

Hill, Davina L. and Wall, Eileen (2014) Dairy cattle in a temperate climate: the effects of weather on milk yield and composition depend on management. *Animal*, 9 (1). pp. 138-149.

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Hill, D. L. and Wall, E. (2015) Dairy cattle in a temperate climate: the effects of weather on milk yield and composition depend on management, *Animal* **9**: 138-149

DOI: <http://dx.doi.org/10.1017/S1751731114002456>

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# **Dairy cattle in a temperate climate: the effects of weather on milk yield and composition depend on management**

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**1 Abstract**

2 A better understanding of how livestock respond to weather is essential to enable  
3 farming to adapt to a changing climate. Climate change is mainly expected to impact  
4 dairy cattle through heat stress and an increase in the frequency of extreme weather  
5 events. We investigated the effects of weather on milk yield and composition (fat and  
6 protein content) in an experimental dairy herd in Scotland over 21 years. Holstein  
7 Friesian cows were either housed indoors in winter and grazed over the summer or  
8 were continuously housed. Milk yield was measured daily, resulting in 762786 test  
9 day records from 1369 individuals, and fat and protein percentage were sampled  
10 once a week, giving 89331 records from 1220 cows per trait. The relative influence  
11 of 11 weather elements, measured from local outdoor weather stations, and two  
12 indices of temperature and humidity (THI), indicators of heat stress, were compared  
13 using separate Maximum Likelihood models for each element or index. Models  
14 containing a direct measure of temperature (dry bulb, wet bulb, grass or soil  
15 temperature) or a THI provided the best fits to milk yield and fat data; wind speed  
16 and the number of hours of sunshine were most important in explaining protein  
17 content. Weather elements summarised across a week's timescale from the test day  
18 usually explained milk yield and fat content better than shorter-scale (three day, test  
19 day, test day-1) metrics. Examining a subset of key weather variables using REML,  
20 we found that THI, wind speed and the number of hours of sunshine influenced milk  
21 yield and composition. The shape and magnitude of these effects depended on  
22 whether animals were inside or outside on the test day. The milk yield of cows  
23 outdoors was lower at the extremes of THI than at average values, and the highest  
24 yields were obtained when THI, recorded at 0900 h, was ~55 units. Cows indoors  
25 decreased milk yield as THI increased. Fat content was lower at higher THIs than at

26 intermediate THIs in both environments. Protein content decreased as THI increased  
27 in animals kept indoors and outdoors, and the rate of decrease was greater when  
28 animals were outside than when they were inside. Moderate wind speeds appeared  
29 to alleviate heat stress. These results show that milk yield and composition are  
30 impacted by extremes of THI under conditions currently experienced in Scotland,  
31 where animals have so far experienced little pressure to adapt to heat stress.

32

### 33 **Keywords**

34 climate change, fat percentage, heat stress, protein percentage, THI

35

### 36 **Implications**

37 Climate change is expected to bring about drier, hotter summers and an increased  
38 frequency of extreme weather events across Europe. Here we show that milk yield  
39 and quality decline at the upper extremes of temperature and humidity even under  
40 conditions currently experienced in Scotland. We identify the values of temperature  
41 and humidity, and of other weather elements, at which performance begins to  
42 decrease. These estimates could be used in conjunction with climate projections to  
43 help policy makers understand the likely economic impact of climate change on dairy  
44 productivity.

45

## 46 **Introduction**

47

48 Climate change will have direct effects on livestock performance and welfare, mainly  
49 through increases in temperature and the frequency of extreme weather events, and  
50 will also affect animals indirectly through changes in the availability of fodder and  
51 pasture and the distribution of pests and parasites (Gauly *et al.*, 2013). High  
52 temperatures are associated with a greater incidence of heat stress in livestock,  
53 which can have negative effects on milk yield (Bohmanova *et al.*, 2007, Hammami *et*  
54 *al.*, 2013), fertility (Hansen, 2009) and health (Sanker *et al.*, 2013), and increase the  
55 risk of mortality (Vitali *et al.*, 2009). Heat stress occurs when animals experience  
56 conditions above their thermal comfort zone and are unable to dissipate enough heat  
57 to maintain thermal balance (Kadzere *et al.*, 2002). This is already costly to the dairy  
58 industry in terms of management interventions and lost productivity (St-Pierre *et al.*,  
59 2003).

60

61 An animal's tolerance to high air temperatures depends on the amount of water  
62 vapour in the air because this influences the rate of heat loss through evaporative  
63 cooling. The association between air temperature and water vapour content can be  
64 expressed as a Temperature Humidity Index (**THI**; Thom, 1959). Milk yield in  
65 Holstein dairy cows, *Bos taurus*, is traditionally said to begin declining at around 72  
66 THI units based on work carried out in subtropical regions (Armstrong, 1994,  
67 Ravagnolo *et al.*, 2000). Thresholds of 68 (Gauly *et al.*, 2013, Renaudeau *et al.*,  
68 2012) or even 60 units (Bruegemann *et al.*, 2012) may, however, be more  
69 characteristic of high yielding herds in temperate zones. The genetic relationship  
70 between heat tolerance and productivity is negative (Ravagnolo and Misztal, 2000),

71 and dairy cattle are becoming more sensitive to heat stress due to optimisation of  
72 breeding and management practices for increased performance (Kadzere *et al.*,  
73 2002, West *et al.*, 2003). The reduction in productivity in heat stressed cows is  
74 largely a result of reduced feed intake, but high temperatures also have a direct  
75 effect on reproductive physiology and metabolism (Renaudeau *et al.*, 2012). Cattle  
76 generate metabolic heat as a by-product of milk synthesis and so higher yielding  
77 animals experience heat stress at lower THIs than lower yielders (Kadzere *et al.*  
78 2002).

