Chapter

Thermal Manipulation: Embryonic Development, Hatchability, and Hatching Quality of Broiler Chicks

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Abstract

Here, PRISMA guidelines were utilized to systematically evaluate the publications reporting the effect of thermal manipulation during embryogenesis on incubation performance, hatchability, and hatching quality of broiler chicks. The search and selection of eligible publications was through databases web of science, PubMed, and Scopus. Publications written in English between 2015 and September 2021 were considered. It is evidenced that during TM, key considerations include duration and strength of TM besides stage of embryonic development. The moderate elevation in incubation temperature (38.5–39.5°C) intermittently (3–18 h/d) between E07 and E18 improves the chick's thermoregulation capacity and reduces any adverse effect of TM on hatchability, and chick quality (e.g., hatch weight and chick length) compared with continuous TM. In addition, high temperature TM (38.5–39.5°C) between E7 and E18 has no significant effect on embryo mortality, hatchability, and chick quality compared to standard incubation temperature (37.8°C). TM above 39.5°C significantly increases and decreases embryo mortality and hatchability, respectively compared with standard incubation temperature. In conclusion, the results of TM studies on embryogenesis, hatchability and hatching quality of broiler chicks are still contradicting, which is a possible limitation for its commercial use.

Keywords: broiler industry, chick quality, epigenetic adaptation, hatchery industry, incubation, thermotolerance acquisition

1. Introduction

In recent decades, the need to increase hatchery efficacy is increasing with demand for quality chicks. Therefore, during incubation, new techniques which are associated with embryo management are increasing with this demand. A possible reason is that the newly developed broiler genotypes have diverged considerably compared to traditional genotypes in terms of the biological, physiological, and biochemical requirements [1]. Thus, manipulation of different incubation conditions

to meet the requirements of modern broiler genotypes is under continuous investigation. Incubation conditions have a significant effect on hatchability, chick quality and post-hatch performance in chicken. In addition, while the first quarter of incubation is critical to chicken embryogenesis [2], the last quarter is very significant to hatch and post hatch performance [3].

Incubation temperature is the most significant incubation condition [4] and there has been an increase in studies regarding thermal manipulation (TM). TM (i.e., increasing or lowering incubation temperature) and broiler chicken embryogenesis has been deeply studied by Collin A, Tzschentke B, Piestun Y, Yahav S, and Halevy O, and the technique enhances chick quality through improved body weight gain, increased expression of genes in the breast muscle, and thermotolerance. Earlier studies laid the foundation for implementation of TM between different days of embryogenesis in addition to key factors such as duration and strength of TM to enhance the chick's ability to cope with environmental challenges of cold and heat stress during post-hatch period [5–10].

In an earlier study, Yahav et al. [11] reported that TM at 39.5°C for 3 hours (h)/day (d) from embryonic age (E) E11–E16 improves the chicks' thermotolerance acquisition. A similar effect was confirmed by [12–16] with TM at 39.5°C for 12 h/d from E7 to E16. Recent studies have also confirmed a long-lasting effect on thermotolerance acquisition in chicks at hatch or 1-day-old chicks, for instance, Piestun et al. [17] and David et al. [18] both with TM at 39.5°C for 12 h/d from E7 to E16, Al-Zghoul et al. [19] with TM at 38.5, 39, 39.5 and 40°C for 18 h/d from E12 to E18 and Al-Zghoul et al. [20] with TM at 39°C for 18 h/d from E10 to E18.

The effect of TM on hatchability in several studies has been reported to differ extensively, with hatchability after TM being higher [11, 21, 22], reduced [9, 12, 13, 23, 24], and not affected [25, 26]. Also, studies from different researchers have shown contradicting results on chick quality parameters, and hatch or chick weight after TM exposure was increased [22, 23, 27], decreased [28], and not affected [21, 25, 29].

Production of optimal quality chicks depends on controlling incubation conditions and understanding the insights into the complex interaction among them. Although various studies have reported the benefits of TM, results are still contradicting and depend on timing, duration, and level of TM. With this background, we systematically reviewed the recent literature regarding the effect of thermal manipulation on embryonic development, hatchability, and hatching quality of broiler chicks.

