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Weather influences feed intake and feed efficiency in a temperate climate

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1 **Weather influences feed intake and feed efficiency in**
2 **a temperate climate**

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INTERPRETIVE SUMMARY

9

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

18 **ABSTRACT**

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

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

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

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45 **KEYWORDS**

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

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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.

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

72 Dairy cows, like other homeothermic animals, experience heat stress when environmental
73 variables such as ambient temperature, humidity, solar radiation and wind speed combine to
74 exceed the body's thermoneutral zone, the range of ambient conditions at which metabolic
75 heat production and heat loss are in equilibrium. High yielding dairy cows require high
76 metabolic rates to support such yields, and this generates considerable metabolic heat
77 (Kadzere et al., 2002). As metabolic heat production increases, a cow's thermoneutral zone
78 shifts to a lower temperature range (Coppock et al., 1982). This means that higher yielding
79 dairy cows experience heat stress at lower temperatures than lower yielding cows (Berman,
80 2005). In response to heat stress, cows reduce nutrient uptake, reallocate energy to
81 thermoregulation, and experience changes in metabolism and endocrine function (Bernabucci
82 et al., 2010; Renaudeau et al., 2012; Rhoads et al., 2009). These adjustments can lead to
83 decreases in milk yield and quality (Bohmanova et al., 2007; Hammami et al., 2013; Hill and
84 Wall, 2015).

85

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

97 Index (**CCI**), which also adjusts ambient temperature for relative humidity, wind speed and
98 solar radiation, was developed specifically to consider the effects of both hot and cold
99 environmental conditions on cattle, and was validated for its effects on DMI (Mader et al.,
100 2010). Although the impact of heat stress on dairy cows has been well-documented in tropical
101 and subtropical regions (e.g. Dikmen and Hansen, 2009; West et al., 2003), a growing number
102 of studies has reported declines in milk yield and quality with increasing THI in temperate
103 regions (reviewed in Van Iaer et al., 2014), including the UK (Dunn et al., 2014; Hill and
104 Wall, 2015), which has a maritime temperate climate with mild summers and winters.

105

106 Here we used eight years' data from a research farm on the west coast of Scotland to
107 investigate the effects of weather on dry matter intake (**DMI**) and the rate of converting dry
108 matter to milk (feed efficiency, **FE**) in Holstein Friesian dairy cows. In southern Scotland
109 temperatures are predicted to increase over the 21st century, especially in summer, with an
110 expected mean daily maximum temperature increase of 4.3°C by the 2080s (Jenkins et al.,
111 2009). The aims of our study were threefold. First, we used Akaike's Information Criterion to
112 compare three thermal indices: a) THI, where wind speed and the number of hours of
113 sunshine were controlled for statistically; b) THI_{adj} ; and c) CCI. As animals show a lagged
114 response to THI with respect to milk yield (Bouraoui et al., 2002; West et al., 2003; Bertocchi
115 et al., 2014), our second aim was to determine a biologically relevant timescale for
116 quantifying the effects of thermal stress on DMI and FE. We did this by comparing the effects
117 of weather on the day of feeding, mean weather spanning the day of feeding plus the 2 days
118 before (3 day means) and mean weather spanning the day of feeding plus 6 days before (7 day
119 means). Third, we tested how genetic selection for milk traits influenced feed intake and FE
120 (whereby a higher FE indicates a greater weight of fat and protein corrected milk produced for
121 a given DMI) under varying weather conditions. We predicted that 1) as thermal indices

122 increase, cows will reduce feed intake to decrease metabolic heat production, and reduce FE
123 to divert more resources from production to thermoregulation. We also predicted that 2) the
124 impact of heat stress on feed intake and FE would be greater in cows of high than average
125 genetic merit because high yielding dairy cows generate more metabolic heat than lower
126 yielding cows.

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129

MATERIALS AND METHODS

130

Subjects, Maintenance and Data Collection

132 The Langhill Holstein Friesian dairy herd was studied at Crichton Royal Farm, Dumfries
133 (55°04695' N, 3°5905' W) between March 2004 and July 2011 inclusive. The herd consisted
134 of ~200 cows, of which approximately half remained indoors throughout the year, while the
135 rest were grazed between April and October. For the remainder of the year all cows were
136 housed in distinct halves of the same building (92.2 × 26.7 m) with access to a shared loafing
137 area (18 × 26.7 m of the building's total space). The continuously housed cows were the focus
138 of our study. They belonged to two genetic lines: Select cows were bred to bulls of the highest
139 genetic merit for kg fat plus protein in the UK, whereas Control cows were bred to bulls close
140 to the UK average for those traits. Bulls were selected at random within a genetic line except
141 that close relatives or sires known to yield calving difficulties were not used. Calving took
142 place all year round, with most calves (65.6 %) being born between October and March of a
143 given year. There were no differences in calving date between the two genetic groups within a
144 given year (Select: ordinal date 168.56±7.78, $N = 316$, Control: 170.5±7.47, $N = 352$;
145 $\beta=1.97\pm10.74$, $t=-0.18$, $P = 0.855$; Linear Mixed effects Model controlling for lactation
146 number and cow identity).

147

148 The cows were housed in a single building in conventional cubicle stalls (210 × 110 cm)
149 supplied with rubber mattresses covered with sawdust. The northernmost half of the NE-
150 facing side of the building was open-sided above a 140 cm high concrete wall. The southern
151 half consisted of a gated section (~3m wide) at either side of an indoor loafing area that was
152 otherwise open to the elements and looked out to grazing fields. The remaining walls
153 consisted of a concrete lower portion (190 cm high), and Yorkshire boarding from the
154 concrete wall to the roof. The wooden panels (115 × 10 cm wide) that made up the Yorkshire
155 boarding were separated by 3 cm gaps between consecutive panels, or a 70 cm gap after every
156 16th panel, to allow free airflow. There was no artificial ventilation. Pillars supported a gabled
157 roof consisting of corrugated cement fiber with Perspex skylights.