79

80 An animal's thermal tolerance is also affected by solar radiation and the velocity of  
81 ambient air (Dikmen and Hansen, 2009, Graunke *et al.*, 2011, Hammami *et al.*,  
82 2013), while increasing precipitation is associated with declining milk production  
83 (Stull *et al.*, 2008). Weather-related stressors could potentially affect performance  
84 immediately or have a delayed impact, and yet few studies have explored the time  
85 interval between weather events occurring and impacting milk traits (St-Pierre *et al.*,  
86 2003). Among those that have, West *et al.*, (2003) found that the effects of mean  
87 daily THI on milk yield were greatest two out of a possible three days after THI was  
88 recorded and Bouraoui *et al.* (2002) found that mean daily THI measured 1-3 days  
89 before the test day had a greater effect on milk yield than test day THI. These time  
90 lags might be related to the duration of digestive processes (Gauly *et al.*, 2013).

91

92 Here we used 21 years' data from a single herd at two dairy research farms on the  
93 east and west coasts of Scotland to investigate the effects of weather on milk yield  
94 and composition (fat and protein content). The study evaluates a range of weather  
95 variables collected from Meteorological Office weather stations located on the

96 grounds of the farms or in the close vicinity, and two THIs that are frequently used to  
97 characterise heat stress in cattle. Although the effects of heat stress on dairy cows  
98 has been well-documented in tropical and sub-tropical regions (e.g. Dikmen and  
99 Hansen, 2009, West *et al.*, 2003), a growing number of studies has reported  
100 associations between THI and milk traits in temperate regions where tolerance to  
101 heat stress is lower (Bruegemann *et al.*, 2011, Dunn *et al.*, 2014, Hammami *et al.*,  
102 2013). Moreover, temperatures are predicted to increase over the 21<sup>st</sup> century in  
103 southern Scotland, especially in summer, with an expected mean daily maximum  
104 temperature increase of 4.3°C by the 2080s with a very slight reduction (0-5%) in  
105 humidity (Jenkins *et al.*, 2009). We therefore aimed to (1) determine the most  
106 biologically relevant way to quantify different weather elements and two THIs with  
107 respect to measurement timescale and summary statistics (mean, maximum,  
108 minimum) and to (2) test how weather currently influences milk yield and  
109 composition in cows with and without access to grazing on the test day  
110 (management group). We hypothesised that productivity would decline under  
111 extreme weather conditions, particularly at the upper extremes of THI, and that the  
112 magnitude of the effects would depend on management.

113

114

## 115 **Material and Methods**

116

### 117 *Subjects, maintenance and data collection*

118 We studied the Langhill Holstein Friesian dairy herd, consisting of approximately 200  
119 cows, between November 1990 and July 2011. The cattle were housed at Langhill  
120 Farm, Roslin, Midlothian (55°52'1"N, 3°10'15"W), hereafter 'Farm 1', until late June

121 2002 and then transferred to Crichton Royal Farm, Dumfries (55°02' N, 3°34' W),  
122 'Farm 2', a distance of 95 km. The management systems are described for Farm 1 in  
123 Veerkamp *et al.* (1994) and for Farm 2 in Pollott and Coffey (2008). Briefly, two  
124 genetic lines were created in 1976: select (**S**) and control (**C**). S cows were bred to  
125 bulls of the highest UK genetic merit for kg fat plus protein while C cows were bred to  
126 bulls that were similar to the national average for these traits. Every year, semen  
127 from 4-5 bulls that were not closely related to the cows nor known to produce calving  
128 difficulties was obtained from nationally available stock and used to serve females  
129 from the same genetic line. Females from the two lines were managed together and  
130 allocated in equal numbers to either a High Forage (**HF**) or Low Forage (**LF**) diet  
131 system. A Total Mixed Ration (**TMR**) of blended concentrates, brewers' grain and  
132 silage was offered *ad libitum* to HF cattle in the ratio 20:5:75 total dry matter (mean  
133 proportions over a full lactation) and to LF cattle in the ratio 45:5:50. All animals  
134 received concentrates in the milking parlour. Females from the same sire were  
135 assigned to the two diet groups in equal numbers.

136

137 At Farm 1, calving took place between early September and January each year.  
138 Cows were kept indoors for approximately 200 days after calving (day 0) and then  
139 grazed. Those that were still indoors at the end of June were moved outside. Most  
140 grazing occurred between April and October, inclusive, depending on the availability  
141 of pasture. At Farm 2, the HF group was grazed between April and October, and  
142 otherwise maintained indoors; LF cows were continuously housed (**CH**). Calving took  
143 place all year round for both HF and LF cows, and the majority of calves were born  
144 during the winter months. Housing at both farms consisted of conventional cubicle  
145 stalls within a single building with a corrugated metal roof and no artificial ventilation.



