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A meta-analysis of the effects of high ambient temperature on growth performance of growing-finishing pigs

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ABSTRACT: High ambient temperature (T) is one of the most important climatic factors influencing pig performance. Increased T occurs sporadically during summer heat waves in temperate climates and year round in tropical climates. Results of published experiments assessing the effects of high T on pig performance are surprisingly variable. Thus, a meta-analysis was performed to aggregate our knowledge and attempt to explain differences in the results across studies on the effect of increased T on ADFI and ADG in growing-finishing pigs. Data for ADFI and ADG were extracted from 86 and 80 trials, respectively, from articles published in scientific journals indexed in PubMed, Science Direct, and from proceedings of scientific meetings through November 2009. Data on ADFI and ADG were analyzed using a linear mixed model that included the linear and the quadratic effects of T and BW, and their interactions as continuous, fixed effects variables, and the trial as a random effect factor (i.e., block). In addition, the effects of housing type (2 levels: individual and group housing) and the year of publication (3 levels: 1970 to 1989, 1990 to 1999, and 2000 to 2009) on the intercept and the linear regression term for T (i.e., the slope) were also tested. Results showed that high T had a curvilinear effect on ADFI and ADG and that this effect was more pronounced in heavier pigs. Across T, ADFI was less when pigs were group-housed. The intercept and the regression coefficient (slope) for T were significantly affected by the year of publication. The effect of increased T was greater in more contemporary works, suggesting that modern genotypes could be more sensitive to heat stress than older genotypes of lesser growth potential. In conclusion, pig performance decreases at an accelerating rate as T is increased. The large between-study variability on the effects of high T on pig performance is partially explained by differences in pig BW and to a lesser extent by the year the study was published.

Key words: feed intake, growing pig, growth, meta-analysis, temperature

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INTRODUCTION

According to Food and Agriculture Organization statistics, more than 50% of world pig production is currently occurring in tropical or subtropical regions (Rosegrant et al., 2001). Despite many challenges faced by the pig industry in these regions, it is expected that pig production in developing countries will sustain future growth (Delgado et al., 1999). Heat stress is a major source of production losses in pig production. For example, the economic losses sustained by the US pork industry from heat stress were estimated at about $300 million per year (St-Pierre et al., 2003). If the predictions of global climate change and the associated projected rise of ambient temperature (**T**) materialize (IPCC, 2007), the heat-stress-related problems in livestock production will increase in the future.

Because of their low capacity for dissipating body heat, pigs rely more on reducing metabolic heat production to maintain a constant body temperature in hot conditions than other domesticated species. The reduction in voluntary feed intake in heat-stressed pigs is considered as the main adaptation to reducing heat production. This reduced feed intake has a direct negative impact on growth performance. Many studies have been published on the effect of high T on the performance of pigs. In a qualitative review, Le Dividich et al. (1998) reported that change in feed consumption varied from 40 to 80 g/d per degree Celsius between 20 and 30°C. This large variability across studies could be explained by differences in animal characteristics (breed, BW, physiological status, sex), environmental conditions (housing, feed composition, management, sanitary status), other environmental factors (i.e., relative humidity) and experimental designs (number of

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pigs, number of temperature treatments, duration of exposure), or a combination of these variables. In practice, all these factors cannot be simultaneously studied within a single experiment. Thus, there is a need to summarize research findings across all the published studies to give a more accurate estimation of the magnitude of the effects of heat stress on pig performance over a large range of environmental and breeding situations.

The objectives of this study are to 1) quantitatively assess the effect of increased T on pig performance, and 2) identify factors modulating the magnitude of the identified response functions. The meta-analysis presented herein focuses entirely on growing-finishing pigs (i.e., greater than 10 kg of initial BW).

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because no animals were used.

Database Description

A database containing data on animal and housing characteristics, dietary composition, ADFI, and ADG in growing-finishing pigs under thermal stress was compiled from 71 published papers in scientific journals indexed in PubMed, Science Direct, and from proceedings of scientific meetings that occurred before December 2009. To be included in the final database, studies had to meet the following criteria: 1) research methods (housing, feeding management) were adequately described, 2) growing-finishing pigs that had initial mean BW greater than 10 kg, 3) animals had free access to feed and water during the experiment, 4) experiments were conducted under controlled T conditions, 5) dietary CP was greater than 12%, 6) the duration of the experiment exceeded 7 d, and 7) at least 2 temperature treatments were used in the experiment. Forty-seven studies reporting 86 trials with 202 temperature treatment means met the criteria for ADFI. The corresponding values for ADG were 43 studies, 80 trials, and 182 temperature means. The main variables in the database regarding animal and housing characteristics, diet composition, and animal responses are reported in Table 1. The response (dependent) variables were ADFI (g/d or g/kg $BW^{0.60}$ per d), ADG (g/d), and feed conversion ratio (**FCR**, kilograms of feed/kilogram of BW gain). Values for all variables could not be determined for all observations. Therefore, the number of observations used for statistical analyses differed between response variables. In some instances, some records were incomplete or not reported uniformly, requiring calculation from the reported data. When a study did not report the outcome for all variables and when it was not possible to calculate a value from the reported data, missing values were considered as missing at random. When the ME content of a diet was not reported, it was estimated using the DE content of the diets, the ME/DE ratios calculated from INRA feed composition tables (Sauvant et al., 2002), and the description of the feedstuffs used in the experimental diets.

Statistical Analyses

Data were analyzed according to St-Pierre (2001), which takes into account the random effect of the study and its possible interaction with fixed effect factors. The MIXED procedure (SAS Inst. Inc., Cary, NC) was used to solve the following base model:

$$Y_{ij} = b_0 + b_1T + b_2T^2 + s_i + a_iT + e_{ij}, \quad [1]$$

where Y_{ij} is the observed outcome for the dependent variable Y in the ith experiment at temperature level T, i = 1, ...n (n = 86 or 80, depending on the dependent variable), b_0 is the overall intercept, T is the ambient temperature (°C), b_1 and b_2 are the regression coefficients for T and T^2 (fixed effects), s_i is the random effect of study (i.e., an intercept shift for each study), a_i is the random interaction of study × T (i.e., a linear term shift for each study), and e_{ij} is the residual error.

