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Evaluating equations estimating change in swine feed intake during heat and cold stress[1]

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ABSTRACT: The objectives of this study were to evaluate heat stress feed intake models for growing swine using a data set assembled from the literature and to develop a series of new equations modeling the influence of the thermal environment and interactions between the thermal environmental and other factors on feed intake. A literature survey was conducted to identify studies assessing intake responses to temperature. The resulting data set comprised 35 studies containing 120 comparisons to thermoneutral intake. Intake as a fraction of thermoneutral intake (FFI) was the primary response variable, where a value of 1 represented no change from thermoneutral intake. The FFI predicted by NRC and a recent model from a meta-analysis (Renaudeau et al.,) were compared to observed values. New parameters for the NRC equation (NRCmod) were derived, and a series of new equations incorporating duration of exposure (TD), temperature cycling (TC), and floor type (TH) were also derived. Root-mean-square prediction error (RMSPE) and concordance correlation coefficients were used to evaluate all models. The RMSPE for the NRC model was 23.6 with mean and slope bias accounting for 12.6% and 51.1% of prediction error, respectively. The TD, TC, and TH models had reduced RMSPE compared with NRC: 12.9 for TD, 12.6 for TC, and 12.9 for TS. Substantial improvements were also made by refitting parameters (NRCmod; RMSPE 13.0%). In NRCmod, TD, TC, and TH, random error was the predominant source, accounting for over 97% of prediction error. The Renaudeau et al. model was also evaluated. Renaudeau et al. had relatively low RMSPE (22.3) for intake but higher RMSPE for FFI (22.6) than NRC, NRCmod, TD, TC, or TH. Additional parameters were derived for the Renaudeau et al. equation to account for housing system and diet characteristics. This adjustment reduced RMSPE of predicting feed intake (16.0) and FFI (16.3) and reduced systematic bias in the equation. This evaluation of equations highlights the effects of novel explanatory variables on feed intake during heat stress, and the comparison can be useful when selecting a model that best explains variability in feed intake responses to heat stress given available input data.

Key words: cold stress, feed intake, heat stress, pigs

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INTRODUCTION

Global population growth (U.S. Census Bureau, 2013) and resource constraints (Vorosmarty et al., 2000; Falkenmark et al., 2009; Hertel, 2011) highlight the need for improved global food security (Godfray et al., 2010; Gomiero et al., 2011). Pork is a key focus due to its global demand (USDA Economic Research Service [**USDA-ERS**], 2014) and socioeconomic importance in the United States (USDA-ERS, 2013). The frequency of extreme weather events is expected to increase (Intergovernmental Panel on Climate Change, 2007), and pigs are sensitive to climate changes (Nardone et al., 2010). Heat stress has extensive economic impacts in the United States (St-Pierre et al., 2003), and these losses will be exacerbated with climate change. The swine model developed for the U.S. National Pork Board was constructed to assess swine responses to climate stress and relies on the equations developed by the NRC (2012). The NRC equations link temperature exceeding the upper critical temperature to changes in metabolizable energy intake and animal performance (NRC, 2012). In comparison to thermoneutral conditions (i.e., 20°C to 24°C), the NRC equations predict a 40% to 50% decrease in feed intake at temperatures of 30°C to 35°C. This decrease in feed intake leads to exacerbated production responses that are inconsistent with those identified in a recent meta-analysis (Renaudeau et al., 2011). Reassessment of equations predicting generalized intake responses to temperature is needed to ensure heat stress effects are appropriately modeled. The objectives of this study were to evaluate models predicting change in generalized feed intake during thermal stress using a data set assembled from the literature and to develop a series of new equations modeling generalized changes in feed intake due to thermal stress. We hypothesized that the NRC model would overestimate intake depression in heat-stressed pigs and that an update to the equation adjusting intake on the basis of temperature would better explain swine feed intake responses to temperature stress.

MATERIALS AND METHODS

Data Collection

A literature survey of the AGRICOLA database was performed using the key words "Growing Swine (Pigs) Heat Stress (Ambient Temperature)." An additional search of the resources available on the Virginia Tech campus was conducted using Google Scholar. The *Journal of Animal Science*, *Canadian Journal of Animal Science*, and *Livestock Production Science* were also specifically searched using the same keywords. Studies were excluded if they failed to report data for swine BW, duration of exposure, ambient temperature, and feed intake. Additionally, studies were selected only if the design included a comparison between heat stress and thermoneutral environments. The resulting data set is available online (National Animal Nutrition Program, 2014) and represents 120 comparisons of heat-stressed and thermoneutral intake sourced from 35 studies.

Within a study, the maximum reported ADG was used as an estimate of the genetic merit of pigs used. To account for BW effects of ADG, the natural log of maximum ADG per unit BW for each study was identified as a metric of genetic merit that was uniform among studies. A subset of the data published more recently than 2005 was used to define the normal distribution of this parameter for modern genotypes. Studies with genetic merit outside this normal distribution (mean ± 3 SD) were eliminated from the data set to ensure the relationships derived would be representative of contemporary animals. This procedure removed 31 treatment means from the data set. Summary statistics of this data set are included in Table 1.

Within each study, 1 or more thermoneutral treatments were identified. Feed intake under each environmental stress treatment was then expressed as a fraction of intake at thermoneutral, where a value of 1 represented thermoneutral intake, a value of 0.5 represented a 50% reduction, and a value of 1.5 represented a 50% increase. Fractional intake (**FFI**) was used as the primary response variable for this work.

Model Evaluations

The literature data were used to evaluate the NRC (2012) predictions for feed intake for heat-stressed growing and finishing pigs on the basis of observed FFI. For each data point where temperature was greater than the lower critical temperature, the NRC (2012) model was used to predict FFI as defined by

$$\mathrm{FFI} = 1 - 0.012914 \times [\mathrm{T} - (\mathrm{LCT} + 3)] - 0.001179 \times [\mathrm{T} - (\mathrm{LCT} + 3)]^2, \quad [1]$$

where T represents temperature (°C) and lower critical temperature (**LCT**) is calculated within the NRC (2012) model on the basis of BW:

$$\mathrm{LCT} = 17.8 - 0.0375 \times \mathrm{BW}. \quad [2]$$

When temperature was less than LCT, the NRC (2012) model predicts FFI on the basis of the measured intake response per degree Celsius below LCT for pigs weighing 25 and 90 kg:

Table 1. Summary of data used in model fitting

Metric	Unit	Mean (Value)	Median	SD	Minimum	Maximum
Studies	number	33				
Comparisons[1]	number	108				
Percentage of treatments						
Conducted in Europe	%	29.9				
Conducted in Asia	%	10.3				
Conducted in UK	%	5.1				
Conducted in SEA	%	3.4				
With heat abatement	%	13.7				
Using chambers	%	39.6				
Conducted outdoors	%	20.7				
On solid floors	%	54.9				
Using individual housing	%	54.0				
Cycling temperatures	%	34.2				
Pigs per pen	number	5.9	1	19.9	1	150
Space per pig	m^2	1.1	1.2	0.41	0.41	2.40
Dietary ME	kcal/kg	3,117	3,250	566	1,500	4,280
Dietary CP	%	17.3	16.8	3.4	12.3	24.8
Duration of exposure	d	35.6	30.0	25.5	1	133
ADG	g/d	612	621	274	234	1,250
	g/kg BW	16.2	11.8	13.8	5.2	82.2
Maximum daily gain	g/d	792	792	229	487	1,250
	g/kg BW	20.5	15.8	14.4	6.8	85.6
Average BW[2]	kg	48.6	52.3	24.7	9.7	104.7
Studies with BW < 25 kg	%	18.8				
Studies with BW > 70 kg	%	29.1				
Ambient temperature (T)	°C	23.5	26.8	10.1	−0.3	36.0
Studies with T < 18°C	%	17.0				
Studies with T > 28°C	%	24.7				
Intake	kg/d	1.78	1.70	0.80	0.36	3.91

[1]Comparisons indicates the total number of treatment comparisons (environmentally stressed as a fraction of thermoneutral intake) available in the data set.