2. Search strategy and selection of publications

The search for potentially eligible publications was conducted using electronic databases Web of science, PubMed, and Scopus. The eligibility was based on the title, abstract, and keywords, and only included articles published in English language. Filters were applied in terms of publication date (2015-01-01 to 2021-09-30 in Web of Science, PubMed, and Scopus).

The developed strings used in the literature search from three databases included: (thermal OR temperature) AND (manipulation) AND (incubation OR embryogenesis OR embryo development) AND (broiler OR chickens OR poultry).

The identified studies from each database were exported to Microsoft Excel workbook to document bibliographic information (author names, title, and publication year). The same software was used to manage and exclude duplicate studies.

Thereafter, the reviewers examined the titles and abstracts, followed by examining the full version of the selected potential studies. At this point, each study was read to extract the aimed set of information. Therefore, the eligibility criteria for the final study selection included:

1. Animal materials are broiler chickens.

2. Study that entirely manipulated incubation temperatures (i.e., studies involving eggshell temperature manipulation or that combined incubation temperatures with other strategies were excluded).

3. Study reports TM age and a control group.

4. Study reports at least one of the following: hatchability, hatch rate, embryo mortality rate, body weight at hatch, body temperature at hatch, and chick quality.

The initial literature search identified a total of 229 articles (125 in Web of Science, 59 in PubMed, and 45 in Scopus database). After the elimination of 89 duplicate articles, 140 studies were available for analysis. Other 72 studies were excluded after evaluating the titles, thus a total of 68 articles were eligible for abstract screening. At this point, 30 studies were excluded because they did not meet the defined criteria, which resulted in 38 studies being available for full-text evaluation. From this, 7 studies were removed based on the previously defined criteria. Finally, 31 studies were selected and included in the definitive systematic review as shown in **Figure 1**.

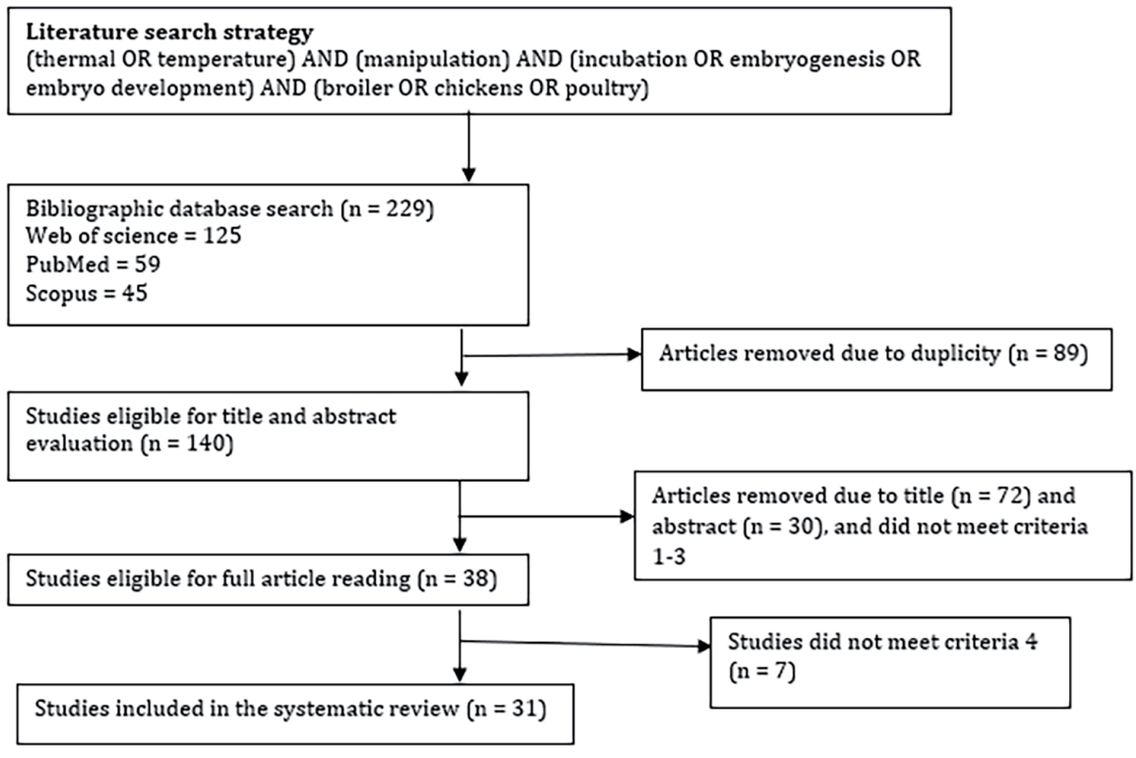

Figure 1.
A flowchart of the summarized study search procedure.