146 At Farm 1, the building had walls of slatted wood and large open doors at each end;  
147 an open ridge in the roof facilitated airflow. The building at Farm 2 had open  
148 windows along the length of one side and a gated but otherwise open section (~3m  
149 wide) on each of two opposite sides surrounding an indoor loafing area.

150

151 Cows were milked twice daily at Farm 1 and three times a day at Farm 2. Milk yield  
152 (kg) was measured and summed for each day. Fat and protein content were  
153 measured twice (Farm 1, Tuesday PM and Wednesday AM) or three times (Farm 2,  
154 Tuesday PM, Wednesday AM and midday) a week, and expressed as percentages  
155 averaged across the two or three milking events. Animals remained in the study for  
156 three lactations unless they were culled due to illness or infertility.

157

#### 158 *Animal data*

159 We extracted milk records collected on days 4-305 of the cows' first three lactations  
160 for animals that were  $\geq 75\%$  Holstein Friesian (mean  $93.0 \pm 0.19\%$ ), discarding  
161 records collected between June 2002 and July 2003 when cows were acclimatising  
162 to Farm 2. This resulted in a dataset containing 762786 test day records for milk  
163 yield from 1369 individuals over 7073 days and 89331 weekly records from 1220  
164 animals over 958 days for fat and protein content. The number of records for each  
165 animal ranged from 3-902 (mean  $557.6 \pm 10.68$ ) for milk yield and 3-129 (mean  
166  $73.2 \pm 10.09$ ) for fat and protein content. Test day milk yield records were matched  
167 with weather data from the same day, and fat and protein records were matched with  
168 weather data measured on the Tuesday of the same week.

169

#### 170 *Weather data*

171 Data on 11 weather elements (Table 1) were downloaded from the British  
 172 Atmospheric Data Centre website (UK Meteorological Office., 2012). These  
 173 consisted of point-samples recorded at 0900 h each day and 24h summaries (mean,  
 174 minimum, maximum, total). For each element we extracted data from the closest  
 175 weather station to Farm 1 for the period 1990-2002 and to Farm 2 for 2003-2011.  
 176 Meteorological Office weather stations that measured most elements of interest were  
 177 active on the grounds of Farm 1 until 1999 and Farm 2 for the duration of the  
 178 experiment. An additional five stations  $\leq 14.4$ km from Farm 1 and one station 29km  
 179 from Farm 2 were used for the remaining elements and to fill in missing values.  
 180 Supplementary Table S1 provides the distances that each weather element was  
 181 measured from the farms, and the elevation at which it was recorded. Using these  
 182 data, we calculated  $THI_1$ :

183 **Equation 1**

$$THI_1 = (T_{db} + T_{wb}) \times 0.72 + 40.6$$

184 where  $T_{db}$  was dry bulb air temperature ( $^{\circ}C$ ) and  $T_{wb}$  was wet bulb temperature ( $^{\circ}C$ ),  
 185 and  $THI_2$ :

186 **Equation 2**

$$THI_2 = (1.8 \times T_{db} + 32) - ((0.55 - 0.0055 \times RH) \times (1.8 \times T_{db} - 26))$$

187 where **RH** was relative humidity (%) (National Research Council, 1971).

188

189 As weather can have a delayed effect on biological processes, and the effects of  
 190 weather depend on the timescale over which animals experience them (Bertocchi et  
 191 al, 2014, Renaudeau *et al.*, 2012, West *et al.*, 2003), we explored the relationship  
 192 between milk traits and all weather variables on the day the cow was milked ('test  
 193 day' or **TD**), the preceding day (**TD-1**), and for the number of hours of sunshine,  
 194 which was measured 0000-2359h, two days before milking (**TD-2**). We calculated a

195 'moving' mean for each daily (0900 h) point sample over the three and seven days  
196 prior to (and including) the TD, and a moving minimum and maximum for the three  
197 variables for which 24h summaries were available (precipitation,  $T_{db}$  and sunshine).  
198 We also noted the presence versus absence of lying snow on the TD and TD-1.  
199 These methods allowed us to compare different ways of expressing the weather  
200 elements, hereafter 'weather metrics'.

201

### 202 *Statistical analysis*

203 Weather at Farms 1 and 2 was compared using separate Generalized Least  
204 Squares models for each weather element or index fitted by Restricted Maximum  
205 Likelihood (**REML**) from the nlme package in R version 3.0.2. (R Development Core  
206 Team, 2013). Harmonic regression allowed us to account for seasonal fluctuations in  
207 weather and we applied a first order autocorrelation structure to deal with non-  
208 independence of weather values between days.

