreme heat stress increases to 19 and 24 in 2050 under SSP1-2.6 and SSP5-8.5, respectively. By 2090, the percentage of cattle affected has declined slightly under SSP1-2.6. This is because SSP1-2.6 envisages that GHG emissions will peak in 2060, at an atmospheric concentration of some 460 ppm CO₂, and this falls to 440 ppm CO₂ by 2100. Under SSP5-8.5, by 2090, more than 60% of the global cattle herd is projected to experience nearly 70 days per year of extreme heat stress. This is because SSP5-8.5 represents a very high GHG-emission future, in which atmospheric CO₂ concentration climbs to 630 ppm by 2060 and accelerates to 1020 ppm by 2100 (Riahi et al., 2017). Acclimation and adaptation can occur within and between generations (Ahmed et al., 2017; Collier et al., 2019), but unabated extreme heat stress may severely affect the animal's reproductive cycle, reduce feed intake and production, and eventually lead to death (Silanikove, 2000).

Similar patterns are shown by the other four species: a doubling or more in the number of extreme stress days per year under SSP1-2.6 in 2050, with that number remaining approximately constant in 2090 as the atmospheric CO₂ concentration peaks and then declines, with 17%–31% of animal numbers being affected, depending on species and breed (temperate or tropical). The effects in 2050 under SSP5-8.5 are larger than under SSP1-2.6 for all species, with approximately a trebling of the proportion of animals affected and the number of days of extreme heat stress. By 2090, the proportion of animals and the number of days per year have nearly doubled again. In most cases in Table 4, the proportion of animals affected

TABLE 3 Number of days per year (days) of extreme heat stress by species, and number of animals affected (N, million), for current conditions and two time slices under two SSPs. Total N, global total in 2010 (Gilbert et al., 2018)

Species	Total N	2000		2050 SSP1-2.6		2090 SSP1-2.6		2050 SSP5-8.5		2090 SSP5-8.5	
		N	Days	N	Days	N	Days	N	Days	N	Days
Cattle	1,432	114	8	252	19	247	18	370	24	876	69
Goats	932	85	6	191	16	215	16	283	21	640	57
Sheep	1,095	117	11	231	23	218	22	336	31	692	77
Pigs	957	87	6	242	18	247	19	369	27	664	77
Poultry	20,117	2,421	11	5,757	28	5,901	28	8,606	36	15,089	87

by extreme heat stress in the temperate zone is larger than the proportion of animals affected in the tropics. This is not the case for goats under SSP5-8.5 in 2050 and 2090 nor for cattle in 2090. The number of animals of each species affected in each IPCC region is shown in Tables S1–S5.

Changes in the number of days per year of extreme heat stress from 2000 to the 2090s under SSP5-8.5 are shown in Figure 1 for the five species. These are mapped in relation to the current global distribution of each species (Gilbert et al., 2018); areas in gray show the presence of animals but no change in the number of days.

3.2 | Changes in the suitability niches of domesticated livestock

Taking 2000 conditions as some indication of “suitability” for cattle (given that this is where they are found currently), Figure 2a shows how the distribution of cattle in the temperate zones could shift in relation to changes in MAT and MAP. In 2000, the largest proportion of cattle is found between 400 and 1500 mm MAP and 4–25°C MAT (cattle in the temperate zone in very low MAP areas are the result of the coarse spatial resolution of the climate data). Under SSP5-8.5 in 2090, the range of MAP for cattle is similar to 2000, but the range of MAT has shifted to about 10–30°C. At the same time, extreme heat stress days in 2090 occur over a larger MAP–MAT space compared to 2000, particularly where conditions are both warmer and wetter. For the tropical cattle herd, animal distribution in MAP–MAT space in Figure 2b contrasts strongly with the temperate herd. The tropical herd in 2090 is distributed across much wetter areas compared to 2000. By the same token, the relative proportion of extreme heat stress days per year in 2090 is far greater in the warmer, wetter areas of the tropics compared to 2000. Similar effects were found for the other four animal species; maps are shown in Figures S2–S5.