In Eq. [1], it is assumed that

$$s_i \approx N(0,\sigma_s^2),\ a_i \approx N(0,\sigma_a^2),$$
$$e_{ij} \approx N(0,\sigma_e^2),\ \text{and } \mathrm{Cov}(s_i, e_{ij}) = 0.$$

The random effects of the study on the quadratic regression coefficient of T (i.e., the study × T^2 interaction) was not included in the model because only 2 T levels were used in most of the published works (68%), thus leaving too few observations to estimate a variance component with reasonable accuracy.

Because the data were extracted from numerous published studies, each with their own experimental design, it was important to properly weigh the observations (the reported means) according to their relative precision (i.e., their SE). Therefore, observations were weighted by the number of animals in each trial to take into consideration the unequal residual variance among trials (Sauvant et al., 2008). An unstructured variance covariance matrix (TYPE = UN in the MIXED procedure) was used to model the random intercepts and slopes, thus allowing for random covariance between slope and intercepts across the random studies (St-Pierre, 2001).

As previously reported (Nienaber et al., 1987; Quiniou et al., 2000a), the effects of T on ADFI and ADG could be affected by the average BW during an experiment. Consequently, the basic model [1] was augmented as follows to account for the effect of BW on animal response to T:

$$Y_{ij} = b_0 + b_1T + b_2T^2 + c_1W + c_2W^2 + c_3TW + s_i + a_iT + e_{ij}, \quad [2]$$

Table 1. Summary statistics for the data included in the data set

Item	No. of studies	No. of observations	Mean	SD	Minimum	Maximum
No. of pigs/trial	47	202	18.4	18.7	3.0	128.0
Climatic variable[1]						
Average temperature, °C	47	202	26.2	5.6	14.0	36.0
Daily range, °C	47	202	0.4	1.2	0.0	6.5
Duration of exposure, d	47	202	45	29	8	152
Relative humidity, %	47	113	63.3	14.0	30.0	95.0
Feed composition						
CP, %	47	202	17.6	2.6	12.0	24.8
ME,[2] MJ/kg	47	202	13.4	0.8	11.4	15.3
Housing condition[3]						
No. of pigs/pen	47	202	2.4	2.4	1.0	16.0
Animal data[4]						
BW,[5] kg	47	202	51.4	24.7	14.0	101.5
ADFI, g/d	47	202	1,837	672	704	3,652
ADFI, g/d per kg of $BW^{0.60}$	47	202	177	28	107	253
BW gain, g/d	43	182	702	185	310	1,189
Feed conversion ratio[6]	43	182	2.62	0.73	1.47	4.91

[1]In 35 of the 47 studies, temperature was maintained constant throughout the day and for the duration of the trial.

[2]When dietary ME values were not reported, estimates were derived either from reported DE values or from diet description and feed composition table (Sauvant et al., 2002).

[3]Pigs were individually housed in 32 of the 44 studies.

[4]Expressed as a percentage of total observations collected, 41.6, 29.0, 11.6, and 1.1% of the observations were obtained from barrows, from a mix between barrows and females, from females, and from boars, respectively. For 17.3% of total observations, the sex type was not reported.

[5]Average BW during the trial.

[6]Calculated as ADFI/ADG, both expressed in kilograms per day.

where W is the mean BW during the experiment (kg), and c_1, c_2, and c_3 are regression coefficients (fixed effects).

Other continuous, independent variables were added to model [2] to assess their possible linear association with animal performance under thermal stress. Factors related to housing conditions (relative humidity, daily T range) and feed composition (diet ME and CP contents) were sequentially added and tested as linear fixed effect covariates in model [2].

Figure 1 shows the distribution of the studies according to their year of publication. Based on this distribution, observations were classified in 3 yr of publication groups: 1) before 1990 (n = 19), 2) between 1990 and 1999 (n = 14), and 3) after 2000 (n = 14). The effects of year of publication (3 levels), sex (5 levels: female, male, barrows, mixed of females and castrated males, and not reported), and housing conditions (2 levels: individual, and grouped housed) were added as fixed effects factors to model [2], as well as their interaction with T and T^2. Terms were sequentially removed from the full model (i.e., model [2] with the addition of all continuous covariates, discrete independent variables, and their 2-way interactions with T and T^2) using the algorithm proposed by Oldick et al. (1999). Goodness of fit was determined by the smallest root mean square error (**RMSE**) and the smallest value of the Bayesian information criterion. Model adequacy was assessed using plots of residuals (observed minus predicted) against predicted values of Y to test for linear prediction bias (St-Pierre, 2003). A correct graphical representation of statistical results in 2 dimensional plots from models of higher dimensional spaces due to the random effect of study requires that the observations on the dependent variables used in the plot be adjusted to take into account the random effect of the study (St-Pierre, 2001).

The quadratic effect of T was significant ($P < 0.05$) for all dependent variables studied, indicating a nonlinear effect of T on all dependent variables. The exact shape of the true, but unknown relationship is probably not a simple quadratic function. Physiological theory would indicate that the nonlinear relationship should consist of a plateau with a threshold change once T reaches a critical threshold temperature (**CT**, °C). Thus, a second analytical approach used a nonlinear model that included a CT. Under this model, ADFI

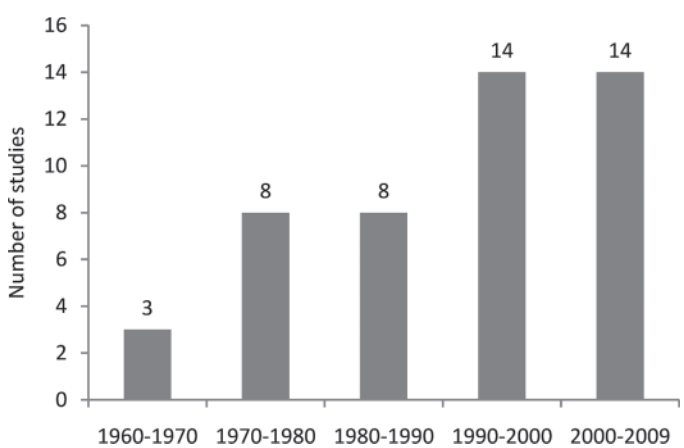

Figure 1. Histogram showing the frequency distribution of studies according to the year of publication.