209

210 We used Akaike's Information Criterion (**AIC**) to determine the most biologically  
211 relevant way to express each weather element and compare the explanatory power  
212 of each element with respect to milk yield, fat content and protein content (models  
213 listed in Supplementary Table S2). AIC has been used previously to compare  
214 temperature indices in explaining milk traits (Bruegemann *et al.*, 2012, Hammami *et*  
215 *al.*, 2013). As the metrics for summarising a given element were closely correlated,  
216 and high proportions of shared variance can lead to unreliable estimates, we fitted  
217 each metric in a separate Linear Mixed effects Model (**LMM**) (Equation 3) using  
218 Maximum Likelihood to produce a series of non-nested models. Information Theory  
219 is an appropriate method for comparing non-nested models provided that models are

220 fitted to identical datasets (e.g. there are no missing values) (Burnham and  
 221 Anderson, 2002). As the full dataset contained missing values where data were  
 222 unavailable for the closest weather stations to a farm, we created a reduced dataset  
 223 of 659918 records (86.5% of the total) and 1357 animals (99.1%) for milk yield, and  
 224 77178 records (86.4% of the total) and 1212 animals (99.3%) for fat and protein  
 225 content by excluding all records with missing weather values. This dataset was used  
 226 only to compare weather metrics. We fitted the following model:

227

228 **Equation 3**

$$y \sim \mu + w + \text{feed group} + \text{genetic group} + (\text{feed group} \times \text{genetic group}) + \text{management} \\ + \text{farm} + \text{lact no.} + \text{DIM} + \text{animal id} + \text{TD} + \text{ordinal calving date} + \epsilon$$

229

230 where  $y$  was the response variable (milk yield, fat or protein content, all normally  
 231 distributed),  $\mu$  was the overall mean and  $w$  was a single weather metric or weather  
 232 metric plus weather metric  $\times$  management interaction term; ‘feed group’ (HF or LF),  
 233 ‘genetic group’ (S or C), ‘management’ on the TD (grazing or housed) and ‘farm’ (1  
 234 or 2) were two-level fixed factors, ‘lactation number’ (1, 2 or 3) was a three-level  
 235 ordered factor, linear and quadratic terms of ‘**DIM**’, (Days 4-305 In Milk where day 0  
 236 was the day of calving) were covariates, animal identity, ordinal calving date and TD  
 237 (continuous date from the beginning of the experiment, 1-7578) were random factors  
 238 (random intercepts only) and  $\epsilon$  was the error structure. We considered farm identity  
 239 to control for potential changes in management and other conditions between the  
 240 two farms, and ordinal calving date (1-367) to control for differences in the time of  
 241 year that cows calved. Fitting TD as a random factor allowed us to account for  
 242 temporal autocorrelation, as well as potential trends related to climate and genetic  
 243 improvements over the study period. To test the hypothesis that productivity declines

244 in extreme weather conditions, we fitted linear, quadratic and cubic terms for all  
245 continuous weather variables (except for snow depth, precipitation and visibility  
246 which were expected to have a linear effect on milk traits), retaining lower order  
247 terms where higher order terms were significant. All continuous terms were mean-  
248 centred to reduce collinearity between polynomial terms of a given variable and to  
249 improve the interpretability of the results. LMMs were fitted using the lme4 package  
250 (Bates *et al.*, 2013) in R. We selected the 'best' model for each weather element  
251 based on the lowest AIC, and considered 7 AIC units to be a meaningful difference  
252 between models (Burnham *et al.*, 2011). The highest ranked model for each weather  
253 element or index was refitted using REML on the same dataset to obtain less biased  
254 parameter estimates, which were calculated using lmerTest (Kuznetsova *et al.*,  
255 2014).

256

257 Next, we tested whether the effects of weather on milk yield and composition  
258 depended on the prevailing management type (indoors or outdoors) in a single LMM  
259 for each response variable (Equation 3) using REML. To avoid fitting variables with  
260 shared variation in the same model, weather variables were limited to precipitation,  
261 WS, sunshine, and THI<sub>2</sub>, based upon Exploratory Factor Analysis (psych package;  
262 Revelle, 2013), correlation coefficients ( $\leq 0.33$  based on TD values) and AIC rankings  
263 (see Results). For each of the three weather elements and THI, the metric belonging  
264 to the highest ranked model was used. We tested for linear effects of precipitation,  
265 and linear, quadratic, cubic and quartic effects of THI<sub>2</sub>, WS and sunshine. Non-  
266 significant interactions were removed from the models (higher order terms before  
267 lower order terms) followed by non-significant main effects using backward  
268 elimination. For each significant interaction between weather and milk traits, a further

269 LMM using REML was undertaken to examine the effect size and shape of the  
270 relationship for the two management groups separately. We used differentiation to  
271 calculate the 'turning points' where performance began to decline for polynomial  
272 relationships between weather and milk traits based on the regression equations of  
273 the post-hoc LMMs. For models fitted by REML, we present estimates of the model  
274 coefficient ( $\beta$ ) with standard errors, t-values and *P*-values assuming significance at  
275  $P < 0.05$ . All statistical tests are two-tailed.

276

277

## 278 **Results**

279

### 280 *Weather conditions at the research farms*

281 The UK has a maritime temperate climate with mild summers and winters.

282 Descriptive statistics for weather at the two research farms are given in Table 1.  $THI_1$

283 and  $THI_2$  showed a strong linear correlation ( $r_p = 0.986$ ,  $t_{6873} = 495.5$ ,  $P < 0.001$ ),

284 although  $THI_1$  was higher than  $THI_2$  ( $t_{6874} = 150.2$ ,  $P < 0.001$ , paired test).  $THI_1$  at

285 0900 h was  $>60$  units across the two farms on 1114 days over the study period

286 (16.2% of TDs), and  $>70$  units on 10 days (0.2%), and  $THI_2$  at 0900 h was  $>60$  units