To summarize these effects, for all species, current distribution in MAP–MAT space shifts up (higher MAT) and to the right (higher MAP), although the effect is stronger for MAP than for MAT, and stronger for animals in the tropics compared with animals in the temperate zones. For all species, both in the tropics and the temperate zones, there is a marked increase in the number of climates (represented by different combinations of MAP and MAT) in which extreme heat stress occurs in 2090 under SSP5-8.5, compared to 2000.

4 | DISCUSSION AND CONCLUSIONS

The results presented here show that through to the end of the century, the major domestic livestock populations will be at increasing risk of extreme heat stress, and in places these risks will be very high. The current climate niche in terms of MAP and MAT for humans, crops, and domesticated livestock overlap considerably, unsurprisingly, and these conditions (within which humans have thrived) have remained largely the same since the mid-Holocene period (6000 years before the present; Xu et al., 2020). The changes in suitability niches for domesticated livestock to the end of the present century as a result of increases in extreme heat stress risk present considerable challenges. We consider these below with respect to (1) animal displacement, (2) adaptation alternatives in lower input livestock production systems, and (3) adaptation alternatives in higher input livestock production systems.

4.1 | Animal displacement

In some regions, local redistribution of livestock populations from areas with high risk of increased extreme heat stress to areas with much lower risk may be possible. For instance, in the southern part of East Africa (SEAF, Figure S1), there are approximately 106 million chickens. Under SSP585 in 2090, some 20 million of them will be at risk of extreme heat stress, compared to 0.1 million in 2000 (Table S5). These at-risk chickens are located mostly on the coastal strip of the SEAF region (Figure 1B), and there are large areas of the SEAF region that will see no increase in extreme heat stress to the end of this century (areas in gray in Figure 1b). Theoretically, the at-risk chickens could be moved to other parts of the region where the risk of extreme heat stress is much lower. The poultry situation in western Africa (WAF, Figure 1) is very different; by 2090 under SSP5-8.5, projections indicate that more than 98% of the region's poultry, numbering 470 million birds, will be at high risk of extreme heat stress. There are few parts of the region (Figure 1b) where poultry could be moved to, under similar management conditions as currently, to reduce the high risk of extreme heat stress (though they might be moved to other regions altogether, theoretically).

Whether such animal redistributions are even possible depends heavily on context. It would depend on a range of factors, including

TABLE 4 Proportion (%) of temperate, tropical, and global animal populations with at least 1 day of extreme heat stress in 2000, 2050, and 2090 under SSP1-2.6 and SSP5-8.5

Species	2000			2050 SSP1-2.6			2090 SSP1-2.6			2050 SSP5-8.5			2090 SSP5-8.5		
	Temp	Trop	Global	Temp	Trop	Global	Temp	Trop	Global	Temp	Trop	Global	Temp	Trop	Global
Cattle	9.7	6.8	8.0	18.2	17.2	17.6	18.1	16.6	17.2	26.7	25.3	25.9	57.4	63.8	61.2
Goats	10.3	8.5	9.1	26.2	17.7	20.5	26.2	17.7	23.1	43.6	23.7	30.3	66.3	69.9	68.7
Sheep	12.5	8.0	10.7	23.4	17.7	21.1	22.0	16.7	19.9	31.3	29.8	30.7	64.7	61.0	63.2
Pigs	8.5	12.5	9.1	25.7	23.3	25.3	26.0	24.5	25.8	39.5	33.6	38.5	69.6	68.3	69.4
Poultry	12.4	11.3	12.0	30.4	25.1	28.6	31.1	25.9	29.3	47.0	34.7	42.8	75.0	75.0	75.0