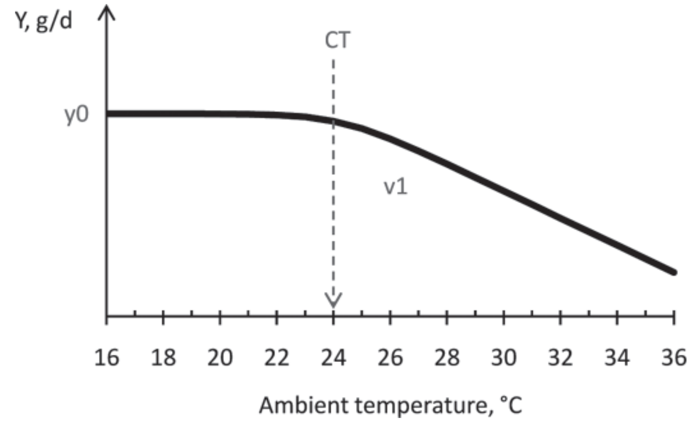

Figure 2. Graphical representation of the model used for the response of ADFI and ADG (Y) to ambient temperature change around a critical temperature point (CT, °C). y0 and v1 = the value of *a* below the CT; v1 = the linear component of the slope of the decline in Y above CT.

and ADG are assumed to remain nearly constant as T is increased as long as T < CT (Figure 2). To model the transition between the plateau when T < CT and the decline in ADFI and ADG when T > CT, a model adapted from Koops and Grossman (1991) was used:

$$Y_{ij} = a\, W^{b} + e_{ij}, \quad [3]$$

where Y_{ij} is the observed value of the dependent variable (ADFI or ADG) adjusted for the random effect of the study i (the empirical BLUP from the model [2]), b is the exponent relating W to Y, and W is the average BW during the trial, and e_{ij} is the residual error, assumed approximately $N(0, \sigma_e^2)$.

In Eq. [3], the parameter a is itself a function of T and CT:

$$a = y_0 + v_1\, s \ln\{1 + \exp[(T - CT)/s]\}, \quad [4]$$

where y_0 is the value of a for T below the CT, v_1 is the linear component of the slope of the decline in Y when T > CT (g/d per °C), and s determines the smoothness of the transition around CT.

In the current study, s was fixed at 0.5, forcing a virtually instantaneous transition between the 2 parts of the function around CT. According to the model developed by Bruce and Clark (1979), the relationship between CT and pig BW is not linear but semi-logarithmic. Consequently, we modeled the relationship between CT and BW using this equation:

$$CT = c + d \ln(1 + W), \quad [5]$$

where c is an intercept term (i.e., the value of CT when W = 0), and d is the marginal change of CT with respect to ln(1 + W).

Parameters of the model expressed by [3], [4], and [5] were estimated using the NLIN procedure of SAS. The residual SD (g/d) and adjusted regression coefficients were calculated according to Gu et al. (1992).

RESULTS AND DISCUSSION

Descriptive Statistics of the Data

Descriptive statistics for the data are reported in Table 1. An average of 18.4 pigs was used per trial, but there was a considerable variability in the number of pigs used across studies (range of 3 to 128 pigs/trial). The average daily ambient T ranged from 14 to 36°C, with a mean of 26.2°C across all studies. Trials averaged 45 d in length, with a minimal and a maximal value of 8 and 152 d, respectively. The average BW of pigs ranged from 14.0 to 101.5 kg, and the number of pigs per pen varied from 1 to 16. Average values across all trials for ADFI, ADG, and FCR were 1,837 g/d, 702 g/d, and 2.62 kg/kg, respectively.

Voluntary Feed Intake

Figure 3 shows a plot of the uncorrected ADFI vs. T. In this figure, the substantial variation in ADFI across studies is quite apparent. Parameters estimates, the SE, and the RMSE and the estimates of the covariance components for model [2] are reported in Table 2. The highly significant T^2 term provides conclusive evidence of a curvilinear relationship between ADFI and T. In contrast, NRC (1987) suggests that there is a linear relationship between ADFI and T. At W = 50, the function is maximized at T* = 20.2°C. Because most of the experimental observations were made between 20 and 32°C (Figure 3), this should not be interpreted as evidence that ADFI declines when T < T*. The residual plot showed no evidence of any prediction bias (linear or nonlinear) for model ADFI (Figure 4). Most residuals were less than |150| g/d, which is equivalent to about 8% of the mean ADFI. There was a strong relationship between adjusted and measured ADFI (adjusted R^2 = 0.98, Figure 5), indicating that observations within study are very predictable. The adjusted ADFI values are nothing else than the observed values corrected for the study effect. However, the random effects of trial [i.e., the variance due to trials on the intercept (σ_s^2 = 181,012) and the linear effect of T (σ_a^2 = 208)] were large and differed significantly from zero ($P <$ 0.001). This implies that both parameters in the quadratic function (i.e., intercept and linear term for T) depend largely on specific factors within each study. In such case, this quantitative analysis has produced a model that is more accurate for explaining the observed ADFI within each study. However, predictions of future outcomes would not be very precise mainly because the actual realization of the future study is unknown (Sauvant et al., 2008). In addition, one can suggest that important unidentified factors, others than those reported in published studies and accounted in the model, have a major impact on the relationship between ambient T and ADFI. In a descriptive review, Le Dividich et al. (1998) showed that high T negatively affects feed consumption in growing and finishing pigs and pointed out a large variability existed among studies regarding the range of decline in ADFI (40 to 80 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ between 20 and 30°C). As suggested by these authors, this high variability is explained by numerous factors including breed, BW, degree of fatness, diet composition, and T range. In addition, pre-experimental rearing conditions and their potential related effects on the animal response to heat stress during the experimental period could be an additional source of variation. Differences in the experimental protocol between studies (e.g., duration of acclimation period to temperature treatment before the experimental period) could also explain some of this variability (Renaudeau et al., 2008). Lastly, results of the present analysis indicate that the decline in ADFI associated with increased T is in fact greatly affected by the BW of the animals. For example, from the ADFI equation reported in Table 2, the decline in ADFI between 20 and 30°C would average 32 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ at a BW of 50 kg, and 78 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ at a BW of 100 kg. These figures are in fact in agreement with the range of values summarized by Le Dividich et al. (1998).

