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EXTRACT FROM

Review:
Impact of Hot Weather on Dairy Cow Reproductive Performance

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Impact of heat stress on dairy cow reproductive performance

Exposure to heat stress during early lactation (breeding season)

Hot climatic conditions may cause cows to be lethargic, negatively affecting their ability to display natural mating behaviour. Lethargy induced by heat stress may help to limit further increases in production of metabolic heat due to activity associated with oestrus (Hansen and Aréchiga, 1999). In heat stressed cows, oestrus cycles tend to be longer, with oestrus expression being reduced in intensity and duration, and more silent heats occur (Thatcher and Collier, 1986; Tippenhauer et al., 2021). The consequences of this are that the number of detected heats and therefore the number of inseminations are reduced, and the proportion of inseminations that do not result in pregnancy is increased (Abilay et al., 1975; Dransfield et al., 1998; Hansen and Aréchiga 1999; Orihuela, 2000; DeRensis and Scaramuzzi, 2003; Tippenhauer et al., 2021).

Hot climatic conditions during the breeding season reduce conception and pregnancy rates. McGowan et al. (1996) analysed reproductive records from 92 Australian dairy herds with historical Bureau of Meteorology weather records. They found that a bent-stick model best fit the data and that a mean seasonal THI above 72 resulted in a significant reduction in conception rate (Figure 3A). Other studies have found the reduction in reproductive performance during the breeding season with increased heat stress to be curvilinear. Cavestany et al. (1985) described a curvilinear relationship between the daily maximum temperature on the day of service and the conception rate to first service. (Figure 3B). The conception rates achieved were lower overall than those reported by Gwazdauskas et al. (1975) and decreased much more rapidly with increased daily maximum temperature. (Figure 3C). This is likely to be due to higher relative humidity levels and little or no shade being provided. Morton and co-workers described a curvilinear relationship between the monthly average daily maximum THI and conception rate for services performed (Figure 3D). This was in contrast with Schuller et al. (2014), who found a very gradual and approximately linear decline in conception rate from a mean daily THI of 41 to 73, followed by a more rapid decline as the mean daily THI exceeded 73 (Figure 3E). One explanation for this may be that the herd studied by Schuller and co-workers had a conception rate of 32%, which was approximately 15% lower than that of the herds studied by Morton and co-workers. Schuller and co-workers concluded that for the herd studied, a mean daily THI of 73 was the most likely threshold for heat stress impacting on conception rate. They noted however that cows appeared to be already sensitive to heat stress at lower THI levels. Mellado et al. (2013) (Figure 3F) also described curvilinear relationships between the maximum THI on the day of insemination and pregnancy rate.

Caution is necessary when considering results of studies that have focused on cow reproductive outcomes based on climatic conditions or cooling strategies only on or near the day of insemination, such as Gwazdauskas et al., 1975; Stevenson et al., 1983; Cavestany et al., 1985; Her et al, 1988; Ealy et al, 1994; Al-Katanani et al., 1999; Garcia-Ispierto et al., 2007, Nabenishi et al., 2011; Mellado et al., 2013; Tippenhauer et al., 2021. This is because there is a high degree of correlation in heat load between days, and failing to account for this may result in over-estimation of the effect of heat load on specific days relative to the day of service. Morton et al. (2007), in their retrospective, observational study, using data from 26 Holstein-Friesian year-round calving dairy herds on the Atherton Tableland, accounted for this high degree of autocorrelation in heat load between days in their analyses. They found that the effect of high heat load on conception rate on a given day relative to the service day was independent of effects on days before and after it, and that these effects could be summed. Morton and co-workers concluded that the effects of high heat load were greatest in the week before insemination and the week after insemination. However, the preceding 5 weeks were also associated with reduced conception rates. Schuller et al. (2014) also found that heat stress both before and after the day of service had negative effect on services per conception. They found that the effect was greatest in the 3 weeks before insemination.

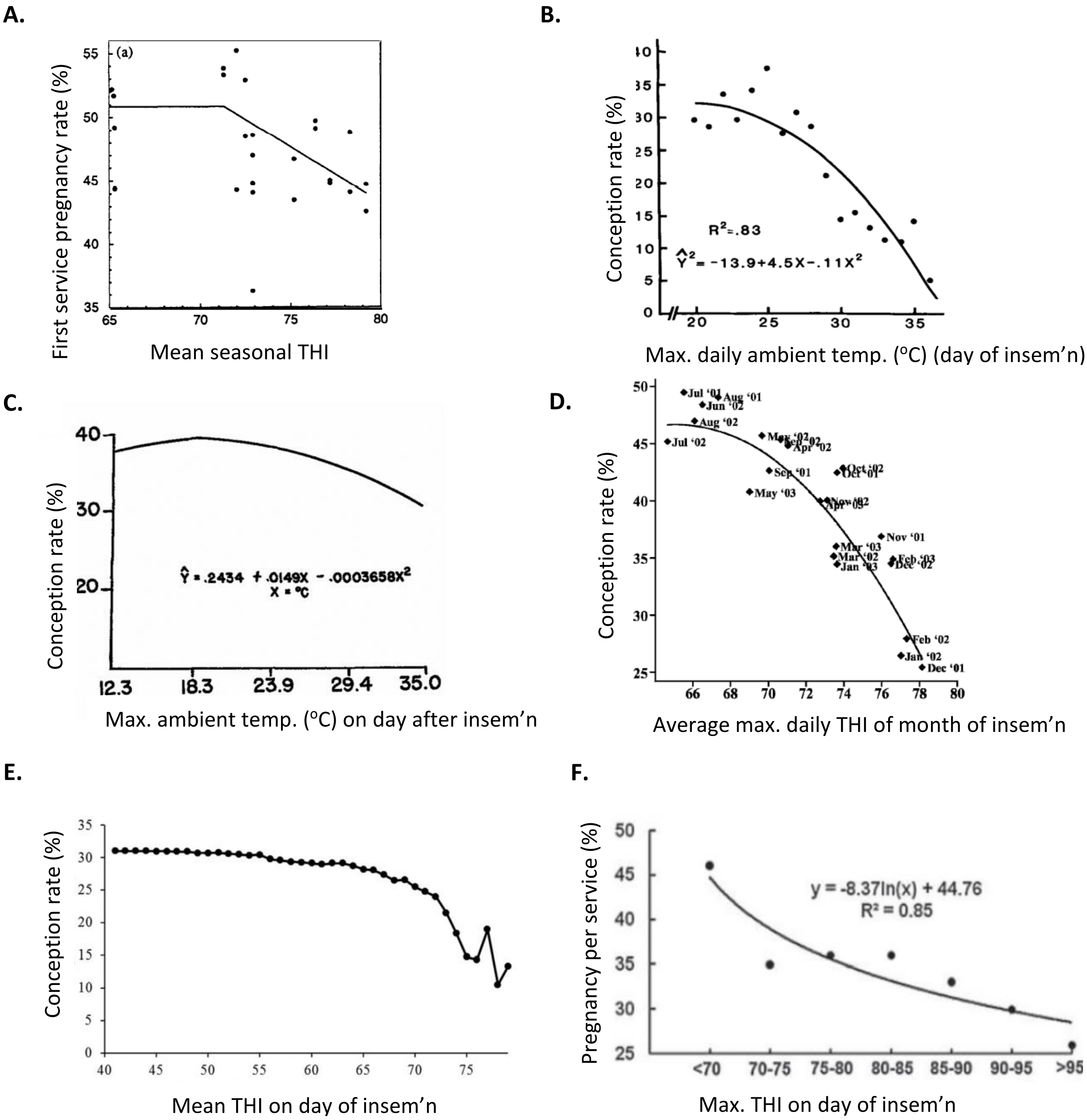

Figure 3. Relationships between maximum daily temperature or mean or maximum temperature-humidity index (THI) and conception rate or pregnancy rate found in studies conducted under different conditions. A. McGowan et al., 1996; B. Cavestany et al., 1985; C. Gwazdauskas et al., 1975; D. Morton et al., 2007; E. Schuller et al., 2014; F. Mellado et al., 2013. (Charts copied from papers).

The finding by Morton and coworkers that the effects of heat stress on conception rate extended from 5 weeks before insemination to one week after insemination are consistent with the reproductive physiology of cows. As well illustrated by Hansen, 2013 (Figure 4), heat stress can affect oocyte competence for fertilization and follicular development. Oocytes can be damaged by heat stress as early as 105 days before ovulation (Torres-Junior et al., 2008). Following fertilisation, in the early stages of cleavage, the embryo is also vulnerable to heat stress (days 1-7). Thermal tolerance then increases by the morula stage. While transcript abundance for some key cytoprotective molecules, including HSPA1A, is higher at the two-cell stage than at the morula stage, the embryo is more susceptible to damage by reactive oxygen species (ROS) produced in response to heat shock at the two-cell stage than in the morula. Intracellular concentrations of the antioxidant glutathione are also low at the two-cell stage (Hansen, 2013).