158

159 Select and Control cows received the same low forage diet consisting of 50 % home-grown
160 silage (grass, maize and ammonia-treated wheat) and 50 % commercial concentrate feed
161 (wheat grain, sugar beet pulp, rapeseed meal, soybean meal, wheat and barley distillers' dark
162 grains, and mineral and vitamin supplements) provided as a Total Mixed Ration (**TMR**; mean
163 proportions of dry matter over a full lactation; Bell et al. 2011). The TMR was evenly
164 distributed into 24 HOKO automatic feed measurement gates (Insentec BV, Marknesse, The
165 Netherlands), giving a ratio of 0.22 feeders per cow. These provided ad libitum feed
166 throughout the day (except between 11:45 and 12:15 when food residues were removed and
167 fresh feed was supplied, and during milking). The number and identity of feeders and the
168 amount of floor space available to the cows at feeding remained constant throughout the year.
169 HOKO data were recorded throughout lactation on a cycle of 3 consecutive days of
170 measurement followed by 3 consecutive days when it was not measured. Water was available
171 from troughs located at either end of the feeding passage. Cows were milked three times a day

172 and received an additional 0.25 kg concentrates in the parlor at each milking event (which is
173 not included in any analysis presented here). Milk yield (kg) was measured and summed for
174 each day. Milk fat and protein were measured three times a week (Tuesday afternoon,
175 Wednesday morning and midday). Cows were weighed (kg) after each milking event and
176 scored for body condition (on an ordinal scale of 1-5 with 0.25 intervals) once a week based
177 on palpation of specific body parts (Lowman et al., 1976). Animals remained in the study for
178 their first three lactations unless they were culled because of infertility or illness.

179

180 *Weather Data*

181 Daily measurements of dry bulb temperature (T_{db}), wind speed (**WS**), relative humidity (**RH**)
182 and sunshine (summarized in Table 1) during the study period were downloaded from the
183 British Atmospheric Data Centre website (UK Meteorological Office, 2012). All data were
184 recorded at a single Meteorological Office weather station located on the grounds of the
185 research farm (85 m NE of the building housing the cows and 50 m above sea level). T_{db} and
186 RH were point-sampled at 0900h, WS was measured 10 m above the ground between 0850-
187 0900h and expressed as a mean, and sunshine was measured using a Campbell-Stokes
188 recorder and expressed as the number of hours over a 24h period (0000-2359). To see how
189 measurements from the weather station reflected indoor conditions, we compared them to raw
190 measurements of T_{db} , RH and WS made in the cattle building for a separate study (Haskell et
191 al., 2013). Indoor data were collected between late April and early July 2009 and matched
192 with Meteorological Office data for time and date.

193

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

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

197 (1)

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

203

204 THI was calculated using

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

205 (2)

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

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

209 (3)

210 from Mader et al. (2006), where

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

211 Finally we calculated CCI using

$$CCI = RH_{adj} + WS_{adj} + GSR_{adj}$$

212 (4)

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

215

216 We calculated ‘moving’ means for THI, nSun, WS, THI_{adj} and CCI over the 3 and 7 days
 217 prior to and including the test date (**TD**; the day of feeding) to allow the effects of weather to
 218 be compared over 3 timescales: TD, 3 days (i.e. TD, TD minus 1 day and TD minus 2 days)
 219 and a week. Weather can have a lagged effect on biological traits, and the effects of a weather
 220 event can depend on its duration (Hill and Wall, 2015; Renaudeau et al., 2012; West et al.,
 221 2003).

222

223 *Animal Data*

224 We summed the total amount of fresh feed consumed per cow over each 24h TD (00:00.00-
 225 23:59.59) to calculate her total daily feed intake. Summarizing data over a 24h period has the
 226 advantage that diurnal patterns in feeding behavior (Stamer *et al.*, 1997) and management
 227 procedures do not need to be addressed. We calculated DMI (g) based on a sample of TMR
 228 dried in a forced-air oven at 60°C, crude protein intake (**CPI**, g) using the semi-automated
 229 Kjeldahl method (Association of Official Analytical Chemists, 1990) and metabolizable
 230 energy intake (**MEI**, MJ) from the prediction equation by Thomas et al. (1988). We refer to
 231 these 3 variables as *feed intake*. Finally, feed efficiency (FE) was estimated by dividing fat
 232 and protein corrected milk yield (**FPCMY**, kg) by DMI in kg where FPCMY is:

$$233 [0.337 \times \text{raw milk (kg)}] + [11.6 \times \text{fat content (kg)}] + [5.999 \times \text{protein content (kg)}]$$

234 (5)

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

237

238 Our dataset contained 73,058 daily feed intake records from 328 cows on 2,427 days and
 239 71,345 daily FE records from 328 cows on 2,418 days. Animals were 97.8±0.11 (mean±SE;
 240 range 87.5-100) % Holstein Friesian and ranged from 0 to 305 days in milk. The number of

241 daily records for each animal over her three lactations ranged from 11-438 (mean±SE:
 242 222.7±6.74) for feed intake and 11-432 (mean±SE: 217.5±6.59) for FE.