As opposed to looking at the ADFI decline over a range of T as done in a descriptive review, the use of a function to represent the quantitative relationship between ADFI and T allows the estimation of the instantaneous rate of decline, the slope calculated as the partial derivative of the function with respect to T. This partial derivative represents the slope of the tangent line to the function (i.e., the instantaneous rate of decline in ADFI at a given T). For a 50-kg pig, values of the partial derivative at 25 and 30°C were −32.3 and −56.3 $g{\cdot}d^{-1}{\cdot}°C^{-1}$, respectively. In other words, the extent to which T affects the change in ADFI depends on the T, as found in prior research (Nienaber et al., 1987; Quiniou et al., 2000c; Renaudeau et al., 2008). Because the decline in ADFI is the most effective mechanism to decrease heat load (Collin et al., 2001), the reduction in feed consumption of pigs under heat stress appears to be a key mechanism to maintain thermal equilibrium especially when ambient T increases noticeably above the upper limit of the thermoneutral zone. In our study, the linear term in the quadratic function varied significantly across studies (i.e., the significant study × T effect). This implies that the rate of decline in ADFI with T differed across studies. To illustrate this point, the 95% confidence interval for the slope of the tangent line can be calculated. From this calculation, there was a 0.95 probability that the instantaneous decline in ADFI at 25°C was between −35.5 and −30.1 $g{\cdot}d^{-1}{\cdot}°C^{-1}$, and between −58.5 and −54.1 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ at 30°C, respectively, for a 50-kg pig.

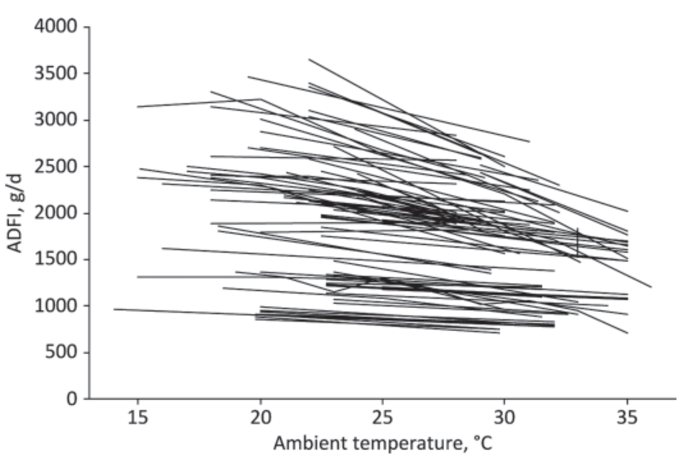

Figure 3. Effect of ambient temperature on ADFI in growing-finishing pigs (47 studies, 86 experiments, 3,714 pigs).

Under practical housing conditions and especially under tropical conditions where buildings are often semi-open, pigs are usually subjected to fluctuation in T throughout the day and across days. Consequently, the application of results collected in closely controlled and constant environment may be inappropriate when applied to variable T conditions. In fact, some evidences show that pigs are totally or partially capable of maintaining feed consumption when exposed to a cycling diurnal T challenge (Morrison et al., 1975; Quiniou et al., 2000b). In the present quantitative analysis, the daily range in ambient T did not explain sufficient variability to be retained in the model. However, this result may be explained by the insufficient number of trials in the database that used cyclic T (less than 16% of the total).

In pigs, feed intake is also influenced by other climatic factors including relative humidity (**RH**) and air renewal, but to a lesser extent than ambient T. Above 80% RH, the effects of heat stress on ADFI are magnified due to a decrease of the rate of evaporative heat loss (Morrison et al., 1968; Granier et al., 1998). In the data set, RH was measured in only 42.6% of the studies, and in most instances (95.7%) the RH was below 80%. This explains why the effect of RH and its interaction with high ambient T was not significant in the present work. Clearly, further work is needed to quantify the effect of RH on pig performance under hot climate.

The quadratic equation modeled a smooth relationship between ADFI and T, without any break point temperature threshold. As pointed out earlier, the prevailing theory on the physiology of heat stress emphasizes a temperature threshold known as critical temperature. Accordingly, we used a near-plateau linear decline threshold model that allowed the determination of a critical threshold temperature. Parameter estimates and associated statistics for this nonlinear model are presented in Table 3. Based on the work of Collin (2000), a plateau with quadratic decline model was fitted to account for the greater rate of ADFI decrease under very high T. The model (Collin, 2000) is as follows:

$$\mathrm{Y} = \mathrm{a} \times \mathrm{W}^{\mathrm{b}}, \text{ with } a = \mathrm{y}_0\,(1 - s\ln\{1 + \exp((\mathrm{T} - \mathrm{CT})/s)]\}/(\mathrm{T} - \mathrm{CT}) + (\mathrm{y}_0 + \mathrm{v}_1\,\{\mathrm{T} - \mathrm{CT}\} + \mathrm{v}_2\,\{\mathrm{T} - \mathrm{CT}\}^2) \times (s\ln\{1 + \exp[(\mathrm{T} - CT)/s)]\}/\{\mathrm{T} - \mathrm{CT}\}).$$

Table 2. Equations for polynomial regression of response of ADFI, ADG, and feed conversion ratio to ambient temperature and average pig BW[1]

Dependent variable	Independent variable	Parameter: Estimates	Parameter: SE	Parameter: *P*-value	RMSE	Covariance component[2]: σ_s^2	Covariance component[2]: σ_a^2	Covariance component[2]: $\sigma_{s,a}$
ADFI, g/d	Intercept[3]	−1,331	288	<0.001	494	181,012	208	−5,501
	T	134	18.5	<0.001				
	T^2	−2.40	3.31×10^{-1}	<0.001				
	W	58.7	5.12	<0.001				
	W^2	-1.05×10^{-1}	3.77×10^{-2}	<0.101				
	T × W	-9.23×10^{-1}	8.85×10^{-2}	<0.001				
ADFI, g/d of kg of $BW^{0.60}$	Intercept[3]	65.2	23.1	0.006	43.4	1,291	1.48	−36.9
	T	10.1	1.61	<0.001				
	T^2	-2.15×10^{-1}	2.88×10^{-2}	<0.001				
	W	1.30	2.07×10^{-1}	<0.001				
	T × W	-4.54×10^{-2}	7.48×10^{-3}	<0.001				
ADG,[4,5] g/d	Intercept[3]	−489	198	0.016	217	35,946	42.1	−1,081
	T	62.2	9.39	<0.001				
	T^2	−1.37	1.58×10^{-1}	<0.001				
	W	21.2	2.80	<0.001				
	W^2	-9.33×10^{-2}	2.07×10^{-2}	<0.001				
	T × W	-2.64×10^{-1}	4.18×10^{-2}	<0.001				
	CP	12.7	5.64	0.038				
FCR,[4] kg/kg	Intercept	4.06	5.00×10^{-1}	<0.001	0.99	0.053*	0.0002	−0.002*
	T	-1.50×10^{-1}	2.89×10^{-2}	<0.001				
	T^2	2.89×10^{-3}	5.32×10^{-4}	<0.001				
	W	1.02×10^{-2}	2.76×10^{-2}	0.002				
	T × W	3.16×10^{-4}	1.18×10^{-4}	0.015				
	CP	-4.51×10^{-2}	1.47×10^{-2}	0.007				

[1]Abbreviations and units: W, average BW (kg); FCR, feed conversion ratio (kg of ADFI/kg of ADG); T, ambient temperature (°C); CP (g/100 g); RMSE: root mean square error (i.e., the square root of the estimated residual variance of the model).