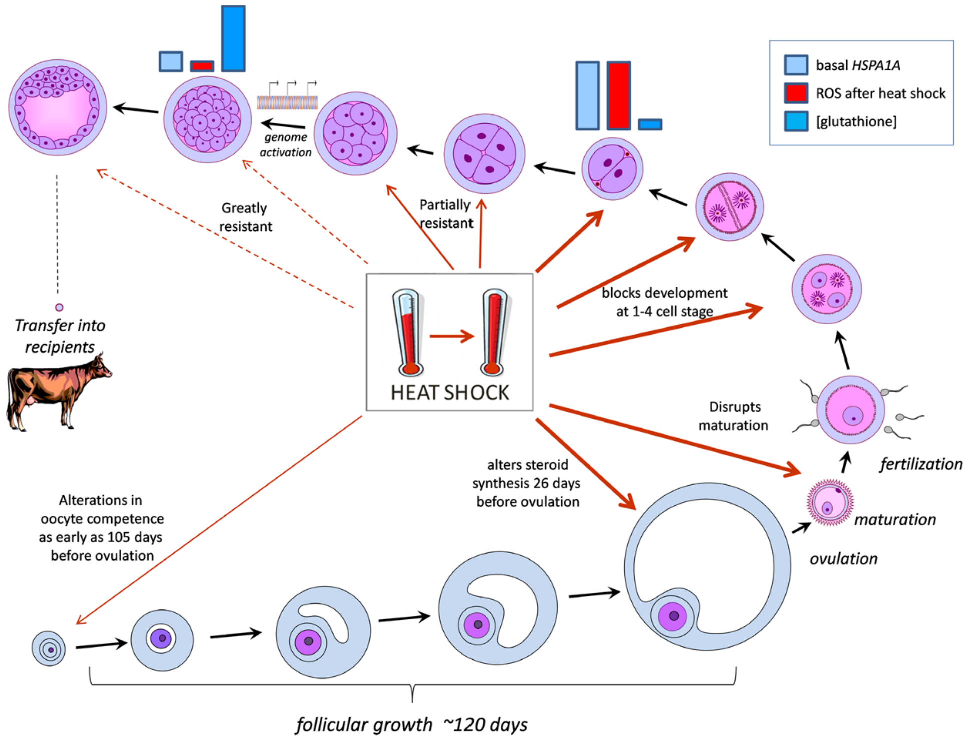

Figure 4. The timing of heat shock (hyperthermal) effects on events leading to blastocyst formation. (Copied from Hansen, 2013).

With an understanding that daily effects of heat load occur over many weeks prior to insemination and are cumulative in their impact on conception on that day of insemination, deciding whether or not to inseminate a cow today based on whether the weather is hot, or cooling cows just on the day of insemination day, will be of little benefit. Farm strategies to reduce the impact of heat stress on dairy cow reproductive performance need to be implemented from at least 5 weeks before the expected insemination date. Furthermore, it is possible to anticipate the potential impacts of current weather conditions on future conception rates.

Some research studies have reported better reproductive performance in multiparous cows then primiparous cows. Badinga et al. (1985) reported that while conception rates of multiparous cows declined rapidly when the maximum daily temperature exceeded 30°C, conception rates of primiparous cows did not decline until 35°C. Schuller et al. (2016) found that multiparous cows were 22% less likely to get pregnant than primiparous cows when artificially inseminated with frozen-thawed semen. In contrast, other studies have founded no difference or lower performance in primiparous cows (Ray et al., 1992; Jonsson et al., 1999; El-Tarabany et al., 2016a).

While it is beyond the scope of this review, it is important to state that inflammatory diseases such as retained foetal membranes, metritis, mastitis, lameness, and digestive and respiratory disorders which occur between calving and breeding may also have negative impacts on the reproductive performance of cow which are independent of effects caused by heat stress and are additive. Inflammatory diseases may affect oocyte competence, early embryo development and the uterine environment (Ribeiro et al., 2016).

Published research studies exploring impacts of heat stress in early lactation on cows' reproductive performance are summarised in Tables 1 and 2.

Table 1. Retrospective, observational studies exploring impacts of heat stress in early lactation on cows' reproductive performance.

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Monty et al., 1974	Arizona, USA.	?	Season inseminated	Hot weather Cool weather	3.3 1.1				
Gwazdauskas et al., 1975	Florida, USA. Jan 1960 – Dec 1971	All breeds. 5,062 services	Season inseminated	Bred Jun-Oct (hot) Bred Nov-May (cool)		33.7 40.1			
Cavestany et al., 1985	Florida, USA. Jul 1979 – Jun 1980	One Holstein herd of 1,800 cows	Season inseminated	Warm months (Jun-Sep: avg max temp. 33.2°C, avg max Rel Humidity 65.3%) Cooler months (Oct-May)		5.3, 4.8, 4.5, 3.5 3.2, 2.6, 2.4, 2.3, 2.6, 3.6, 3.5, 4.5	9, 7, 12, 11 13, 29, 33, 26, 32, 23, 25, 17	Calving to concept-tion (d)	171, 167, 149, 134 118, 105, 99, 103, 115, 140, 149, 173
Badinga et al., 1985	Florida, USA. 1975 - 1977	One mixed breed herd 12,038 inseminations	Day after insemination	March (23.9°C) July (32.2°C)		52 32			
Ray et al., 1992	Arizona, USA.	19,266 cows	Season calved	Winter Spring Summer Fall	1.90^{c} 2.23^{b} 2.34^{a} 1.89^{c}			Inter-calving period (d)	369.0^{c} 385.6^{a} 386.8^{a} 371.8^{b}
Bagnato and Oltenacu, 1994	Italy. 1966-1984	Italian Friesian herds	Season inseminated	Warm months (Jun-Sep: max temp. 33 to 44°C) Cooler months				Calving to concept-tion (d)	+5-10
Thompson et al., 1996	Texas, USA. 1992-1993	119 herds Holstein cows	Season inseminated	Winter Spring Summer Fall			Odds ratio: Summer: 0.53 vs. other seasons		
Al-Katanani et al., 1999	Sth Georgia, Nth and Sth Florida, USA.	17 Holstein herds	July	Sth Georgia Nth Florida Sth Florida				90d NRR (%)	18.9 7.0 4.7

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Al-Katanani et al., 1999	Sth Georgia. Nth and Sth Florida, USA	17 Holstein herds	Days rel. to insemination: -10 0 +10	Temperature: >20ºC vs ≤20ºC >20ºC vs ≤20ºC >20oC vs ≤20oC				90d NRR (%)	 36.5v60.1 41.4v59.6 41.1v56.9
Alnimer et al., 2002	Italy.	90 cows	Season inseminated	Summer Winter				Pregnancy rate (%)	56.3 81
Lopez-Gatius et al., 2005	NE Spain. Jan 2002-Oct 2003	2 H-F herds 5,883 inseminations	Season inseminated	Warm Cool			32.9 37.2		
Garcia-Ispierto et al., 2007	NE Spain. Jan 2002-Dec 2004	4 H-F herds 10,964 inseminations	Season inseminated	Hot weather Cool weather		27.9 35.0			
Garcia-Ispierto et al., 2007	NE Spain. Jan 2002-Dec 2004	4 H-F herds 10,964 inseminations	Days rel. to insemination: -3 0 +1	Max THI: <70 71-75 76-80 81-85 <70 71-75 76-80 81-85 Max temperature: <20°C 21–25°C 26–30°C 31–35°C				Odds ratio for CR	 1.48 1.47 1.5 1.1 1.73 1.53 1.11 1.3 1.5 1.2 1.0 1.0
Morton et al., 2007	Atherton, Far North Qld., Australia. 2001-2003	26 mainly Holstein herds				-2.5% per day with max THI ≥82 or 18 h when THI >72, from 35 days before to 6 days after service			
Flamenbaum and Galon, 2010	Israel. 2005	22 herds	Season ± intensive or moderate cooling	Summer: Intensively cooled Moderately cooled Winter: Intensively cooled Moderately cooled		 19 12 39 39			

Reference	**Study location and period**	**Sample population**	**Comparison**	**Groups**	**Services per conception**	**Conception rate (%)**	**Pregnancy at first AI (%)**	**Other parameter**	
Flamenbaum and Galon, 2010	Israel. 2007	48 herds	Summer:Winter ratio of ECM produced	High S:W ratio: Winter CR Summer CR Low S:W ratio: Winter CR Summer CR		 36 19 40 27			
Nabenishi et al., 2011	SW Japan. Jan 2006-Dec2008	170 Holstein herds		Jul-Sep: avg max THI = 77.4 Oct-Jun: avg max THI = 63.5		29.5 (CRFS) 38.2 (CRFS)			
Mellado et al., 2013	NE Mexico. Time period not specified	Holstein herd of 5,000 cows 18,037 inseminations Dry lot with shade and fans	Day of insemination	Max THI: <70 70-75 75-80 80-85 85-90 90-95 >95			 46 35 36 36 33.5 32 26		
Schuller et al., 2014	Sachsen-Anhalt, Germany. May 2010-Oct 2012	1 Holstein herd of 1150 cows	Period rel. to insemination: 42 days before 21 days before 2 days before Day of insemination 3 days after insemination 21 days after insemination 31 days after insemination	Mean daily THI ≥73 vs ≤73		Odds ratio: 0.69 0.39 0.64 0.61 0.57 0.52 0.64			
Mellado et al., 2014	Nth. Mexico. 2004-2012	Holstein herd of 2,525 cows 64,666 inseminations Dry lot	Season inseminated	 Warm Cool			Heifers: Cows: 43 22 48 28		
Pereira et al., 2015	Brazil. July 2012–Jan 2013	4 Holstein herds Freestall barn and outside pen	Season inseminated	Hot weather Cool weather	5.55 2.70				