the adaptation options available in the original location, and in the new location, the availability and price of feed, and the costs of production. Because the distribution of domesticated livestock and cropping is highly correlated with human population distribution (Reid et al., 2000; Xu et al., 2020), as the human climate niche changes, so domesticated livestock distributions can be expected to change also. The feasibility of animal redistribution could thus also include the costs of energy along what may be new value chains to supply livestock products to possibly different centers of demand. Furthermore, the socio-economic and cultural barriers to managed animal movements may be daunting. In many transhumant and pastoral livestock systems, for example, rangeland fragmentation and the privatization of communal grazing lands have already placed considerable constraints on traditional seasonal livestock movement, and these constraints may become increasingly severe (Hobbs et al., 2008). The places where extreme heat stress risk is projected to increase may affect livestock keepers as well as their livestock. Human labor capacity is projected to decline markedly during the current century because of heat stress risk (Watts et al., 2018); the ability of some livestock keepers to manage their animals may be significantly constrained.

In general, reconfiguration and relocation of agricultural systems could be a highly effective adaptation strategy for moderate levels of climate change, moving crop, and livestock production to the land areas best suited to prevailing (and shifting) climatic conditions (Janssens et al., 2020). Any such movement toward regional land use optimization, including use of grazing lands, will depend on policy objectives of national governments and on the development and implementation of collaborative trading and security agreements. It should also be noted that livestock production suitability will increase in some places, via a reduction in the colder temperatures that constrain production as well as warmer temperatures. Although not a focus of our analysis here, some locations in these higher latitudes will be much less affected by extreme heat stress risk in the future. The biological potential of livestock production in some of these locations may be considerably higher than it is today.

4.2 | Adaptation to extreme heat stress in lower input livestock production systems

Adaptation to extreme heat stress will become an imperative, as the climate niche occupied by domesticated livestock becomes warmer and wetter and the risks become more pervasive spatially. Adaptation options have been reviewed in several places (e.g., Godde et al., 2021; Rojas-Downing et al., 2017). In lower input livestock systems, various lower cost adaptation strategies may be effective in reducing the impacts of heat stress in smallholder systems. These include the use of simple sheds to provide shade, animal baths, roof soaking, and installing fans in sheds, for example (Bang et al., 2021; York et al., 2017). Certain arrangements of shade trees in silvopastoral livestock production systems, particularly in Latin America, have been shown to be an effective means of reducing heat stress (Cuartas Cardona et al., 2014; Ibrahim et al., 2006; Pezzopane et al., 2019).