3. General characteristics of the studies included in the systematic review

Table 1 summarizes the information that was extracted from the final selected studies. The studies in the systematic review were published between 2015 and 2021, and 31 papers were finally included. Intermittent TM profile (3–18 h/d) was used in most studies (24 papers, 77%) compared with continuous (24 h/d) (6 papers, 19%),

Reference	Control group temperature profile	TM profile	TM age/ embryonic day (E)	Outcome
Piestun et al. [17]	37.8°C	Intermittent (12 hours (h)), continuous (24 h)/day (d) at 39.5 °C	E7–E16	There was no negative effect of intermittent TM on embryo development. Continuous TM negatively affected embryo weight, and significantly decreased the ratio of embryo weight to egg weight from E16 to E21.
Al-Zghoul et al. [19]	37.8°C	39°C for 9, 12, and 18 h/d	E12–E18	TM significantly reduced hatchability compared to control.
Al-Zghoul et al. [30]	37.8°C	39°C for 9, 12, or 18 h/d	E12–E18	1-d-old chick body temperature was higher in 9 h TM than the other TM and control groups.
Wilsterman et al. [26]	37.5°C	38.6°C	E0–E5, E5–E18	They found no differences in hatchability and hatch weight among the groups.
Rajkumar et al. [31]	37.5°C	39.5°C for 3 h/d	E16–E18	TM did not have a significant effect on hatchability and hatch weight.
Janisch et al. [32]	37.8°C	High (38.8°C) and low (36.8°C)	E7–E10, E10–E13	Low TM resulted in significant increase in hatch weight compared with high TM and the control group.
Krischek et al. [33]	37.8°C	High (38.8°C) and low (36.8°C)	E7 and E10, E10 and E13	Low TM significantly decreased embryo weights (body, liver, heart) compared to high TM and control, which were similar at some level.
Aminoroaya et al. [34]	37.6°C	39°C for 3 h/d	E12–E14, E15–E17	TM did not significantly affect hatch weight and there was no significant difference among the groups in hatchability.
Elmehdawi et al. [35]	37.4°C	38.4°C	E18–E20	TM did not negatively affect hatchability, chick weight, chick length, rectal temperature, and chick quality score compared to control.

Reference	Control group temperature profile	TM profile	TM age/ embryonic day (E)	Outcome
Almeida et al. [36]	37.5°C at 60% RH	Low (36°C), or high (39°C) at 60% RH	E13–E21	Differences between control and high TM were not significant for incubation period but it was longer in cold TM treatment. Differences between control and low TM treatment for hatchability were not significant but it increased in high TM group.
Al-Zghoul et al. [37]	37.8°C	39°C for 9, 12, and 18 h	E12–E18	TM slightly increased embryonic body weight in comparison to control on E18. No significant difference between TM groups was observed from E12 to E16.
Narinç et al. [38]	37.8°C at 55% RH	39.6 °C at 60% RH for 6 h/d	E0–E8, E10–E18	TM significantly lowered hatchability and chick quality but lowest in late TM treatments compared with control. No statistically significant difference was observed between TM and control groups for hatch weight.
Morita et al. [39]	37.5°C	Low 36°C and high 39°C	E13–E21	TM did not have a significant effect on hatch weight compared with control. Hatchability was increased in high TM but lower and similar in low TM and control treatments.
Al-Rukibat et al. [40]	37.8°C	38.5°C and 40°C	6 h at E16, 9 h at E17, and 12 h at E18	TM did not influence hatchability.
Zaboli et al. [41]	37.8°C	39.5°C for 12 h/d	E7–E16	TM reduced hatchability by 4%, reduced hatch weight, and delayed hatch time (6 h later) compared with control.
Al-Zghoul [42]	37.8°C	38.5, 39, 39.5, and 40°C for 18 h/d	E12–E18	1-d-old chick body temperature was higher with TM at 38.5°C than the other TM and control groups.
Vinoth et al. [43]	37.5°C	40.5°C for 3 h/d	E15–E17	TM had no significant effect on hatchability. 1-d-old chick weight did not differ between the groups.
Al-Zghoul et al. [44]	37.8°C	39.5°C for 18 h/d	E10–E18	There was no difference between the groups in hatchability, but hatch weight was significantly reduced in TM group compared with control.