[2]σ_s^2 is the variance estimate for the random intercept due to study; σ_a^2 is the estimated variance for the random linear term for T (i.e., the study × T interaction); $\sigma_{s,a}^2$ is the covariance estimate between random intercept and slope.

[3]The intercept was significantly affected by housing condition (individual vs. group housed; $P < 0.01$).

[4]The intercept was significantly affected by the year of publication (1970 to 1989, 1990 to 1999, 2000 to 2009; $P < 0.01$).

[5]The linear effect of T was affected by the year of publication ($P < 0.01$).

*Variance or covariance estimate was not significantly different from zero ($P > 0.05$).

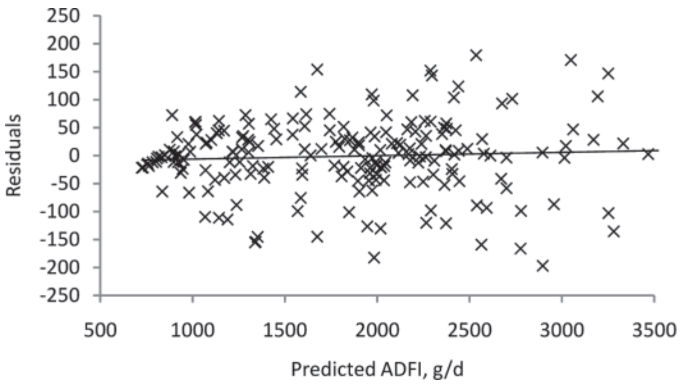

Figure 4. Plot of residuals (observed – predicted) against predicted ADFI from the mixed model analysis. The line represents the regression of residuals on predicted ADFI [$Y = -12.62\ (13.85) + 0.0062\ (0.0071) \times$ predicted ADFI; $R^2 = 0.003$; $P > 0.05$].

This model, however, did not fit the data better than the simpler threshold and linear decrease model [3]. Its residual SD (183 g/d) was not different that of model [3]; nor was its estimate of CT [$CT = 39.9 + 4.10\ \ln(1 + W)$]. Therefore, we concluded that a plateau with linear decline model was sufficient to describe the ADFI response to T. The estimated exponent b relating ADFI to BW was 0.69 in model 3 (Table 3). This value is comparable with the value used by NRC when DE intake was related to BW in growing pigs kept in thermoneutral conditions (i.e., an exponent between 0.50 and 0.70). Based on our fitted model (Table 3) and for a 50-kg pig, ADFI remains approximately constant below 23.6°C and thereafter declines by 25 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ when T > 23.6°C (Figure 6). In grouped-housed growing pigs (70 kg of BW on average), ADFI decreased steadily by 95 $g{\cdot}d^{-1}{\cdot}°C^{-1}$ above 25.5°C (Huynh et al., 2005). First, the discrepancy between both studies could be explained by difference in BW. However, in this later experiment, pigs were submitted to 9 successive T levels (from 16 to 32°C) for only 1 d without a previous acclimation period, which could explain the greater effect of T above CT on ADFI reported by these authors compared with our results. In fact, it has been shown

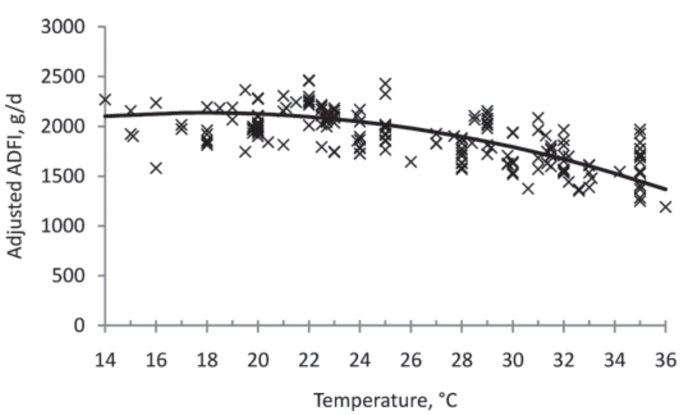

Figure 5. Average daily feed intake vs. model-predicted ADFI (solid line) in response to ambient temperature (solid line calculated from the Eq. [1] for an average BW of 50 kg).

Table 3. Plateau linear decline regression analysis of response of ADFI and ADG to ambient temperature in growing finishing pigs

Dependent variable (Y)	Parameter estimate[1]									RSD, g/d	Adjusted R^2
	y_0	SE	v_1	SE	c	SE	d	SE	b	SE		
ADFI, g/d	140	13.1	−3.42	4.58×10^{-1}	40.9	4.94	−4.40	1.20	0.69	2.30×10^{-2}	181	0.91
ADG, g/d	281	36.8	−9.32	2.06	36.7	5.19	−3.07	1.31	0.27	3.34×10^{-1}	123	0.97

[1]ADFI and ADG responses (adjusted for the experiment effect) to ambient temperature according to a plateau linear model: $Y = a \times W^b$, with $a = y_0 + 0.5\ v_1 \ln\{1 + \exp[(T - CT)/0.5]\}$, and $CT = c + d \ln(1 + W)$, where W is the average BW during the trial (kg), T is the ambient temperature (°C), and CT is the critical temperature (°C). Residual SD (RSD, g/d) and adjusted regression coefficient were calculated according to Gu et al. (1992). y_0 = the value of *a* below the CT; v_1 = the linear component of the slope of the decline in Y above CT; c = the value of CT for a null BW; b = power of the BW for the estimation of the metabolic BW; and d = the marginal change of CT with respect to $\ln(1 + W)$.