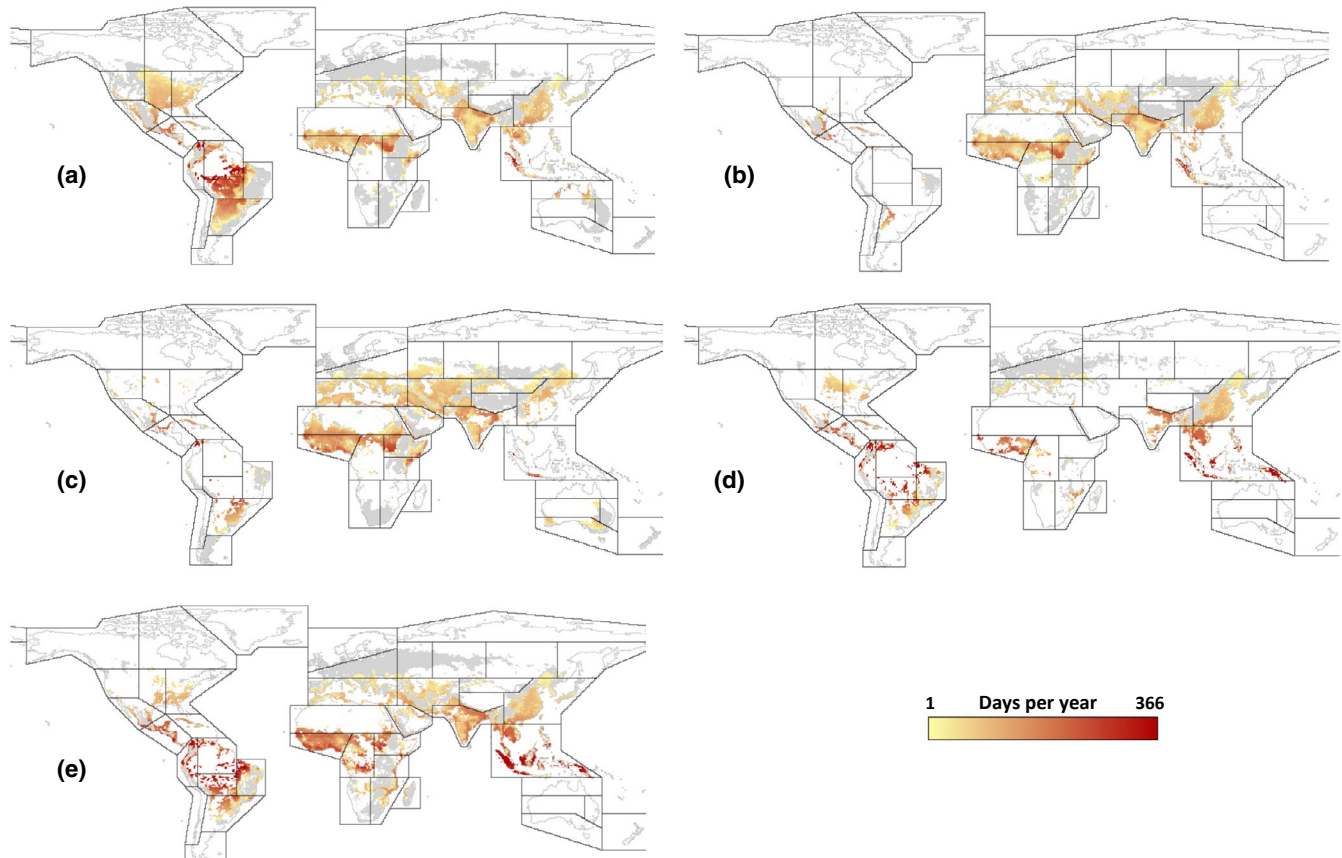


FIGURE 1 Change in the number of days per year above “extreme stress” values from 2000 to the 2090s for SSP5-8.5, estimated using the temperature humidity index (THI). Data mapped for each species’ current global distribution (Gilbert et al., 2018). Gray areas show no change from zero. Regional boundaries shown are for the IPCC subregions (Iturbide et al., 2020). (a) cattle, (b) goats, (c) sheep, (d) pigs, (e) poultry

