Weather influences feed intake and feed efficiency in a temperate climate

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INTERPRETIVE SUMMARY

Weather influences feed intake and feed efficiency in a temperate climate. *By Hill and Wall*. We tested how feed intake and the rate of converting dry matter to milk (feed efficiency, FE) vary in response to weather and genetic merit in Holstein Friesians under temperate conditions. Cows of high genetic merit (Select) had higher milk yield, dry matter intake and FE than Controls. As an index of temperature and humidity (THI) increased, both genetic lines decreased dry matter intake and milk yield and, importantly, increased FE. Improvements in FE may partially offset the costs of reduced milk yield under a warming climate, at least under conditions of mild heat stress.

ABSTRACT

A key goal for livestock science is to ensure that food production meets the needs of an increasing global population. Climate change may heighten this challenge through increases in mean temperatures and in the intensity, duration and spatial distribution of extreme weather events, such as heat waves. Under high ambient temperatures, livestock are expected to decrease dry matter intake (DMI) to reduce their metabolic heat production. High yielding dairy cows require high DMI to support their levels of milk production, but this may increase susceptibility to heat stress. Here, we tested how feed intake and the rate of converting dry matter to milk (feed efficiency, FE) vary in response to natural fluctuations in weather conditions in a housed experimental herd of lactating Holstein Friesians in the UK. Cows belonged to two lines: those selected for high genetic merit for milk traits (Select) and those at the UK average (Control). We predicted that 1) feed intake and FE would vary with an index of temperature and humidity (THI), wind speed and the number of hours of sunshine, and that 2) the effects of (1) would depend on the cows' genetic merit. Animals received a mixed ration, available ad libitum, from automatic feed measurement gates. Using >73,000 daily feed intake and FE records from 328 cows over eight years, we found that Select cows produced more fat and protein corrected milk (FPCM), and had higher DMI and FE than Controls. Cows of both lines decreased DMI and FPCM but, importantly, increased FE as THI increased. This suggests that improvements in the efficiency of converting feed to milk may partially offset the costs of reduced milk yield owing to a warmer climate, at least under conditions of mild heat stress. The rate of increase in FE with THI was steeper in Select cows than in Controls, which raises the possibility that Select cows use more effective coping tactics. This is, to our knowledge, the first longitudinal study of the effects of weather on feed efficiency. Understanding how weather influences feed intake and efficiency can help us to

develop management and selection practices that optimize productivity under unfavorable weather conditions. This will be an important aspect of climate resilience in future.

KEYWORDS

Comprehensive Climate Index, crude protein intake, feed conversion ratio, metabolizable energy intake

INTRODUCTION

Producing enough food to meet the needs of the growing human population is an important challenge, especially given concerns over climate change. One way to address this challenge is in improving feed efficiency, the amount of meat or milk produced per unit of dry matter. Improving feed efficiency allows producers to increase their net output while minimizing feed costs and environmental impacts (Reynolds et al., 2011).

Individual cattle can vary in dry matter intake (**DMI**) above or below what is expected based on their growth rate or size (Herd & Arthur, 2009). They also differ in the amount of manure, methane and carbon dioxide they produce for a given unit of DMI, and in their abilities to generate and conserve heat energy (Arndt et al., 2015; DiGiacomo et al., 2014). Animals that have a higher core body temperature, all else being equal (e.g. feed intake), are expected to direct a greater proportion of feed energy into metabolic heat production than into productivity, which reduces their production efficiency. Support for this comes from studies showing that beef cattle that are more efficient at directing feed to growth have lower rectal temperatures (Martello et al., 2016) and produce less metabolic heat (Basarab et al., 2003; Nkrumah et al., 2006) than less efficient animals. Similarly, dairy cows that convert feed into milk more efficiently produce less heat as a proportion of gross energy intake (Arndt et al., 2015) and have lower skin surface temperatures than less efficient cows (DiGiacomo et al., 2014). This suggests that efficient dairy cows might be less susceptible to thermal stress (stresses associated with high or low temperatures) than less efficient cows as a consequence of better thermoregulatory abilities in the former.

Dairy cows, like other homeothermic animals, experience heat stress when environmental variables such as ambient temperature, humidity, solar radiation and wind speed combine to exceed the body's thermoneutral zone, the range of ambient conditions at which metabolic heat production and heat loss are in equilibrium. High yielding dairy cows require high metabolic rates to support such yields, and this generates considerable metabolic heat (Kadzere et al., 2002). As metabolic heat production increases, a cow's thermoneutral zone shifts to a lower temperature range (Coppock et al., 1982). This means that higher yielding dairy cows experience heat stress at lower temperatures than lower yielding cows (Berman, 2005). In response to heat stress, cows reduce nutrient uptake, reallocate energy to thermoregulation, and experience changes in metabolism and endocrine function (Bernabucci et al., 2010; Renaudeau et al., 2012; Rhoads et al., 2009). These adjustments can lead to decreases in milk yield and quality (Bohmanova et al., 2007; Hammami et al., 2013; Hill and Wall, 2015).

The environmental conditions associated with heat stress can be quantified using Temperature Humidity Indices (**THI**), which are based on different weightings of ambient temperature and humidity. Evaporative cooling is the main means of energy loss in ruminants (Blaxter, 1962), but, when ambient humidity is high, the process is hampered by a reduced moisture gradient between the air and respiratory surfaces. The thermal tolerance of cattle is also influenced by the velocity of ambient air (which influences rates of latent and sensible heat loss) and solar radiation (Dikmen and Hansen, 2009; Graunke et al., 2011; Hammami et al., 2013). This led Mader et al. (2006) to formulate a single metric that adjusts ambient temperature for relative humidity, wind speed and solar radiation, termed 'adjusted THI' (hereafter THI_{adj}). THI_{adj} explained milk traits more effectively than THI in a study carried out under temperate conditions (Hammami et al., 2013). Building upon these indices, the Comprehensive Climate

Index (**CCI**), which also adjusts ambient temperature for relative humidity, wind speed and solar radiation, was developed specifically to consider the effects of both hot and cold environmental conditions on cattle, and was validated for its effects on DMI (Mader et al., 2010). Although the impact of heat stress on dairy cows has been well-documented in tropical and subtropical regions (e.g. Dikmen and Hansen, 2009; West et al., 2003), a growing number of studies has reported declines in milk yield and quality with increasing THI in temperate regions (reviewed in Van Iaer et al., 2014), including the UK (Dunn et al., 2014; Hill and Wall, 2015), which has a maritime temperate climate with mild summers and winters.

Here we used eight years' data from a research farm on the west coast of Scotland to investigate the effects of weather on dry matter intake (**DMI**) and the rate of converting dry matter to milk (feed efficiency, **FE**) in Holstein Friesian dairy cows. In southern Scotland temperatures are predicted to increase over the 21st century, especially in summer, with an expected mean daily maximum temperature increase of 4.3°C by the 2080s (Jenkins et al., 2009). The aims of our study were threefold. First, we used Akaike's Information Criterion to compare three thermal indices: a) THI, where wind speed and the number of hours of sunshine were controlled for statistically; b) THI_{adj}; and c) CCI. As animals show a lagged response to THI with respect to milk yield (Bouraoui et al., 2002; West et al., 2003; Bertocchi et al., 2014), our second aim was to determine a biologically relevant timescale for quantifying the effects of thermal stress on DMI and FE. We did this by comparing the effects of weather on the day of feeding, mean weather spanning the day of feeding plus the 2 days before (3 day means) and mean weather spanning the day of feeding plus 6 days before (7 day means). Third, we tested how genetic selection for milk traits influenced feed intake and FE (whereby a higher FE indicates a greater weight of fat and protein corrected milk produced for a given DMI) under varying weather conditions. We predicted that 1) as thermal indices increase, cows will reduce feed intake to decrease metabolic heat production, and reduce FE to divert more resources from production to thermoregulation. We also predicted that 2) the impact of heat stress on feed intake and FE would be greater in cows of high than average genetic merit because high yielding dairy cows generate more metabolic heat than lower yielding cows.

MATERIALS AND METHODS

Subjects, Maintenance and Data Collection

The Langhill Holstein Friesian dairy herd was studied at Crichton Royal Farm, Dumfries (55°04695' N, 3°5905' W) between March 2004 and July 2011 inclusive. The herd consisted of ~200 cows, of which approximately half remained indoors throughout the year, while the rest were grazed between April and October. For the remainder of the year all cows were housed in distinct halves of the same building (92.2 × 26.7 m) with access to a shared loafing area (18 × 26.7 m of the building's total space). The continuously housed cows were the focus of our study. They belonged to two genetic lines: Select cows were bred to bulls of the highest genetic merit for kg fat plus protein in the UK, whereas Control cows were bred to bulls close to the UK average for those traits. Bulls were selected at random within a genetic line except that close relatives or sires known to yield calving difficulties were not used. Calving took place all year round, with most calves (65.6 %) being born between October and March of a given year. There were no differences in calving date between the two genetic groups within a given year (Select: ordinal date 168.56±7.78, N = 316, Control: 170.5±7.47, N = 352; β=1.97±10.74, t=-0.18, P = 0.855; Linear Mixed effects Model controlling for lactation number and cow identity).