243

244 *Statistical Analysis*

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

251

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

$$\begin{aligned}
 y_{ijk} \sim & \mu + w_{ij} + \text{genetic group}_i + (\text{genetic group}_i \times w_{ij}) + \text{lactation number}_{ijk} + DIM_{ijk} \\
 & + LW_{ijk} + CS_{ijk} + \cos\left(\frac{2\pi TD}{365.25}\right) + \text{sine}\left(\frac{2\pi TD}{365.25}\right) + \cos\left(\frac{2\pi CD}{365.25}\right) \\
 & + \text{sine}\left(\frac{2\pi CD}{365.25}\right) + \text{animal id}_{jk} + \varepsilon_{ijk}
 \end{aligned}$$

262

(6)

263 where y was a single normally distributed response variable (DMI, CPI, MEI or FE) for
264 animal i on test day j that gave birth on calving date k , μ was the overall mean, w was
265 weather (expressed as one of the following a) $\text{THI} + \text{nSun} + \text{WS}$, b) THI_{adj} , or c) CCI)
266 experienced by animal i over one of the three timescales (see above); genetic group (S or C)
267 was a two-level fixed factor for animal i on day j , and lactation number (1, 2 or 3) was a
268 three-level ordered factor; **DIM** was days in milk (days 0-305 for feed intake and days 4-305
269 for FE; day 0 was the day of calving), **CS** was condition score (a proxy for the cow's energy
270 reserves; a decline in CS suggests tissue mobilization to compensate for a negative energy
271 balance (Bauman and Currie, 1980)), and **LW** is live weight. Animal identity was a random
272 factor (random intercepts only) and ϵ was the unexplained variation for animal i on test day j
273 that calved on date k . TD (running test date, 1 to 2676) and **CD** (running calving date, 1 to
274 2945) were expressed as harmonic terms in the model to accommodate potential seasonal
275 trends in management (e.g. stocking density) and photoperiod. The denominator of each sine
276 and cosine term represents the periodicity of the waves. In this case, 365.25 days represents a
277 wave for predictable annual variability (taking into account leap years). We tested for linear,
278 quadratic and cubic effects of all weather variables, DIM and LW, and linear and quadratic
279 effects of CS. Weather variables, DIM, LW and CS were mean-centered to reduce collinearity
280 between higher and lower order terms of a given variable and to improve the interpretability
281 of the estimates. We fitted nSun in the model rather than GSR owing to the high correlation
282 between GSR and THI ($r_p = 0.641$, $t_{2392} = 40.82$, $P < 0.001$) compared to nSun and THI ($r_p =$
283 0.318 , $t_{2392} = 16.40$, $P < 0.001$). These methods generated nine non-nested models (3 weather
284 metrics \times 3 timescales) per response variable. For each response variable, we determined the
285 'best' model with respect to timescale and weather metric based on the lowest AIC, and
286 considered 7 AIC units to be a meaningful difference (Burnham *et al.*, 2011).

287

288 Models were re-fitted based on the full datasets using REML (retaining the same explanatory
289 variables, including autocorrelation parameters) to obtain less biased estimates. To provide
290 context for our results we repeated the THI+WS+nSun analysis with FPCMY (days 4-305 of
291 lactation), as a (normally distributed) response variable using REML. We reached the final
292 models using backward elimination of non-significant ($P \geq 0.05$) interactions (higher order
293 terms removed before lower order terms) and then main effects, retaining lower order terms
294 where higher order terms were significant. We used differentiation of the regression equations
295 to calculate 'turning points' in polynomial relationships between weather and responses. For
296 all models fitted by REML we present estimates of model coefficients (β) with standard
297 errors, t-values and P -values. All statistical tests are two-tailed, and significance is assumed at
298 $P < 0.05$.

299

300

301

RESULTS

302

Weather at the Research Farm

304 T_{db} , THI, THI_{adj} and CCI followed similar seasonal patterns, with peaks in July and troughs
305 between December and February (Fig. 1, Fig. 2). T_{db} at 0900h was $0.22 \pm 0.03^\circ\text{C}$ warmer than
306 mean T_{db} calculated from daily minimum and maximum values ($t_{2419} = 6.3$, $P < 0.001$, paired
307 test). T_{db} at 0900h and mean T_{db} were closely correlated (Table 2). THI and THI_{adj} showed a
308 strong linear correlation (Table 2), although THI was higher than THI_{adj} ($t_{2318} = 5.1$, $P <$
309 0.001 , paired test; Table 1, Fig. 2). CCI was closely correlated with THI, and slightly less so
310 with THI_{adj} (Table 2). THI at 0900h was >60 units on 315 days over the study period (13.2 %
311 of TDs), and >70 units on 6 days (0.3 %); THI_{adj} at 0900h was >60 units on 414 days (17.9 %

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

314

315 THI, THI_{adj} and CCI decreased over the study period (THI: $\beta = -0.0006 \pm 0.0002$, $t = 2.8$, $P =$
316 0.005 ; THI_{adj}: $\beta = -0.0008 \pm 0.0003$, $t = 3.0$, $P = 0.003$; CCI: $\beta = -0.0002 \pm 0.00005$, $t = 3.5$,
317 $P < 0.001$), but nSun ($\beta = 0.0002 \pm 0.0001$, $t = 0.18$, $P = 0.854$) and WS did not change ($\beta =$
318 0.00009 ± 0.0001 , $t = 0.88$, $P = 0.380$).