Reference	Control group temperature profile	TM profile	TM age/ embryonic day (E)	Outcome
Al-Zghoul and El-Bahr [45]	37.8°C	38.5, 39, 39.5, and 40°C for 18 h/d at 56% RH	E12–E18	While TM at 38.5 and 39°C did not influence the hatchability, TM 39.5 and 40°C lowered hatchability compared with control group. Similar embryonic weights were found for all the groups.
Dalab and Ali [46]	37.8°C	39°C for 18 h/d	E7–E11, E11–E15, E15–E18, E7–E18	TM significantly influenced the hatchability. Early TM significantly improved hatchability versus control. Late and long TM adversely affected hatchability and chick quality compared with control.
David et al. [18]	37.8°C	39.5°C for 12 h/d	E7–E16	Significantly decreased hatch body temperature was found in TM chickens.
Saleh and Al-Zghoul [47]	37.8°C	39°C for 18 h/d	E10–E18	TM significantly reduced hatchability but did not significantly affect body weight of 1-d-old chicks compared to control.
Amjadian and Shahir [48]	37.8°C	39.5°C for 3 h/d	E11–E16	There was no significant effect of TM on hatchability and embryonic mortality and TM did not influence chick body weight and hatch body temperature.
Saleh et al. [49]	37.8°C	39°C for 18 h/d	E10–E18	No significant difference was identified in embryonic mortality, hatchability, and hatch weight between the control and TM treatment. TM led to significantly decreased hatch body temperature.
Tarkhan et al. [50]	37.8°C	39°C for 18 h/d	E10–E18	TM significantly reduced hatchability and body temperature in 1-d-old chicks compared with control but no significant increase in weight was found in 1-d-old chicks between the groups.
Nyuiadzi et al. [51]	37.6°C	37.6°C at 56%, and interruption of 15°C for 30 min at 81% RH.	E18–E19	No significant effect of TM on hatchability was observed. At hatching, body temperature was higher in TM than in control chicks, but hatch weight was not affected by TM.

Reference	Control group temperature profile	TM profile	TM age/ embryonic day (E)	Outcome
Basaki et al. [52]	37.5°C	Low (33°C) and high (41°C) for 3 h/d	E15–E17	Survival rate, embryos with deformities, hatchability, and hatch weight were not significantly different between groups.
Rocha et al. [2]	37.5°C	Low (36°C) and high (39°C) for 6 h/d	E0–E5	Hatch weight in low TM chicks was higher than control and high TM.
Khaleel et al. [53]	37.8°C	36 and 39°C for 18 h/d	E7–E16	TM did not significantly affect hatchability.
Brannan et al. [54]	37.5°C	39.5°C for 12 h/d	E7–E16	TM increased and decreased embryo mortality and hatchability, respectively but had no influence on hatch weight.
Yalcin et al. [55]	37.8°C	38.8°C for 6 h/d	E10–E14	TM did not affect relative embryo weight on E19 and hatchability but found strain differences in hatch weight.

Table 1.
Overview of thermal manipulation studies during incubation of broiler chicken eggs.

and a combination of both intermittent and continuous in only one study [17], in which no depressing effect of intermittent (12 h/d) TM between E7 and E16 on embryogenesis was reported, however, continuous (24 h/d) reduced embryo weight from E16 to E21.

Among the 24 intermittent TM studies, 20 articles reported the TM effect on hatchability, of which 65% found no significant effect, 30% being reduced, and a comparative study by Dalab and Ali [46] reported increased and decreased hatchability at different embryonic age. Meanwhile, embryo and/or hatch weight and chick quality were reported in 18 articles, of which 12 (67%) found no significant effect, three studies reported increased [2, 38, 50], and three reported reduced effect of TM on embryo and/or hatch weight and chick quality [42, 45, 46].