The cows were housed in a single building in conventional cubicle stalls (210 × 110 cm) supplied with rubber mattresses covered with sawdust. The northernmost half of the NE-facing side of the building was open-sided above a 140 cm high concrete wall. The southern half consisted of a gated section (~3m wide) at either side of an indoor loafing area that was otherwise open to the elements and looked out to grazing fields. The remaining walls consisted of a concrete lower portion (190 cm high), and Yorkshire boarding from the concrete wall to the roof. The wooden panels (115 × 10 cm wide) that made up the Yorkshire boarding were separated by 3 cm gaps between consecutive panels, or a 70 cm gap after every 16th panel, to allow free airflow. There was no artificial ventilation. Pillars supported a gabled roof consisting of corrugated cement fiber with Perspex skylights.

Select and Control cows received the same low forage diet consisting of 50 % home-grown silage (grass, maize and ammonia-treated wheat) and 50 % commercial concentrate feed (wheat grain, sugar beet pulp, rapeseed meal, soybean meal, wheat and barley distillers' dark grains, and mineral and vitamin supplements) provided as a Total Mixed Ration (**TMR**; mean proportions of dry matter over a full lactation; Bell et al. 2011). The TMR was evenly distributed into 24 HOKO automatic feed measurement gates (Insentec BV, Marknesse, The Netherlands), giving a ratio of 0.22 feeders per cow. These provided ad libitum feed throughout the day (except between 11:45 and 12:15 when food residues were removed and fresh feed was supplied, and during milking). The number and identity of feeders and the amount of floor space available to the cows at feeding remained constant throughout the year. HOKO data were recorded throughout lactation on a cycle of 3 consecutive days of measurement followed by 3 consecutive days when it was not measured. Water was available from troughs located at either end of the feeding passage. Cows were milked three times a day and received an additional 0.25 kg concentrates in the parlor at each milking event (which is not included in any analysis presented here). Milk yield (kg) was measured and summed for each day. Milk fat and protein were measured three times a week (Tuesday afternoon, Wednesday morning and midday). Cows were weighed (kg) after each milking event and scored for body condition (on an ordinal scale of 1-5 with 0.25 intervals) once a week based on palpation of specific body parts (Lowman et al., 1976). Animals remained in the study for their first three lactations unless they were culled because of infertility or illness.

Weather Data

Daily measurements of dry bulb temperature (**T_{db}**), wind speed (**WS**), relative humidity (**RH**) and sunshine (summarized in Table 1) during the study period were downloaded from the British Atmospheric Data Centre website (UK Meteorological Office, 2012). All data were recorded at a single Meteorological Office weather station located on the grounds of the research farm (85 m NE of the building housing the cows and 50 m above sea level). T_{db} and RH were point-sampled at 0900h, WS was measured 10 m above the ground between 0850-0900h and expressed as a mean, and sunshine was measured using a Campbell-Stokes recorder and expressed as the number of hours over a 24h period (0000-2359). To see how measurements from the weather station reflected indoor conditions, we compared them to raw measurements of T_{db}, RH and WS made in the cattle building for a separate study (Haskell et al., 2013). Indoor data were collected between late April and early July 2009 and matched with Meteorological Office data for time and date.

Global Solar Radiation (**GSR**, the total amount of direct solar radiation and diffuse solar radiation falling on a horizontal surface in a given day) was estimated using the Ångstrom–Prescott model (Ångstrom, 1924; Prescott, 1940):

$$GSR = I_x \left(A_a + A_b \frac{nSun}{N}\right) \tag{1}$$

where I_x is extra-terrestrial radiation (MJ/m per day), **nSun** is the number of hours of sunshine (h/day), N is day length (h /day) and A_a and A_b are site-specific empirical constants. We solved Equation (1) using the sirad package in R based on constants from the Meteosat Second Generation-based calibration (Bojanowski, 2013) and expressed the output as W/m^2 per day.

THI was calculated using

$$THI = (1.8 \times T_{db} + 32) - \big((0.55 - 0.0055 \times RH) \times (1.8 \times T_{db} - 26)\big) \tag{2}$$

from the National Research Council (US) (1971). Many formulations of THI have been devised, and we chose this one because it is used frequently in the agricultural literature (e.g. Hammami *et al.*, 2013). We calculated adjusted THI using

$$THI_{adj} = [4.51 + THI_2 - (1.992 \times WS) + (0.0068 \times GSR)] \tag{3}$$

from Mader et al. (2006), where

$$THI_2 = (0.8 \times T_{db}) + \left((\frac{RH}{100}) \times (T_{db} - 14.4)\right) + 46.4$$

Finally we calculated CCI using

$$CCI = RH_{adj} + WS_{adj} + GSR_{adj} \tag{4}$$

from Mader et al. (2010). RH_{adj}, WS_{adj} and GSR_{adj} are defined in Appendix 1 of the present paper.

We calculated 'moving' means for THI, nSun, WS, THI_{adj} and CCI over the 3 and 7 days prior to and including the test date (**TD**; the day of feeding) to allow the effects of weather to be compared over 3 timescales: TD, 3 days (i.e. TD, TD minus 1 day and TD minus 2 days) and a week. Weather can have a lagged effect on biological traits, and the effects of a weather event can depend on its duration (Hill and Wall, 2015; Renaudeau et al., 2012; West et al., 2003).

Animal Data

We summed the total amount of fresh feed consumed per cow over each 24h TD (00:00.00-23:59.59) to calculate her total daily feed intake. Summarizing data over a 24h period has the advantage that diurnal patterns in feeding behavior (Stamer *et al.*, 1997) and management procedures do not need to be addressed. We calculated DMI (g) based on a sample of TMR dried in a forced-air oven at 60°C, crude protein intake (**CPI**, g) using the semi-automated Kjeldahl method (Association of Official Analytical Chemists, 1990) and metabolizable energy intake (**MEI**, MJ) from the prediction equation by Thomas et al. (1988). We refer to these 3 variables as *feed intake*. Finally, feed efficiency (FE) was estimated by dividing fat and protein corrected milk yield (**FPCMY**, kg) by DMI in kg where FPCMY is:

$$[0.337 \times \text{raw milk (kg)}] + [11.6 \times \text{fat content (kg)}] + [5.999 \times \text{protein content (kg)}] \quad (5)$$

following Manzanilla Pech et al. (2014). As milk fat and protein were not sampled daily, we based our estimates on measurements from the closest sampling date to the TD.

Our dataset contained 73,058 daily feed intake records from 328 cows on 2,427 days and 71,345 daily FE records from 328 cows on 2,418 days. Animals were 97.8±0.11 (mean±SE; range 87.5-100) % Holstein Friesian and ranged from 0 to 305 days in milk. The number of daily records for each animal over her three lactations ranged from 11-438 (mean±SE: 222.7±6.74) for feed intake and 11-432 (mean±SE: 217.5±6.59) for FE.

Statistical Analysis

Data were analyzed using R. 3.1.1 (R Core Team, 2014). We tested whether THI, WS, nSun, THI_{adj} and CCI changed over the study period using separate generalized least squares models for each weather element or index. These were fitted by restricted maximum likelihood (**REML**) using the nlme library in R (Pinheiro *et al.*, 2014). We accounted for seasonal fluctuations in weather using harmonic regression and for non-independence of weather from one day to the next by applying a first-order autocorrelation structure.

We compared the 3 timescales over which weather was summarized (TD, 3 day means and weekly means) and the 3 methods of describing weather (hereafter *weather metrics* i.e. THI + WS + sun vs THI_{adj} vs CCI) using Akaike's information criterion (**AIC**). This approach is described in Hill and Wall (2015). Non-nested models can be compared using AIC provided that models be fitted to identical datasets (Burnham and Anderson, 2002). We therefore removed missing values using case-wise deletion to create two reduced datasets of 69,316 records (94.8 % of the total) for feed intake and 67,704 records (94.9 % of the total) for FE. The same numbers of individuals were included in the full and reduced datasets. We fitted the following linear mixed effects model (**LMM**) with a fifth-order autocorrelation structure using maximum likelihood:

$$y_{ijk} \sim \mu + w_{ij} + genetic\ group_i + (genetic\ group_i \times w_{ij}) + lactation\ number_{ijk} + DIM_{ijk} + LW_{ijk} + CS_{ijk} + \cos\left(\frac{2\pi\ TD}{365.25}\right) + \text{sine}\left(\frac{2\pi\ TD}{365.25}\right) + \cos\left(\frac{2\pi\ CD}{365.25}\right) + \text{sine}\left(\frac{2\pi\ CD}{365.25}\right) + animal\ id_{jk} + \varepsilon_{ijk} \quad (6)$$