319

320 There was no difference in T_{db} measured outdoors ($13.3 \pm 0.26^\circ\text{C}$, $N = 75$) and in the center of
321 the loafing area ($13.3 \pm 0.26^\circ\text{C}$, $N = 76$; $\beta = 0.00002 \pm 0.05$, $t < 0.01$, $P > 0.999$, General Linear
322 Model, **LM**, controlling for date; T_{db} data were square-root transformed to normalize), but
323 conditions were cooler outside than in the middle of the feed face ($14.6 \pm 0.27^\circ\text{C}$, $N = 76$; $\beta =$
324 1.6 ± 0.05 , $t = 3.3$, $P = 0.004$). Outdoor T_{db} measurements were strongly and positively
325 correlated with measurements made in the loafing area ($r_s = 0.94$, $t_{73} = 24.6$, $P < 0.001$) and at
326 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
327 the feed face (0.07 ± 0.03 m/s; $\beta = 3.7 \pm 0.42$, $z = 8.9$, $P < 0.001$, Generalized Linear Model with
328 poisson errors, controlling for date) and the loafing area ($0.56 \pm 0.08^\circ\text{C}$; $\beta = 1.7 \pm 0.17$, $z = 10.5$,
329 $P < 0.001$). Outdoor WS was positively correlated with WS in the loafing area ($r_s = 0.40$, $t_{73} =$
330 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
331 between the three sites (feed face: 72.2 ± 1.30 %, loafing: 70.3 ± 1.30 %, outdoors: 72.1 ± 1.32
332 %; $F_{2,222} = 0.66$, $P = 0.520$, LM, controlling for date), and outdoor RH was positively
333 correlated with RH at the feed face ($r_s = 0.78$, $t_{72} = 10.52$, $P < 0.001$) and the loafing area ($r_s =$
334 0.84 , $t_{72} = 13.06$, $P < 0.001$).

335

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

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

347

348 *Comparing Timescales for Quantifying Weather Metrics using Maximum Likelihood*

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

356

357 *How did Genetic Merit Influence Milk Yield and Feeding Traits?*

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

362

363 *How Did THI, Wind Speed and the Number of Hours of Sunshine Influence Feeding*364 *Traits in Cows of High and Average Genetic Merit?*

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

387 steeper on days with fewer hours of sunshine (Fig. 5a-c). Select cows decreased DMI and CPI
388 with increasing sunshine hours at a greater rate than Controls (Fig. 5a-b), but nSun did not
389 affect the two genetic groups differently for MEI or FE (Fig. 5c-d).

390

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

392 Feed intake increased with days in milk until day 123.1 ± 0.16 (mean across the 3 feed intake
393 traits), then decreased and finally increased again on day 276.3 ± 8.68 (Table 5, Supplementary
394 Table S1, Supplementary Figure S1). FE decreased with days in milk (Table 5,
395 Supplementary Figure S1). Feed intake increased with increasing live weight to a weight of
396 638.1 ± 5.76 kg (mean across the 3 traits), and then decreased (Supplementary Figure S2a-c).
397 FE decreased with increasing live weight in cows lighter than 488.3 kg, and then increased
398 with live weight until cows reached a weight of 706.4 kg, before decreasing with increasing
399 live weight (Supplementary Figure S2d). DMI, MEI and FE increased with increasing CS
400 until cows reached a score of 2.2 ± 0.22 units, before decreasing with increasing CS
401 (Supplementary Figure S3). CPI was not influenced by CS (Supplementary Table S1)

402

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

404 As THI_{adj} increased, feed intake decreased and FE increased (Supplementary Table S2, Fig.
405 3f-i). The rate of decrease with increasing THI_{adj} was greater in Select than in Control cows
406 for DMI and CPI, but did not differ between genetic groups for MEI (Supplementary Table
407 S2, Fig. 3f-i). The slope of the relationship between THI_{adj} and FE was steeper for Control
408 than Select cows (Supplementary Table S2).

409

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

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

416

417

418

DISCUSSION

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

433

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

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

460 temperatures. CCI models were better at explaining DMI, CPI and FE than THI_{adj} models,
461 which offers statistical support for this possibility.

462

463 *Comparing Timescales for Quantifying Weather Metrics*

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

475

476 *Feed Intake Decreased and Feed Efficiency Increased with Increasing THI*

477 Our observation that feed intake decreased with increasing THI supports work on DMI in
478 dairy cows (Bouraoui et al., 2002; Gorniak et al., 2014; West, 2003), on DMI in cattle steers
479 (Kang et al., 2016) and on DMI and MEI in sheep (Dixon et al., 1999). Decreases in DMI
480 under conditions of heat stress are associated with decreases in daily and resting metabolic
481 heat production, longer digestion times and a shift from fat to glucose utilization in dairy
482 cows (Eslamizad et al., 2015). In southern Georgia, USA, DMI decreased 0.51 kg for every 1
483 unit increase in test day THI between approximately 73 and 82 THI units (West et al., 2003).
484 Ominski et al. (2002) reported a 6.5 % decline in DMI during 5 days' experimental exposure

485 to heat stress (mean daily THI ~73.5) compared to control conditions (THI ~68.8) in lactating
486 Holsteins in Manitoba, Canada. We observed lower declines (3.8 and 4.3 % in Select and
487 Control cows, respectively) than Ominski et al. (2002) for the same THI values, perhaps
488 owing to a shorter duration of exposure in our study. Severe heat stress can bring about
489 declines in cows' DMI as high as 55 % compared to thermoneutral conditions (National
490 Research Council, 1981). By contrast, at the highest THI recorded in our study, DMI
491 decreased by 11.5 and 12.8 % (Select and Control cows, respectively) compared to peak
492 intake. Under the environmental conditions and feeding regime experienced in our study,
493 cows received the nutrients and energy necessary to support their productive functions
494 (National Research Council, 2001). Nevertheless, predicted increases in temperature (IPCC,
495 2013) combined with increased maintenance requirements as a consequence of heat stress
496 (reviewed in Baumgard and Rhodes, 2012) mean that producers should stay alert to cows'
497 energetic and nutritional requirements falling below these levels even in temperate regions.
498