Embryo mortality was reported in four of 24 intermittent TM studies, of which three studies observed no significant difference in embryo mortality between intermittent TM and control groups [48, 49, 52]. However, Brannan et al. [54] identified increased embryo mortality in intermittent TM groups compared with control group.

Hatch or chick body temperature was reported in eight of 24 intermittent TM studies, which included no significant effect [48, 52], increased [30, 42, 51], and reduced [18, 49, 50].

From the six continuous TM studies, the application increased [39], and had no significant effect on hatchability [26, 35, 36] compared with control groups. Moreover, continuous TM increased [32], decreased [33] and had no significant effect on embryo, chick weight, or chick quality [26, 35, 39]. Furthermore, Elmehdawi et al. [35] reported no negative effect of continuous TM on hatch body temperature compared with control treatment.

In all the studies, the set standard incubation temperature was the control treatment, which was compared to TM treatments. 37.8°C was used as the standard incubation temperature in most studies (20 papers, 65%), followed by 37.5°C (8 papers,

26%). Only Aminoroaya et al. [34], Nyuiadzi et al. [51], and Elmehdawi et al. [35] used 37.6 and 37.4°C, respectively.

While most studies (23 papers, 74%) only used high-temperature TM (i.e., 1–3°C above the set standard incubation temperature), 7 papers were comparative studies of low and high-temperature TM, and only one study used low-temperature TM at 37.6°C but on 18 and 19 d of incubation, embryos were subjected to short cold exposure of 15°C for 30 minutes [51]. The above authors found no significant effect of TM from E18 to E19 on hatchability and hatch weight, but hatch body temperature was elevated compared with control group (37.6°C). In addition, studies involving low-temperature TM, the adjustments varied between 1 and 4.5°C below the set standard incubation temperature.

Three studies compared various high-temperature TM; both 38.5 and 40°C did not have any effect on hatchability [40]. Meanwhile, Al-Zghoul and El-Bahr [44] compared 38.5, 39, 39.5, and 40°C for 18 h/d from E12 to E18 and observed that 38.5 and 39°C did not impact hatchability however, 39.5 and 40°C reduced hatchability compared with control group (37.8°C). The latter TM setup was used by Al-Zghoul [42], who reported increased 1-d-old chick body temperature at 38.5°C compared with other TM and control treatments.

Three studies compared TM duration, which Al-Zghoul et al. [19] and Al-Zghoul et al. [37] identified depressed hatchability and increased embryo body weight on E18, respectively, at 39°C regardless of TM duration (9, 12, or 18 h/d) from E12 to E18. Using similar TM profile to Al-Zghoul et al. [19], Al-Zghoul et al. [37], and Al-Zghoul et al. [45] reported elevated body temperature in 1-d-old chicks at 9 h/d TM duration compared with other TM durations and control (37.8°C) treatment.

Among the seven comparative studies, low-temperature TM resulted in increased hatch weight [2, 32], reduced embryo weights [33], and both low and high-temperatures were not significantly different in hatch weight, embryo mortality, and deformed embryos [52]. Meanwhile, high-temperature TM resulted in higher hatchability [36, 39], and both low and high-temperature treatments did not impact and significantly differ in hatchability [52, 53]. Furthermore, continuous TM was used in most comparative studies [32, 33, 36, 39] compared with intermittent [2, 52, 53].

The main RH used in control and low-temperature TM studies was 56% and, 65% in high-temperature TM studies. In **Table 1**, we only reported RH of four studies (four papers, 14%) that used the different RH protocol from the above.

The embryonic age at the time of TM varied between E7 and E18 in most studies (24 papers, 77%), followed by E18–E20 and E0–E8 (three papers each) and one study by Morita et al. [39] reported the timing of TM from E13 to E21, which resulted in no significant influence on hatch weight but higher hatchability in high-temperature TM than low-temperature treatments.