where *y* was a single normally distributed response variable (DMI, CPI, MEI or FE) for animal *i* on test day *j* that gave birth on calving date *k*), *μ* was the overall mean, *w* was weather (expressed as one of the following a) THI + nSun + WS, b) THI_{adj}, or c) CCI) experienced by animal *i* over one of the three timescales (see above); genetic group (S or C) was a two-level fixed factor for animal *i* on day *j*, and lactation number (1, 2 or 3) was a three-level ordered factor; **DIM** was days in milk (days 0-305 for feed intake and days 4-305 for FE; day 0 was the day of calving), **CS** was condition score (a proxy for the cow's energy reserves; a decline in CS suggests tissue mobilization to compensate for a negative energy balance (Bauman and Currie, 1980)), and **LW** is live weight. Animal identity was a random factor (random intercepts only) and ε was the unexplained variation for animal *i* on test day *j* that calved on date *k*. TD (running test date, 1 to 2676) and **CD** (running calving date, 1 to 2945) were expressed as harmonic terms in the model to accommodate potential seasonal trends in management (e.g. stocking density) and photoperiod. The denominator of each sine and cosine term represents the periodicity of the waves. In this case, 365.25 days represents a wave for predictable annual variability (taking into account leap years). We tested for linear, quadratic and cubic effects of all weather variables, DIM and LW, and linear and quadratic effects of CS. Weather variables, DIM, LW and CS were mean-centered to reduce collinearity between higher and lower order terms of a given variable and to improve the interpretability of the estimates. We fitted nSun in the model rather than GSR owing to the high correlation between GSR and THI ($r_p = 0.641$, $t_{2392} = 40.82$, $P < 0.001$) compared to nSun and THI ($r_p = 0.318$, $t_{2392} = 16.40$, $P < 0.001$). These methods generated nine non-nested models (3 weather metrics × 3 timescales) per response variable. For each response variable, we determined the ‘best’ model with respect to timescale and weather metric based on the lowest AIC, and considered 7 AIC units to be a meaningful difference (Burnham *et al.*, 2011).

Models were re-fitted based on the full datasets using REML (retaining the same explanatory variables, including autocorrelation parameters) to obtain less biased estimates. To provide context for our results we repeated the THI+WS+nSun analysis with FPCMY (days 4-305 of lactation), as a (normally distributed) response variable using REML. We reached the final models using backward elimination of non-significant ($P \geq 0.05$) interactions (higher order terms removed before lower order terms) and then main effects, retaining lower order terms where higher order terms were significant. We used differentiation of the regression equations to calculate 'turning points' in polynomial relationships between weather and responses. For all models fitted by REML we present estimates of model coefficients (β) with standard errors, t-values and *P*-values. All statistical tests are two-tailed, and significance is assumed at $P < 0.05$.

RESULTS

Weather at the Research Farm

T_{db}, THI, THI_{adj} and CCI followed similar seasonal patterns, with peaks in July and troughs between December and February (Fig. 1, Fig. 2). T_{db} at 0900h was 0.22±0.03°C warmer than mean T_{db} calculated from daily minimum and maximum values ($t_{2419} = 6.3$, $P < 0.001$, paired test). T_{db} at 0900h and mean T_{db} were closely correlated (Table 2). THI and THI_{adj} showed a strong linear correlation (Table 2), although THI was higher than THI_{adj} ($t_{2318} = 5.1$, $P < 0.001$, paired test; Table 1, Fig. 2). CCI was closely correlated with THI, and slightly less so with THI_{adj} (Table 2). THI at 0900h was >60 units on 315 days over the study period (13.2 % of TDs), and >70 units on 6 days (0.3 %); THI_{adj} at 0900h was >60 units on 414 days (17.9 %

of TDs) and >70 units on 27 days (1.2 %). nSun was greatest in May and lowest in December and January.

THI, THI_{adj} and CCI decreased over the study period (THI: β = -0.0006±0.0002, t = 2.8, P = 0.005; THI_{adj}: β = -0.0008±0.0003, t = 3.0, P = 0.003; CCI: β = -0.0002±0.00005, t = 3.5, P<0.001), but nSun (β = 0.0002±0.0001, t = 0.18, P = 0.854) and WS did not change (β = 0.00009±0.0001, t = 0.88, P = 0.380).

There was no difference in T_{db} measured outdoors (13.3±0.26˚C, N = 75) and in the center of the loafing area (13.3±0.26˚C, N = 76; β = 0.00002±0.05, t <0.01, P > 0.999, General Linear Model, **LM**, controlling for date; T_{db} data were square-root transformed to normalize), but conditions were cooler outside than in the middle of the feed face (14.6±0.27˚C, N = 76; β = 1.6±0.05, t = 3.3, P = 0.004). Outdoor T_{db} measurements were strongly and positively correlated with measurements made in the loafing area (r_s = 0.94, t_{73} = 24.6, P < 0.001) and at the feed face (r_s = 0.94, t_{73} = 23.6, P < 0.001). WS was higher outside (3.14±0.21 m/s) than at the feed face (0.07±0.03 m/s; β = 3.7±0.42, z= 8.9, P < 0.001, Generalized Linear Model with poisson errors, controlling for date) and the loafing area (0.56±0.08˚C; β = 1.7±0.17, z = 10.5, P < 0.001). Outdoor WS was positively correlated with WS in the loafing area (r_s = 0.40, t_{73} = 3.76, P < 0.001), but not at the feed face (r_s = 0.14, t_{73} = 1.17, P = 0.244). RH did not differ between the three sites (feed face: 72.2±1.30 %, loafing: 70.3±1.30 %, outdoors: 72.1±1.32 %; $F_{2,222}$ = 0.66, P = 0.520, LM, controlling for date), and outdoor RH was positively correlated with RH at the feed face (r_s = 0.78, t_{72} = 10.52, P < 0.001) and the loafing area (r_s = 0.84, t_{72} = 13.06, P < 0.001).

How Well Did Three Weather Metrics Explain Feed Intake and Feed Efficiency?

Maximum likelihood models testing for the effects of THI+WS+nSun explained feed intake and FE better than models testing for the effects of THI_{adj} or CCI (Table 3). CCI models fitted the data better than THI_{adj} models for DMI, CPI and FE. CCI and THI_{adj} explained MEI equally well. THI, THI_{adj} and CCI were similar in the shape of their relationships with the four feeding traits, except at their lower extremes (Fig. 3, Supplementary Fig. S4). Indeed, at the lowest index values, THI_{adj} and CCI followed different directions in their relationships with two feed intake traits (DMI and CPI): feed intake was highest at the lowest THI_{adj} values, whereas feed intake increased with CCI at low CCI values. By comparison, THI and CCI (which were closely correlated; Table 2) had the same sign for their relationships with these traits.

Comparing Timescales for Quantifying Weather Metrics using Maximum Likelihood

Focusing on models for THI+WS+nSun, weather averaged over 3 days explained CPI and FE best, whereas weekly averages were best for MEI. Weekly and 3 day means performed equally well for DMI (Table 3). Models for THI_{adj} followed the same pattern as for THI+WS+nSun. For CCI, 3 day means explained CPI and ME data best, and weekly means were best for DMI and FE (Table 3). Overall, weather variables averaged over 3 days generated lower AIC values than those averaged over different timescales, so all further analyses were based on 3 day means.

How did Genetic Merit Influence Milk Yield and Feeding Traits?

Cows of high genetic merit for milk fat and protein (Select cows) produced more fat and protein corrected milk, consumed more feed (expressed as dry matter, crude protein or metabolizable energy) and had a higher FE than Control cows (Table 4, Table 5, Supplementary Table S1).

How Did THI, Wind Speed and the Number of Hours of Sunshine Influence Feeding Traits in Cows of High and Average Genetic Merit?

DMI, CPI and MEI showed similar cubic relationships with THI: there was little or no effect of THI on feed intake at low THI values, followed by a decline in feed intake with increasing THI at higher THI values (Table 5, Supplementary Table S1, Fig. 3a-c). DMI reached a maximum of 21.35 kg in Select cows and 19.18 kg in Controls at 38.9 THI units. Between 55 and 65 THI units, declines in DMI averaged 80.01 g for every 1 unit increase in THI for both genetic groups (Fig. 3a). This relationship resulted in a 5.31% decrease in DMI in Select animals and 5.91% in Controls between 65 THI units and peak DMI at 38.9 units. DMI decreased 11.5 % in Select cows and 12.8 % in Controls between 73.9 THI units (the highest THI recorded at 0900h) and 38.9 THI units. FPCMY showed an overall decrease with increasing THI (Supplementary Table S1, Fig. 3e). THI did not affect the feed intake or FPCMY of Select and Control cows differently (Table 5, Supplementary Table S1, Fig. 3a-c, e). The relationship between THI and FE, by contrast, varied with genetic merit: FE increased with increasing THI after 33.19 THI units in Select cows, and after 40.17 THI units in Control cows (Table 5, Fig. 3d). Feed intake showed an overall increase with WS in cows of both genetic groups, and the rate of increase was greater in Select than in Control cows (Table 5, Supplementary Table S1, Fig. 4a-c). The effects of WS on FE also varied with genetic group: FE in Control cows decreased with increasing WS until WS reached 4.3 m/s and then FE increased with increasing WS, whereas FE in Select cows decreased until WS reached 5.6 m/s (Table 5, Fig. 4d). There was a trend towards a decrease in FPCMY with increasing WS, but the relationship was not statistically significant (Supplementary Table S1). The three feed intake traits decreased as nSun increased, whereas FE and FPCMY increased as nSun increased (Table 5, Supplementary Table S1, Fig. 5a-e). The rate of decline in feed intake was steeper on days with fewer hours of sunshine (Fig. 5a-c). Select cows decreased DMI and CPI with increasing sunshine hours at a greater rate than Controls (Fig. 5a-b), but nSun did not affect the two genetic groups differently for MEI or FE (Fig. 5c-d).