[2]When studies assessed long-term influence of environmental stress, the average of the starting and BW was taken. If studies did not report a start and finish weight and ran over a few days, the start weight was assumed to be equal to average weight.

$$\mathrm{FFI} = 1 + \frac{(\mathrm{LCT}-\mathrm{T}) \times \left[\dfrac{1.5 + \dfrac{\mathrm{BW}-25}{90-25} \times}{(3.0-1.5)} \right]}{100}. \quad [3]$$

This fractional adjustment was applied to baseline predicted intake (**I_{base}**) in a multiplicative manner to yield an estimate of heat or cold adjusted intake (I_{adj}):

$$I_{adj} = I_{base} \times \mathrm{FFI}. \quad [4]$$

In this representation, FFI of 1 denotes no effect of temperature on intake, and FFI greater than and less than 1 denote intake stimulation and depression, respectively. To avoid excessive overprediction of intake, the NRC (2012) model also imposes a restriction on feed intake representative of gut fill. To evaluate the NRC (2012) FFI estimate, Eq. [1] through [3] were used to calculate LCT and FFI for each treatment observation on the basis of treatment-specific BW and temperatures, and the resulting observed FFI were compared with measured FFI. The root-mean-square error of prediction (**RMSPE**) and concordance correlation coefficient (**CCC**; Lin, 1989) were calculated and partitioned to assess mean and slope biases. Residuals were graphed against predicted FFI for formal analysis and against temperature to visually assess goodness of fit across different temperatures.

To more completely evaluate the current models available to predict FFI, the model by Renaudeau et al. (2011; **R2011**) was also used to calculate FFI. The function was derived from a meta-analysis and predicts feed intake (FI; kg/d) and is predominantly influenced by BW:

$$\mathrm{FI\ (kg/d)} = (a \times \mathrm{BW}^{0.69}) / 1{,}000, \quad [5]$$

where a is a function of temperature,

$$a = 140 - 3.42 \times \ln(1 + e^{\mathrm{T}-\mathrm{CT}}), \quad [6]$$

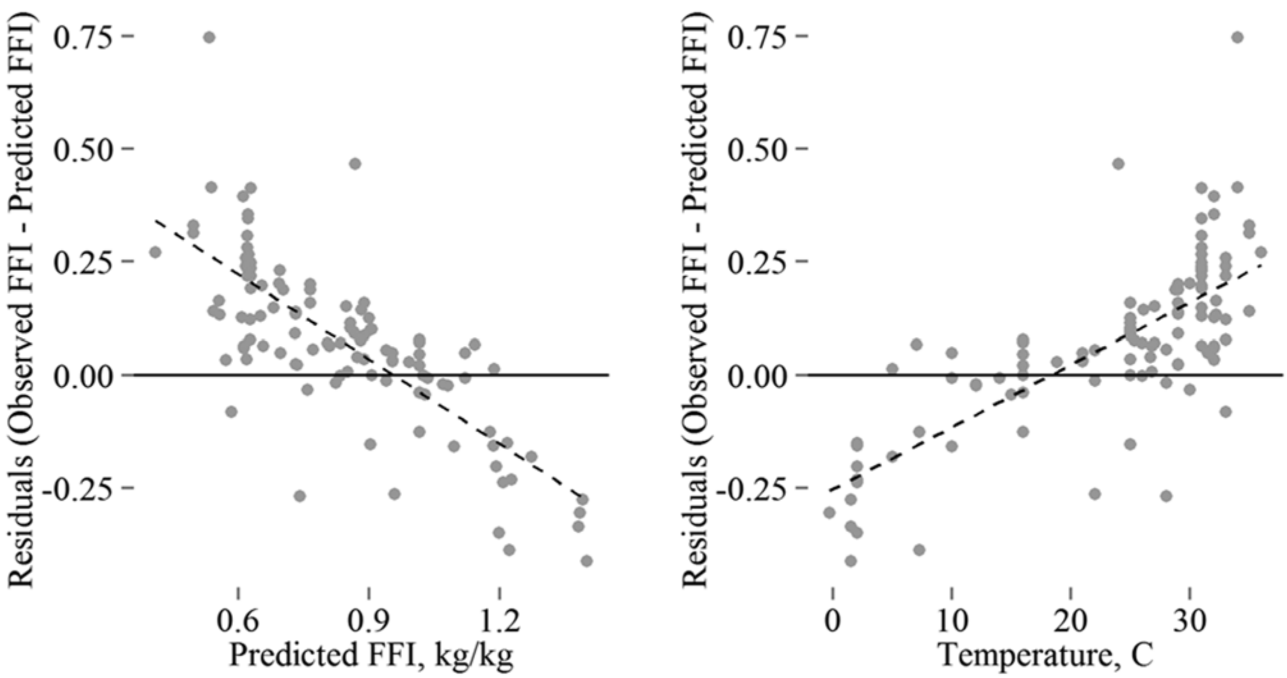

Figure 1. Residuals (observed intake as a fraction of thermoneutral intake [FFI] minus NRC predicted FFI) graphed over predicted FFI and temperature. The left graph shows the clear mean and slope bias of the model predictions. The right graph shows the trend in residuals with respect to temperature.

and is dependent on critical temperature (**CT**), which is calculated as

$$CT = 40.9 - 4.4 \times \ln(1 + BW), \quad [7]$$

To calculate FFI using the R2011 model, the absolute intake values were simulated for each available data point and predicted temperature-stressed feed intake was divided by the corresponding predicted thermoneutral intake.

Model Improvement

Initial analyses of the NRC equations indicated they were biased (Fig. 1). New parameters were derived by fitting the NRC (2012) equation to the assembled data using R statistical software (R Core Team, 2014). Because Eq. [3] was based on interpolating a response from 2 experimentally derived means, it was inappropriate to fit new parameters to this function. As such, the quadratic form of Eq. [1] was relied on to simulate responses to heat and cold stress. As intake was anticipated to decrease at an increasing rate with temperature increases, the quadratic form was expected to be a sufficient model across the range of mean temperatures (1.5°C to 41°C) represented within the data. This new model (**NRCmod**) retained the polynomial form of the NRC heat stress equation, and new parameters were fit by mixed-model linear regression (R Core Team, 2014). Although it is recommended that models derived from literature data include a random effect for study (St-Pierre, 2001; Sauvant et al., 2008), the response variable in this model was standardized among studies as it was expressed as a fraction of thermoneutral intake within a study. To determine whether a random effect for study improved the model, the NRC equation was rederived with and without a study intercept. The coefficients did not differ among models, and RMSPE and CCC were nearly identical. On the basis of this comparison, a study effect was deemed unnecessary in the FFI models as the data were already standardized among studies. Analysis of the residuals was performed to compare model mean and slope biases to the original NRC model biases. Again, residuals were also graphed vs. temperature to assess trends in accuracy across temperatures. The mean absolute error, RMSPE, and CCC were also calculated to compare error among NRC and the new NRCmod coefficients.

As factors other than mean temperature may account for some of the variability in feed intake responses to temperature, a set of new equations was derived that made use of stress duration, the change in temperature from night to day (cycling), and location. The equations were designed to minimize input data requirements and optimize RMSPE and CCC.

The first model related temperature and duration of exposure to FFI (**TD**; Eq. [8]):

$$FFI = c1 + c2 \times [T - (LCT + 3)] + c3 \times [T - (LCT + 3)]^2 + c4 \times Dur, \quad [8]$$

where c1 through c4 are coefficients, T is temperature (°C), and Dur is duration of exposure (d). The general equation form from NRC (2012) in terms of expressing the effects as FFI was retained so that these equations could be easily substituted, provided the extra input data are available.

Duration of exposure is a complex variable. In acute heat stress situations, there appears to be marginal abatement in the intake depression associated with heat stress (Verhagen, 1987; Renaudeau et al., 2007). This relationship suggests a potential quadratic relationship between duration and temperature. Insufficient data were available for chronic heat stress situations to define a quadratic relationship, and therefore, a linear relationship was used.