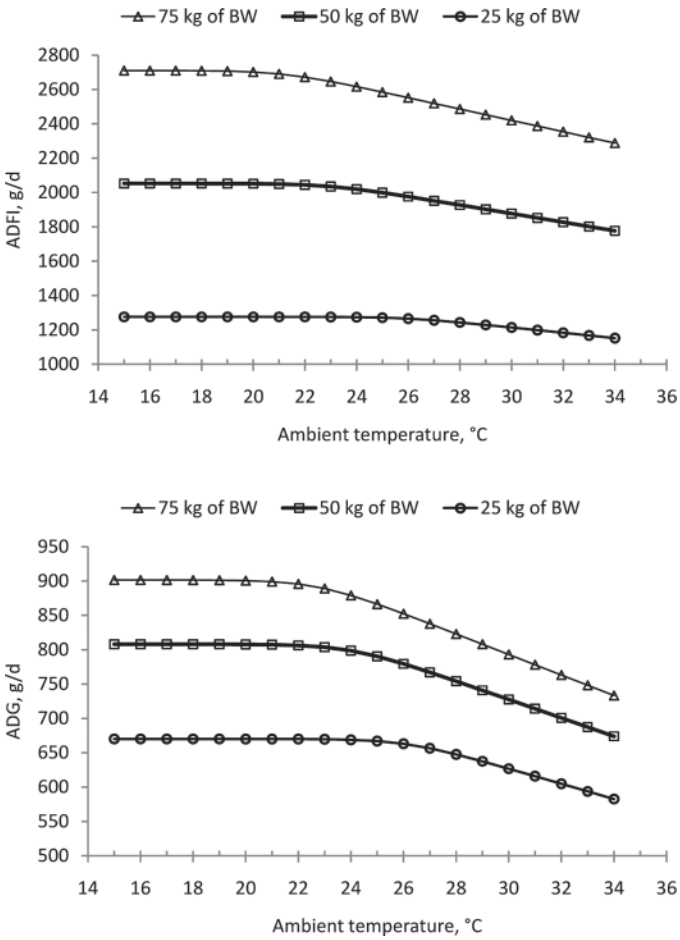

Figure 6. Effects of ambient temperature and pig BW on ADFI and ADG. The ADFI and ADG responses were calculated using the nonlinear models reported in Table 3.

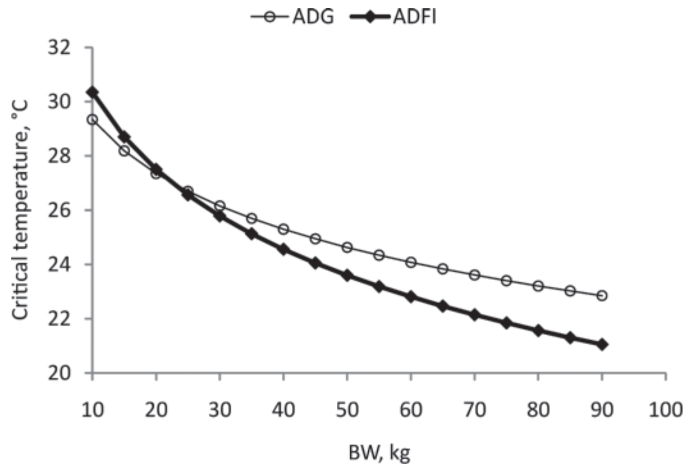

Figure 7. Effect of pig BW on the critical temperature for ADFI and BW. Responses were calculated using the nonlinear models reported in Table 3.

that the reduction in ADFI during thermal acclimation occurs mainly within the first 2 to 3 d of exposure (Renaudeau et al., 2010).

According to the results from the mixed model analysis (Table 2), the significant interaction between T and average W ($P < 0.001$) means that heavier pigs are more sensitive to high ambient T than lighter pigs. Based on the resulting equation, it is estimated that on average (i.e., across studies) the reduction in ADFI from 20 to 30°C are 9, 32, and 55 $g \cdot d^{-1} \cdot °C^{-1}$ at 25, 50, and 75 kg of BW, respectively (Figure 5). Similar results were previously reported by Quiniou et al. (2000a). According to the results from the plateau and linear decline model (Table 3), CT for ADFI decreased as the BW increased following this relationship:

$$CT = 40.9 - 4.4 \ln(1 + BW). \quad [6]$$

Using Eq. [6], the threshold T at which ADFI begin to decline drops from 30.3 to 21.0°C between 10 and 90 kg of BW (Figure 7). These results are in agreement with a decrease of the upper limit of the thermal neutral zone with increasing pig BW (Holmes and Close, 1977). The greater susceptibility of heavier pigs is mainly related to their increased metabolic rate at thermoneutrality in relation to their relatively high feed intake. In addition, heavy pigs have much smaller ratio of surface area to mass and a greater thermal insulation (increased subcutaneous tissue content) than young, light pigs (Bruce and Clark, 1979). Consequently, their ability to dissipate heat is theoretically less than that of piglets, which could partly explain their greater sensitivity to increased ambient T.

The housing conditions (individual vs. group) significantly affected the intercept of the mixed model for ADFI (−1,331 vs. −1,445 g/d). Therefore, across T, ADFI is less by an average of 114 g/d when pigs are group housed. This result can be attributed to differences in competition at the feeder (Hyun and Ellis, 2002). However, housing conditions did not interact with the linear or quadratic terms associated with T. Thus, the intake difference between the 2 housing conditions does not appear to change with ambient T.

Growth Rate and Feed Conversion

Figure 8 shows a plot of the uncorrected ADG and FCR vs. T, with observations from a given trial connected by a common line. As for ADFI, the trial effect appears large for both ADG and FCR. Parameter estimates for the mixed model analysis of ADG and FCR are reported in Table 2. The variance components for study and study × T are relatively large for both dependent variables, indicating that many unknown and unaccounted for factors, specific to each study, remain to be identified. Residual plots for model predictions and the relationship between model predicted and experiment-adjusted ADG and FCR are shown in Figures 9 and 10, respectively. According to Figure 9, there was no evidence for a prediction bias for ADG prediction ($P > 0.05$) even though 4 treatments means were overestimated (strongly negative residuals). However, there was an apparent positive slope bias for FCR prediction ($P = 0.04$), indicating that standard residuals tended to be positive at a high level of predicted

FCR (Figure 9). Recall that model [2] was fitted using a weight on the observations equal to the number of pigs in each treatment mean. Algebraically, the method used in PROC MIXED guarantees that the sum of the weighted residuals is equal to zero (i.e., the average of the weighted residuals is equal to zero), and that the slope of the regression between the weighted residuals and the predicted values is also equal to zero (St-Pierre, 2003). Thus, the slight positive slope observed when regressing the standard residuals (as opposed to the weighted residuals) on the predicted values of FCR in Figure 9 only means that the weighting scheme used produced parameter estimates that were slightly, but significantly different than those that would be obtained if the observations had not been weighted.