How Did Feeding Traits Vary with Days in Milk, Live Weight and Condition Score?

Feed intake increased with days in milk until day 123.1±0.16 (mean across the 3 feed intake traits), then decreased and finally increased again on day 276.3±8.68 (Table 5, Supplementary Table S1, Supplementary Figure S1). FE decreased with days in milk (Table 5, Supplementary Figure S1). Feed intake increased with increasing live weight to a weight of 638.1±5.76 kg (mean across the 3 traits), and then decreased (Supplementary Figure S2a-c). FE decreased with increasing live weight in cows lighter than 488.3 kg, and then increased with live weight until cows reached a weight of 706.4 kg, before decreasing with increasing live weight (Supplementary Figure S2d). DMI, MEI and FE increased with increasing CS until cows reached a score of 2.2±0.22 units, before decreasing with increasing CS (Supplementary Figure S3). CPI was not influenced by CS (Supplementary Table S1)

How Did THI_{adj} Influence Feeding Traits in Cows of High and Average Genetic Merit?

As THI_{adj} increased, feed intake decreased and FE increased (Supplementary Table S2, Fig. 3f-i). The rate of decrease with increasing THI_{adj} was greater in Select than in Control cows for DMI and CPI, but did not differ between genetic groups for MEI (Supplementary Table S2, Fig. 3f-i). The slope of the relationship between THI_{adj} and FE was steeper for Control than Select cows (Supplementary Table S2).

How Did CCI Influence Feeding Traits in Cows of High and Average Genetic Merit?

Feed intake increased with increasing CCI values when CCI was very low, and then decreased as CCI increased (Supplementary Table S3, Supplementary Figure S4a-c). The relationship between feed intake and CCI was cubic for DMI and quadratic for CPI and MEI. FE showed an overall increase with CCI (Supplementary Table S3), and Select cows showed a steeper rate of increase in FE with CCI than Control cows (Supplementary Figure S4d).

DISCUSSION

In dairy cows, increased feed efficiency is favorable from an economic perspective because a greater share of the energy in feed is converted into milk (Reynolds et al., 2011). It also minimizes the environmental impact of production because fewer resources are lost as manure, methane and carbon dioxide per kilogram of milk produced (Arndt et al., 2015). The main aim of the present study was to determine how feed intake and feed efficiency vary in response to natural fluctuations in weather in housed cows in a temperate climate. Cows decreased feed intake (expressed as DMI, CPI and MEI) and FPCMY, but became more efficient at converting dry matter to milk as THI increased. Feed intake increased with increasing WS, but decreased as the number of hours of sunshine increased. As cows received a TMR, which precluded the selection of different feed components, variation in CPI and MEI with weather arose largely from changes in DMI. Nevertheless, differences between the three feed intake traits in their responses to CCI and THI_{adj} suggest that weather can have subtle effects on the content or intake of CP and ME that are not fully explained by variation in DMI, perhaps due to differences in the density of components within the ration.

How Well Did THI, THI_{adj} and CCI Explain Feed Intake and Feed Efficiency?

CCI was developed as an indicator of the thermal comfort of cattle over a range of hot and cold conditions (Mader et al., 2010). Hammami et al. (2013) found that THI_{adj} and CCI explained production traits and somatic cell count more effectively than THI (calculated using Equation 2 in the present study). THI_{adj} and CCI take into account WS and solar radiation but THI does not. Here, we fitted a model containing not only THI but also WS and nSun as individual main effects, and compared its performance to alternative models containing THI_{adj} and CCI. Our former model was better at explaining feed intake and FE than models containing THI_{adj} or CCI. This is probably because individual weather variables capture the complex ambient conditions experienced by the animal more comprehensively than single metrics, which are constrained by weightings that might be more appropriate under some conditions than others. For example, distinct thermal indices differ between climatic regions in their effectiveness as proxies of the environmental conditions associated with heat stress (Bohmanova et al., 2007). The superior performance of individual weather variables compared to metrics that condense the same variables into a single value suggests that a model containing main effects of T_{db}, RH, WS and nSun would perform better than one containing THI, WS and nSun. Consistent with this idea, Dikmen & Hansen (2009) found that a model that fitted both T_{db} and RH as main effects explained rectal temperature in lactating dairy cows as well or better than models containing one of 8 THI. Although models including individual weather variables appear to describe feed and production traits more closely, thermal indices are valuable because they condense complex ambient conditions into a single value that can be easily compared between studies or commercial settings. All three indices were similar in the shape of their relationships with the four feeding traits, except at their lower extremes. Interestingly, at low index values, THI_{adj} and CCI followed different directions in their relationships with two feed intake traits. This could reflect the apparently greater suitability of CCI compared to THI_{adj} for explaining feed intake at cooler temperatures. CCI models were better at explaining DMI, CPI and FE than THI_{adj} models, which offers statistical support for this possibility.

Comparing Timescales for Quantifying Weather Metrics

Moving mean weather measurements spanning three days before and including feeding (i.e. means of weather across the TD, TD minus 1 and TD minus 2) usually explained feed intake and FE better than TD or seven-day means. This is consistent with Bertocchi et al. (2014), who reported that the THI recorded 2 days before the TD explained milk quality better than measurements taken 1, 3, 4 or 5 days before the TD in Holsteins in northern Italy. Similarly, West et al. (2003) found that mean THI recorded 3 days before the TD explained DMI in Holsteins in southern Georgia better than THI recorded on the TD, or 1 or 2 days before the TD (although a 2-day lag of mean T_{db} performed best overall). These lags reflect the time an animal spends consuming, digesting and metabolizing feed (West et al., 2003). We also propose that expressing lags as moving means allows short-lived periods of harsh weather to be captured in the analysis.

Feed Intake Decreased and Feed Efficiency Increased with Increasing THI

Our observation that feed intake decreased with increasing THI supports work on DMI in dairy cows (Bouraoui et al., 2002; Gorniak et al., 2014; West, 2003), on DMI in cattle steers (Kang et al., 2016) and on DMI and MEI in sheep (Dixon et al., 1999). Decreases in DMI under conditions of heat stress are associated with decreases in daily and resting metabolic heat production, longer digestion times and a shift from fat to glucose utilization in dairy cows (Eslamizad et al., 2015). In southern Georgia, USA, DMI decreased 0.51 kg for every 1 unit increase in test day THI between approximately 73 and 82 THI units (West et al., 2003). Ominski et al. (2002) reported a 6.5 % decline in DMI during 5 days' experimental exposure to heat stress (mean daily THI ~73.5) compared to control conditions (THI ~68.8) in lactating Holsteins in Manitoba, Canada. We observed lower declines (3.8 and 4.3 % in Select and Control cows, respectively) than Ominski et al. (2002) for the same THI values, perhaps owing to a shorter duration of exposure in our study. Severe heat stress can bring about declines in cows' DMI as high as 55 % compared to thermoneutral conditions (National Research Council, 1981). By contrast, at the highest THI recorded in our study, DMI decreased by 11.5 and 12.8 % (Select and Control cows, respectively) compared to peak intake. Under the environmental conditions and feeding regime experienced in our study, cows received the nutrients and energy necessary to support their productive functions (National Research Council, 2001). Nevertheless, predicted increases in temperature (IPCC, 2013) combined with increased maintenance requirements as a consequence of heat stress (reviewed in Baumgard and Rhodes, 2012) mean that producers should stay alert to cows' energetic and nutritional requirements falling below these levels even in temperate regions.

We had expected the impact of THI on feed intake to be greater in cows of high than average genetic merit. Contrary to our prediction, however, the slopes did not differ between the two groups. There at least three reasons, which are not mutually exclusive, as to why this could be the case. 1) Cows may not have experienced warm enough temperatures for a difference to be detected (i.e. for heat stress to occur and affect feed intakes). However, feed intake varied with THI within genetic groups, so cows were clearly affected by the range of temperatures in the study. 2) THI alone may not have fully captured the response of cows to weather. The observation that THI, THI_{adj}, CCI, WS and nSun affected high genetic merit cows differently from Controls with respect to some of the feed intake traits is consistent with this possibility. 3) Select cows might have modified other aspects of feeding in order to maintain the same overall DMI. This might involve feeding at a cooler time of day (Adin et al., 2008) or adjusting meal characteristics (Hill & Wall, in prep). Such questions can be addressed using individual animal feed intake recording systems, such as that used in the present study, which provide detailed information on intake, duration and timing of individual visits.