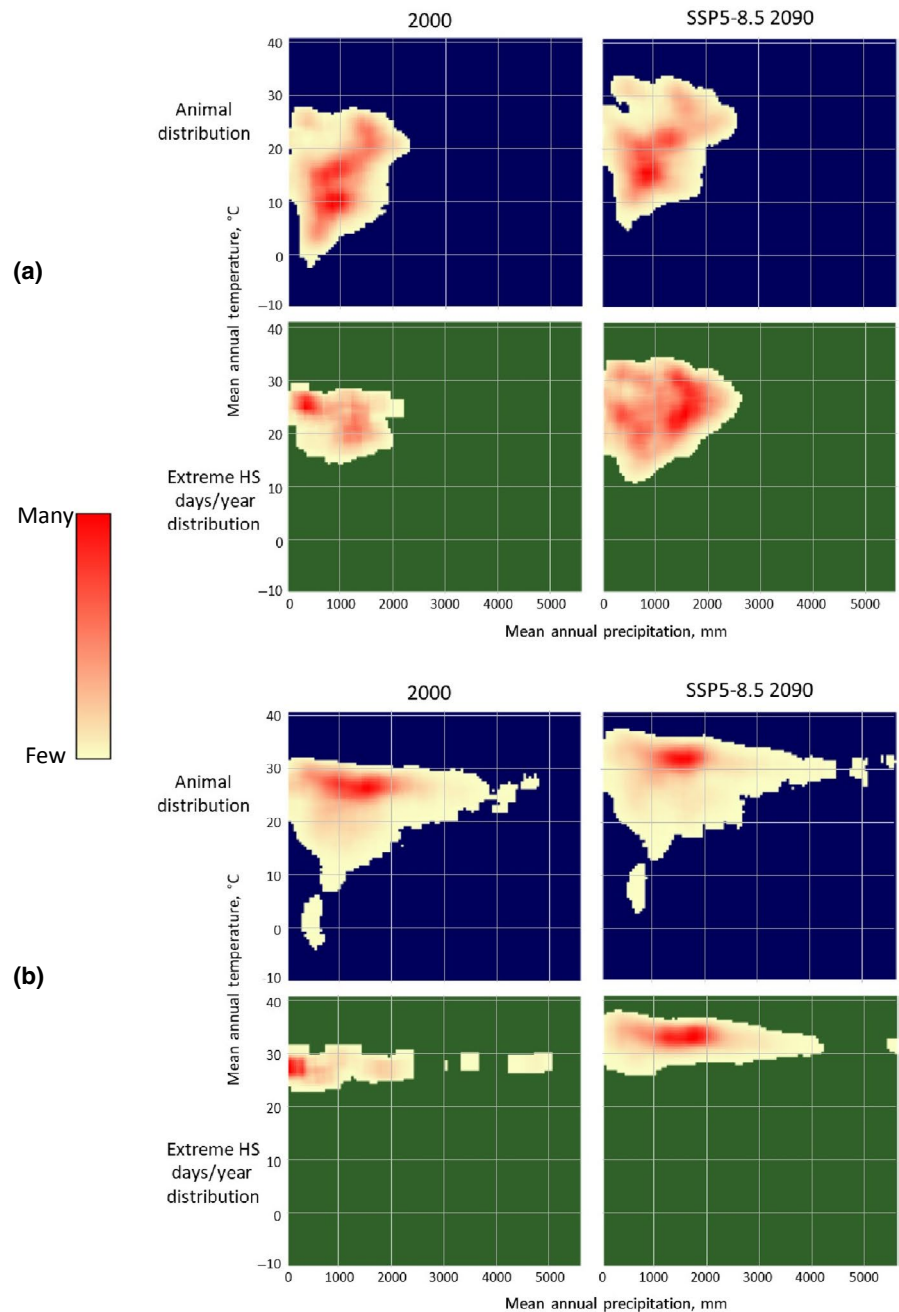
Exploiting existing variation in heat tolerance among different breeds and species may be a key adaptation strategy. This includes shifts such as from large ruminants to more heat-resilient goats for dairy production in Mediterranean systems or from cattle to camels in pastoral systems in East Africa, for instance (Kagunyu & Wanjohi, 2014; Silanikove & Koluman, 2015; Wako et al., 2017).

Cross-breeding highly selected breeds with indigenous breeds may offer adaptation benefits in some situations, although its effectiveness as an adaptation appears dependent on context (Moore & Ghahramani, 2014; Wilkes et al., 2017). There is some scope for genetic improvement in animals to increase tolerance to heat stress, such as making use of the slick hair gene in cattle (Ortiz-Colón et al., 2018) or the naked neck gene in poultry (Nawab et al., 2018). Although there are prospects for fast-track genetic improvement programs for domesticated livestock (Clark et al., 2020), the extent and pervasiveness of projected future extreme heat stress risk indicate that extensive livestock systems in some parts of the global tropics may cease to be viable, in the absence of marked increases in heat tolerance in livestock in these systems. Poultry and pigs face major heat stress challenges in many parts of the tropics where they are currently raised; the same is true for all five major domesticated species in West Africa and South Asia.