Pigs are particularly sensitive to diurnal temperature cycling during heat stress as rapid temperature changes apparently impair acclimation mechanisms (Lopez et al., 1991a,b; Renaudeau et al., 2007). To account for the impact of studies assessing cycling vs. constant temperatures, the data set was divided into 2 subsets based on whether cycling temperatures were assessed. One model was fit on the basis of the cycling data set, and 1 was fit on the basis of the noncycling data. The resulting conditional equation (**TC**) predicting FFI is given as

$$FFI = \begin{cases} c1 + c2 \times [T - (LCT + 3)] + c3 \times \\ \quad [T - (LCT + 3)^2] + c4 \times HighT, & \text{if } NC = 1, \\ c5 + c6 \times [T - (LCT + 3)], & \text{otherwise}, \end{cases} \quad [9]$$

where c1 through c6 are the coefficients to be fit, NC is a binary indicator of night cooling, and HighT is daily high temperature (°C). When night cooling occurs, the first equation (c1 through c4) should be used; otherwise, the second equation (c5 and c6) should be used.

Housing conditions are also thought to affect pigs responses to heat stress. Solid floors, rather than slatted floors, have been shown to reduce productivity in swine during thermoneutral and heat stressed conditions (Stansbury et al., 1987). To account for the differences in responses to heat stress on solid compared with slotted floors, a third FFI prediction (**TH**) was compiled:

$$FFI = \begin{cases} c1 + c2 \times [T - (LCT + 3)] + \\ \quad c3 \times [T - (LCT + 3)]^2, & \text{if Solid} = 1, \\ c4 + c5 \times [T - (LCT + 3)], & \text{otherwise}, \end{cases} \quad [10]$$

where Solid is a binary indicator variable for solid floors and c1 to c5 are coefficients to be derived. In Eq. [10], when solid floors are used, intake should be predicted with the first equation (c1 through c3); otherwise, the second equation should be used (c4 and c5).

A series of additional parameters are likely to affect feed intake responses to temperature. The biological influence of heat stress is impacted by duration of exposure to extreme temperatures (Renaudeau et al., 2007), night cooling (Xin and DeShazer, 1991; Patience et al., 2005), relative humidity (Huynh et al., 2005), diet composition (Jørgensen et al., 1996; Kerr et al., 2003), and genetics (Brown-Brandl et al., 2001; Sutherland et al., 2006), among others. In particular, ME content (Baldwin and Sainz, 1995; Rodrigues et al., 2012), protein and AA balance (Kerr et al., 2003; Spencer et al., 2005; Wolp et al., 2012), dietary additives (Zier-Rush et al., 2014) ,and mineral concentrations (Haydon et al., 1990; Kim et al., 2009) all affect responses to heat stress. To understand the relationships among variables, a mixed-effect linear model of absolute intake was also derived from the data set. Feed intake as a fraction of metabolic BW ($BW^{0.6}$) was used as a response variable. As this was not standardized among studies, a random intercept for study was included in the model. Equation [11] represents the initial model; 2-way interactions between temperature and all other variables (interactions not listed in Eq. [11]) were also evaluated within the model. All variables are as defined in Table 2.

$$\begin{aligned} FI\_MBW = {} & T + Dur + Tspan + BW + Eur + UK + \\ & SEA + SA + Abatement + ADG + CP + ME + \\ & Mesh + Solid + Slat + on12 + Room + \\ & Outside + Density + Individual, \end{aligned} \quad [11]$$

Because of the high correlation among some explanatory variables, the equation was derived using a 2-phase stepwise procedure. All variables were included initially and were sequentially eliminated if both the main effect and the interaction with temperature were insignificant. Once a model in which all parameters were statistically significant was identified, previously dropped parameters were individually added back into the equation, and corrected Akaike information criteria (Hurvich and Tsai, 1993) were compared to identify whether the added parameter improved the model likelihood. This second phase was added to account for concerns with dropping a significant parameter early in the stepwise regression due to nonsignificance. No dropped parameters were added back into the model.

The mixed model, although informative, had minimal practical field applicability, and an equation derived specifically for field use was desired. A series of attempts was made to derive a field-applicable feed intake model; however, the existing representation from Renaudeau et al. (2011) had improved RMSPE and CCC compared with the independently derived feed intake models. As such, a series of adjustments were derived for the R2011 equation. All adjustments to this model were derived in a stepwise manner, where all parameters in Table 2 were included initially and parameters were sequentially

Table 2. Model and variable definitions

Variable	Definition
T − (LCT+3)	Difference between the observed temperature and the l10ower critical temperature plus 3°[1]
Dur	Duration of exposure to temperature (d)
Tspan	Difference between high and low temperatures
Eur	1 if study was conducted in continental Europe, otherwise 0
Asia	1 if study was conducted in Asia, otherwise 0
UK	1 if study was conducted in the United Kingdom, otherwise 0
SEA	1 if study was conducted in Oceana, otherwise 0
SA	1 if study was conducted in South America
NC	1 if study used cycling temperatures, otherwise 0
Abatement	1 is study employed fans or sprinklers to abate heat stress
CP	Crude protein content of the diet (% DM)
ME	Metabolizable energy content of the diet (mcal/kg)
Mesh	1 if floor was specified as wire mesh or expanded metal, otherwise 0
Solid	1 if floor was specified as solid or concrete, otherwise 0
Slat	1 in floor was specified as plastic, concrete or metal slats, otherwise 0
On12	1 if an 11- to 13-h photoperiod was used, otherwise 0
Outside	1 if study was conducted outdoors or with outdoor access, otherwise 0
Chamber	1 if study was conducted in a metabolism crate or chamber, otherwise 0
m2Pigs	Square meters available per pig (m^2/pig)
Individual	1 if pigs were housed individually, otherwise 0
ADG	Average daily gain (g)
Potential	Maximum reported ADG within a study divided by mean BW (g/d/kg)

[1]Lower critical temperature (LCT) was calculated following NRC (2012).

eliminated because of nonsignificance. A random study effect was included in deriving Eq. [13] and [14] because feed intake, rather than FFI, was used as a response variable. Although assuming an intercept of 0, the R2011 equation follows the general format

$$FI = a + b \times BW^{0.69} . \quad [12]$$

The existing representation of critical temperature was assumed to be accurate because efforts to derive bias adjustments to predict critical temperature as a function of housing density, floor type, and potential growth rate resulted in no significant parameters. New parameters were derived to estimate the slope of intake per unit $BW^{0.69}$ (Eq. [13]), and additional terms accounting for temperature, diet, and duration of exposure were also added:

$$b = c1 + c2 \times \ln(1 + e^{T-40.9+4.4\times\ln(1+BW)}) + c3 \times T + c4 \times T^2 + c5 \times CP + c6 \times Dur + c7 \times Dur^2 . \quad [13]$$

Equation [12] was designed to replace Eq. [6] (defined above) from the R2011 calculation scheme. The parameters used in Eq. [13] were those that were statistically significant in a stepwise regression analysis beginning with the continuous parameters identified as significant in Eq. [11]. The residuals of Eq. [13] were biased against several additional diet and housing parameters, so an intercept function was also calculated to better account for these main effects of feed intake:

$$a = c1 + c2 \times \log(ADG) + c3 \times HighT + c4 \times ME . \quad [14]$$

Equations [13] and [14] were combined and used to estimate feed intake as described in Eq. [12].

The adjusted Renaudeau et al. (2011) model (**RMod**) was used to estimate FFI and FI, and the RMSPE, CCC, and mean and slope biases were compared to those from the other models. Residual analyses were used to identify what additional explanatory variables may help to explain more variation in FI. The same adjustments were attempted for the NRC equation; however, the FFI metric was less sensitive to the additional explanatory variables, and the RMSPE and CCC of the FFI equations were higher than the adjusted R2011 model (data not presented).

Model Verification

The data set used in evaluation and derivation of new FFI and FI models was collected in June 2014. Studies published between June 2014 and May 2015 were collected to evaluate the equations derived herein. Although numerous studies within this time period evaluated the effects of fetal stress on downstream growth performance, only 6 studies (23 treatment means) were identified that reported production responses of growing or finishing pigs to thermal stress using a thermoneutral control group with unrestricted intake and 1 or more thermal-stressed groups. This evaluation data set was used to evaluate the repeatability of the fit statistics for each equation derived here (NRCmod, TC, TD, TH, RMod).