Our measurements of FE agree with those carried out by other authors under similar environmental conditions (e.g. Su et al. (2013) recorded 1.66±0.02 kg fat corrected milk per kg DMI at 50.6 THI units at 0900h). Although both FPCMY and DMI declined with increasing THI in our study, the concurrent increase in FE indicates that the decline in milk yield was less than the decline in DMI at a given THI. Our findings cannot be attributed to changes in condition score, body mass, stage of lactation or lactation number, which affect FE through changes in energy balance and maintenance requirements (Reynolds et al., 2011), because these were controlled for statistically in our analyses. The increase in FE with increasing THI supports work carried out by Kang et al. (2016) under similar environmental conditions. Kang et al. (2016) found that FE in housed steers increased from March (mean THI 49 units) to the warmer month of April (56 THI units). Studies carried out in warmer regions, however, have reported lower FE under hot (high 24h ambient temperature >21˚C in Britt et al., 2003; mean daily THI 76.5 in Su et al., 2013) than mild (≤21˚C; THI 53) conditions (Britt et al., 2003; Su et al., 2013). In contrast to our findings, the difference in FE was driven by THI having more pronounced effects on milk yield than on DMI under warmer conditions in these studies (Britt et al., 2003). Taken together, these results support previous suggestions that FE increases with mild heat stress but rapidly decreases when heat stress becomes more severe (Baumgard and Rhoads, 2012; Yunianto et al., 1997). This may reflect the increased energetic cost of evaporative cooling under severe compared to mild heat stress (Yunianto et al., 1997).

Feed Intake Increased with Increasing Wind Speed

Cows in our study were exposed to natural ventilation from windows, open areas and slits between timber panels, but were sheltered from strong winds. Moderate WS can alleviate the effects of high ambient temperatures on rectal temperature (Dikmen and Hansen, 2009) and productivity (Hill and Wall, 2015) in dairy cows. We found that FE decreased with increasing WS, presumably because cows increased feed intake but not milk yield as WS increased. The rate of increase in feed intake with increasing WS was greater in Select than in Control cows because higher yielding cows have a greater heat increment to offload.

Feed Intake Decreased and Feed Efficiency Increased as Sunshine Hours Increased

The number of hours of sunshine is presumably a function of both solar radiation, which could reach cows directly through the open areas in the building or indirectly from the roof, and photoperiod. Other studies have observed a positive relationship between milk production and day length, perhaps owing to a decline in melatonin production with increasing photoperiod (Dahl et al., 2000). Although we accounted for seasonality in our study, it is possible that endocrine mechanisms stimulated by residual changes in photoperiod explain the positive influence of sunshine on FPCMY and FE. Holstein heifers experimentally subjected to photoperiods of 16h L: 8h D converted feed into body mass more efficiency than heifers that experienced 8h L: 16h D irrespective of whether they received ad libitum or restricted feed (Petitclerc et al., 1983). In contrast to our results, Swedish red and white bulls on an ad libitum concentrate diet and Holstein heifers fed concentrates and forage ad libitum increased DMI as day length increased (Mossberg and Jönsson, 1996; Petitclerc et al., 1983). The findings of Mossberg and Jönsson (1996) and Petitclerc et al. (1983) and our adjustments for seasonality suggest that the declines in DMI with increasing sunshine in the present study are more likely to be a consequence of increased solar radiation on the animals rather than photoperiod. Interestingly, the effects of sunshine differed between the two genetic lines in our study: Select cows decreased DMI and CPI with increasing sunshine hours at a greater rate than Controls.

Implications for Climate Change

We observed decreases in feed intake and FPCMY with increasing THI under conditions currently experienced in a temperate region, suggesting that temperate herds may be more sensitive to ambient heat than is currently recognized. Dunn et al (2014) predicted a steady increase in the number of days on which THI exceeds 70 units in the UK over the 21st century. In south-east England, the number of days over 70 THI units was predicted to exceed 40 days/year by 2100 (Dunn et al., 2014). Although these predicted conditions are milder than those currently experienced in many regions that rely on dairy farming, the low tolerance of temperate zone animals to high THI is cause for concern. Nevertheless, our finding that FE increased with increasing THI suggests that some of the future costs of lost productivity may be offset by reduced economic expenditure on feed per kg milk, at least under conditions of mild heat stress.

Temperatures inside cattle sheds are 3-6°C warmer than outdoors in northern Europe (Seedorf et al., 1998), and up to 3.5°C warmer or 6 THI units higher indoors than outdoors in central Europe (Erbez et al., 2010). In our study the feed face was just 1.23˚C warmer than outside and humidity inside the building did not differ from values measured outdoors during the months for which indoor data were available (late April to early July). The responses to temperature and humidity that we describe are therefore likely to reflect those in a grazing system (though potential interactions with feed type, and physical activity and other behaviors between housed and grazing animals should be considered). It is worth noting that stocking density was higher between November and March than the other months of our study because cows from a separate study were housed with our study subjects for the winter. Body heat from the additional animals may have therefore helped to buffer our subjects from the cold. For animals grazing on warm days, WS is expected to have a more pronounced effect in alleviating heat load than we observed in our housed cows.

CONCLUSIONS

This is, to our knowledge, the first longitudinal study of the effects of weather on feed efficiency in dairy cows. Our first objective was to compare how well three thermal indices described feed intake and feed efficiency. Models considering THI, wind speed and sunshine were more effective at explaining cows' responses to temperate weather conditions than models containing single metrics (THI_{adj} or CCI). Next, we showed that moving mean weather measurements spanning the TD and the two preceding days (three-day means) explained feeding traits better than TD or seven-day means, which probably reflects the duration of digestive processes. Finally, we found that milk yield, feed intake and FE are influenced by current weather conditions in a temperate climate. As THI and CCI increased, feed intake decreased, as predicted, but the efficiency of converting dry matter to milk increased. Interestingly, high genetic merit and Control cows differed in their responses to weather, which suggests that they differ in their sensitivities to weather or their coping tactics. Understanding how weather influences feed intake and efficiency can help shape management and selective breeding strategies, and will become an important aspect of resilience to future climate change. Heritable genetic variation exists for FE (Berry and Crowley, 2013), and so using feed intake records to identify cows that maintain efficiency under different weather conditions provides opportunities to breed for improved resilience to weather-related stress.

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Table 1. Descriptive statistics for weather data recorded at the closest Meteorological Office station (source id: 19259) to the research farm (2004 to 2011; N = 2676 daily records) and for Global Solar Radiation, THI, THI_{adj} and CCI calculated from Meteorological Office data using Equations (1, (2, (3 and (4 respectively

Weather element	**Recording regime**	**Accuracy**	**Mean±s.e.m**	**Min**	**Max**	**90 % CI**
Dry bulb temperature, T_{db}	PS	0.1°C	9.9±0.11	-8.9	25.2	0.8 to 17.2
	Minimum during 24h (0900-0900)	0.1°C	6.1±0.10	-13.0	18.4	-2.4 to 13.6
	Maximum during 24h (0900-0900)	0.1°C	13.2±0.11	-4.1	30.7	4.2 to 21.4
Relative humidity, RH	PS	0.1%	80.1±0.24	28.1	100	59.3 to 96.3
Wind speed, WS	0850-0900 mean	1 m/s	2.9±0.06	0	26.7	0.5 to 9.8
Sunshine, nSun	No. hours over 24h (0000-2359)	0.1 h	3.8±0.07	0	14.7	0.0 to 11.2
Global solar radiation, GSR	24h mean based on (1)	0.1 w/s	100.25±1.43	12.1	298.56	14.4 to 240.1
Weather index	**Equation**		**Mean±s.e.m**	**Min**	**Max**	**90 % CI**
Temperature Humidity Index, THI	(2)		50.6±0.17	20.8	73.9	35.7 to 62.4
Adjusted THI, THI_{adj}	(3)		50.0±0.20	-8.5	78.2	34.1 to 65.3
Comprehensive Climate Index, CCI	(4)		1.1±0.04	-5.2	9.1	-2.1 to 4.1

Recording regime indicates whether values are point-samples (PS) taken at 0900h or 24h summaries (mean, minimum, maximum, total). We present the range (Min and Max) and 90 % confidence intervals (CI) to give an indication of the frequency of weather extremes during the study.