Only seven studies compared embryo age at the timing of TM; hatchability and hatch weight were not affected by high-temperature TM at E0–E5 and E5–E18 [26], and E12–E14 and E15–E17 [34]. Also, Al-Rukibat et al. [40] showed no effect on hatchability after TM at 38.5 or 40°C for 6 h at E16, 9 h at E17 and 12 h at E18. However, TM at 39°C for 18 h/d at early embryonic age (E7–E11) significantly enhanced hatchability but in late (E11–E18) and long-term (E7–E18) negatively affected hatchability and chick quality compared with control (37.8°C) [46]. Janisch et al. [32] reported significant increase in hatch weight with low-temperature TM between (E7–E10) and (E10–E13) and Krischek et al. [33] found a significant decrease in embryo weights at low-temperature TM at E7–E10 and E10–E13 compared with high-temperature and control treatments (37.8°C). Narinç et al. [38] identified

significantly depressed hatchability and chick quality in late (E10–E18) TM compared with early (E0–E8) and control (37.8°C) treatments however, all treatments were not statistically different in hatch weight.

4. Discussion

This present review used a methodological approach to conduct a comprehensive literature search, which enabled a logical interpretation of the recent results obtained from broiler chicken incubation published studies. Thus, the effects of thermal manipulation on incubation performance, hatchability and hatching quality of broiler chicks could be examined.

4.1 Thermal manipulation and thermotolerance acquistion

The hatchery industry is expected to change dramatically with increasing demand for quality chicks and production efficacy. It is well established that incubation conditions significantly influence incubation and post-hatch performance besides, hatching quality in chickens [4]. During perinatal stage (critical period), incubation conditions may result in persistent variations in the epigenetic programming of different body systems and their roles in chickens [56]. One condition of interest is incubation temperature, which when manipulated by short or long-term may induce epigenetic adaptation thus enhancing development and maturation of particular body systems and their functions, which begins during the early periods of embryonic development [10].

TM is well known for inducing improved thermotolerance acquisition (thermoregulatory functions) in chickens, which is evidenced by reduced body temperature at hatch and during the first days post-hatch. Intermittent manipulation in incubation temperature between different embryonic ages resulted in thermoregulatory functions being boosted; 3 h of 39.5°C/d from E16 to E18 [21], 39.5°C for 12 h/d at E7–E16 [15, 16, 24], and 60 minutes exposure to 15°C at E18–E19 [57]. In our review, the similar effect was confirmed by [49, 50] at 38.5–39.5°C for 18 h/d from E10 to E18 and, David et al. [18] at 39.5°C for 18 h/d from E7 to E16. It's clear that thermotolerance acquisition in broiler chickens can be enhanced by application of TM between E7 to E18, a period that is termed the critical stage and, the ideal embryonic age for TM.

It is scientifically proven that successful TM should be between E7 and E18, a period which enables efficient alternation in threshold stimulus of the regulatory systems during the development and maturing of the thermoregulatory mechanism (hypothalamus-hypophysis-thyroid axis) and the stress control (hypothalamus-hypophysis-adrenal axis) [9, 11, 12, 58]. It is clearly reported that thermotolerance acquisition is improved via reduced plasma triiodothyronine (T_3) concentrations and basal metabolism, accompanied with lowered body temperature [15, 16, 24]. In addition, T_3 is the thyroid hormone of interest in the last week of incubation because it is vital for increasing extra energy requirements during hatching [14].

However, some recent studies have reported that TM increased [30, 51] and had no influence on hatch body temperature [48, 52]. These differences may be associated with the possible elevation or similarity in hormones that regulate metabolism (T_3) and growth (GH) leading to elevated or similar metabolic rate and heat production, accompanied with elevated and similar body temperature in thermal manipulated chickens and both thermal manipulated and control treatments, respectively [36, 39].

4.2 Thermal manipulation and embryo, hatch, or chick weight

Short-term (intermittent) alteration in incubation temperature during varying age of embryogenesis can boost muscle growth and development at hatch and in the first weeks post-hatch (early period (E0–E5) [22]; mid-term (E16–E18) [59]; long-term (E12–E18 and E10–E21) [60]). In the current review, the similar effect was identified with short and long-term TM (36.8°C for 24 h/d from E7 to E13 [32]; 39°C for 9–18 h/d from E10 to E18 [37, 50]; 36.°C for 6 h/d from E10 to E5 [2]), which was indicated by increased embryo, hatch and 1-day-old chick weight. In addition, it is evidenced that TM has significant effect on proliferation and differentiation of satellite cells, and thus growth and development of embryonic and chick muscles [61].