RESULTS AND DISCUSSION

NRC Model Evaluation

Average BW and temperatures reported for each treatment comparison were used to predict LCT and FFI following Eq. [1] through [3]. Figure 1 shows the relationship between the residuals and the prediction of FFI using the NRC equation. This relationship demonstrates significant mean ($P < 0.001$) and slope bias ($P < 0.001$). The disparity between the NRC-calculated FFI

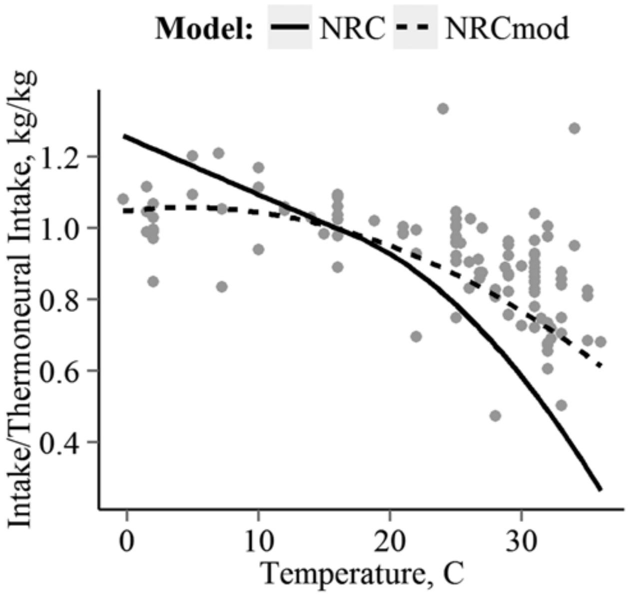

Figure 2. Comparison of NRC predicted and NRCmod predicted intake and a fraction of thermoneutral intake (FFI) compared with the experimentally observed FFI. The NRC line appears above the experimental data at low temperatures and below the data at high temperatures. The new NRCmod line runs through the center of the data across the entire temperature range. Average BW were used to derive these lines for demonstration.

Table 3. Original and revised NRC parameters and associated fit statistics for predictions of the percent depression in feed intake during cold or heat stress

Term	NRC[1]	NRCmod[2]	SE	P^3
Intercept	1.00	1.01	0.028	0.001
[T − (LCT+3)]	-1.29×10^{-2}	-1.02×10^{-2}	1.40×10^{-3}	0.001
$[T - (LCT+3)]^2$	-1.18×10^{-3}	-4.49×10^{-4}	1.58×10^{-5}	0.001
Fit Statistics	NRC[1]	NRCmod[2]	Evaluation	
RMSPE, % Mean[4]	23.6	13.02	23.8	
Mean,[5] % MSE	12.6	0.03	14.5	
Slope, % MSE	51.1	2.2	0.02	
Residual, % MSE	36.3	97.8	85.4	
CCC[6]	0.498	0.576	0.142	
MAE[7]	0.071	0.002		

[1]Equation parameters from NRC (2012). Although the evaluation of the NRC was based on Eq. [1] and [3], only the parameters for Eq. [1] are presented here for comparison to NRCmod.

[2]New parameters fit to equation form presented in NRC (2012).

[3]Significance of coefficients for parameters fitted to NRCmod equation.

[4]Root-mean-square error of prediction (RMSPE).

[5]Proportions of mean squared prediction error partitioned to mean bias, slope bias, and residual error, with the latter expressed as a percentage of mean squared prediction error.

[6]Concordance correlation coefficient.

[7]Mean absolute error.

and the literature data is depicted in Fig. 2. The RMSPE of 23.6% was a concern as this error would compound with errors in the feed intake prediction, likely yielding poor accuracy and precision in estimating intake. The CCC (0.498) also indicated poor accuracy and precision of the FFI estimates compared with the measured data (Table 3). The mean bias indicated that FFI tended to be underpredicted by 7% units as temperature increased from 0°C to 40°C. This systematic underprediction of FFI may be due to inappropriate specification of the relationships between FFI and temperature. Alternatively, failure to account for known FFI influences such as night cooling, duration of exposure, housing, heat abatement strategies, or genetics may contribute to the biases in predicting FFI (Christianson et al., 1982; Nienaber et al., 1999; Renaudeau et al., 2011). The significant mean bias (underpredicting FFI by 7%) supports the hypothesis that the environmental stress module of the NRC (2012) model overpredicted the negative implications of heat stress on swine feed intake. As the environmental stress module of the NRC (2012) model was designed on the basis of 1 experiment involving group-housed pigs (Quiniou et al., 2000) and was intended only for explanatory purposes, this poor representation of the behavior is not unexpected. Although a slope bias was revealed by the residuals, previous literature supports the use of a quadratic relationship between temperature and intake depression (Stahly and Cromwell, 1979; Close, 1987). The behavior of these data indicates that the equation form is likely adequate but that the parameters may have been fit from an unrepresentative data set or a set that did not contain sufficient extremes in temperature to accurately model the real shape of the response.

Fitting New Parameters

Table 3 includes a comparison between the new and old parameters and the fit statistics for NRC and NRCmod. The new parameters yield an intake response curve with a less severe slope (Fig. 2). The intake depression predicted by the new equation more closely resembles FFI response estimated in previous metastudies (Renaudeau et al., 2011) and in studies measuring intake response (Fuller, 1965; Close, 1987; Rinaldo et al., 2000). The RMSPE of NRCmod was 13.02% of mean FFI, which represents a 45% reduction when compared with the NRC predictions. The CCC also improved (0.576), indicating greater agreement between measured and predicted observations. Additionally, both coefficients in the FFI model were significantly different from 0 ($P < 0.001$; Table 3). The reduced systematic bias and improved error of the NRCmod suggest it as a useful alternative for quantifying changes in intake during heat stress.

Figure 3 shows the residuals from NRCmod plotted against the new predicted values and across temperature. The mean and slope bias of NRCmod were not significant and represented substantial reductions in bias compared with NRC (Fig. 3). The trend of residuals with

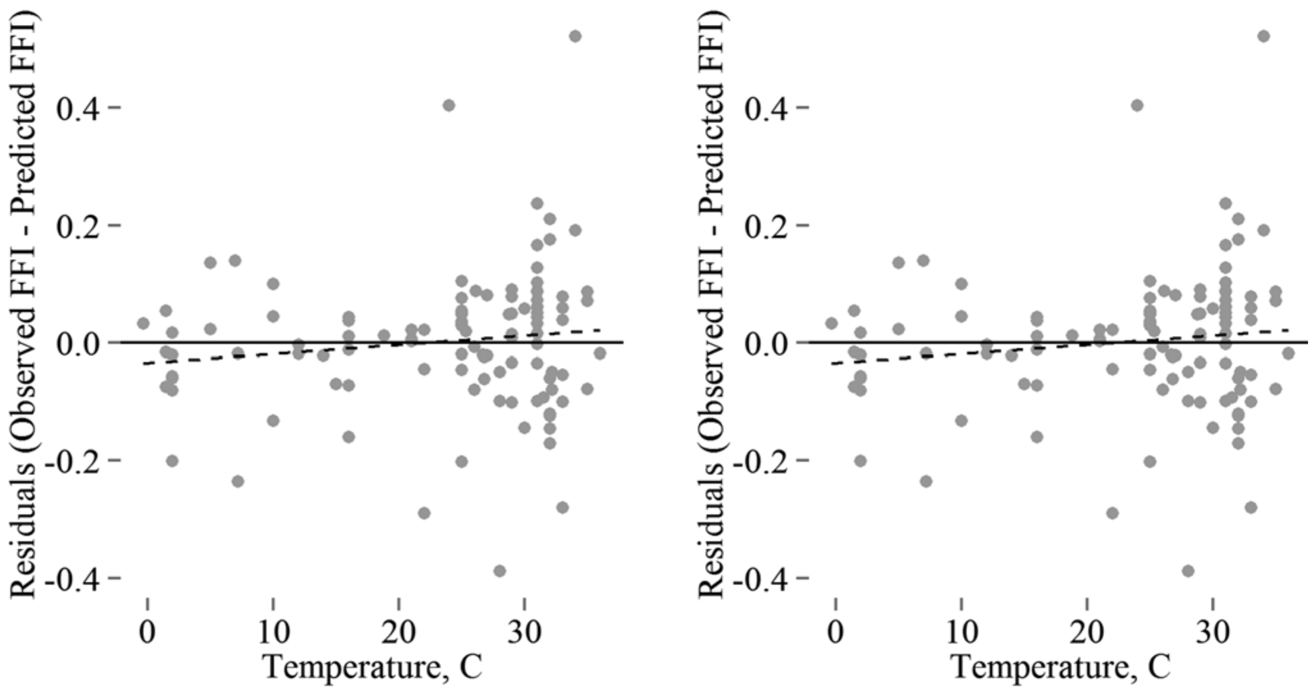

Figure 3. Residuals (predicted minus observed intake vs. predicted intake) all expressed as a fraction of thermoneutral intake (FFI) vs. temperature. The left graph shows that fitting the new parameters substantially reduced the mean and slope bias. The right graph shows no trend in residuals with respect to temperature.