499 We had expected the impact of THI on feed intake to be greater in cows of high than average
500 genetic merit. Contrary to our prediction, however, the slopes did not differ between the two
501 groups. There at least three reasons, which are not mutually exclusive, as to why this could be
502 the case. 1) Cows may not have experienced warm enough temperatures for a difference to be
503 detected (i.e. for heat stress to occur and affect feed intakes). However, feed intake varied
504 with THI within genetic groups, so cows were clearly affected by the range of temperatures in
505 the study. 2) THI alone may not have fully captured the response of cows to weather. The
506 observation that THI, THI_{adj}, CCI, WS and nSun affected high genetic merit cows differently
507 from Controls with respect to some of the feed intake traits is consistent with this possibility.
508 3) Select cows might have modified other aspects of feeding in order to maintain the same
509 overall DMI. This might involve feeding at a cooler time of day (Adin et al., 2008) or

510 adjusting meal characteristics (Hill & Wall, in prep). Such questions can be addressed using
511 individual animal feed intake recording systems, such as that used in the present study, which
512 provide detailed information on intake, duration and timing of individual visits.

513

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

534

535 *Feed Intake Increased with Increasing Wind Speed*

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

543

544 *Feed Intake Decreased and Feed Efficiency Increased as Sunshine Hours Increased*

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

560 photoperiod. Interestingly, the effects of sunshine differed between the two genetic lines in
561 our study: Select cows decreased DMI and CPI with increasing sunshine hours at a greater
562 rate than Controls.

563

564 *Implications for Climate Change*

565 We observed decreases in feed intake and FPCMY with increasing THI under conditions
566 currently experienced in a temperate region, suggesting that temperate herds may be more
567 sensitive to ambient heat than is currently recognized. Dunn et al (2014) predicted a steady
568 increase in the number of days on which THI exceeds 70 units in the UK over the 21st
569 century. In south-east England, the number of days over 70 THI units was predicted to exceed
570 40 days/year by 2100 (Dunn et al., 2014). Although these predicted conditions are milder than
571 those currently experienced in many regions that rely on dairy farming, the low tolerance of
572 temperate zone animals to high THI is cause for concern. Nevertheless, our finding that FE
573 increased with increasing THI suggests that some of the future costs of lost productivity may
574 be offset by reduced economic expenditure on feed per kg milk, at least under conditions of
575 mild heat stress.

576

577 Temperatures inside cattle sheds are 3-6°C warmer than outdoors in northern Europe (Seedorf
578 et al., 1998), and up to 3.5°C warmer or 6 THI units higher indoors than outdoors in central
579 Europe (Erbez et al., 2010). In our study the feed face was just 1.23°C warmer than outside
580 and humidity inside the building did not differ from values measured outdoors during the
581 months for which indoor data were available (late April to early July). The responses to
582 temperature and humidity that we describe are therefore likely to reflect those in a grazing
583 system (though potential interactions with feed type, and physical activity and other behaviors
584 between housed and grazing animals should be considered). It is worth noting that stocking

585 density was higher between November and March than the other months of our study because
586 cows from a separate study were housed with our study subjects for the winter. Body heat
587 from the additional animals may have therefore helped to buffer our subjects from the cold.
588 For animals grazing on warm days, WS is expected to have a more pronounced effect in
589 alleviating heat load than we observed in our housed cows.

590

591

CONCLUSIONS

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

609

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610

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619

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WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

807 **Table 1.** Descriptive statistics for weather data recorded at the closest Meteorological Office station (source id:
 808 19259) to the research farm (2004 to 2011; N = 2676 daily records) and for Global Solar Radiation, THI, THI_{adj}
 809 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

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

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

813 **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

814 T_{db} is dry bulb temperature, THI is temperature humidity index and THI_{adj} is THI adjusted for wind speed and

815 global solar radiation. $P < 0.001$ for all correlations.

816

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

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

Weather metric	Time-scale	DMI		MEI		CPI		FE	
		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

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

824

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

825 **Table 4.** Least squares means \pm standard errors for daily intake of dry matter (DMI), metabolizable energy (MEI), crude protein (CPI), feed efficiency (FE), and fat and
 826 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	<i>N</i>	mean	s.e.m	mean	s.e.m	<i>N</i>
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)

827 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
 828 for groups within FPCM and FE.