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Polsky et al., 2017	Brazil. Feb 2014–Feb 2015	1700 Holstein cows	% time 9-11 days before service with vaginal temp: High (≥22.9%) Low (<22.9%)	 Avg THI: ≤65 65-70 ≥70 ≤65 65-70 ≥70	 3.76 4.24 8.14 3.46 4.83 3.96				
Kim and Jeong, 2019	Korea. 2011-2016	426 cows, 790 lactations. Breed not specified	Summer vs other seasons	 Spring Summer Autumn Winter		Odds ratio^: Reference 0.44 0.73 0.88			
Penev et al., 2020	Southern Bulgaria. 2015-2018	H-F herd Freestall 10,000kg/lact.		Max THI: ≤72 73-78 79-89 ≥90	 2.5 2.4 2.8 4.3			Calving to concept-tion (d)	 130.4 137.9 150.5 206.7
Penev et al., 2020	Southern Bulgaria. 2015-2018	H-F herd Freestall 10,000kg/lact.	Month of insemination	Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec		39.3 39.4 33.3 40.0 30.4 37.8 19.4 16.7 38.1 35.9 51.6 40.7			
Tippenhauer et al., 2021	NE Germany. Jul 2018-May 2019	8 Holstein herds	Days rel. to insemination: -7	Avg THI: <50 50-55 56-60 61-65 66-70 >70			All inseminations: 40.9^{a} 37.8^{a} 40.4^{a} 32.9^{b} 31.9^{b} 16.3_{c}	High oestrus intensity (%)	 77.7^{ab} 74.9^{bc} 74.8^{abc} 70.9^{cd} 68.1^{d} 51.0^{e}

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Rolando et al., 2022	Lima, Peru. Aug 2010-Jul 2013	4 Holstein herds	Warm season (Jan-Apr)	THI		1.74% decrease per unit max THI	0.84% decrease per unit max THI		
Menta et al., 2022	Central California, USA. 2012-2014	2 Holstein herds	Thermoneutral (TN) or heat stress (HS) 4 weeks pre-calving and 4 weeks post calving	Avg THI: Primiparous cows: TN-TN: 57.8 & 63.4 TN-HS: 68.2 & 72.0 HS-TN: 71.3 & 65.5 HS-HS: 72.2 & 72.6 Multiparous cows: TN-TN: 57.9 & 63.8 TN-HS: 68.2 & 72.0 HS-TN: 71.4 & 65.7 HS-HS: 72.2 & 72.7			Day 32 Day 60 43.6 40.3 40.1 34.8 40.7 37.2 36.2 32.1 36.2 30.4 23.3 19.8 33.2 28.2 30.9 25.7	Pregnancy loss (%)	7.2 13.2 8.5 11.5 15.5 12.0 13.8 14.3

- * 90-day non-return-rate to first service
- ^First service conception rate

.ns Non significant difference

Table 2. Prospective cohort studies exploring impacts of heat stress in early lactation on cows' reproductive performance.

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Gwazdauskas et al. (1973)	Uni. of Florida., USA. Sep. 1970-Aug 1971	Not specified	Uterine temp. on day of insemination Ambient temperature on day after insemination			Refer to paper for overall analysis of variance for conception			
De Rensis et al., 2002	Bergamo, Italy. May 1999-Mar 2000	6 Holstein herds	Season inseminated	Summer Winter Summer Winter				Pregnancy rate (%)	Day 90: 33 46 Day135: 62 76
Turk et al., 2015	Croatia. Jun 2011-Jul 2013	32 H-F heifers Open-sided freestall	Season inseminated	Summer Winter Summer Winter	% of Heifers: 1: 50.0, 2: 44.4, 3: 0, 4: 5.6 1: 71.4, 2: 28.6, 3: 0, 4: 0 Primiparous cows 1: 17.6, 2: 35.6, 3: 23.5, 4: 23.5 1: 70.0, 2: 30.0, 3: 0, 4: 0			Calving to conception (days)	159 91
Pereira et al., 2015	Minas Gerais State, Brazil. Jul 2012 – Jan 2013	4 Holstein herds	Season inseminated All cows vs synchronised cows	All cows: Hot season Cool season Synchronised cows: Hot season Cool season	4.67 (32 days) 5.56 (60 days) 2.20 (32 days) 2.70 (60 days) 25.3 (32 days) 20.9 (60 days) 50.5 (32 days) 41.3 (60 days)				

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Pregnancy at first AI (%)	Other parameter	
Stefanska et al., 2024	Poland.	5 Holstein	Days rel. to calving day:	Avg THI:				Inter-	
	Jun-Sep 2018	herds	0	<68	47.4	1.63b	103	calving	378
		Open-sided		68-72	56.9	1.93ab	118	period (d)	393
		freestalls		>72	76.2	2.94a	159		434
			+7	Avg THI:					
				<68	53.4	1.65	109		384
				68-72	63.0	1.75	121		396
				>72	80.0	2.22	148		423
			14	Avg THI:					
				<68	51.0	1.73	108		383
				68-72	48.2	2.16	115		390
				>72	75.9	2.5	149		424
			21	Avg THI:					
				<68	56.8	1.85	117		392
				68-72	60.1	1.89	121		396
				>72	72.8	2.71	151		426

.[ns] Non significant difference

Exposure to heat stress during the dry period (late gestation)

Following dry off, 6-8 weeks of gestation remain before calving. During this non-lactating period, the udder is remodelled in readiness for the onset of the next lactation. During the dry period, a cow would be expected to be less susceptible to heat stress, as she produces less metabolic heat than during lactation (Collier et al., 2017). This is confirmed by the smaller increases in body temperatures measured in heat-stressed dry cows compared to heat-stressed lactating cows in studies conducted in environmental chambers and in pens under hot conditions with or without evaporative cooling (Rhoads et al., 2009; Wheelock et al., 2010; Lamp et al., 2015; Weng et al., 2018). Despite this, however, heat stress during the dry period has substantial impacts on cows' performance in the following lactation.

Remodelling of the udder during the dry period comprises two functional phases. Firstly, involution, in which senescent mammary epithelial cells are removed through the processes of apoptosis and autophagy. Secondly, redevelopment, in which new mammary epithelial cells proliferate (Ouellet et al., 2020). Late gestation heat stress has been shown to compromise mammary gland remodelling, impacting on the number of mammary cells and their secretory capacity, and resulting in reduced lactation performance in the following lactation (Tao et al., 2011). Heat stress experienced by cows in either phase – involution and redevelopment – or both phases has been shown to negatively impact lactation performance (Fabris et al., 2019). Further to its effects on udder remodelling, late gestation heat stress also negatively impacts voluntary feed intake and therefore nutrient uptake and supply to the mammary gland. This effect contributes to reduced lactation performance observed in early - mid lactation (Ouellet et al., 2020). Thirteen prospective, cohort studies reported average daily milk yields over varying numbers of days in milk (DIM) of cows heat stressed in late gestation and cows that were not heat stressed. On average, cows heat stressed in late gestation produced 3.4 kg less milk per day (9.1% reduction). See Table 4. While substantial, this milk yield loss is of much smaller magnitude than that observed when cows are heat stressed during lactation (up to 40% or more).

While the effects of late gestation heat stress on lactation performance of cows in the subsequent lactation have been well described, there are fewer reports of the effects of late gestation heat stress on reproductive performance of cows. Furthermore, in some reviews on the effects of late gestation heat stress on cows, reproductive performance in the subsequent lactation is not discussed at all (Tao et al., 2019; Ouellet et al., 2020).

A retrospective, observational study by Moore et al. (1992) in Mississippi, USA using 341 lactations found no correlation between late-gestation heat stress and reproductive performance in the subsequent lactation. However, in a study by Thompson and Dahl (2012) cows heat stressed in the dry period had more days from calving to first oestrus and more days open in the subsequent lactation. In a study by Stevenson et al. (2022) in Kansas, USA, the conception rate of cows heat stressed in late gestation was 6.7% lower (39.0% vs. 45.7%) than that of cooled cows. In a Mexican study by Rodriguez-Godina et al. (2024), the difference in conception rate of cows heat stressed and cooled in late gestation was 17.6% (42.6% vs. 60.2%). Prospective, cohort studies by Collier et al., 1982; Lewis et al., 1984; Avendano-Reyes et al., 2006; Adin et al., 2009; Karimi et al., 2015 and Scanavez et al., 2019 reported higher reproductive performance in cows that were cooled in late gestation rather than heat stressed. However, the differences were not statistically significant, but these studies had small sample sizes. Interestingly, Lewis and co-workers examined the ovaries of cows in their study and found that those provided with shade in late gestation had larger ovaries with greater diameter of the largest follicle and corpus luteum, and a higher percentage of ovaries with a corpus luteum compared to cows not provided with shade (Lewis et al., 1984).