respect to temperature was also substantially reduced (NRCmod did not exhibit systematic prediction bias across temperatures). The RMSPE analysis indicated that 97.8% of the prediction error was random.

The new model relied on a continuous relationship between FFI and temperature, whereas the NRC (2012) model used a discontinuous relationship. The NRC cold stress equation assumed a 1.5% or 3% decrease in feed intake per unit T below LCT for 25 and 90 kg pigs. The data representing cold-stressed production was measured in environments with temperature ranging from 1.5°C to 16°C on pigs with BW averaging 48.3 kg and ranging from 24.6 to 73.2 kg. The NRC (2012) model estimated an average 2.25% change in FFI per degree Celsius below LCT. The average increase in FFI from the data used in this study was 0.45% per degree Celsius below LCT. The average increase in FFI was lower than the 25-kg pig from NRC (2012) even though the average BW of pigs herein was 48.3 kg. This comparison further supports a systematic overprediction of FFI in NRC (2012).

Additional Fractional Feed Intake Models

A series of additional FFI models was derived to explain variability in FFI as a function of temperature and duration of exposure, temperature cycling, and housing type (Fig. 4). The coefficients and fit statistics associated with these models are included in Table 4. All models resulted in improved RMSPE compared with the NRC and NRCmod models (Tables 3 and 4) and are preferable for field use if the additional input data are available. The reduced bias and improved error of these new models (Tables 3 and 4) suggest that explanatory variables representing duration of exposure to thermal stress, presence of cycling temperatures, and type of housing should be included in future efforts to model swine responses to temperature. As data were preselected on the basis of estimated genetic merit, other factors not considered here may also affect feed intake responses to thermal environment. Although efforts were made to derive significant effects of other housing, genetic merit, and diet parameters, all parameters were dropped from the model during fitting, suggesting that NRCmod was a robust representation of fractional feed intake.

The TD model resulted in significant coefficients for a linear effect of duration of exposure (Table 4). Conflicting relationships between intake and duration of exposure to environmental stress have been reported (Verhagen, 1987; Sutherland et al., 2006; Renaudeau et al., 2007). In acute heat stress studies, pigs appear to acclimate to the environmental conditions after a short-term decrease in performance (Renaudeau et al., 2007). The TD model supported this hypothesis as the duration coefficient was positive, meaning that intake increased with increasing duration of exposure, suggesting that pigs acclimate to thermal stress. Previous research suggests that acclimation begins within a week of exposure and continues for several days, and the acclimation response varies according to the

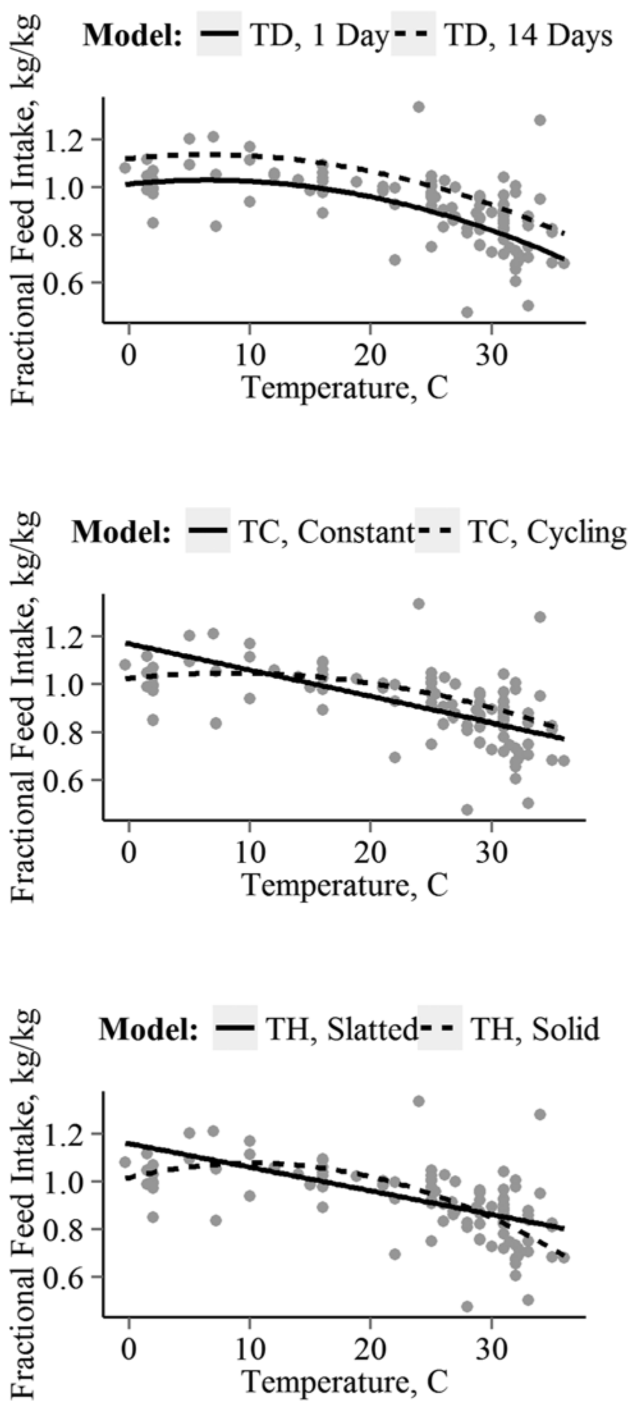

Figure 4. Comparison of intake as a percentage of thermoneutral intake (FFI) predicted by the TD, TC, and TH equations. Comparisons between factors influencing FFI are noted in each legend.

severity of thermal stress (Verhagen, 1987; Renaudeau et al., 2007; Renaudeau et al., 2010). The predicted responses from the TD model (Fig. 4) suggest substantial improvement in FFI after 2 wk of exposure, which agrees with these previous findings. However, as only a linear effect could be identified, this equation fails to capture the acute reduction in intake occurring at the start of a prolonged bout of heat stress (Sutherland et al., 2006). As more consistent time series data on heat stress responses are reported, additional efforts should be made to better represent this phenomenon.

The TC model was useful for simulating production scenarios with cycling temperatures. As previous studies would suggest (Xin and DeShazer, 1991; Nyachoti et al., 2004; Patience et al., 2005), temperature cycling affected FFI. High temperature tended to affect FFI ($P = 0.062$) when temperatures cycled diurnally, but responses to thermal stress were linear across temperatures when cycling did not occur. Heat-stressed climates with temperature cycling can result in exceptionally poor feed intake as pigs have a more difficult time adapting to the elevated environmental temperatures (Lopez et al., 1991a; Xin and DeShazer, 1991; Patience et al., 2005). In contrast, night cooling has been proposed as a way to improve feed intake during times of heat stress because it allows a period of time within the thermoneutral zone for pigs to recover (Ames and Ray, 1983). This recovery is evidenced by shifts in eating behavior (Xin and DeShazer, 1992) and physiological parameters (Patience et al., 2005). The comparison of constant and cycling environments (Fig. 4) indicated that FFI was predicted to be slightly greater under heat stress when the temperature cycled than during constant heat stress. However, the model also predicted that the positive effect of cold stress on FFI was less pronounced when the temperature cycled compared to when temperature was constant. Low-temperature data were limited, and thus, the results need to be verified as additional data come available. During extreme heat stress (T > 30°C), the projected differences in FFI between constant and cycling temperatures diminished. This may be reflective of the thermal environment no longer cycling in and out of the thermoneutral zone. If temperature is cycling above the thermoneutral zone, animals will no longer experience the daily time period in the thermoneutral zone which has been associated with moderate abatement in stress (Patience et al., 2005; Segura et al., 2006).