4.3 | Adaptation to extreme heat stress in higher input livestock production systems

Higher input livestock production systems include confined, intensive systems, and these are generally based on higher yielding animals, which are more susceptible to heat stress (Godde et al., 2021). Such production systems may need increasing investments in farm infrastructure if they are to adapt to increasing heat stress risk. There is a wide range of different ventilation systems, cooling systems, and building designs for confined and seasonally confined intensive livestock systems (pigs, poultry, beef, dairy) in temperate regions. The literature on the economic consequences and profitability of different infrastructural options under different climate change scenarios in Europe and North America is already extensive (e.g., Derner et al., 2018; Hempel et al., 2019; Mikovits et al., 2019; Schaubberger et al., 2019; Vitt et al., 2017), given that the economic costs of combatting increasing heat stress may increase sharply. If such systems become increasingly energy and capital intensive, and if energy costs are high, economic viability may be threatened, and they may become increasingly vulnerable to disruptions in energy supply (Godde et al., 2021) with investments in more distributed generation, including locally with solar panels, a potential replacement for grid-based electricity.

FIGURE 2 Relative distribution of cattle (dark blue plots) and of extreme heat stress days per year (dark green plots) in relation to mean annual precipitation and mean annual temperature, 2000 (left-hand panels) and 2090 under SSP5-8.5 (right-hand panels). Here (and in Figures S2–S5), the data were smoothed using a low-pass filter and bins with sparse data (<1%) omitted. (a) Cattle in the temperate zones, (b) cattle in the tropical zones



4.4 | Concluding comments: Limits to adaptation?

Our broad-scale analysis shows that current domesticated livestock niches will become hotter and wetter, and extreme heat stress will become more pervasive. By the 2050s, some locations will become too hot and humid for animals to thrive without considerable adaptation. In such areas, extensive animal production may no longer be viable. This applies particularly to low input systems, where the costs of (and constraints to) adaptation may become prohibitive. Even for the higher input systems, in places where extreme heat stress risk increases, adaptation costs will increase because of increasing energy and infrastructure costs, threatening economic viability.

In lower income countries, vulnerability to the health impacts of climate change will be shaped by the existing burden of ill-health and

is expected to be highest in poor and socio-economically marginalized populations (Labbé et al., 2016). For many in the rural areas, livestock may be their primary asset. The labor capacity of rural populations in rural areas under a warming climate is likely to decrease further, beyond the 5% decrease estimated since 2000 (Watts et al., 2018). Loss of labor capacity may have critical implications for the vulnerability of those relying on subsistence farming and livestock keeping.

Much is unknown about the potential impacts of increased heat stress on domesticated livestock populations and the resulting production and productivity effects, particularly in species other than cattle. The analysis above concerned the longer term impacts of heat stress on domesticated livestock. An additional element in the estimation of heat stress impacts relates to the effects of heat waves, or relatively short periods of consecutive days when heat stress is

severe or extreme (Gaughan et al., 2009). Heat waves of a few days' duration can reduce animal performance and cause substantial economic losses to the livestock industry (Hahn et al., 2002, cited in Gaughan et al., 2009; Garner et al., 2017; Lees et al., 2019).

In addition to further information on effects of heat waves on animal productivity, particularly in extensive systems, studies are needed that integrate heat stress effects with what is known about likely future impacts of climate change on feed and feed supply, and with information on projected shifts in climate-sensitive diseases and disease vectors and their impacts on livestock. Although a proxy of heat stress such as THI may provide useful information on the potential extent and scope of the problem in the future at broad scale, there is a need for considerably more research on impacts and adaptation options that can provide more context-specific, actionable information so that livestock keepers and policy makers can adapt to the impact of climate changes.

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Results from the study are included as Supplementary Information accompanying this article. Other data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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