Published research studies exploring impacts of late gestation heat stress on reproductive and lactation performances of cows in the subsequent lactation are summarised in Tables 3 and 4.

Table 3. Retrospective, observational studies exploring impacts of heat stress in late gestation on reproductive and lactation performances of cows in subsequent lactation.

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Calving to conception (days)	Milk yield (kg)
Thompson and Dahl, 2012	Florida, USA. 2007-2010	2,613 cows	Hot season (Jun-Aug) vs Cool season (Dec-Feb). Avg. max. THI: Jun-Aug: 76.2 Dec-Feb: 54.8	Cows dry during hot season (Jun-Aug) Cows dry during cool season (Dec-Feb)	1.6[a] 1.5[b]		131.1[a] 125.9[b]	10,547/lact[a] 11,005/lact[b]
Stevenson et al., 2022	Kansas, USA. 2017-2021 Days 230-239 of gestation	Holstein >10,000kg/lact. Freestall, open sided TMR	Cows with different ear temps in Hotter season (May-Sep) and Cooler season (Oct-Apr). Avg. max THI: May-Sep: 78, 90, 91, 88, 81 Oct-Apr: 64, 51, 45, 41, 37, 54, 67	Hotter season (May-Sep): High ear temp. cows Med. ear temp. cows Cooler season (Oct-Apr): Med.-Low ear temp. cows Low ear temp. cows		39.0 45.7		 43.7[ns] 43.5[ns] 45.0ns 44.0[ns]
Rodriguez-Godina et al., 2024	Nth. Mexico. 2016-2021	Holstein herd of 3,000 cows >10,000kg/lact		Avg. THI in dry period: >80 70-80 Avg. THI <70	 5.6 ± 3.8[c] 6.3 ± 3.9[b] 6.5 ± 3.6[a]	 42.6[c] 51.1[b] 60.2[a]		 10,691[c]/305d lact 10,799[b]/305d lact 10,926[a]/305d lact

.[ns] Non significant difference

Table 4. Prospective, cohort studies exploring impacts of heat stress in late gestation on reproductive and lactation performances of cows in subsequent lactation.

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Calving to conception (days)	Milk yield (kg)	
								HOT	COOL
Lewis et al., 1984	Uni. Florida, USA. 1978	31 Holstein cows and heifers	Heat stressed vs Cooled for 85-115 days pre-calving	No shade Shade	2.4ns 2.6ns		91.6ns 114.4ns		
Wolfenson et al., 1988	Israel. 1986	85 Israeli-Holstein cows. Open sided shade shed TMR	Heat stressed vs Cooled for 60 days pre-calving	Not cooled Cooled with fans and sprinklers for 8 hours per day (06:00 to 18:00)				37.2 (mean kg/day to 150 DIM)	40.7
Avendano-Reyes et al., 2006 (Expt. 1)	NW Mexico. 2000	38 Holstein cows. Partially shaded pens TMR	Heat stressed vs Cooled for 60 days pre-calving Avg. max. THI: May: 89.5 Jun: 93.8 Jul: 94.3 Aug: 96.9 Sep: 91.2	Not cooled Cooled by wetting twice daily for 2 min at 11:30 and 14:30	2.0ns 1.5ns		102.7ns 86.9ns	20.3ns	22.3ns
Avendano-Reyes et al., 2006 (Expt. 2)	NW Mexico. 2001-2003	52 Holstein cows. Partially shaded pens TMR	Heat stressed vs Cooled for 60 days pre-calving Avg. max. THI: May: 88.4, 88.7, 90.0 Jun: 92.7, 93.6, 94.0 Jul: 94.3, 94.8, 94.6 Aug: 95.0, 94.8, 95.2 Sep: 92.4, 92.0, 92.6	Not cooled Cooled with fans and misting for 8 hours per day (10:00 to 18:00)	2.5ns 1.9ns		89.1ns 70.3ns	25.5ns	28.1ns

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Calving to conception (days)	Milk yield (kg)	
								HOT	COOL
Urdaz et al., 2006	California, USA. 2002	475 Holstein cows Dry lot pens with shade structures	Heat stressed vs Cooled for ≥14 days pre-calving Avg. max. THI: 71	Feedbunk with sprinklers Feedbunk with sprinklers, fans and shade cloth				38.7 (mean kg/day to 60 DIM)	40.1
Adin et al., 2009 (Expt. 1)	Israel. 2009	72 cows. Breed not specified Closed-sided freestall	Heat stressed vs Cooled for 56 days pre-calving	Hot = Shade only Cool = Shade plus fans and sprinklers				38.4 (mean kg/day to 150 DIM)	37.1
Adin et al., 2009 (Expt. 2)	Israel. 2009	72 cows. Breed not specified Loose housing facility	Heat stressed vs Cooled for 56 days pre-calving	Hot = Shade only Cool = Shade plus fans and sprinklers				39.3 (mean kg/day to 150 DIM)	41.4
Do Amaral et al., 2009	Florida, USA. 2007	16 Holstein cows Freestall	Heat stressed vs Cooled for 46 days pre-calving	Not cooled Cooled with fans and sprinklers				26.2 (mean kg/day to 140 DIM)	33.7
Do Amaral et al., 2011	Florida, USA. 2008	21 Holstein cows Freestall	Heat stressed vs Cooled for 46 days pre-calving	Not cooled Cooled with fans and sprinklers				32.2 (mean kg/day to 140 DIM)	34.5
Tao et al., 2011	Florida, USA. 2008	29 Holstein cows Freestall	Heat stressed vs Cooled for 46 days pre-calving	Not cooled Cooled with fans and sprinklers				28.9 (mean ECM/day to 280 DIM)	33.9
Tao et al., 2012a	Florida, USA. Jun-Nov 2010	32 Holstein cows Freestall	Heat stressed vs Cooled for 46 days pre-calving	Not cooled Cooled with fans and sprinklers				27.7 (mean ECM/day to 294 DIM)	34.0

Reference	Study location and period	Sample population	Comparison	Groups	Services per conception	Conception rate (%)	Calving to conception (days)	Milk yield (kg) HOT	COOL
Karimi et al., 2015	Iran. 2012	20 Holstein cows Freestall	Heat stressed vs Cooled for 21 days pre-calving Mean THI: 69.7	Not cooled Cooled with fans and sprinklers from 07:00 to 19:00 daily	2.2[ns] 1.9[ns]		106.7[ns] 97.0[ns]		
Fabris et al., 2017	Florida, USA. 2015	60 Holstein cows Freestall	Heat stressed vs Cooled for 46 days pre-calving Mean THI: 78	Not cooled Cooled with fans and sprinklers				35.9	40.7
Fabris et al., 2019	Florida, USA. 2016	60 Holstein cows Freestall	Heat stressed for all, none of part of dry period Mean THI: 75	Not cooled Cooled entire dry period Cooled* for 3 weeks, then hot Hot for 3 weeks, then cooled* (* fans and sprinklers)				36.3 36.1 36.3	 40.2
Scanavez et al., 2019	Kansas, USA. Jun-Aug 2017	241 cows from 3 Holstein herds Loose housing and freestall. No fans and sprinklers	Dry cows above or below mean vaginal temperature No cooling. Mean THI: 74-76	High vaginal temp. cows Low vaginal temp. cows	No significant difference			46.2 (mean kg/day to 90 DIM)	49.3

.[ns] Non significant difference

Inter-generational impacts of heat stress in the pregnant cow

Developmental programming and epigenetics

The Developmental Origins of Health and Disease (DOHaD) hypothesis states that a number of maternal and environmental factors (nutrition, health, and exposure to hypoxia, toxins, pollutants and other insults) during pre-natal development can have profound short term and long term impacts on health and disease risk throughout post-natal life (Fleming et al., 2015). There is now strong evidence for this theory, otherwise known as developmental programming (Barker, 1990), in humans, and in small and large animal models. Impacts have been found on the cardiovascular, metabolic, endocrine and reproductive systems, and on the risks of obesity, various diseases and premature death (Meesters et al., 2024).

Heat stress in-utero induces changes in gene activity and function that are not associated with any changes in DNA sequence. It reduces the expression levels of the epigenetic modifications from histones, DNA methylation, and DNA hydroxymethylation at all stages of the oocyte and embryo (Ouellet et al., 2020). Heat stress also reduces cleavage rate, blastocyst rate, oocyte mitochondrial-membrane potential level, adenosine-triphosphate (ATP) level, mitochondrial DNA copy number, and transzonal projection level. It also affects mitochondrial distribution in oocytes and significantly increases reactive oxygen species, apoptosis levels and mitochondrial autophagy levels (Feng et al., 2024).

The Dutch winter famine in World War II, from November 1944 to May 1945, provided a stark demonstration of developmental programming on long-term human health (Roseboom et al., 2001). An example of how developmental programming impacts on the health of offspring in dairy cattle is provided by Swartz et al. (2021), who found an association between mammary gland health (mastitis) in cows and their daughters. Heat stress during gestation is also an example of developmental programming in dairy cattle.