The TH model was designed to identify differences between pigs in housing systems with solid or slatted floors. The predicted response to heat on slatted floors was linear with temperature, and during periods of high heat (T > 28°C) animals in environments with slatted floors consumed more feed than animals housed on solid floors. During moderate heat stress (24°C < T < 28°C), the opposite was true. This differential benefit of alternative flooring systems may be reflective of the efficacy of different heat abatement strategies. As temperature increases, time spent huddling decreases, wallowing behavior increases, and time spent lying on slatted floors (if available) increases (Huynh et al., 2005). Lying on solid floors may be an effective cooling mechanism during moderate heat stress, but as the temperature of the floor increases as a function of room temperatures, this

Table 4. Parameters and associated fit statistics for new equation forms predicting the percent depression in growing pig feed intake associated with temperature stress[1]

Term[2]	TD	TD SE	TD *P*	TC NC = 1	SE	*P*	TC NC = 0	SE	*P*	TH Solid	SE	*P*	TH Slatted	SE	*P*
Int.	0.97	0.02	<0.001	0.59	0.22	0.011	0.97	0.02	<0.001	1.04	0.04	<0.001	0.98	0.02	<0.001
[T − (LCT+3)]	-8.8×10^{-3}	9.5×10^{-4}	0.073	-2.3×10^{-2}	7.8×10^{-3}	0.006	-1.1×10^{-2}	2.0×10^{-3}	<0.001	-9.2×10^{-3}	1.7×10^{-3}	<0.001	-9.9×10^{-3}	1.9×10^{-3}	<0.001
$[T - (LCT+3)]^2$	-3.8×10^{-4}	1.1×10^{-4}	<0.001	-3.1×10^{-4}	1.4×10^{-4}	0.031				-5.8×10^{-4}	2.2×10^{-4}	0.011			
Dur	8.2×10^{-3}	4.5×10^{-4}	<0.001												
HighT				1.7×10^{-2}	9.0×10^{-3}	0.062									

Fit statistics	TD Derivation	TD Evaluation	TC Derivation	TC Evaluation	TH Derivation	TH Evaluation
RMSPE[3]	12.9	22.1	12.6	29.0	12.9	26.0
Mean bias, % MSE	0.52	15.6	<0.01	4.8	<0.01	25.7
Slope bias, % MSE	0.26	6.97	<0.01	29.2	<0.01	1.76
CCC[4]	0.563	0.274	0.558	−0.13	0.536	0.006
MAE[5]	0.008	−0.070	0.079	−0.050	<0.001	-0.112

[1]Significance of coefficients in the duration (TD), temperature cycling (TC), and floor type (TH) models indicated by *P*-values.

[2]Int. is the intercept of each equation, and T is the temperature variable, T − (LCT+3).

[3]Root-mean-square error of prediction (RMSPE) in all these models, the mean and slope errors summed to less than 1% of the mean squared prediction error.

[4]Concordance correlation coefficient.

[5]Mean absolute error

heat abatement behavior becomes less effective. During cold stress, the model again suggests increased FFI for animals on slatted floors compared with solid floors. This may be because the increased ventilation on slatted floors results in a more cold-stressed environment than the solid floors, which provide more insulation.

Genetic Potential, Housing, Environment, and Experimental Effects

A mixed effect linear model was derived in a stepwise manner to identify how feed intake was affected by variables representing genetic potential, housing system, thermal environment, and experimental protocol. The final model is summarized in Table 5. Temperature interacted with heat abatement, dietary protein, days of exposure, housing density parameters, photoperiod, study location parameters, floor-type parameters, and temperature span. Heat abatement, ADG, days of exposure, housing density parameters, housing-type parameters, photoperiod, study location, experimental protocol, and BW also had direct effects on feed intake. This result is in agreement with previous studies that suggest that housing system (Morrison et al., 2007), stocking density (Jensen et al., 2012; Hemsworth et al., 2013), diet (Wolp et al., 2012), heat abatement strategy (Bull et al., 1997), and duration of exposure to heat stress (Pearce et al., 2013) affect physiological and behavioral responses to heat stress.

A notable interaction was identified between space available and temperature. When evaluated with NRCmod, animals with more available space tended to consume more feed during thermal stress than was predicted by temperature alone (Fig. 5). Group housing is likely beneficial for high-risk or stressed animals as evaluation of NRCmod suggested heat-stressed pigs tend to consume more feed when group housed than when individually housed (Fig. 5). The mean space allowance in this data set, 1.2 m^2/pig, was larger than typical industry space allowances, suggesting a potential need to reconsider housing density for high-risk or stressed animals. Although statistically significant in Table 5, the responses to housing density and group housing are not well defined (Fig. 5), and the slope of the residuals against either parameter was not statistically significant. Additionally, the additional factors accounted for in RMod resulted in minimal patterning of residuals by housing characteristics.

Table 5. General linear model relating feed intake per kilogram of metabolic BW to thermal, environmental, genetic, and experimental conditions

Factor[1]	Estimate	SE	P^2
Intercept	-0.110	0.097	0.277
Abatement	-0.892	0.137	<0.001
ADG	9.77×10^{-5}	1.32×10^{-5}	<0.001
Chamber	-0.144	0.040	0.002
Days	5.37×10^{-3}	8.11×10^{-4}	<0.001
m2Pigs	−0.117	0.032	<0.001
ME	1.19×10^{-4}	3.32×10^{-5}	0.004
Mesh	−0.099	0.028	0.012
on12	0.134	0.032	<0.001
SA	−0.333	0.075	<0.001
SEA	−0.286	0.060	0.001
Solid	0.287	0.039	<0.001
Span	−0.019	3.47×10^{-3}	<0.001
Temp	-4.93×10^{-3}	1.96×10^{-3}	0.017
Weight	-4.78×10^{-3}	2.05×10^{-4}	0.022
Temp:Abatement.	0.013	3.49×10^{-3}	0.001
Temp:Chamber	2.33×10^{-3}	8.24×10^{-4}	0.006
Temp:CP	-1.87×10^{-4}	5.78×10^{-5}	0.002
Temp:Days	-6.47×10^{-5}	2.36×10^{-5}	0.008
Temp:Individual	2.39×10^{-3}	9.29×10^{-5}	0.026
Temp:m2Pigs	5.11×10^{-3}	1.32×10^{-3}	<0.001
Temp:on12	-4.56×10^{-3}	9.73×10^{-4}	<0.001
Temp:SA	6.54×10^{-3}	1.87×10^{-3}	0.001
Temp:Solid	-7.96×10^{-3}	1.27×10^{-3}	<0.001
Temp:Span	9.02×10^{-4}	1.46×10^{-4}	<0.001

[1]Factors include main effects and interactions between temperature and various additional explanatory variables. Interactions are shown using the form X:Y.

[2]Significance of factors determined by *P*-values.

As indicated in Table 5, myriad factors affect feed intake. Swine responses to thermal stress can be represented by empirical predictions (Renaudeau et al., 2010, 2011; NRC, 2012) such as the model derived here or more mechanistic representations of heat exchange (Bruce and Clark, 1979; Black et al., 1986; Knap, 1998; Black et al., 1999). Although mechanistic approaches may be a long-term solution to modeling feed intake, improved biological understanding of the relative contributions and priorities of factors governing feed intake must be achieved before we can derive robust parameters for these models. As noted in Black (2014), appropriate parameterization of mechanistic feed intake models remains a paramount challenge to be addressed by future research. The data set collected in this study was not conducive to deriving a mechanistic model, and thus, an empirical approach was taken to understand how these interactions among environmental factors affected feed intake.