The plot of predicted and observed ADG corrected for the trial effect vs. T suggests that the model fits the data set well except at the lower T (Figure 10). The RMSE for ADG and FCR predictions (217 g/d and 0.99 kg/kg, respectively) were high compared with the average ADG and FCR of the data set (707 g/d and 2.62 kg/kg, respectively; Table 2). As discussed for ADFI, these increased RMSE reflected an increased random variation induced by trial within study effect.

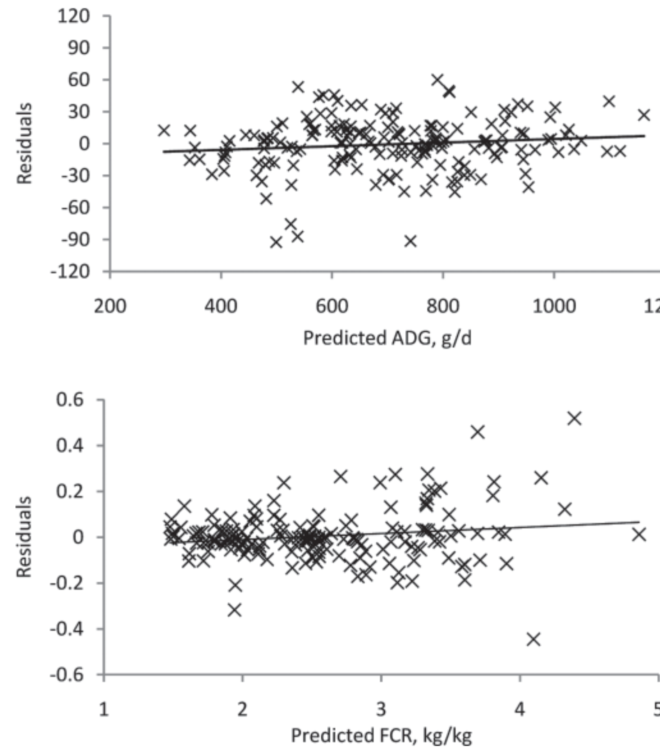

Figure 9. Plot of residuals (observed minus predicted) against predicted ADG and feed conversion ratio (FCR = ADFI/ADG) from the mixed model analysis (Eq. [1]). The line represents the regression of residuals on predicted ADG [Y = −12.6 (7.5) + 0.017 (0.010) × predicted ADG; R^2 = 0.015; $P > 0.05$] or on predicted FCR [Y = −0.062 (0.034) + 0.026 (0.012) × predicted FCR; R^2 = 0.026; $P = 0.04$].

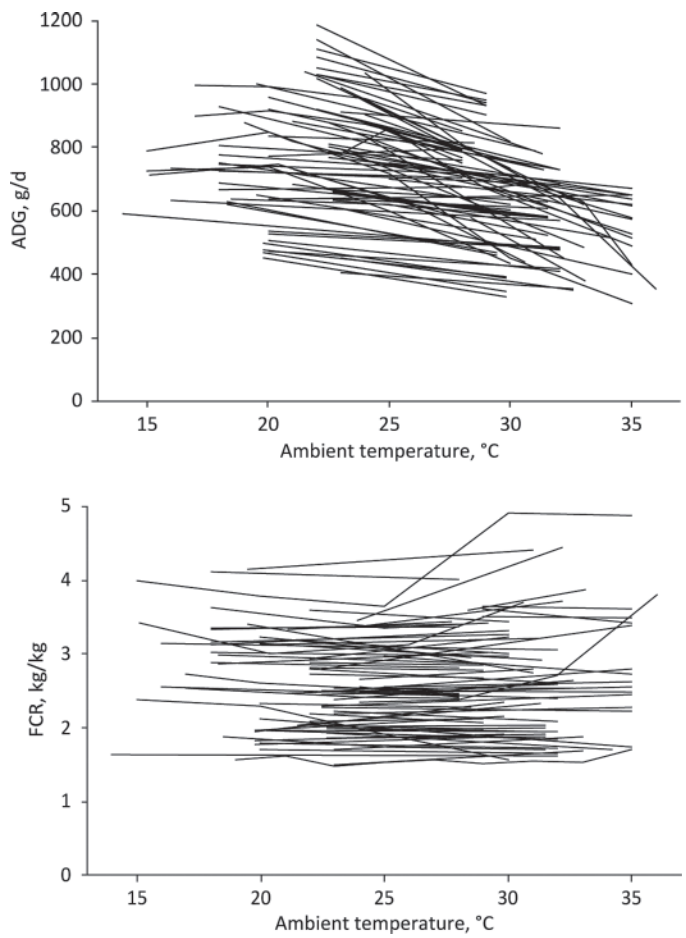

Figure 8. Effect of ambient temperature on ADG and feed conversion ratio (FCR = ADFI/ADG) in growing-finishing pigs (43 studies, 80 experiments, 3,609 pigs).

Based on the parameter estimates for the mixed model of ADG (Table 2), the estimated reduction in ADG for a 50-kg BW pig is about 18 g·d^{-1}·°C^{-1} when T is raised from 20 to 30°C. Under this range of T, FCR would remain nearly constant at a ratio of 2.70, indicating that the decreased ADG associated with heat stress is primarily a result of a decrease in feed intake. Therefore, the use of techniques that reduce the effect of heat stress on ADFI may be beneficial to maintaining growth performance under heat stress. At a very high T level, the FCR showed a slight increase (+0.2 kg/kg from 30 to 36°C), suggesting that pigs becomes less efficient in using feed for growth under severe heat stress conditions (Figure 10). It is unclear whether the marginal efficiency for growth is affected by severe heat stress as well.

In agreement with the effect of T on ADFI, the response of ADG to increased T was also curvilinear. At 25 and 30°C, the instantaneous rates of ADFI change were −10.9 and −24.6 g·d^{-1}·°C^{-1}, respectively, for a 50-kg-of-BW pig. The 95% confidence intervals were very narrow and ranged between −11.9 and −9.9 g·d^{-1}·°C^{-1} and between −25.6 and −23.5 g·d^{-1}·°C^{-1} at 25 and 30°C, respectively. Similarly, Nichols et al. (1982), Nienaber and Hahn (1983), and Nienaber et al. (1987) reported that the extent to which high T affects growth performance depends on the T level.