287 on 626 days (9.1% of TDs) and  $>70$  units on 8 days (0.1%). THI values peaked in

288 July and were lowest between December and February, while the number of hours

289 of sunshine was greatest in May and lowest in December and January. The research

290 farms received  $<1$ h sunshine over 24h on 2343 days (33.4%) and  $>9$ h on 668 days

291 (9.5%), and WS was  $<5$  knots at 0900 h on 2464 days (36.1%) and  $>20$  knots on

292 415 days (6.1%). Higher values of ppt,  $T_{db}$ ,  $T_{wb}$ ,  $THI_1$ ,  $THI_2$ ,  $T_s$  and  $T_g$  were recorded

293 at Farm 2 than at Farm 1, whereas WS, visibility, snow depth and RH were greater

294 at Farm 1 (Table 1). There was no difference in  $P_{MSL}$  or the number of hours of  
 295 sunshine at the two farms. THI increased over the 12-years of study at Farm 1 (THI<sub>1</sub>:  
 296  $\beta = 0.17 \pm 0.04$ ,  $t = 4.34$ ,  $P < 0.001$ ; THI<sub>2</sub>:  $\beta = 0.13 \pm 0.04$ ,  $t = 2.95$ ,  $P = 0.003$ ), but did  
 297 not change over the 8 years at Farm 2 (THI<sub>1</sub>:  $\beta = -0.11 \pm 0.07$ ,  $t = 1.63$ ,  $P = 0.103$ ;  
 298 THI<sub>2</sub>:  $\beta = 0.13 \pm 0.08$ ,  $t = 1.64$ ,  $P = 0.101$ ). The number of hours of sunshine  
 299 increased over the study period at Farm 1 ( $\beta = 0.09 \pm 0.02$ ,  $t = 4.85$ ,  $P < 0.001$ ), but  
 300 did not change over the years of the study at Farm 2 ( $\beta = -0.02 \pm 0.04$ ,  $t = 0.47$ ,  $P =$   
 301  $0.636$ ). WS decreased over the time at Farm 1 ( $\beta = -0.21 \pm 0.05$ ,  $t = 3.90$ ,  $P < 0.001$ ),  
 302 but did not change at Farm 2 ( $\beta = 0.12 \pm 0.07$ ,  $t = 1.80$ ,  $P = 0.072$ ). Precipitation did  
 303 not change over the study period at Farm 1 ( $\beta = 0.02 \pm 0.03$ ,  $t = 0.49$ ,  $P = 0.625$ ) or at  
 304 Farm 2 ( $\beta = 0.10 \pm 0.06$ ,  $t = 1.55$ ,  $P = 0.122$ ). Daily maximum temperatures exceeded  
 305 point samples measured at 0900 h by 3.3°C ( $t_{6919} = 120.6$ ,  $P < 0.001$ ), and daily  
 306 minimum temperatures were 3.7°C cooler than point samples ( $t_{6919} = 123.0$ ,  
 307  $P < 0.001$ ).

308

### 309 *Comparing the effects of weather elements and metrics on milk yield and quality*

310 Models testing for the effects of  $T_s$  provided the best fits to the data for both milk  
 311 yield and fat content, while WS models provided the best fit to protein content data  
 312 (Table 2; Supplementary Table S3). Weather elements and indices were ranked in  
 313 the same order for milk yield and fat content (albeit with ties for THI<sub>1</sub>, THI<sub>2</sub> and  $T_{db}$   
 314 for fat content), but followed a different order for protein content except at the end of  
 315 the scale ( $P_{MSL}$ , ppt and snow were ranked 12<sup>th</sup>, 11<sup>th</sup> and 13<sup>th</sup> across all 3 milk traits).  
 316 Models testing for direct measures of temperature ( $T_s$ , THI<sub>2</sub>,  $T_{db}$ , THI<sub>1</sub>,  $T_{wb}$  and  $T_g$ )  
 317 were ranked above all other models for milk yield and fat content, and in the top 9 of  
 318 13 elements or indices for protein content. THI<sub>2</sub> showed a better fit to the data than

319 THI<sub>1</sub> for milk yield, but the two THIs did not differ in explanatory power for milk fat  
320 and protein (Table 2). Among models that did not contain direct temperature  
321 variables, the number of hours of sunshine (7<sup>th</sup>) and RH (8<sup>th</sup>) were ranked highest for  
322 milk yield and fat content, and the number of hours of sunshine was ranked second  
323 for protein content (Table 2).

324

325 Models testing for interactions between weather and management fitted the data  
326 better or (for the effects of WS and snow on fat content, and the effects of T<sub>db</sub>, THI<sub>1</sub>,  
327 T<sub>wb</sub> and snow on protein content) not significantly worse than models without the  
328 interaction term. In all but one case (TD T<sub>s</sub>), metrics applied over a week's timescale  
329 provided better fits for milk yield than metrics applied over shorter timescales.  
330 Similarly, weekly summaries were ranked more highly (or equally highly in the cases  
331 of RH, ppt and snow) than shorter term metrics for fat content, with the exception of  
332 WS, where TD was the best metric. TD or three-day metrics were usually most  
333 effective at explaining the effects of temperature variables on protein content, while  
334 weekly summaries usually explained the effects of other weather elements on  
335 protein content better than shorter term metrics. For T<sub>db</sub>, where data were available  
336 both as 0900 h point samples and as 24h summaries, metrics derived from point-  
337 samples ranked more highly than those based on 24h summaries for all three milk  
338 traits. Models containing metrics with higher order polynomial effects usually  
339 explained the data better than those containing lower order polynomials for milk yield  
340 and fat content, although this was less frequently the case for milk protein  
341 (Supplementary Table S3). Although models varied in explanatory power, the best  
342 metric for each weather element or index significantly influenced all three milk traits



343 when tested individually using REML, with the exception of snow on protein content,  
344 for which no metric was significant (Supplementary Table S4).