Impacts of developmental programming may extend over several generations. This occurs when an animal is exposed to a stressor in-utero, between its conception and birth, that affects the oocytes (female gametes, germ cells) or the developing foetus (Huber et al., 2020; Laporta 2021). Table 5 shows the means by which each generation may be exposed to a stressor such as heat stress, directly or indirectly.

Table 5. Means of exposure to heat stress by generation, F_0 to F_3.

Generation		Means of exposure to heat stress
Dam	F_0	Directly exposed to heat stress during pregnancy of F_1
Daughter	F_1	Exposed to heat stress in-utero. Epigenetic reprogramming of oocytes that will give F_2 generation
Grand-daughter	F_2	Not exposed to heat stress, but the product of the heat stress exposed, epigenetic modified F_1 oocytes which is fertilised
Grand grand-daughter	F_3	Not exposed to heat stress, but may inherit epigenetic modified F_1 oocytes by transgenerational transamination via F_2

For the purpose of modelling the impact of heat stress on dairy cow reproductive performance it is important to understand the magnitude of effects of maternal heat stress on daughters, grand-daughters and grand grand-daughters (F_1, F_2 and F_3), so that they can be compared to the direct effects of heat stress on the dam. The inter-generational impacts of heat stress through developmental programming have been investigated through retrospective analysis of vast quantities of phenotypic, pedigree and genomic information for millions of dairy cows worldwide collected and stored in various databases (Wathes, 2022; Meesters et al., 2024). Prospective, cohort studies have also been conducted.

Impacts on daughters (F_1 generation)

The reproductive performance, lactation performance and survival of daughters (F_1) are influenced by parity and level of maternal milk yield per lactation. Daughters of higher parity cows have higher reproductive performance, and daughters of cows with higher lactation performance have lower reproductive performance (Bafandeh et al., 2023; Harati et al., 2024).

Gestation length, organ development, birth weight and weaning weight

If heat stress (hyperthermia) is experienced by the dam during late gestation (dry period), her developing foetus (F_1 generation) also becomes hyperthermic as it is unable to control its own body temperature independent of the dam. This has many immediate and long-lasting negative consequences for the F_1 generation.

In utero heat stress during late gestation, which is a period of rapid growth and development, leads to reduced bodyweight at birth. Retarded foetal growth may be due three contributing factors: 1) Shortened gestation length, thereby reducing total time for foetal development, 2) altered placental development and blood flow, and morphological changes to the placenta which reduce nutrient supply to the foetus. (Collier et al., 1982; Reynolds et al., 2006, Thompson et al., 2013; Potadle et al., 2019), and 3) the direct effect of foetal hyperthermia on metabolism of the foetus (Tao et al., 2012; Ouellet, 2023).

Twenty two prospective, cohort studies reported birthweights of calves which were exposed to in-utero heat stress in late gestation and calves that were not exposed. On average, calves exposed to in-utero heat stress in late gestation weighed 4.0 kg less (9% reduction) at birth. Twelve studies reported gestation length. On average, the gestation length of calves exposed to in-utero heat stress in late gestation was 1.9 days fewer (1% reduction). Seven prospective, cohort studies reported weaning weight of calves. See Table 6. On average, calves exposed to in-utero heat stress in late gestation weighed 7.3 kg less (0.9% reduction) at weaning. While the impact of in-utero heat stress during late gestation on birth weight and weaning weight are quite consistent across studies, reported growth rates from birth to weaning are more variable, reflecting differences in the calf feeding regimes used in studies.

In-utero heat stress in late gestation also impairs growth and development of many organs and tissues in the foetus which play key metabolic and immune functions (Monteiro et al., 2016a; Dado-Senn et al., 2021). At birth, the thymus, spleen, thyroid gland, heart and mammary gland are smaller in in-utero heat stressed calves relative to calves kept cool in-utero. In-utero heat stressed calves have an impaired capacity to acquire passive immunity after birth through absorption of colostral immunoglobulin G (IgG) (Tao et al., 2012b; Laporta et al., 2017). This is likely to be due to more rapid gut closure (Ahmed et al., 2021). Cellular immunity is also impaired in in-utero heat stressed calves. This may be associated with under-developed immune organs i.e. thymus, spleen (Ahmed et al., 2021). In-utero heat stressed calves exhibit altered metabolic responses when exposed to heat stress pre-weaning, with insulin resistance in muscle and fat tissues and greater glucose uptake through non-insulin dependent tissues. This indicates altered nutrient partitioning which may contribute to reduced pre-weaning growth (Monteiro et al., 2016a). At weaning the adrenal glands and kidneys of in-utero heat stressed calves are larger than those of calves kept cool in-utero; however, the mammary gland and ovaries relative to bodyweight are smaller (Dado-Senn et al., 2021).

Reproductive performance

Daughters (F_1s) exposed to heat stress in-utero may have reduced reproductive performance. Environmental stressors such as heat stress imposed on daughters in-utero may programme different changes, depending on the stage of gestation (early, mid or late gestation) and the duration of the exposure (Yao et al., 2020). In early and mid gestation, the ovaries and hypothalamic-pituitary axis develop, and any alteration in their function may impair reproductive performance by compromising the animal's ovarian reserve, the finite number of follicles and oocytes in the ovaries that females are born with, which then declines over time (Monniaux et al., 2014; Mossa and Evans, 2023).

Monteiro et al. (2016b) compared the reproductive performance of daughters exposed to heat stress in-utero and those cooled in-utero during late gestation, as maiden heifers and in their first three lactations. They did not find any significant differences in the risk of conception between the two groups. Laporta et al. (2020) also found no significant differences in reproductive performance between daughters exposed to heat stress in-utero and those cooled in-utero in late gestation. Age at first insemination, age at first calving, and conception risks for the first, second and third lactations were similar. However, Akbarinejad et al. (2017) found that overall, across four lactations, in-utero heat stress resulted in significantly longer Days to First Service (DFS), reduced First Service Conception Rate (FSCR), higher Services per Conception (SPC) and longer Calving-to-Conception Interval (CCI). In each of the four lactations, these reproductive performance parameters (DFS, FSCR, SPC and CCI) were numerically higher in daughters not exposed to heat stress in-utero. (Figure 5A). These findings provide evidence that the impacts of in-utero heat stress on the reproductive performance of F_1s are long lasting.

There is uncertainty as to precisely when in-utero heat stress has the greatest impact on daughters' subsequent reproductive performance - early, mid or late gestation - as the findings of studies conducted to date have not been consistent. Akbarinejad and co-workers (2017) found that heat stress in-utero in either early, mid or late gestation resulted in a longer Calving-to-Conception Interval (CCI) (Figure 5B). They also measured plasma levels of anti-Mullerian hormone (AMH) which is positively associated with ovarian reserve in cows, and found that plasma AMH concentrations were lower in daughters exposed to heat stress in-utero in mid and late gestation, indicating that the pool of primordial follicles in the ovaries may have been diminished. This led Akbarinejad and co-workers to conclude that in-utero heat stress had its greatest impact on the reproductive performance of daughters when it occurred in mid and late gestation (and especially mid gestation).

This is not consistent with the findings of Succa et al. (2020), Recce et al. (2021) and Makiabadi et al. (2023). Succu et al. (2020) compared AMH and the number of follicles greater than 3mm diameter (antral follicle count, AFC) of daughters exposed to heat stress in-utero in early gestation vs late gestation, as markers of the size of the ovarian reserve. They found that those exposed in early gestation had smaller ovarian reserves than those exposed in late gestation. No significant differences were found in age at first conception, age at first calving and number of services per conception between daughters exposed to heat stress in-utero in early gestation vs late gestation. This may be due to the small number of animals enrolled in the study. Recce et al. (2021) found that the daughters (F_1s) exposed to heat stress in-utero in early gestation had a longer Calving-to-First Service Interval (CFSI) and a longer Calving-to-Conception Interval (CCI), with an increase of one day. The results of Makiabadi et al. (2023) for reproductive performance parameters of daughters exposed to heat stress in-utero were inconclusive. However, they also compared plasma AMH concentrations of daughters (F_1s) exposed to heat stress in-utero in early gestation only, in early and mid gestation, in mid and late gestation, and in late gestation only, and based on their results determined that the most critical gestational stage to manage heat stress was early gestation. Conclusions about fertility based on the assessment of the size of the ovarian reserve, using the markers AMH and AFC, should be made with caution, as their association may be weak, with other factors such as farm management practices having a greater influence on reproductive performance (Mossa and Evans, 2023).