TM at 39.5°C for 12 or 24 h/d from E7 to E16 result in accelerated myoblast proliferation and cell differentiation, which is evidenced by increased myoblast number (25–48%) in the pectoral muscle and increased expression of myogenin in embryonic muscles, respectively [17]. Similarly, Al-Zghoul et al. [37] and Al-Zghoul and El-Bahr [44] found upregulation of MyoD, myogenin, insulin-like growth factor 1 (IGF-1), and growth hormone (GH) after TM at 38.5–39°C for 9–18 h from E12 to E18 in embryos and 1-d-old chicks. Furthermore, a linear increase in embryo breast muscle weight with embryonic age was observed but significantly elevated in the TM-treated embryos compared with controls during the second quarter of embryogenesis. The interpretation of the above findings explains the possible reasons for elevated embryo, hatch and 1-day-old chick weight after TM. However, the ability of myoblasts to proliferate declined in the embryos after TM compared with embryos incubated at 37.8°C in the last quarter of incubation [17]. Furthermore, Piestun et al. [59] reported increased muscle hypertrophy in thermal manipulated embryos at 39.5°C for 3 or 6 h/d from E16 to E18. This was evidenced by upregulation of myogenin, and IGF-1 mRNA expressions in TM embryos compared with control treatment.

Studies by Zaboli et al. [41], Al-Zghoul et al. [45], and Dalab and Ali [46] reported depressed embryo, hatch, or chick weight due to intermittent high-temperature TM, which partially agrees with Piestun et al. [14]. However, Piestun et al. [14] reported that only continuous (24 h) elevation in incubation temperature (39.5°C) from E7 to E16 negatively affected embryo growth and development and hatch weight. Although the above variation could have resulted from differences in factors such as breed or strain, flock age, incubation layout, and embryo age at the time of TM, the contradicting results due to TM length may suggest a strong gap for continuous studies on the length of TM.

In the current review, TM did not influence embryo, hatch, or chick weight in 67% of the intermittent TM studies that reported the above parameter. This result has been attributed to a possible similarity in plasma T3, T4, and GH leading to similar metabolic growth rate and heat production, which result in incubation duration and chick body weight being similar in both thermal manipulated and control treatments [36, 39].

Interestingly, Janisch et al. [32] and Rocha et al. [2] observed increased hatch weight at low-temperature TM compared with high-temperatures. This result may be associated with the variations based on factors such embryo age at TM, strain, and incubation temperature profile. However, it is well established that yolk weight is a critical factor that accounts for 20% of hatch weight [62]. At low incubation temperatures, nutrient metabolic rate, and the embryo's ability to draw liquids from the yolk sac are reduced, which result in increased yolk weights at hatch [63], and consequently, elevated hatch weight.

4.3 Thermal manipulation and hatchability

The effect of TM on hatchability in the present review is contradictive, with 65% of 20 studies that reported hatchability found no significant effect, 30% being reduced, and a comparative study by Dalab and Ali [46] reported increased and decreased hatchability with intermittent TM at different embryonic age. Also, earlier studies regarding TM and hatchability have shown contradicting results, for instance, Yahav et al. [11] and Piestun et al. [22] reported significantly increased hatchability with TM at 39.5°C for 3 h/d from E8 to E10 and 38.1°C for 24 h/d from E0 to E5, respectively. Yahav et al. [29] identified no effect on hatchability at 38.5°C for 3 h/d from E8 to E10. Piestun et al. [24] found decreased hatchability with TM at 39.5°C for 12 h/d from E7 to E16.

It is well documented that hatchability is depressed by overheating embryos however, length, strength, and embryo age at the time of high-temperature TM determine the effects of the application on hatchability [25]. Reduced hatchability has been associated with reduction in corticosterone concentrations at internal pipping after TM at 39°C for 2 h/d from E13 to E17 [64]. Continuous TM at 39.5°C from E7 to E16 depressed embryonic growth and development, which was accompanied by lower hatchability compared with intermittent and control treatments [14]. Low hatchability was associated with reduced development of pipping muscle (musculus complexus) on E18 and E19 day, which muscle is stated to have a significant role during hatching [14].