Based on the parameter estimates for the mixed model (Table 2), the effect of increased T on ADG from

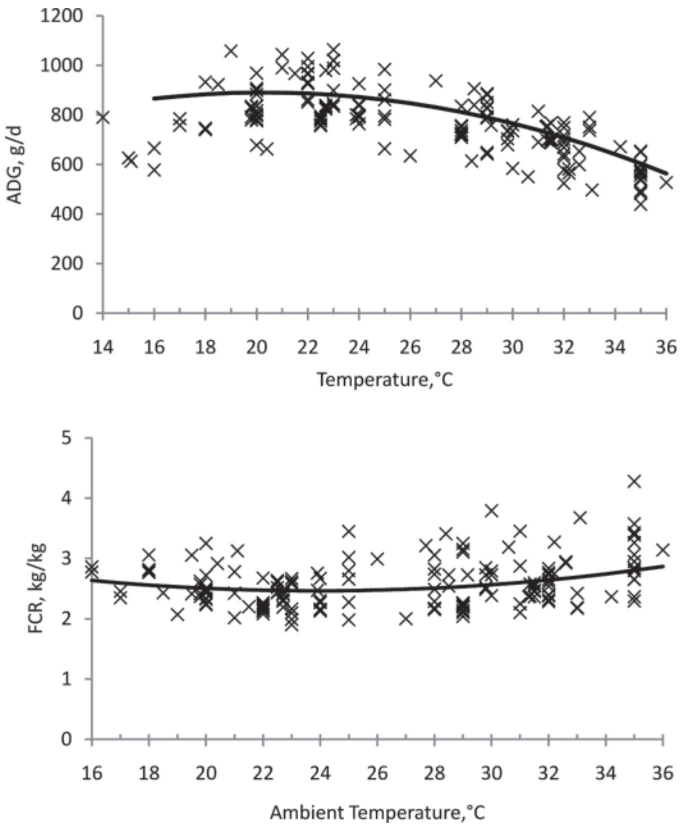

Figure 10. Prediction of the ADG and feed conversion ratio (FCR = ADFI/ADG) vs. model-predicted ADG or FCR (solid lines) in response to ambient temperature (solid line calculated from Eq. [2] and [3] for an average BW of 50 kg).

20 to 30°C is 2-fold greater at 75 than at 25 kg (25 vs. 11 g·d^{-1}·°C^{-1}). According to the plateau and linear decline model for ADG, CT declines from 29.3°C at 10 kg of BW to 22.9°C at 90 kg (Figure 7). This matches the results obtained for ADFI and indicates that older, heavier pigs are more susceptible to high ambient T than young pigs. According to Figure 7, the CT values for ADG and ADFI are quite similar at BW less than 40 kg. Above this BW, the CT value for ADG becomes noticeably greater than for ADFI. In young pigs, the energy requirement for maximal growth usually exceeds the ad libitum-energy intake. Consequently, the reduced feed intake under heat stress has a direct negative effect on growth performance. In contrast, the greater energy consumption relative to requirements in heavier pigs explains the reduced CT for ADG than for ADFI in those pigs.

The intercept and the linear term for T in the equation for the mixed model of ADG (Table 2) were significantly influenced by the year of the study publication. The effect of year of publication on the intercept of this equation was −892, −786, and −489 g/d, for works published from 1960 to 1989, from 1990 to 1999, and from 2000 to 2009, respectively. The effect of year of publication on the linear term of the same equation was 72.2, 70.3, and 62.2 g·d^{-1}·°C^{-1}, for works published from 1960 to 1989, from 1990 to 1999, and from 2000 to 2009, respectively.

The intercept, but not the linear term for T in the equation for the mixed model of FCR (Table 2), was affected by the year of publication. The effect of year of publication on the intercept of this equation was 4.57, 4.32, and 4.06 for works published from 1960 to 1989, from 1990 to 1999, and from 2000 to 2009, respectively. Using a standard 50-kg pig housed at 20°C the mixed model equation indicates that the ADG was much greater and the FCR less in reports published from 2000 to 2009 than in those published from 1960 to 1989 (1,000 vs. 785 g/d and 2.0 vs. 2.4 kg/kg, respectively; $P < 0.01$). Intermediate values were found for studies published from 1990 to 1999 (885 g/d and 2.2 kg/kg, respectively). Between 20 and 30°C and at an average BW of 50 kg, the decline in ADG for each publication period was estimated at 12, 18, and 25 g·d^{-1}·°C^{-1} in works published from 1960 to 1989, 1990 to 1999, and from 2000 to 2009, respectively. The change in FCR from 20 to 30°C (+0.05 kg/kg) was similar across all years of publication. Even though many factors could be involved (e.g., difference in breeding conditions), the greater effect of increased T on growth performance in recent works could be explained by an improvement in the genetic potential for growth in pigs. In other words, genetic selection aimed at increasing the amount and efficiency of lean growth in pigs would lead to animals with a reduced capacity for coping with heat stress. Nienaber et al. (1997) observed that the threshold T at which heat stress affects performance is reduced in increased lean growth potential pigs compared with moderate growth genetic lines. This increased sensitivity of modern pigs to high ambient T is probably related to their greater metabolic heat production associated with greater production. In addition, according to Noblet et al. (1999), the maintenance requirements are also greater when synthetic line pigs are compared with conventional Large White pigs in connection to breed variations in fasting heat production due to change in weights of metabolically active body compartments such as viscera and lean mass.

In Table 2, dietary CP was found to affect the intercept of the equations relating ADG or FCR to ambient T (Eq. [3] and [4]); the linear term for T, however, was not affected by CP. An increase in dietary CP has a positive effect on ADG and feed efficiency. In most of the published studies assessing effects of CP level on performance under heat stress, the low CP diets were not supplemented with synthetic AA to meet the AA requirement for growth. This would explain why pigs fed reduced CP diets had poorer growth performance than those fed normal diets.

In conclusion, this analysis provides quantitative relationships between major performance variables and increased T. This study shows that factors other than those traditionally studied can interact with ambient T to affect performance. It is assumed that the animal sanitary status, climatic factors other than temperature, and animal performance before starting the experiment could explain the large variability observed for the effects of T among studies. Future work is needed to more precisely quantify the relative importance of these factors and to improve the accuracy of the model predicting the effect of increased T on growth performance of pigs. This may become even more important for pig production under tropical countries and in the context of potential climate change and mitigation strategies to reduce the associated impact on pig productivity.

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