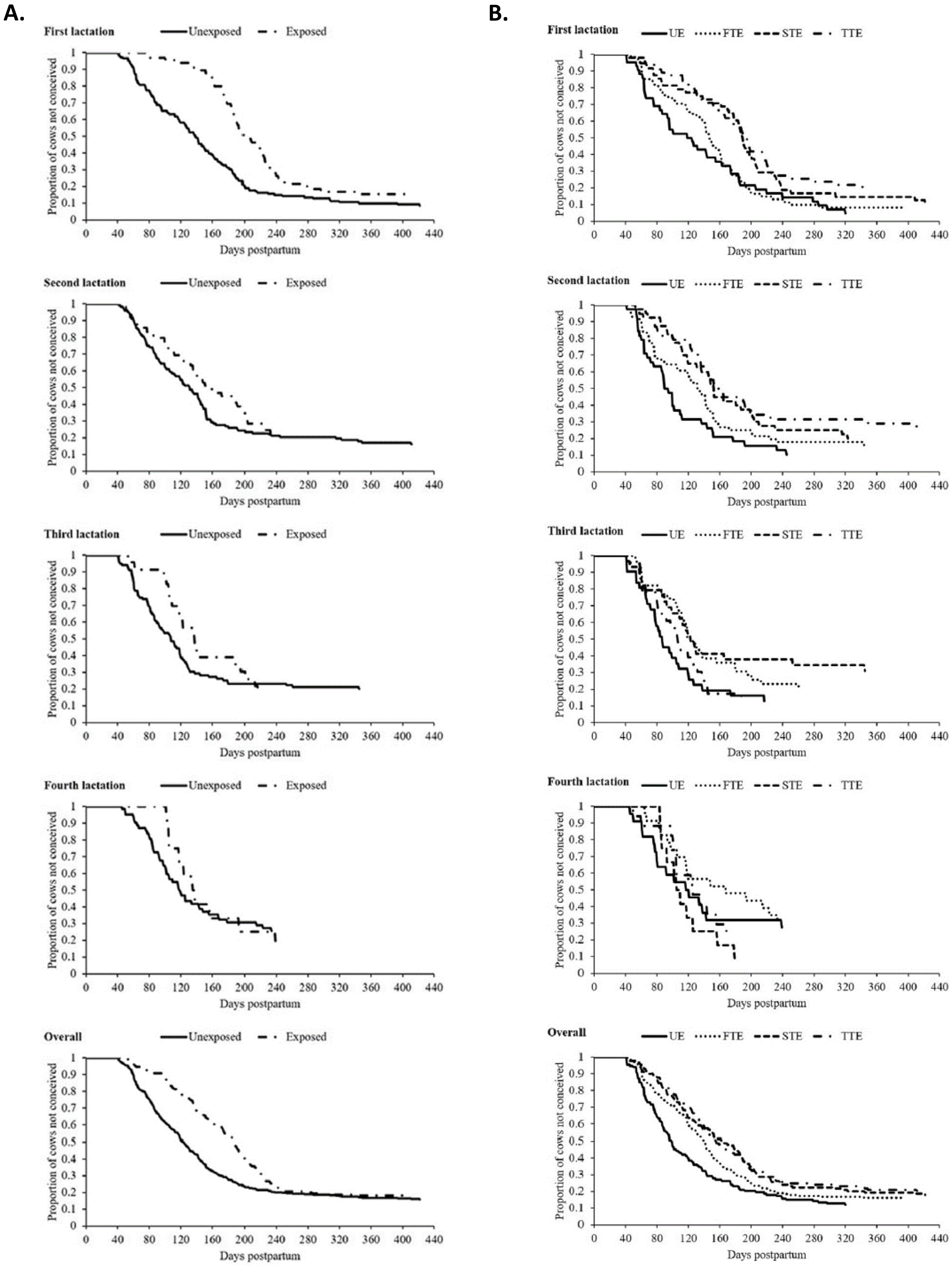

Figure 5. A. Time to conception in daughters (F_1s) exposed to heat stress in-utero, during their first, second, third and fourth lactations, and overall. B. Time to conception in daughters (F_1s) exposed to heat stress in-utero during their first, second, third and fourth lactations, and overall, considering heat stress exposure during different trimesters of gestation (UN = unexposed, FTE = first trimester exposed, STE = second trimester exposed and TTE = third trimester exposed) (Copied from Akbarinejad et al., 2017).

Lactation performance

Daughters (F_1s) exposed to heat stress in-utero have reduced lactation performance (Monteiro et al. (2016); Laporta et al. (2020). Laporta and co-workers found that heifers heat stressed in-utero (F_1) produced less milk up to 245 DIM in not only their first lactation but also their second and third lactations. (Figure 6). Their milk component were also altered. These impacts indicate that impairment of the development and function of the mammary gland, which is initiated in-utero, persists and is potentially permanent (Dado-Senn et al., 2020). In early gestation, the mammary band and bud form and in late gestation exponential growth of the mammary tissue occurs. At birth, the mammary gland comprises a fat pad and a small area of parenchyma with rudimentary branching ducts (Dado-Seen et al., 2022). Adverse conditions at any stage of gestation which result in alterations to the epigenetic state of the foetal genome lead to impaired mammary gland development and lactation performance (Skibiel et al., 2018b).

Brown et al. (2015) and Brown et al. (2016), in their retrospective, observational studies, found that while daughters (F_1s) conceived in summer produced less milk over a full lactation than those conceived in winter, they performed better during hot conditions in late spring or summer. Brown and co-workers (2016) suggested that cows heat stressed at the time of their conception may develop altered thermoregulatory mechanisms as adults that improve their thermotolerance. The results of the experiment by Ahmed et al. (2017) support this hypothesis. They found that cows subjected to heat stress in late gestation had higher skin surface temperature at 17:00 hours vs cows that did not. They suggested that this may be due to increased skin perfusion, which enables greater dissipation of heat from the cow's body. Brown et al. (2015) found that in most instances, daughters conceived during winter produced significantly more milk over their first three lactations than those that conceived in summer. Pinedo and De Vries (2017) also showed in their large retrospective, observational study that cows conceived in winter had better subsequent reproductive performance, lactation performance and survival than cows conceived in summer.

Skibiel et al. (2018a) compared the morphology of mammary gland tissue of daughters (F_1s) that were either heat stressed or kept cool in-utero during late gestation (i.e. their dams' entire dry period) and were then reared as a single cohort and monitored through their first lactation. Biopsies were collected at 21 and 42 days in milk. Skibiel and co-workers found that daughters (F_1s) heat stressed in-utero had a similar number of alveoli to daughters (F_1s) kept cool in-utero, but they were 46% smaller in area and therefore lower in capacity for milk storage and synthesis. Daughters (F_1s) heat stressed in-utero also had a higher proportion of connective tissue in their mammary glands at 21 and 42 DIM.

A study by Dado-Senn et al. (2021) of the impacts of in-utero heat stress on early-life growth and organ development included a comparison of mammary gland tissue at birth and at weaning of daughters (F_1) born to dams that were either heat stressed or kept cool in-utero during late gestation (i.e. through the entire dry period) and then reared as a single cohort. Dado-Senn and co-workers found that the mammary mass, including the fat pad, was reduced in heifers heat stressed in-utero, as reported previously at weaning in heifers on a limited plane of nutrition from birth. Furthermore, they found that heifers heat-stressed in-utero had fewer ductal structures in their mammary parenchyma at birth, which are essential for later development of secretory tissue (i.e. the number of mammary epithelial cells and their secretory activity) and therefore milk production during lactation.

Survival

Daughters (F_1) heat stressed in-utero have increased disease risk and reduced survival (Monteiro et al., 2016b; Pinedo and De Vries, 2017; Laporta et al., 2020; Toledo et al., 2020). Laporta et al. (2020) found that they were less likely to survive to their first calving (71% vs 82%) and that their total lifespan was 356 days less (1,113 days vs 1,469 days), with their times in the milking herd reduced by 4.9 months (20.9 months vs 25.8 months). (Figure 7 and Tables 9 and 10).

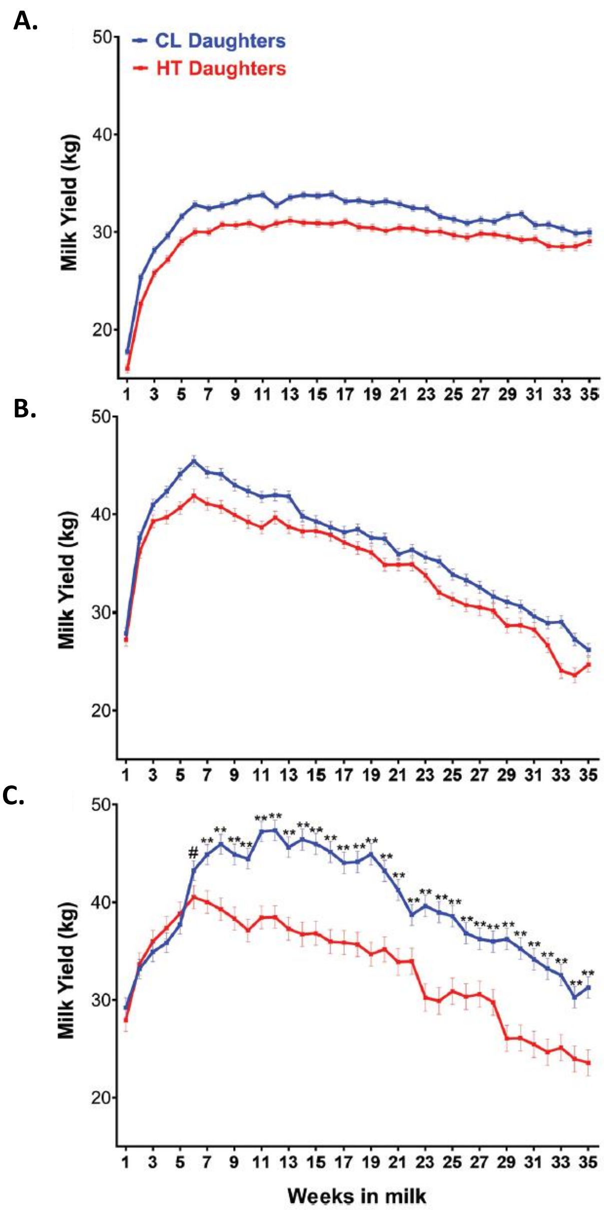

Figure 6. Milk yields of daughters (F_1s) born to cows under cooling (CL; access to fans, shade, and water soakers) or heat stress (HT; only access to shade) during late gestation (~46 days) in A. first lactation, B. second lactation, C. third lactation. All daughters had access to active cooling (shade of a freestall barn, fans, and water soakers) during their first, second, and third lactations. (Copied from Laporta et al., 2020).