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

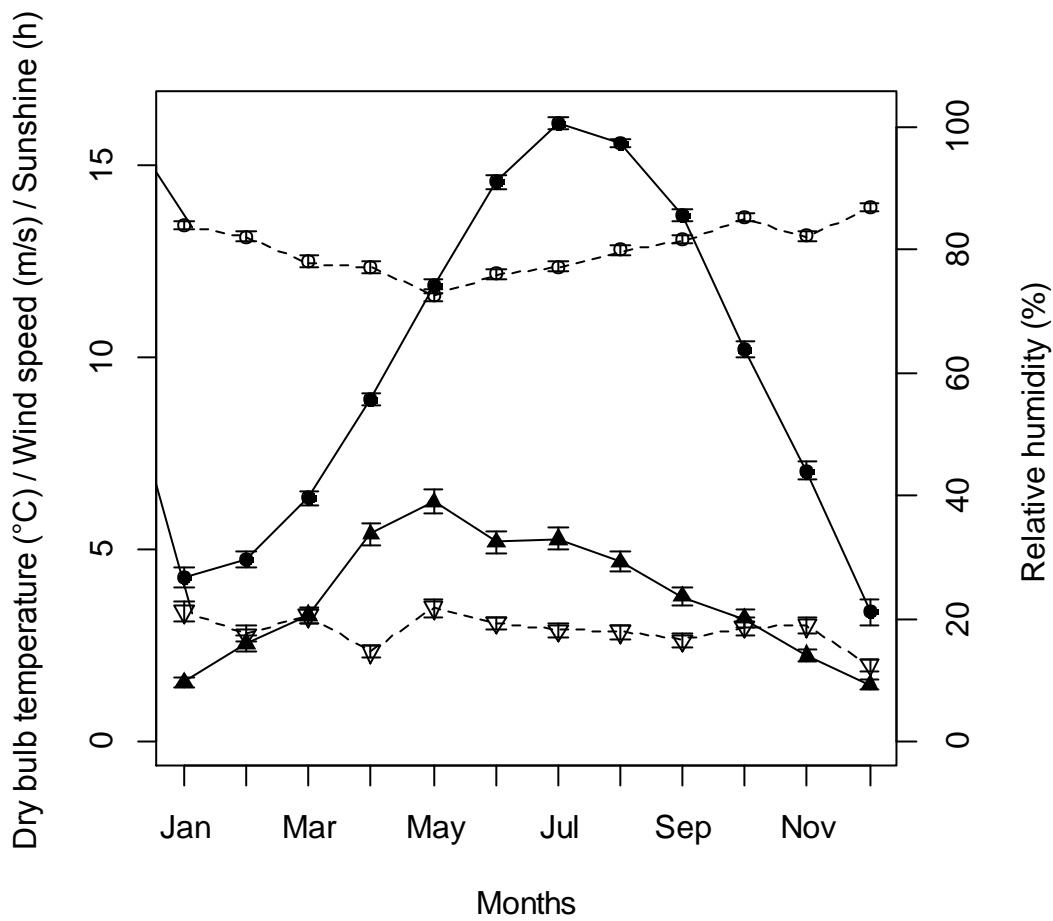
829 **Table 5.** LMMs to test the effect of weather (THI, wind speed and hours of sunshine; means summarized over 3
 830 days) and genetic group (Select or Control) on dry matter intake (73,058 records) and feed efficiency (71,345
 831 records) in 328 Holstein Friesian cows during the years 2004-2011

Fixed effects	Dry matter intake (g)				Feed efficiency (kg milk / kg DMI)			
	β	s.e.m	<i>t</i>	<i>P</i>	β	s.e.m	<i>t</i>	<i>P</i>
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

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

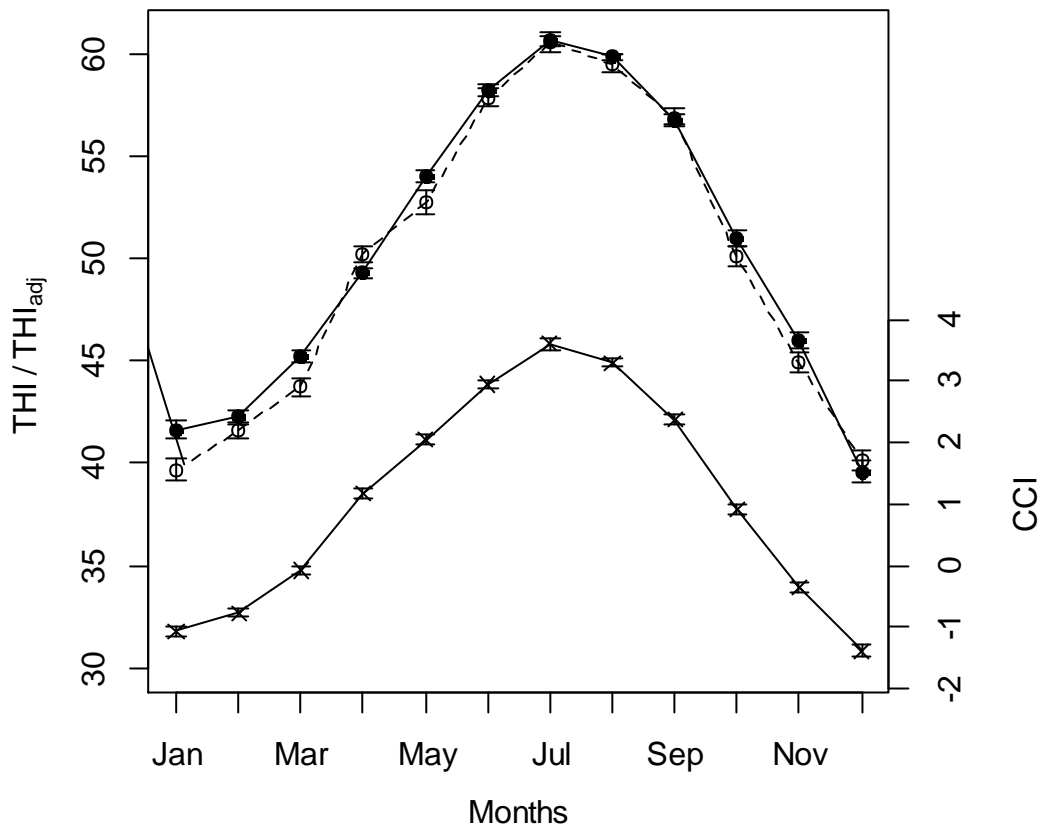
φ_1	0.162	0.175
φ_2	0.169	0.176
φ_3	0.151	0.146
φ_4	0.096	0.089
φ_5	0.055	0.075
<hr/>		
Random effect	% σ	% σ
<hr/>		
Animal identity	36.360	30.126
Residual	63.640	69.874