Table 2. Pearson's correlations between weather variables and indices recorded at the research farm

	r_p	d.f.	*t*
0900h T_{db} and mean T_{db}	0.945	2419	6.3
THI and THI_{adj}	0.824	2317	70.1
CCI and THI	0.931	2317	122.3
CCI and THI_{adj}	0.823	2317	69.8

T_{db} is dry bulb temperature, THI is temperature humidity index and THI_{adj} is THI adjusted for wind speed and global solar radiation. $P<0.001$ for all correlations.

Table 3. Information-theoretic comparison of models fitted using Maximum Likelihood to compare the effects of weather index and measurement timescale on daily dry matter intake (DMI), metabolizable energy intake (MEI), crude protein intake (CPI) and feed efficiency (FE) in 328 Holstein Friesian cows (69,316 records for DMI, MEI and CPI, and 67,941 records for FE)

		DMI		MEI		CPI		FE	
Weather metric	Time-scale	Rank	AIC	Rank	AIC	Rank	AIC	Rank	AIC
THI, WS, sun	TD	e	1292608	f	679058	f	498876	f	37051
	3 day	a	1292262	b	678747	a	498526	a	36902
	week	a	1292263	a	678720	b	498641	b	36917
THI_{adj}	TD	g	1292672	h	679124	h	498998	h	37081
	3 day	d	1292459	de	678922	d	498733	e	37010
	week	d	1292454	c	678903	e	498752	g	37060
CCI	TD	f	1292635	g	679101	g	498946	g	37061
	3 day	c	1292408	d	678917	b	498640	d	36991
	week	b	1292401	e	678925	c	498713	c	36955

Models are ranked from best (lowest AIC) to worst within each feeding trait; ‘a’ represents the most favorable rank, and different lower case letters indicate meaningful differences (≥7 AIC units). Models are based on Equation (6) and differ from each other only in the terms indicated in the first column.

Table 4. Least squares means ± standard errors for daily intake of dry matter (DMI), metabolizable energy (MEI), crude protein (CPI), feed efficiency (FE), and fat and protein corrected milk yield (FPCM) for each genetic group (GG: S, Select and C, Control), lactation number (1, 2 and 3)

		DMI (kg)		**CPI (g)**		**MEI (MJ)**			**FE (kg milk: kg DMI)**		**FPCM (kg)**		
		mean	s.e.m	mean	s.e.m	mean	s.e.m	*N*	mean	s.e.m	mean	s.e.m	*N*
GG	**C**	19.01	0.15	3426.6	23.11	223.8	1.78	38,752 (167)	1.649	0.014	31.2	0.34	37,823 (167)
	S	21.18	0.15	3813.9	23.93	249.3	1.83	34,306 (161)	1.778	0.015	37.2	0.35	33,522 (161)
Lact no.	**1**	16.64	0.15	3050.4	24.35	196.0	1.83	32,982 (288)	1.633	0.015	27.1	0.35	32,325 (288)
	2	19.58	0.15	3522.9	24.61	230.9	1.84	23,250 (226)	1.634	0.015	30.9	0.35	22,644 (225)
	3	20.82	0.16	3706.5	26.20	244.4	1.91	16,826 (154)	1.681	0.016	35.7	0.38	16,376 (153)

Sample sizes are given under *N* as the number of records and (in brackets) individuals used to calculate each mean. *N* was equal for all groups within DMI, MEI and CPI, and for groups within FPCM and FE.

Table 5. LMMs to test the effect of weather (THI, wind speed and hours of sunshine; means summarized over 3 days) and genetic group (Select or Control) on dry matter intake (73,058 records) and feed efficiency (71,345 records) in 328 Holstein Friesian cows during the years 2004-2011

	Dry matter intake (g)				Feed efficiency (kg milk / kg DMI)			
Fixed effects	*β*	s.e.m	*t*	*P*	*β*	s.e.m	*t*	*P*
Intercept	19013.496	145.713	130.5	<0.001	1.64918	0.01424	115.8	<0.001
THI	-32.898	4.630	-7.1	<0.001	0.00187	0.00050	3.7	<0.001
THI^2	-2.047	0.208	-9.8	<0.001	0.00009	0.00002	4.0	<0.001
THI^3	-0.038	0.013	-2.9	0.003	<0	<0.00001	-1.7	*0.098*
WS	50.549	9.158	5.5	<0.001	-0.00409	0.00109	-3.7	<0.001
WS^2	-17.055	3.174	-5.4	<0.001	0.00171	0.00038	4.5	<0.001
WS^3	1.234	0.279	4.4	<0.001	-0.00012	0.00003	-3.6	<0.001
nSun	-35.078	7.505	-4.7	<0.001	0.00333	0.00075	4.4	<0.001
nSun^2	10.311	1.858	5.6	<0.001	-0.00089	0.00022	-4.0	<0.001
nSun^3	-0.799	0.256	-3.1	0.002	0.00012	0.00003	3.9	<0.001
Lact no^2	2950.198	58.228	50.7	<0.001	0.03444	0.00736	4.7	<0.001
Lact no^3	-695.540	45.650	-15.2	<0.001	0.01903	0.00574	3.3	0.001
GG	2166.106	198.514	10.9	<0.001	0.12888	0.01884	6.8	<0.001
DIM	-9.391	0.699	-13.4	<0.001	-0.00085	0.00009	-9.6	<0.001
DIM^2	-0.151	0.004	-39.4	<0.001	0.00001	<0.00001	22.6	<0.001
DIM^3	0.001	<0.001	29.1	<0.001	<0	<0.00001	-23.2	<0.001
LW	0.353	0.622	0.6	0.570	0.00068	0.00011	6.5	<0.001
LW^2	-0.028	0.004	-6.5	<0.001	<0	<0.00001	-3.3	0.001
LW^3	<0.001	<0.001	0.3	*0.727*	<0	<0.00001	-5.4	<0.001
CS	-32.898	4.630	-7.1	<0.001	-0.04296	0.00618	-7.0	<0.001
CS^2	-2.047	0.208	-9.8	<0.001	-0.04366	0.00761	-5.7	<0.001
THI×GG	-0.834	4.806	-0.2	*0.862*	0.00121	0.00058	2.1	0.036
THI^2×GG	-0.170	0.348	-0.5	*0.625*	0.00004	0.00004	0.9	*0.363*
THI^3×GG	0.007	0.025	0.3	*0.770*	<0	<0.00001	-0.7	*0.481*
WS×GG	24.563	10.745	2.3	0.022	-0.00255	0.00130	-2.0	0.049
WS^2×GG	-2.958	2.558	-1.2	*0.248*	-0.00002	0.00031	-0.1	*0.942*
WS^3×GG	-0.056	0.557	-0.1	*0.920*	0.00001	0.00007	0.2	*0.877*
nSun×GG	-18.791	8.631	-2.2	0.030	0.00042	0.00106	0.4	*0.691*
nSun^2×GG	2.975	1.994	1.5	*0.136*	-0.00022	0.00024	-0.9	*0.348*
nSun^3×GG	-0.115	0.512	-0.2	*0.822*	0.00009	0.00006	1.5	*0.146*
Cosine (TD)	-453.773	44.836	-10.1	<0.001	0.04813	0.00538	8.9	<0.001
Sine (TD)	642.437	47.950	13.4	<0.001	-0.05860	0.00581	-10.1	<0.001
Cosine (CD)	145.061	67.534	2.1	0.032	-0.00053	0.00801	-0.1	*0.947*
Sine (CD)	125.926	71.179	1.8	*0.077*	-0.02721	0.00843	-3.2	0.001

φ_1	0.162	0.175
φ_2	0.169	0.176
φ_3	0.151	0.146
φ_4	0.096	0.089
φ_5	0.055	0.075
Random effect	**% σ**	**% σ**
Animal identity	36.360	30.126
Residual	63.640	69.874

TD = running test day (the day of feeding); CD = running calving date; THI = temperature humidity index; WS = wind speed; nSun = the number of hours of sunshine; GG = genetic group; DIM = days in milk; LW = live weight; CS = condition score; φ_n = the estimate of correlation at lag n

‘Control’ was the reference (baseline) genetic group

Linear, quadratic (^2) and cubic (^3) effects were tested for where indicated; lactation number is an ordered factor.

Non-significant effects that were not components of significant interactions were removed from the final models; their *P*-values are italicized.

Parameter estimates (*β*) and standard errors marked <0.001 for dry matter intake or <0.00001for feed efficiency were positive values, and those marked <0 were between 0 and -0.001 for dry matter intake or between 0 and -0.00001 for feed efficiency.