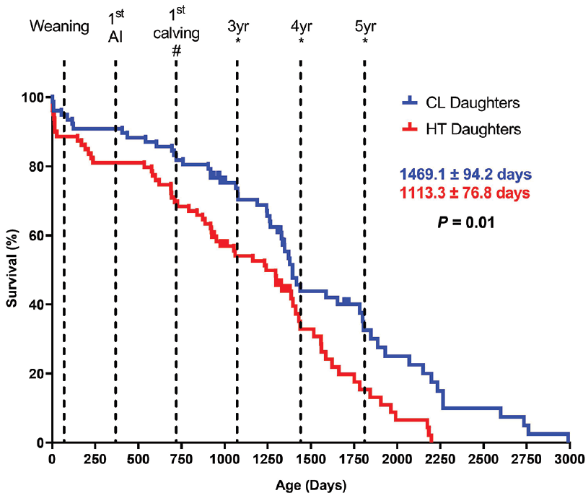

Figure 7. Survival of daughters (F_1s) born to cows under cooling (CL; access to fans, shade, and water soakers) or heat stress (HT; only access to shade) during late gestation (~46 days). (Copied from Laporta et al., 2020).

Published research studies exploring impacts of in-utero heat stress in late gestation on gestation length, birth weight and weaning weight of daughters (F_1s) are summarised in Table 6. Published research studies exploring impacts of in-utero heat stress in late gestation on reproductive performance of F_1s are summarised in Tables 7 and 8. Published research studies exploring impacts of in-utero heat stress in late gestation on lactation performance and survival of F_1s are summarised in Tables 9 and 10.

Table 6. Prospective, cohort studies exploring impacts of in-utero heat stress in late gestation on gestation length, birth weight and weaning weight of daughters (F_1s).

Reference	Study location and period	Facility	Cows	Climatic conditions	Cooling system (if used)	Gestation length (days)		Birth weight (kg)		Weaning weight (kg)		Weight at 12 months (kg)	
						HOT	COOL	HOT	COOL	HOT	COOL	HOT	COOL
Collier et al., 1982	Arizona, USA. 1978	Pens with or without shade	31 Holstein cows and heifers		Hot = No shade Cool = Shade	281	281	36.6	39.7				
Wolfenson et al., 1988	Israel. 1986	Open sided shade shed	85 Israeli Holstein cows		Hot = Shade only Cool = Shade plus sprinklers and fans from 6:00 to 18:00			40.6	43.2				
Avendano-Reyes et al., 2006 (Expt. 1)	NW Mexico. 2000	Partially shaded pens TMR	38 Holstein cows	Avg. max. THI: May: 89.5 June: 93.8 July: 94.3 Aug: 96.9 Sep: 91.2	Hot = Shade only Cool = Shade plus soaking with hose for 2 min at 11:30 and 14:30			30.1	32.4				
Avendano-Reyes et al., 2006 (Expt. 2)	NW Mexico. 2001-2003	Partially shaded pens TMR	52 Holstein cows	Avg. max. THI: May: 88.4, 88.7, 90.0 June: 92.7, 93.6, 94.0 July: 94.3, 94.8, 94.6 Aug: 95.0, 94.8, 95.2 Sep: 92.4, 92.0, 92.6	Hot = Shade only Cool = Fans and misting from 10:00 to 18:00 daily			33.7	37.9				
Adin et al., 2009	Israel. 2009	Loose housing facility	72 cows. Breed not specified		Hot = Shade only Cool = Shade plus fans and sprinklers	274	278	40.8	43.6				
Do Amaral et al., 2009	Florida, USA. 2007	Freestall	16 Holstein cows		Hot = Shade only Cool = Shade plus fans and sprinklers			31	44				
Do Amaral et al., 2011	Florida, USA. 2008	Freestall	16 Holstein cows		Hot = Shade only Cool = Shade plus fans and sprinklers			39.5	44.5				
Tao et al., 2011	Florida, USA. May-Nov 2009	Freestall	29 cows	THI: 76.6 THI: 76.6	Hot = Shade only Cool = Shade plus fans and sprinklers			41.6	46.5				

Reference	Study location and period	Facility	Cows	Climatic conditions	Cooling system (if used)	Gestation length (days)		Birth weight (kg)		Weaning weight (kg)		Weight at 12 months (kg)	
						HOT	COOL	HOT	COOL	HOT	COOL	HOT	COOL
Tao et al., 2012a	Florida, USA 2010	Freestall	32 Holstein cows	Mean THI: 78.3	Hot = Shade only Cool = Shade plus fans and sprinklers	272	276						
Tao et al., 2012b*	Florida, USA 2010	Freestall	21 Holstein cows		Hot = Shade only Cool = Shade plus fans and sprinklers			36.5	42.5	65.9	78.9		
Tao et al., 2014	Florida, USA 2012	Freestall	20 Holstein cows	Mean THI: 75.2 and 74.4	Hot = Shade only Cool = Shade plus fans and sprinklers	277	279	40.2	45.0	68.2ns	71.3ns		
Monteiro et al., 2014*	Florida, USA 2011	Freestall	20 Holstein cows		Hot = Shade only Cool = Shade plus fans and sprinklers	272	275	38.3	43.1	67	76		
Karimi et al., 2015	Iran 2012	Freestall	20 Holstein cows	Mean THI: 69.7	Hot = Shade only Cool = Shade plus fans and sprinklers from 07:00 to 19:00 daily	277	278	40.7	43.4				
Monteiro et al., 2016a	Florida, USA 2014	Freestall	20 Holstein cows		Hot = Shade only Cool = Shade plus fans and sprinklers	276	276	35.7ns	36.3ns	61.4	71.7		
Monteiro et al., 2016b	Florida, USA 2007 to 2011 (5 experiments)	Freestall			Hot = Shade only Cool = Shade plus fans and sprinklers			39.1	44.8			325	345
Guo at al, 2016	Florida, USA 2014	Freestall	38 Holstein cows	Mean THI: 78	Hot = Shade only Cool = Shade plus fans			39.8	42.6				
Laporta et al., 2017	Florida, USA 2015	Freestall	60 Holstein cows			275	279	39.0	41.9	75.3	78.9		
Skibiel et al., 2017	Florida, USA 2015	Freestall	60 Holstein cows	Mean THI: 78 THI: Always >68 day and night	Hot = Shade only Cool = Shade plus fans and sprinklers	273	275	38.8	42.3	68.3	73.6		
Akbarinejad et al., 2017	Iran 2001-2015	?	1 Holstein herd	Unexposed HS in early gest'n HS in mid gest'n HS in late gest'n				 41.2 41.3 39.6	41.9				

Reference	Study location and period	Facility	Cows	Climatic conditions	Cooling system (if used)	Gestation length (days)		Birth weight (kg)		Weaning weight (kg)		Weight at 12 months (kg)	
						HOT	COOL	HOT	COOL	HOT	COOL	HOT	COOL
Skibiel et al., 2018a	Florida, USA 2015	Freestall	35 Holstein first lactation heifers	Mean THI: 78 THI: Always >68 day and night	Hot = Shade only Cool = Shade plus fans and sprinklers	276	275ns	37.6	39.5ns				
Fabris et al., 2019	Florida, USA 2016	Freestall	60 Holstein cows	THI: Always >68 day and night	Hot = Shade only Cool = Shade plus fans and sprinklers	275	277	38.3	42.6				
Dado-Senn et al., 2020a	Florida, USA 2018	Freestall	60 Holstein cows	THI: Always >68 day and night	Hot = Shade only Cool = Shade plus fans and sprinklers	275	276	40.1	42.5	75.0	81.6		
Makiabadi et al., 2023	Isfahan, Iran 2009 - 2020	Not specified	1 Holstein herd 3 stages of gestation	HS in early gest'n only HS in early & mid gest'n HS in mid & late gest'n HS in late gest'n only	-			39.5 39.4 38.4 38.3					

* Heifer calves only

.[ns] Non significant difference

Table 7. Retrospective, observational studies exploring impacts of in-utero heat stress on reproductive performance of daughters (F_1s).