832 TD = running test day (the day of feeding); CD = running calving date; THI = temperature humidity index; WS
833 = wind speed; nSun = the number of hours of sunshine; GG = genetic group; DIM = days in milk; LW = live
834 weight; CS = condition score; φ_n = the estimate of correlation at lag n
835 ‘Control’ was the reference (baseline) genetic group
836 Linear, quadratic (²) and cubic (³) effects were tested for where indicated; lactation number is an ordered
837 factor.
838 Non-significant effects that were not components of significant interactions were removed from the final models;
839 their *P*-values are italicized.
840 Parameter estimates (β) and standard errors marked <0.001 for dry matter intake or <0.00001 for feed efficiency
841 were positive values, and those marked <0 were between 0 and -0.001 for dry matter intake or between 0 and -
842 0.00001 for feed efficiency.



843

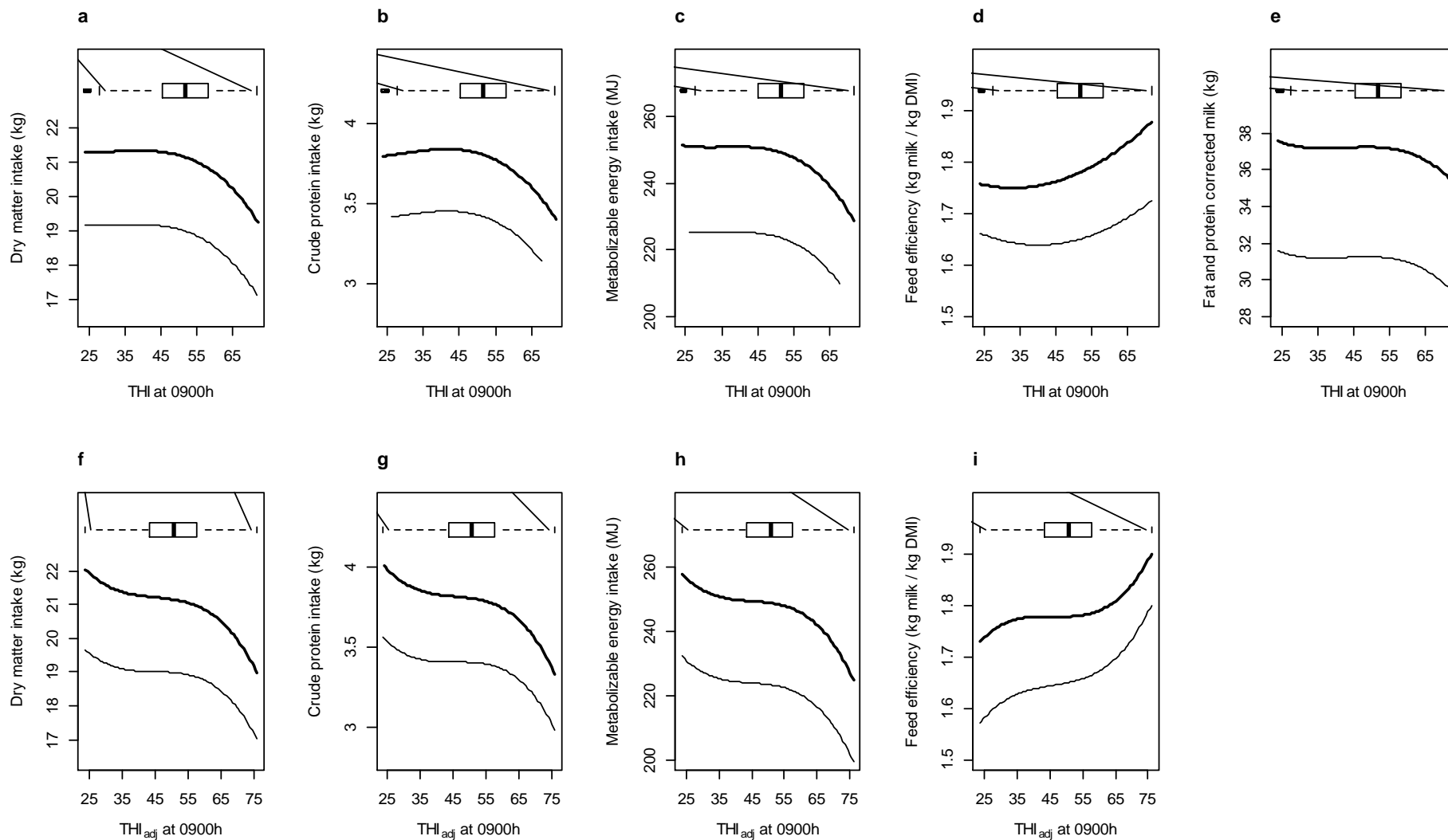
844 **Fig. 1** Mean monthly dry bulb temperature (closed circles), wind speed (open triangles), the number of
 845 hours of sunshine (closed triangles) and relative humidity (open circles) ± 1 standard error measured
 846 daily at the research farm, Dumfries, Scotland, during the study period (2004-2011).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



848

849 **Fig. 2** Mean monthly THI (Temperature Humidity Index, closed circles), THI_{adj} (THI adjusted for
 850 wind speed and global solar radiation, open circles) and CCI (Comprehensive Climate Index, crosses)
 851 ±1 standard error based on values measured daily at 0900h at the research farm, Dumfries, Scotland,
 852 during the study period (2004-2011)