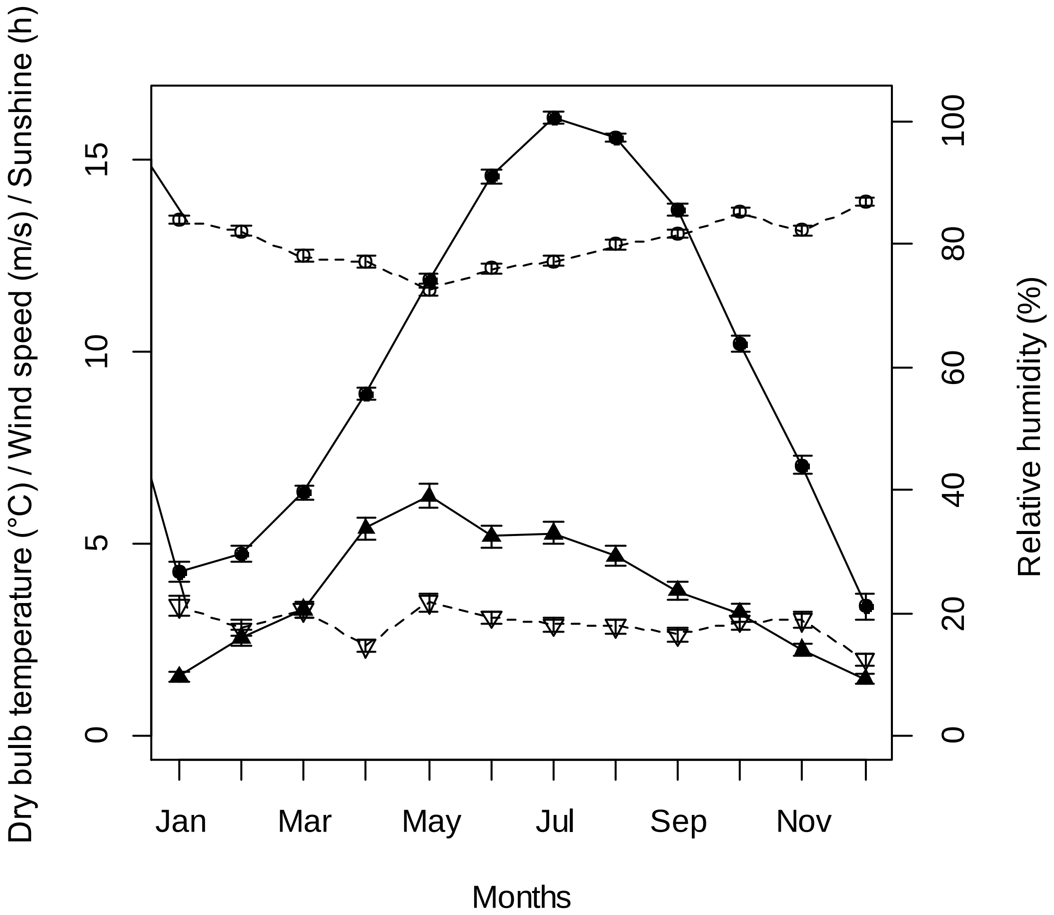

Fig. 1 Mean monthly dry bulb temperature (closed circles), wind speed (open triangles), the number of hours of sunshine (closed triangles) and relative humidity (open circles) ±1 standard error measured daily at the research farm, Dumfries, Scotland, during the study period (2004-2011). Weather values were point-sampled at 0900h except for the number of hours of sunshine over 24h

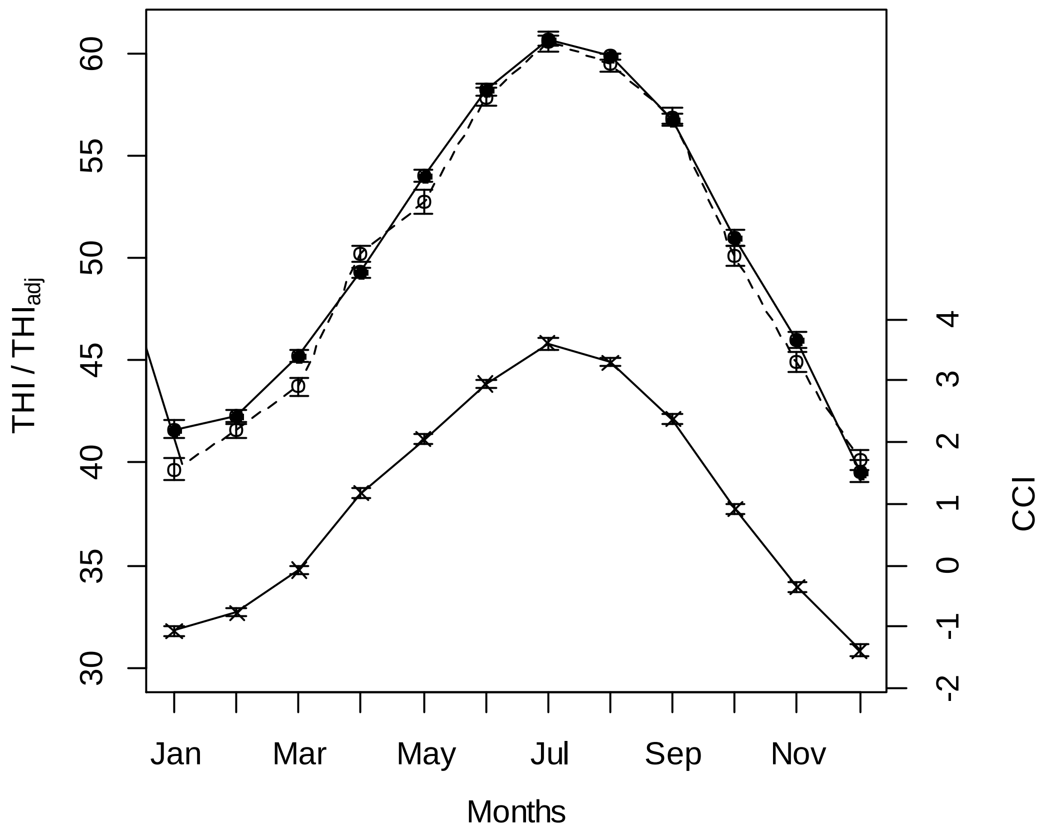

Fig. 2 Mean monthly THI (Temperature Humidity Index, closed circles), THI_{adj} (THI adjusted for wind speed and global solar radiation, open circles) and CCI (Comprehensive Climate Index, crosses) ±1 standard error based on values measured daily at 0900h at the research farm, Dumfries, Scotland, during the study period (2004-2011)

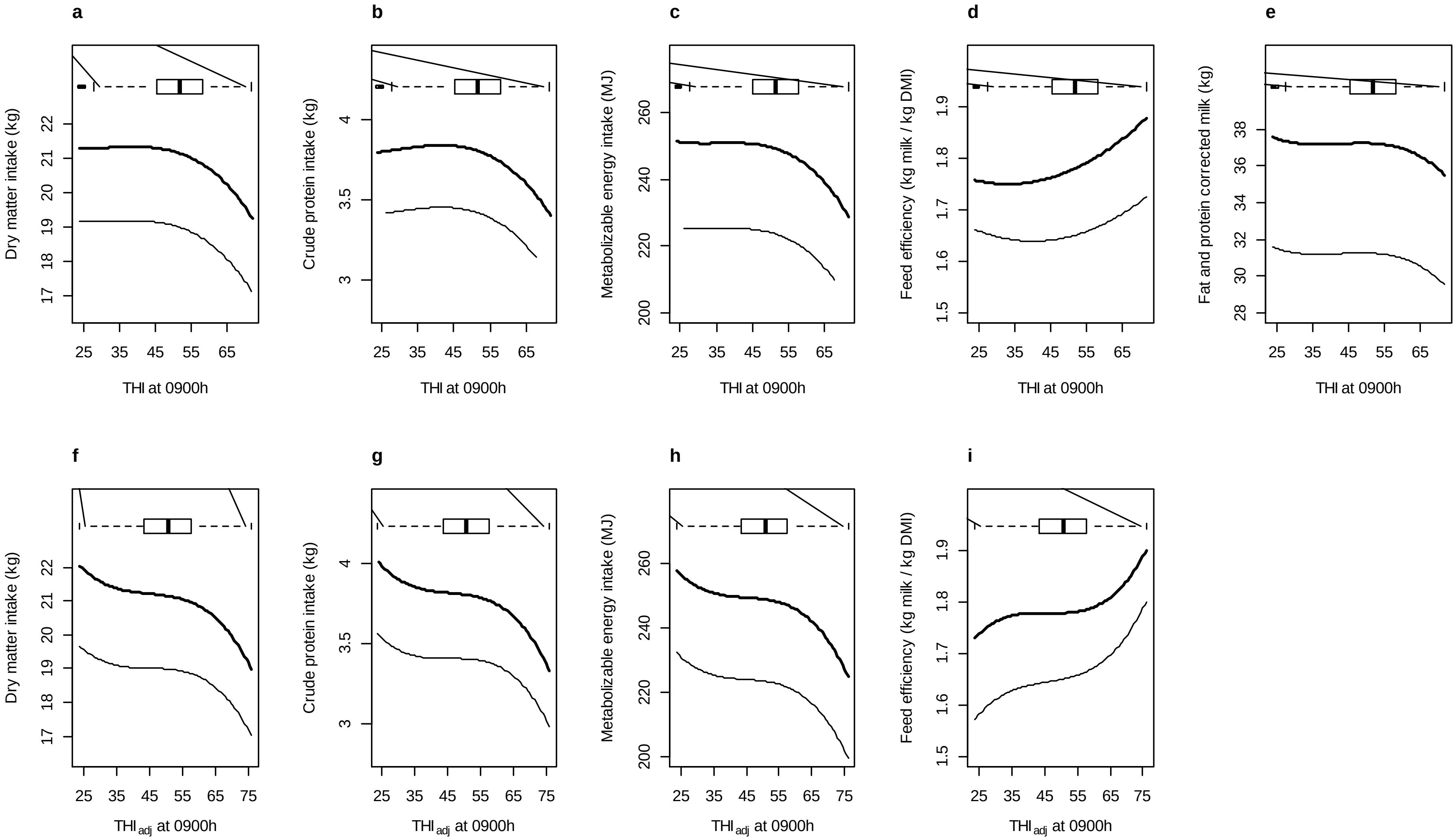
a
b
c
d
e
f
g
h
i
Dry matter intake (kg)
Crude protein intake (kg)
Metabolizable energy intake (MJ)
Feed efficiency (kg milk / kg DMI)
Fat and protein corrected milk (kg)
THI at 0900h
THI_{adj} at 0900h
17
18
19
20
21
22
3
3.5
4
200
220
240
260
1.5
1.6
1.7
1.8
1.9
28
30
32
34
36
38
25
35
45
55
65
75