The empirical feed intake prediction evaluated (R2011) model showed slight bias when compared with the available data (Table 6; Fig. 6). Although the RMSPE of 22.3% was reasonable for a feed intake prediction, slope bias contributed 12% of mean squared error (**MSE**), indicating some structural misrepresentation within the equation. On the basis of the residual analysis collected, the primary source of slope bias was due to additional sources of systematic variation within the data rather than poor representation of the average response to temperature. The R2011 model had high RMSPE (22.6%) for predicting FFI compared with the NRCmod, TC, TD, and TH equations. The primary contributor to error was slope bias (58.7% MSE), suggesting that FFI was increasingly overpredicted at higher FFI predictions. When considered in terms of the slight slope bias in predicting intake, this bias is not unexpected and was likely due to systematic variation within the data.

The derivation of adjustment parameters to account for additional variables affecting the slope of intake on BW substantially reduced bias in predicting feed intake (Fig. 6). After the intercept and slope adjustments were added (Table 6), the RMod model had an RMSPE of only 16.0% with minimal mean (0.04% MSE) and slope (1.9% MSE) bias. The concordance of the RMod model was excellent (0.96), demonstrating the good agreement between the modeled and measured estimates of feed intake. As a random effect for study was included in the model derivation procedure, it is important to note that these fit statistics are not adjusted for the study effect. On average, the RMod model overpredicted intake by only 6 g; this margin of error is small considering the average intake within the data set was 1.73 kg. The RMod function was unbiased against housing parameters (Fig. 6) and genetic merit (not shown). As such, although the function does not contain variables for these additional factors, the RMod equation may be a useful method of predicting intake of growing-finishing pigs during thermal stress when a more mechanistic approach is impractical.

When RMod was used to predict FFI, the RMSPE was more favorable than with R2011, but it was still greater than RMSPE from NRCMod, TC, TD, and TH. One benefit of the RMod function was the more robust method of calculating a critical temperature. Whereas the NRC predicted lower critical temperature, the R2011 and RMod equations relied on a critical inflection temperature, which allowed for more flexibility in the equations. The RMod function employed a more biologically interpretable calculation of critical temperature, which returned better fit than the simple linear relationship with lower critical temperature employed in NRC (2012). Considering that an intake equation (RMod) could predict intake with an RMSPE of 16.0% and CCC of 0.96, one must consider whether a FFI equation is the best way to account for the effect

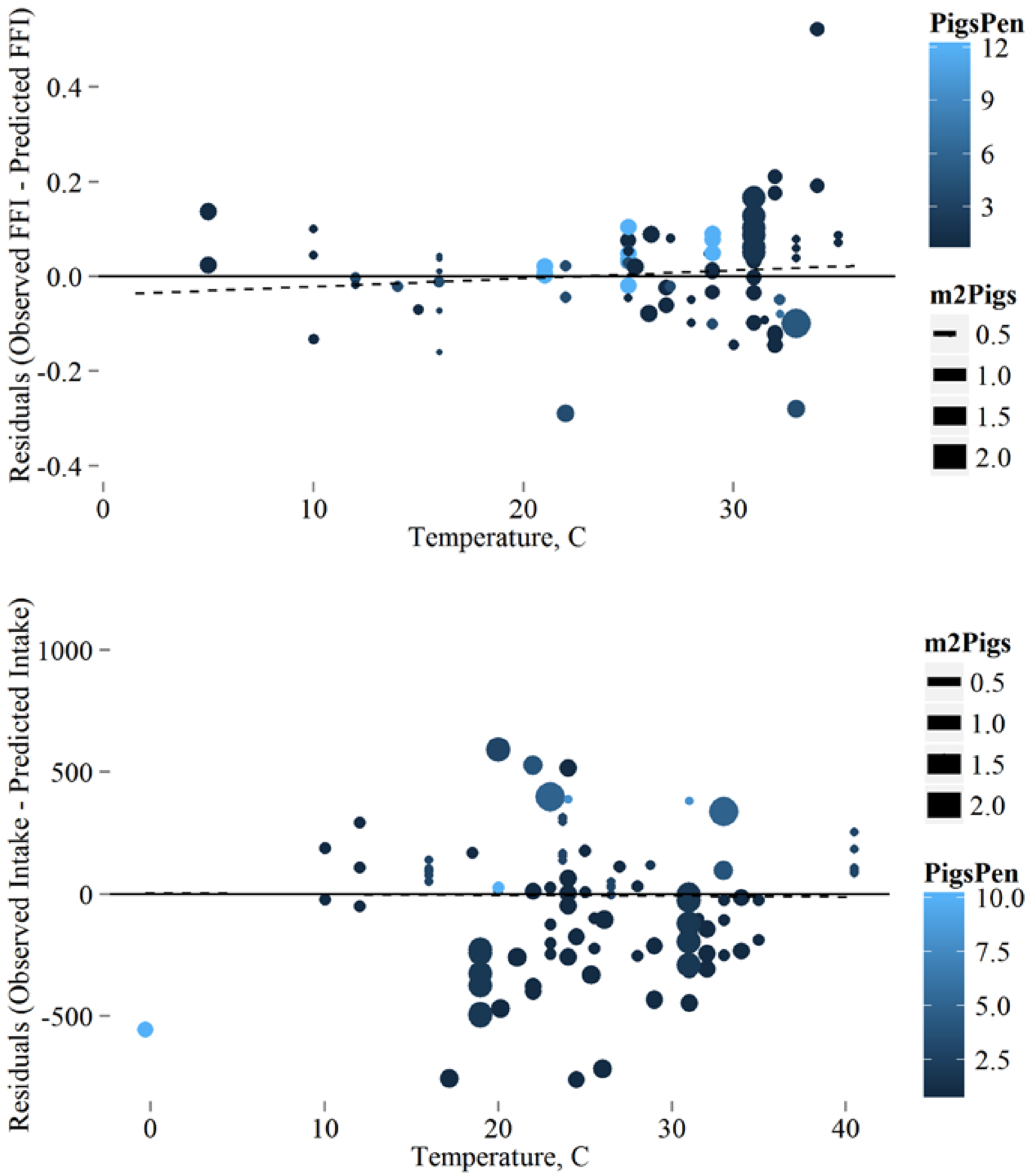

Figure 5. Residuals of the modified NRC (2012) equation (NRCmod) function (predicted minus observed fractional feed intake [FFI]) and the Rmod function (predicted minus observed feed intake) compared across temperatures when considering housing density (m2Pigs) and number of pigs per pen (PigsPen). Data sets differ because of improved data availability in the thermoneutral zone when fitting intake rather than fractional feed intake.

of temperature on intake. Given a typical RMSPE for an empirical intake equation (20%), the additional 12% variation introduced by applying a FFI equation to predict intake during thermal stress would almost undoubtedly result in a less precise estimate of intake than produced from an empirical intake equation that accounts for temperature (R2011, RMod).