345

346 *How does weather influence milk yield in dairy cattle?*

347 Milk yield was influenced by two-way interactions between management and each of  
348 the individual weather variables (weekly mean THI<sub>2</sub> at 0900 h, weekly maximum  
349 number of hours of sunshine, weekly mean WS and weekly mean ppt), the  
350 interaction between diet and genetic group, and main effects of farm identity,  
351 lactation number and DIM (Table 3) as follows. When cows were outside, milk yield  
352 increased with THI to 24.0 kg at 54.9 THI units, and then decreased as THI  
353 continued to increase (Figure 1, Table 3). When cattle were indoors, by contrast,  
354 increasing THI values were associated with an overall decrease in milk yield from a  
355 local maximum of 26.5 kg of milk at 32.8 THI units. Animals outdoors increased milk  
356 yield with WS to 24.1 kg at 9.1 knots, and then gradually decreased milk yield as WS  
357 increased (Figure 1, Table 3). Those indoors increased milk yield with increasing WS  
358 when WS was low, and showed no change in milk yield at higher WS. In animals  
359 indoors and outdoors, milk yield increased and then decreased as the number of  
360 hours of sunshine increased (Table 3). Performance began to decline at lower  
361 values of sunshine when animals were indoors (26.0 kg milk at 2.4 h sunshine) than  
362 when they were outdoors (24.5 kg milk at 12.8 h sunshine (Figure 1). Cattle  
363 experienced a decrease in milk yield with increasing ppt, and the rate of decline was  
364 greater in animals outdoors than indoors. Individuals produced more milk indoors  
365 than outdoors, at Farm 1 than Farm 2 and in later lactations than in earlier lactations,  
366 and milk production decreased over a given lactation (Table 3; Table 4). Milk yield  
367 was greater in S than C (effect of genetic group in HF animals:  $\beta = 4.64 \pm 0.31$ ,  $t =$

368 14.74,  $P < 0.001$ ; effect of genetic group in LF animals:  $\beta = 4.45 \pm 0.49$ ,  $t = 9.00$ ,  
369  $P < 0.001$ ) animals, and in LF than HF animals (effect of feed group in C animals:  $\beta =$   
370  $1.75 \pm 0.03$ ,  $t = 51.39$ ,  $P < 0.001$ ; effect of feed group in S animals:  $\beta = 2.21 \pm 0.03$ ,  $t =$   
371  $74.67$ ,  $P < 0.001$ ), and the difference in milk yield between LF and HF cattle was  
372 greater in S than in C animals.

373

#### 374 *How does weather influence milk fat?*

375 The proportion of fat in milk was influenced by two-way interactions between  
376 management and weekly mean  $THI_2$  at 0900 h, management and weekly minimum  
377 sunshine, and between diet and genetic group, and main effects of TD WS, farm  
378 identity, lactation number and DIM, but not by the maximum ppt over the last three  
379 days (Table 3). Fat content showed an overall decrease with THI for animals  
380 outdoors. For animals indoors, milk fat increased to a local maximum of 3.8% at 50.2  
381  $THI$  units, and then decreased with  $THI$  (Figure 1, Table 3). Animals outdoors and  
382 indoors increased and then decreased fat content as WS increased; performance  
383 began to decline at a lower WS for animals indoors (3.8% at 13.3 knots) than  
384 outdoors (3.7% at 15.5 knots; Figure 1, Table 3). Cattle kept indoors increased fat  
385 content as the number of hours of sunshine increased, whereas cattle outdoors  
386 gradually decreased fat content as the number of hours of sunshine increased  
387 (Figure 1, Table 3). Cows produced milk with a higher proportion of fat when  
388 outdoors than indoors (Table 3; Table 4), at Farm 1 than Farm 2, and in later  
389 lactations than in earlier lactations. Milk fat decreased during the first days of a given  
390 lactation and then increased (Table 3). Fat content was greater in S than C animals  
391 (effect of genetic group in HF animals:  $\beta = 0.09 \pm 0.03$ ,  $t = 2.77$ ,  $P = 0.006$ ); effect of  
392 genetic group in LF animals:  $\beta = 0.16 \pm 0.04$ ,  $t = 4.17$ ,  $P < 0.001$ ) and in HF than LF

393 animals (effect of feed group in C cows:  $\beta = -0.24 \pm 0.01$ ,  $t = 18.36$ ,  $P < 0.001$ ; effect of  
 394 feed group in S cows:  $\beta = -0.24 \pm 0.01$ ,  $t = 20.19$ ,  $P < 0.001$ ), and the difference in fat  
 395 content between S and C cattle was greater in LF than in HF individuals.