Meanwhile, embryo mortality rate and incubation duration or hatching time have been associated with hatchability. Brannan et al. [54], for instance, revealed increased embryonic mortalities (mid and late) after TM, which periods of development overlap with the plateau in eggshell temperature during TM at 39.5°C from E7 to E16, consequently, reduced hatchability. In addition, the above authors stated that fluctuating effect of TM on hatchability is associated with harmful levels of incubator temperature on embryo development besides, flock age, genotype, incubation design, etc. Almeida et al. [36] reported longer incubation period at low-temperature TM, which was followed by reduced hatchability compared with standard incubation and high TM.

Furthermore, reduced hatchability is linked to decreased chick quality, which is a well-known indicator for incubation challenges and investigated for assessment of incubation conditions [65]. While Elmehdawi et al. [35] identified no negative effect of high-temperature (38.4°C) TM from E18 to E20 on hatchability and chick quality, Dalab and Ali [46] observed lower hatchability and chick quality after TM at 39°C for 18/h from E15 E7 to E18. Similar to hatchability, the effect of exposure of embryos to low or high temperatures on chick quality is thought to depend on length and level of TM besides the stage of embryo development at the timing of TM [25].

Tzschentke [10] reported that slight increase in incubation temperature is expected to yield no depressing effects of TM in the last stages of embryogenesis, a period in which the development of mechanisms that regulates temperature in peripheral and central nervous systems, besides other body systems and their roles are completed. This could be the possible reason for no significant effect of TM on hatchability in most studies in the current review.

4.4 Thermal manipulation and eggshell temperature

Studies by Morita et al. [39] and Amjadian and Shahir [48] identified that exposure of embryos to high temperatures increased eggshell temperature in comparison to standard incubation temperature. The eggshell temperature reflects embryo body temperature [66]. The air temperature and heat transfer between the egg and the

incubator affect embryo body temperature, however, the correlation between heat production by the embryo and heat loss by the incubator determine the embryo temperature [67, 68]. It is established that the rate of chicken embryo heat production is proportional to increase in embryo development thus embryo body temperature reflects embryo development [69]. This could explain the longer incubation duration for low-temperature TM compared with control and high-treatments observed by Almeida et al. [36] and Morita et al. [39]. Earlier, Willemsen et al. [70] found significantly higher eggshell temperature (41.1°C) in high-temperature (40.6°C) compared with 35.5°C in low-temperature (34.6°C) thermal manipulated embryos, which was significantly reduced in comparison to 38.3°C of control temperature (37.6°C) from E17 to E18. Similarly, Piestun et al. [24] found that eggshell temperature was higher in thermal manipulated eggs at 39.5°C compared with standard incubation (37.8°C), accompanied by elevated hatching process of 6 h earlier. However, between E19 and E21, the eggshell temperature decreased although both the thermal treated and untreated eggs were placed in the same hatcher. Delay in hatching period has been linked to depressed metabolism in embryos after exposure to lower incubation temperatures than the standard [25].

In the current review, 65% of studies used 37.8°C as the standard incubation temperature, which also acted as the control treatment. During TM, any elevation in incubation temperature (above 37.8°C), RH is adjusted to 65% to eliminate excessive water loss from the eggs [14]. In addition, setting RH at 60% from E0 to E21 was thought to reduce the influence of RH on embryogenesis and embryonic mortality [36].

5. Conclusions

Thermal manipulation is an important approach that has been deeply studied due to its role in alleviating the effects of heat stress on broiler chickens. The success of this application depends on duration and strength of exposure in addition to embryo age at the timing of TM. The ideal embryonic stage for TM is between E7 and E18, in which thermoregulatory roles are enhanced. While intermittent TM has no adverse effects on embryonic development, hatchability, and hatching quality of broiler chicks, continuous TM depresses the above parameters. High-temperature (39–39.5°C) TM accelerates hatching time, shortens the incubation period, but has no significant effect on embryoinc development, hatchability and chick quality compared to low TM and incubation at standard temperature (37.8°C). Interestingly, in some studies, TM below 37.8°C was shown to increase chick weight at hatch compared with TM above 37.8°C. Furthermore, there is need for more comparative studies between low and high-temperature TM and the duration of TM because on addition to the available studies being insufficient, their results are also controversial. Additionally, a meta-analysis to provide an insight into contradicting results of TM application is thought of as a sound option. Also, there is need to continue studies on TM to identify the exact duration and intensity of TM and embryonic age to obtain higher hatchability and improved chick quality.

Conflict of interest

The author declares no conflict of interest.

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