Although significant relationships could be identified to adjust R2011 to account for dietary protein and energy concentrations, ADG, daily high temperature, and days of exposure to thermal stress, parameters rep-

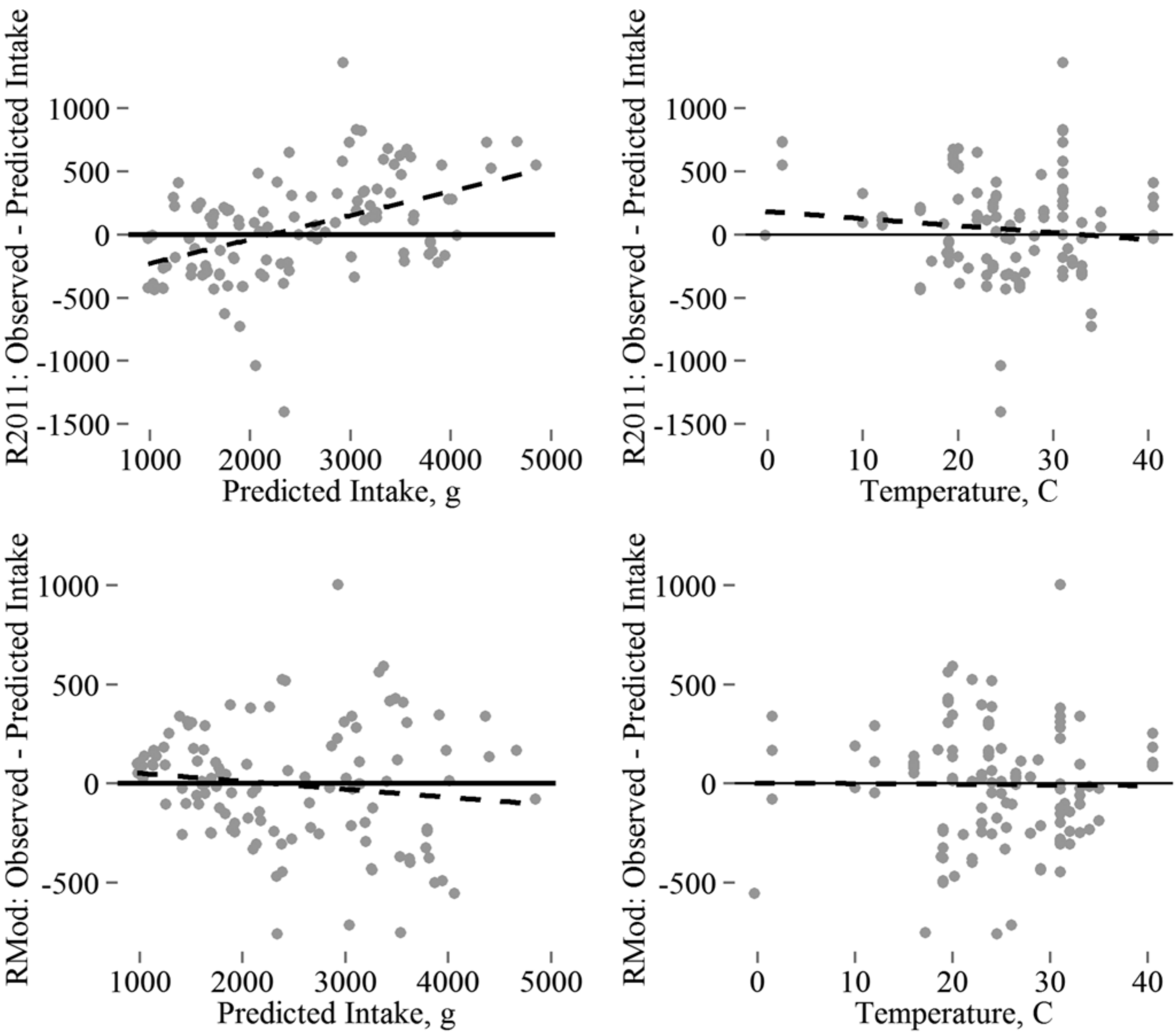

Figure 6. Residuals (predicted minus observed intake vs. predicted intake) of the R2011 (Renaudeau et al., [2011] model) and RMod (Eq. [13] and Eq. [14]) feed intake predictions vs. predicted values or temperature. The left graphs demonstrate the change in mean and slope bias. The right graphs show the reduction in the trend between the residuals and ambient temperature.

resenting the influence of housing parameters on feed intake could not be identified. As additional data that evaluate multiple housing densities across multiple temperatures become available, this relationship should be reevaluated and, likely, included in the model.

Evaluation and Limitations

The evaluations of equations derived herein are presented in Tables 3, 4, and 6. Feed intakes reported from the 23 treatment means available for evaluation had a higher mean (2.0 kg) and lower SD (0.62 kg) than the measurements in the derivation data set (Table 1). Additionally, no cold stress data were available in the evaluation data set, pigs were almost exclusively individually housed, and growth rate averaged 721 g/d compared with 685 g/d in the derivation data set. The limited number of treatments resulted in minimal range in breed, housing structures, diet composition, and other essential parameters. These discrepancies limit the likelihood that the evaluation data set is an appropriate tool to assess the reproducibility of the fit statistics for the equations derived herein. The fit statistics reflect this. The RMSPE and CCC for the FFI predictions from NRCMod, TD, TC, TH, and RMod demonstrate poor fit against the evaluation data set. The intake prediction (RMod) was more durable against the evaluation data set (RMSPE 16.3%), but there was a slope bias to the predictions (28.3% MSE). With only 6 studies of data and no study effects included in the fit statistics, it is very easy for 1 study to pull the residuals into a slope bias, and thus, this bias should be interpreted with care. Until a larger, more comprehensive and representa-

Table 6. Parameters and fit statistics for the intercept and slope adjustments derived for the Renaudeau equation

Slope adjustment[1]	Value	SE	P^2
Intercept	194.1	28.3	<0.001
$\ln(1+e^{T-CT})$	−3.48	1.32	0.009
T	−2.76	1.24	0.028
T^2	0.061	0.035	0.079
CP	−3.03	1.27	0.021
Days	0.76	0.33	0.024
$Days^2$	-4.4×10^{-3}	2.2×10^{-3}	0.060
Intercept adjustment[1]	Value	SE	P^2
Intercept	−3259.5	667.1	<0.001
ln(ADG)	600.1	76.1	<0.001
HighT	10.8	2.59	<0.001
ME	−0.27	0.13	0.050
Intake fit statistics[3]	R2011	RMod	Eval[4]
RMSPE, % mean	22.3	16.0	17.1
Mean bias, % MSE	1.27	0.04	4.30
Slope bias, % MSE	12.3	1.90	4.56
Mean bias, g/d	45.1	−5.8	69.3
Slope bias, g/g	0.18	−0.041	−0.12
CCC	0.90	0.96	0.84
MAE[5]	45.12	−5.84	69.3
FFI fit statistics[6]	R2011[7]	RMod[7]	Eval[4]
RMSPE, % mean	22.6	16.3	23.4
Mean bias, % MSE	0.01	1.05	12.6
Slope bias, % MSE	58.7	28.3	17.4
Mean bias, g/d	−0.002	−0.02	−0.07
Slope bias, g/g	−0.805	−0.63	−0.40
CCC	0.26	0.35	0.56
MAE	−0.002	−0.015	−0.015

[1]The slope adjustment and intercept adjustments correspond to Eq. [13] and [14], respectively.

[2]Significance of parameters was identified by *P*-values.

[3]Fit statistics for measured compared with modeled feed intake included root-mean-square prediction error (RMSPE) and concordance correlation coefficient (CCC).

[4]Fit statistics for modeled intake or fractional feed intake (FFI) against the evaluation data set.

[5]Mean absolute error.

[6]Fit statistics for measured compared with modeled FFI.

[7]Model presented by Renaudeau et al. (2011; R2011) or modified in Eq. [13] and [14] (RMod).

tive evaluation data set is available, the evaluation results have very limited interpretation.

Predicting intake is a great challenge in animal nutrition modeling. The equations evaluated in this project were designed to exactly replace Eq. [8] to [14] of the 2012 swine NRC model (NRC, 2012). Given the good fit statistics from the Renaudeau model, those equations should also be considered by users interested in improved representation of generalized animal responses to thermal stress. Additionally, as the absolute intake models (R2011 and RMod) had reasonable RMSPE and eliminated the need for an additional equation explaining the shape of the response to temperature, the need for FFI equations appears limited. For users relying on the model, these intake adjustment equations can be employed before balancing a ration as an adjustment in the assumed animal feed intake. In addition to the factors addressed in this study, intake varies with gender, genotype, physical environment, health status, feed form, and many other variables. In response to this high variability, on-farm intake monitoring systems have shown promise in improving production efficiency by allowing more precise estimates of actual feed consumption in the facility (Nyachoti et al., 2004), which provides opportunities to improve productivity and limit environmental impact (Pomar et al., 2009; Andretta et al., 2014). Understanding of climate interactions with feed intake would benefit from a standardized reporting of health status, physical environment, genotype, and feed form in publications. Reporting this information allows for use of meta-analytic techniques to interrogate the cross-study similarities and differences attributable to these additional parameters.

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