396

397 *How does weather influence milk protein?*

398 The proportion of protein in milk was influenced by two-way interactions between  
 399 management and 3 separate weather variables (mean THI<sub>2</sub> over the last 3 days,  
 400 weekly mean WS, weekly mean ppt), and main effects of weekly maximum number  
 401 of hours of sunshine, diet, genetic group, farm identity, lactation number and DIM  
 402 (Table 3). Protein content decreased as THI increased in animals kept outdoors and  
 403 indoors, and the rate of decrease was greater when animals were outside than when  
 404 they were inside (Figure 1, Table 3). Animals outdoors gradually increased protein  
 405 content as WS increased, whereas protein content was not influenced by WS when  
 406 animals were indoors. Examining cattle kept indoors and outdoors separately, those  
 407 indoors showed a tendency to increase protein content with increasing ppt ( $\beta =$   
 408  $0.002 \pm 0.001$ ,  $t = 1.80$ ,  $P = 0.072$ ), but there was no effect of ppt ( $\beta = -$   
 409  $0.0001 \pm 0.0016$ ,  $t = 0.06$ ,  $P = 0.636$ ) on protein content when cattle were outdoors.  
 410 Cattle indoors and outdoors decreased protein content as the number of hours of  
 411 sunshine increased. Cows produced more milk protein when housed outdoors than  
 412 indoors, at Farm 1 than Farm 2 and in lactations 2 and 3 than in lactation 1 (Table 3;  
 413 Table 4). Protein content decreased during the first days of a given lactation and  
 414 then increased (Table 3). Protein content was greater in Select than Control animals  
 415 (effect of genetic group in HF animals:  $\beta = 0.05 \pm 0.01$ ,  $t = 3.48$ ,  $P < 0.001$ ; effect of  
 416 genetic group in LF animals:  $\beta = 0.10 \pm 0.02$ ,  $t = 5.79$ ,  $P < 0.001$ ) and in HF than in LF  
 417 cattle (effect of feed group in C animals:  $\beta = 0.04 \pm 0.01$ ,  $t = 7.58$ ,  $P < 0.001$ ; effect of

418 feed group in S animals:  $\beta = 0.06 \pm 0.01$ ,  $t = 11.80$ ,  $P < 0.001$ ), and the difference in  
419 milk protein between S and C cattle was greater in LF than in HF animals.

420

421

## 422 **Discussion**

423

424 A better understanding of the response of livestock to current and future weather  
425 patterns is essential to enable farming to adapt to a changing climate (Gauly *et al.*,  
426 2013). We investigated the effects of weather over a 21 year-period on milk yield and  
427 composition under different management systems in a dairy herd at two Scottish  
428 farms. The relative influence of 11 weather elements and two THIs, indicators of heat  
429 stress, was compared. Models containing direct measures of temperature provided  
430 the best fits to milk yield and milk fat data; the number of hours of sunshine and  
431 relative humidity were also important. Models considering wind speed explained  
432 protein content best, while those containing sunshine, humidity and temperature also  
433 performed well. The importance of direct temperature metrics in explaining  
434 productivity is consistent with a wealth of studies on the impact of heat stress in dairy  
435 cattle (Renaudeau *et al.*, 2012). Relatively few studies have assessed the impact of  
436 other weather variables on milk traits, but thermal indices that account for wind  
437 speed and solar radiation perform better than those that do not (Hammami *et al.*,  
438 2013).

439

440 In our study, weather metrics summarised across a week's timescale from the test  
441 day usually explained milk traits (particularly yield and fat content) better than shorter  
442 scale summaries. Previous studies found that weather measured prior to the test day

443 (up to three days before) explained test day milk traits better than weather measured  
444 on the test day (Bertocchi et al., 2014, Bouraoui et al. 2002, West et al. 2003), which  
445 may be associated with the duration of digestive processes in ruminants (Gauly et  
446 al., 2013). The higher explanatory power of longer versus shorter timescales may  
447 also reflect the greater potential for extreme weather conditions, which might have a  
448 disproportionate effect on subsequent milk yield, to be captured in the analysis. The  
449 pattern was less clear for protein content, with weekly, three-day and TD scales  
450 performing similarly well. This suggests that weather has a more sustained impact  
451 on milk yield and fat content than on milk protein. Although recent studies have used  
452 summaries of the three days preceding milk sampling to describe weather conditions  
453 (e.g. Lambertz et al., 2014), our results suggest that weekly summaries may be more  
454 appropriate, at least for milk yield and fat content.

455

456 The effects of weather (THI<sub>2</sub>, sunshine, wind speed and precipitation) measured  
457 from outdoor weather stations on milk yield depended on whether cattle were  
458 indoors or outdoors on the test day. Cattle that were rotated between an indoor and  
459 outdoor environment responded according to the prevailing environment and  
460 produced more milk when they were indoors than outdoors. Similarly, grazing cows  
461 produced less fat-corrected milk than animals without access to grazing in another  
462 study (Lambertz et al., 2014). We assume that these results are largely a  
463 consequence of differences in diet: animals maintained indoors in our study received  
464 *ad libitum* TMR with some forage, while those outdoors ate mainly grass. TMR  
465 maximises metabolisable energy (ME) and nutrient uptake in high producing cows  
466 and can be obtained and digested more quickly than grass (Agnew and Yan, 2000).  
467 Accordingly, many studies show an increase in milk yield with feed intake (Agnew et

468 *al.*, 1998). Further to diet effects on relative productivity, the difference in the shapes  
469 of the productivity curves for animals inside and outside is probably due to  
470 differences in weather conditions experienced by cattle in the two environments.