Fig. 3 The effects of temperature humidity index (THI; top row) and temperature adjusted for humidity, wind speed and solar radiation (THI_{adj}; bottom row) on (a, f) daily dry matter intake, (b, g) daily crude protein intake, (c, h) daily metabolizable energy intake, and (d, i) feed efficiency (kg fat and protein corrected milk yield / kg dry matter intake) and fat and protein corrected milk yield (e) in 328 dairy cattle on a research farm in Scotland. Cows belonged to Select (thick line) genetic merit or Control (thin line) groups. Temperature and humidity were recorded at a single outdoor weather station 85 m from the cattle building. The median THI for the study period is represented by the thick line in the center of each boxplot, the left and right limits of the box are the 1st and 3rd quartiles of the data, respectively, and the whiskers show the range of the data minus values > 1.5 times the interquartile range (open circles). Curves are adjusted for all significant terms in equation (6), and statistical estimates for the effects presented here are provided in Tables 5 and Supplementary Table S1 for THI and THI_{adj}, respectively. a-c and f-h are based on 73,058 records and d and i are based on 71,345 records. Models testing for the effects of THI (controlling for WS and sunshine; top row) explained feed intake and FE better than models testing for the effects of THI_{adj}

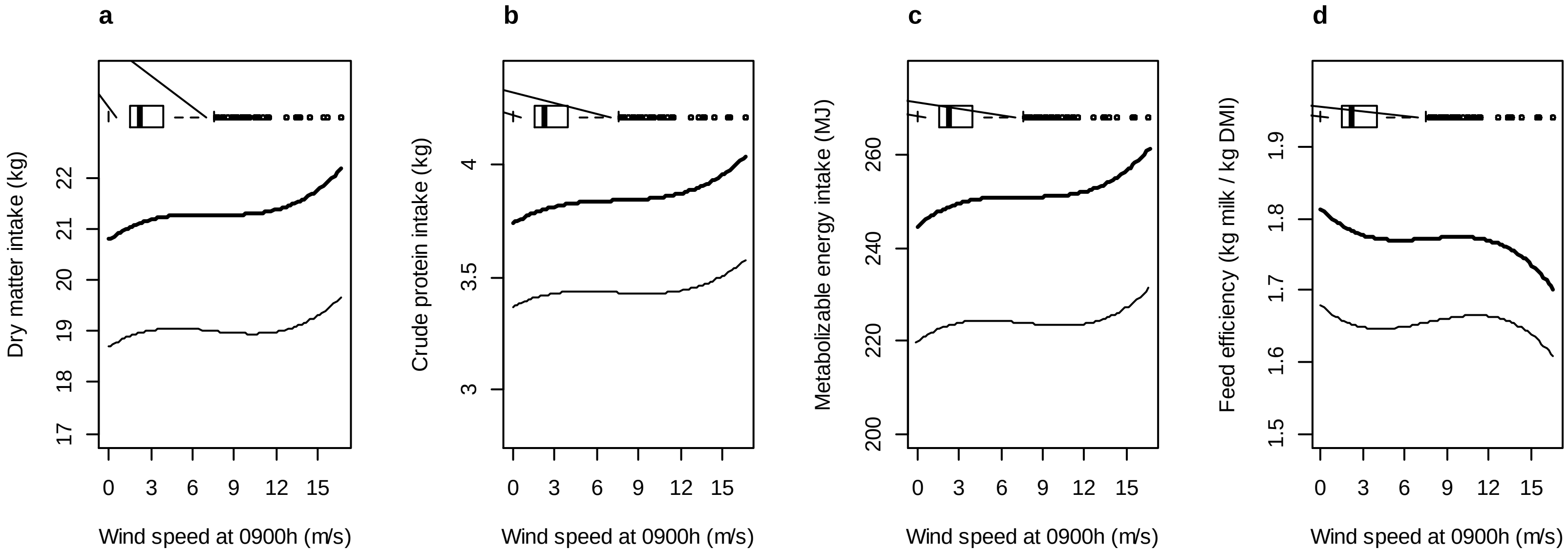

Fig. 4 The effects of wind speed on (a) daily dry matter intake, (b) daily crude protein intake, (c) daily metabolizable energy intake and (d) feed efficiency in a herd of dairy cattle depended on the cows' genetic line. Cows belonged to Select (thick line) genetic merit or Control (thin line) groups. Wind speed was recorded at a single outdoor weather station 85 m from the cattle building. All curves are adjusted for the terms in equation (6), where significant, and statistical estimates for the effects presented here are provided in Tables 5 and Supplementary Table S1. Wind speed did not have a statistically significant effect on fat and protein corrected milk yield (not shown)

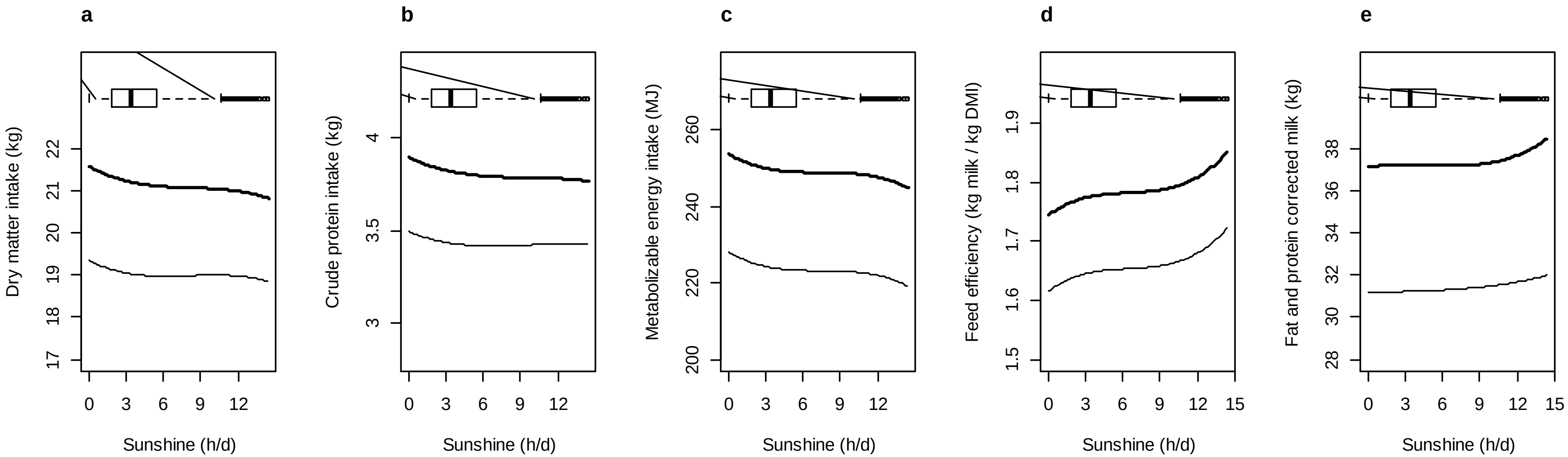

Fig. 5 The effects of sunshine on (a) daily dry matter intake, (b) daily crude protein intake, (c) daily metabolizable energy intake, (d) feed efficiency and (e) fat and protein corrected milk yield in 328 dairy cows belonging to Select (thick line) genetic merit or Control (thin line) groups. The number of hours of sunshine per day was recorded at a single outdoor weather station at the farm. Curves are adjusted for all terms in equation (6), where significant, and statistical estimates for the effects presented here are provided in Table 5 and Supplementary Table S1. a-c are based on 73,058 records, d-e are based on 71,345 records