Reference	Study location and period	Sample population	Comparison	Groups	Days to first service	Services per conception	Conception rate (%)	Calving to conception (days)
Akbarinejad et al., 2017	Tehran province, Iran 2001-2015	1 Holstein herd	3 stages of gestation over 4 lactations	Unexposed HS in early gest'n HS in mid gest'n HS in late gest'n	69.5 83.4 92.9 86.7	2.05 2.36 2.57 2.74	41.9 (FSCR) 35.8 32.1 25.5	109.4 129.8 150.0 146.3
Pinedo and De Vries, 2017	Florida, USA, 2000 - 2012	152 Holstein herds	Season of conception: Summer (Jul-Sep. avg THI: 91) = Hot Winter (Dec-Feb. avg THI: 63) = Cool	Parity 1 Parity 2 Parity 3	Hot Cool 168 161 145 140 129 129			Hot Cool 183 176 179 176 170 169
Laporta et al., 2020	Florida, USA, 2008 - 2018	156 cows	Dams heat stressed (HS) vs cooled (CL) for 46 days pre-calving	Maiden heifer First Lactation Second lactation Third lactation			Conception risk Hot Cool 0.44 0.43 0.4 0.31^{ns} 0.21 0.31^{ns} 0.27 0.15^{ns}	
Recce et al., 2021	Santa Fe and Cordoba provinces, Argentina, 2000-2013	43 Holstein herds	Number of high THI cycles (≥3days with THI≥72) in first stage of gestation	1 high THI cycles 2 high THI cycles >2 high THI cycles	+1.7 days if > 2 high THI cycles			+1 day per high THI cycle
Makiabadi et al., 2023	Isfahan, Iran 2009 - 2020	1 Holstein herd	3 stages of gestation	HS in early gest'n only HS in early & mid gest'n HS in mid & late gest'n HS in late gest'n only	63.1 64.2 64.2 62.8	2.31 2.20 2.26 2.34	46.2 (FSCR) 44.0 42.4 41.0	109.7 106.8 109.5 110.7

.^{ns} Non significant difference

Table 8. Prospective, cohort studies exploring impacts of in-utero heat stress on reproductive performance of daughters (F_1s).

Reference	Study location and period	Sample population	Comparison	Groups	Days to first service	Services per conception	Conception rate (%)	Calving to conception (days)
Monteiro et al., 2016b	Florida, USA. 2007 to 2011 (5 experiments)	Holstein cows	Last 46 days of gestation	Hot = Shade only Cool = Shade plus fans and sprinklers		2.6^{ns} 2.3^{ns}		
Succa et al., 2020	Sardinia, Italy. 2015-2016	4 H-F herds	Heat stress at different stages of gestation: Early (conceived in summer. Avg THI: 69) Late (conceived in winter. Avg THI: 55)	Early gestation Late gestation		1.48 1.54		

.^{ns} Non significant difference

Table 9. Retrospective, observational studies exploring impacts of in-utero heat stress on lactation performance and survival of daughters (F_1s).

Reference	Study location and period	Sample population	Comparison	Groups of F_1s	Milk yield (kg)		Survival (%)	
					HOT	COOL	HOT	COOL
Brown et al., 2015	Georgia, Florida, Texas, USA. 2014	75,465 cows that had completed 3 lactations	Season of conception: Summer (Jun-Aug) Winter (Dec-Feb)	Summer conceived Winter conceived	+82-399kg/lactation (305 DIM)			
Brown et al., 2016	Georgia, Florida, Texas, USA. 2014	235,805 primiparous cows	Season of conception: Summer (Jun-Aug) Winter (Dec-Feb)	Summer conceived Winter conceived	+172-423kg/lactation (305 DIM)			
Pinedo and De Vries, 2017	Florida, USA. 2000 - 2012	152 Holstein herds	Season of conception: Summer (Jul-Sep. avg THI: 91) Winter (Dec-Feb. avg THI: 63)	Parity 1 Parity 2 Parity 3	7,410 7,263 7,525 (305d)	6,983 7,447 7,660	Odds ratio of survival to second calving Summer: Reference	Winter: 1.15
Laporta et al., 2020	Florida, USA. 2018 - 2018	156 cows	Heat stressed (HS) vs cooled (CL) for 46 days pre-calving	First Lactation Second lactation Third lactation	29.2 34.3 33.1	31.4 36.7 39.6	Lifespan 1,113 days	1,469 days
Toledo et al., 2020	Florida, USA. 2008 - 2010	1 Holstein herd Pasture with min. shade and pivot soakers in dry period	Last 60 days of gestation: Hot (May-Jul avg THI: 75) Cool (Nov-Jan. avg THI: 56)	To parity 1 To parity 2 To parity 3	8,762 (305-days)	8,889[ns]	86.0 77.0 62.6	86.1[ns] 77.1[ns] 56.9

.[ns] Non significant difference

Table 10. Prospective, cohort studies exploring impacts of in-utero heat stress on lactation performance and survival of daughters (F_1s).

Reference	Study location and period	Sample population	Comparison	Groups of F_1s	Milk yield (kg)		Survival (%)	
					HOT	COOL	HOT	COOL
Monteiro et al., 2016b	Florida, USA. 2007 to 2011 (5 experiments)	Holstein cows Freestall barn TMR	Last 46 days of gestation in summer with shade only vs shade, sprinklers and fans	Hot Cool	26.9* (avg per day)	32.0*	65.9^	85.4^
Skibiel et al., 2018a	Florida, USA. 2014 – 2017	Holstein cows Freestall barn TMR	Last 46 days of gestation in summer with shade only vs shade, sprinklers and fans	Hot Cool	30.2*	31.5*		

* = first lactation
^= to end of first lactation

Impacts on grand-daughters and grand grand-daughters (F_2 and F_3 generations)

Maternal heat stress in late gestation (dry period) has been found to negatively impact not only daughters (F_1) but also grand-daughters (F_2) and grand grand-daughters (F_3). Laporta et al. (2020) found that grand-daughters (F_2) generated from an F_1 heat stressed oocyte also had lower milk yields in their first 3 lactations compared to grand-daughters generated from an F_1 oocyte kept cool during late gestation. (Table X). The total lifespan of grand-daughters (F_2) generated from an F_1 heat stressed oocyte was shorter than that of grand-daughters (F_2) (980 days vs 1,349 days); however, the difference was not statistically significant. The lower lactation performance of grand-daughters (F_2) of cows heat stressed in late gestation may be partly due to the stunted development of their mammary glands' epithelial microstructure and cellular turnover, and reduced oestrogen receptor α which is necessary for ductal structures in the mammary gland, despite there being no macrostructural differences evident pre-weaning (Larsen and Laporta, 2024). The microstructural changes were similar to those found in their mothers (F_1) by Dado-Senn et al. (2022). It is interesting that the grand-daughters (F_2) of cows heat stressed in late gestation did not exhibit reduced birth weight and stature, as observed in their mothers (F_1), and had growth rates to breeding that were very similar to those of the grand-daughters (F_2) of cows kept cool in late gestation (Larsen and Laporta, 2024).

Two retrospective, observational studies (Weller et al., 2021; Macciotta et al., 2023) looked for associations between dams (F_0) and grand grand-daughters (F_3) which may indicate transgenerational epigenetic inheritance in the grand-daughters (F_3) through the germ line had occurred from dams (F_0) heat stressed in late gestation. Weller and coworkers analysed large Israeli Holstein datasets to assess the impact of month of birth (as an indicator of the level of heat stress during gestation) on milk production of 4 generations and found that the milk production levels of F_2 and F_3 animals were associated with the birth month, season of pregnancy and THI values experienced by F_0 pregnant cows. Similarly, Macciotta and coworkers analysed data from commercial Italian Simmentals herds in NE Italy and found that F_0 and F_1 gestations in winter and spring positively affected F_3 milk production, while F_0 and F_1 gestations during summer and autumn had negative impacts on F_3 milk production. The studies by Macciotta et al. (2023) and Weller et al. (2021) therefore provide evidence that inter-generational effects of maternal heat stress in late gestation may extend to the fourth generation (F_3) through trans-generational epigenetic inheritance, as these effects cannot be explained by genetics or direct environmental effects.

Published research studies exploring impacts of in-utero heat stress on lactation performance and survival of daughters and grand-daughters (F_1s and F_2s) are summarised in Table 11.

Table 11. Prospective, cohort studies exploring impacts of in-utero heat stress on lactation performance and survival of daughters and grand-daughters (F_1s and F_2s).

Reference	Study location and period	Sample population	Comparison	Groups	Milk yield (kg)		Survival (%)	
					HOT	COOL	HOT	COOL
Laporta et al., 2020	Florida, USA. 2008 - 2018	156 cows	Dams heat stressed (HS) vs cooled (CL) for 46 days pre-calving	**Daughters (F_1):**			Lifespan	
				First Lactation	29.2	31.4		
				Second lactation	34.3	36.7	1,113 days	1,469 days
				Third lactation	33.1	39.6		
				Grand-daughters (F_2):				
				First Lactation	29.9	31.2		
				Second lactation	27.8	39.8		
				Third lactation	33.7	38.6		

.[ns] Non significant difference

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