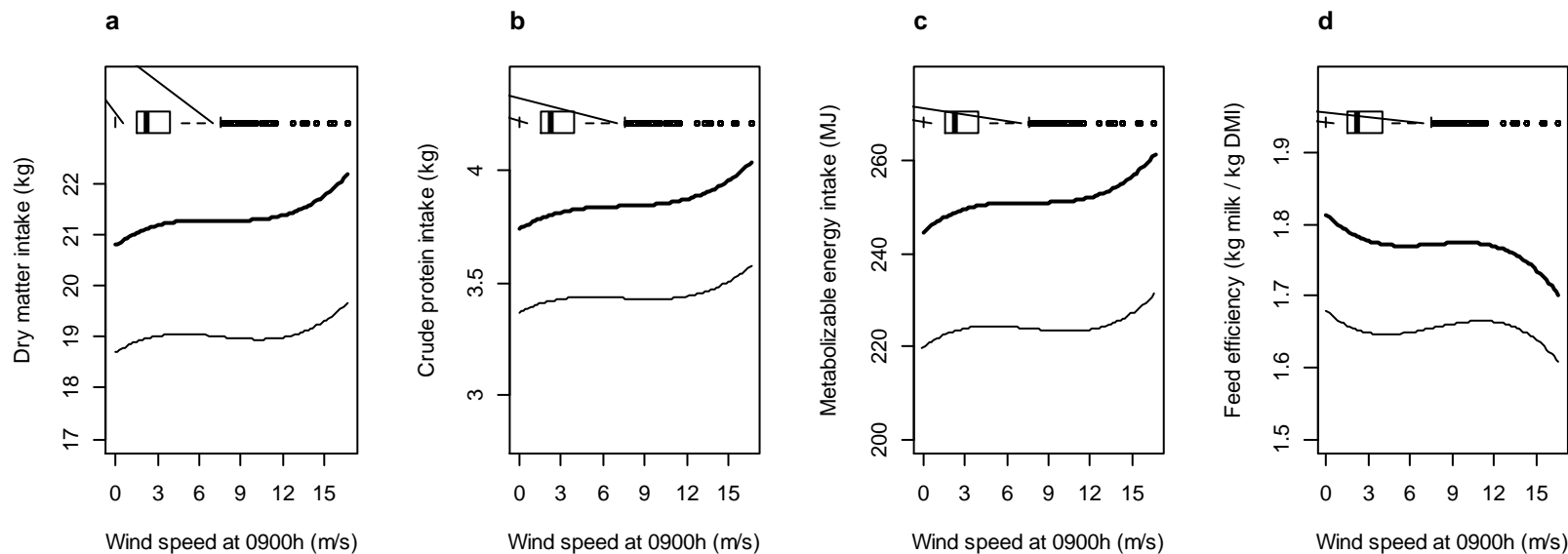
WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY



WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

854 **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)
855 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
856 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
857 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
858 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
859 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
860 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
861 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
862 (controlling for WS and sunshine; top row) explained feed intake and FE better than models testing for the effects of THI_{adj}

WEATHER INFLUENCES FEED INTAKE AND EFFICIENCY

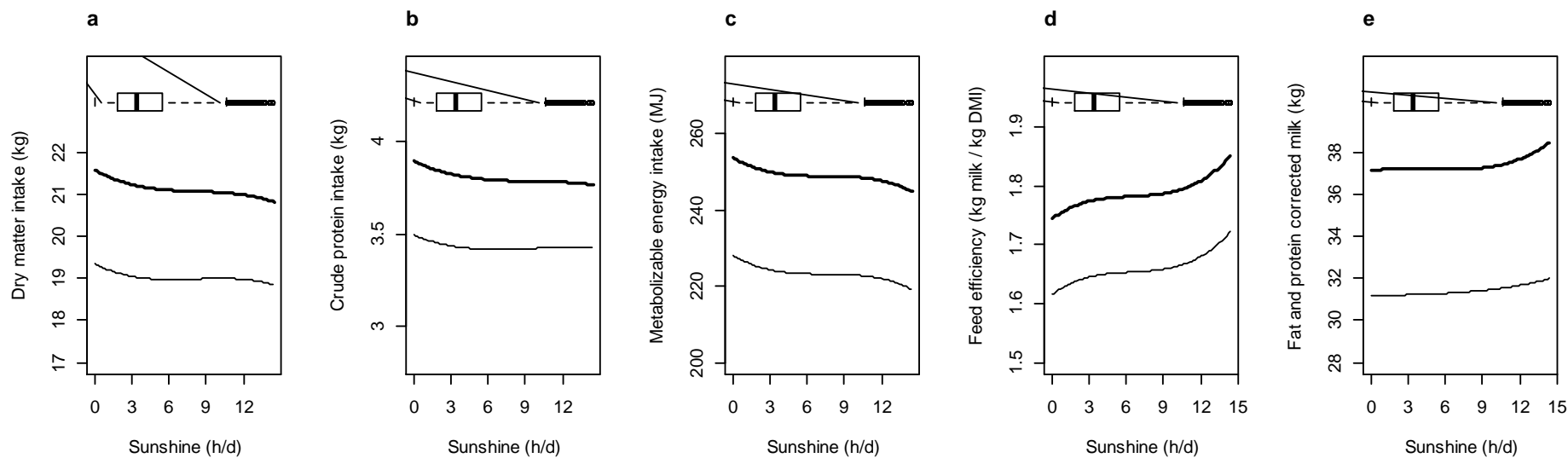


863

864 **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
 865 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
 866 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
 867 statistical estimates for the effects presented here are provided in Tables 5 and Supplementary Table S1. Wind speed did not have a statistically significant
 868 effect on fat and protein corrected milk yield (not shown)

869

870



871

872 **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)

873 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

874 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

875 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

876 71,345 records

877