471

472 When animals were outside they produced less milk during extremes of THI than  
473 during average conditions, as predicted. Other authors have reported similar  
474 declines in milk yield at low THIs or cold temperatures (Bruegemann *et al.*, 2012,  
475 Rodriguez *et al.*, 1985). The rate of decrease in milk yield in our study was greater at  
476 higher values of THI than at lower values, consistent with the idea that endotherms  
477 are more tolerant of low than high body temperatures (Hansen, 2009). Cows that  
478 were indoors showed an overall decrease in milk yield with increasing THI  
479 (measured from an outdoor weather station). In northern Europe, temperatures  
480 inside cattle buildings are 3-5°C warmer than outdoors (Seedorf *et al.*, 1998).  
481 Therefore animals indoors will be less susceptible to cold stress but may experience  
482 higher temperatures than animals outside on the same day. Indoor temperatures are  
483 also likely to increase with stocking density, although density will be lower during the  
484 summer than the winter in systems with summer grazing. It would be interesting to  
485 measure microclimatic conditions inside the barn to determine how closely the  
486 animals' immediate environment is associated with different weather elements, and  
487 how microclimate influences performance. Another question worth exploring is  
488 whether a carryover effect of weather on performance exists for animals that were  
489 recently moved indoors. Similarly, the effects of weather on animals outside may  
490 depend on how long they have been outdoors.

491

492 Dikmen and Hansen (2009) observed a weak negative relationship between a dairy  
493 cow's rectal temperature and wind speed, which together with our results on wind  
494 speed and milk yield, suggests that moderate winds can alleviate losses associated  
495 with heat stress. We observed a decline in milk production with increasing  
496 precipitation, and the decline was greater in animals outdoors than indoors. Stull *et*  
497 *al.* (2008) also reported a decrease in milk yield in cattle as precipitation increased.  
498 Precipitation is likely to affect an animal's thermal and energy balance due to a  
499 reduction in the insulative properties of its coat after wetting and the increased  
500 energy necessary to heat a layer of moist rather than dry air trapped within the coat.  
501 High precipitation and wind speeds can increase stress levels, thus reducing the  
502 availability of energy for milk production (Webster *et al.*, 2008). Beef cattle reduced  
503 feed intake but increased rumination during wet weather (Graunke *et al.*, 2011),  
504 which implies that productivity might also be reduced on rainy days in dairy cows via  
505 feed intake. On the whole, milk yield decreased as the number of hours of sunshine  
506 increased when cattle were indoors, perhaps in response to increased radiant heat  
507 from the roof.

508

509 Weather influenced milk composition as well as yield in our study. The proportion of  
510 fat in milk showed a sharp decrease with increasing THI in animals outdoors, and  
511 was lower at the upper extreme of THI than at low and intermediate THI values when  
512 cattle were indoors. Similar to milk yield, fat content was highest at moderate wind  
513 speeds. Most previous studies also report a decrease in the proportion of fat in milk  
514 (Bouraoui *et al.*, 2002, Hammami *et al.*, 2013, Smith *et al.*, 2013) or total milk fat  
515 (Lambertz *et al.*, 2014) under conditions of heat stress or increasing temperature,  
516 although others found no effect (Knapp and Grummer, 1991, Wheelock *et al.*, 2010).

517 While an increase in the number of sunshine hours was associated with an increase  
518 in milk yield in cows outdoors and a decrease in milk yield in cows indoors, the  
519 inverse was true for fat content. More concentrated milk yields can arise where milk  
520 production is reduced and fat synthesis remains constant, so one possibility is that  
521 sunshine influences milk fat simply through its effects on milk yield. This could be  
522 tested by evaluating the effects of sunshine on total milk fat.

523

524 Protein content decreased as THI increased in animals kept indoors and outdoors,  
525 and the rate of decrease was greater when animals were outside than when they  
526 were inside. A decline in milk protein with THI was reported by several other authors  
527 (e.g. Bouraoui *et al.*, 2002, Bruegemann *et al.*, 2012, Gantner *et al.*, 2011, Hammami  
528 *et al.*, 2013). Our results also agree with those of Lambertz *et al.* (2014), who  
529 reported a more marked decline in total protein yield with increasing THI in cows with  
530 access to pasture than those without. The increase in milk protein content with  
531 increasing wind speed when animals were outdoors was probably due to the action  
532 of wind in alleviating heat stress, while an increasing level of radiant heat from  
533 sunshine would have contributed to heat stress.

534

535 The points at which performance began to decline with increasing THI were lower in  
536 our study than in previous work (e.g. Gauly *et al.*, 2013, Ravagnolo *et al.*, 2000,  
537 Zimbelman *et al.*, 2013) for two reasons. First, ours were calculated from daily 0900  
538 h point samples from local weather stations. Temperature values at 0900 are  
539 probably a slight underestimation of the mean temperature over a 24h period.  
540 Second, animals in Scotland are probably less well adapted to heat stress and are



541 thus likely to have lower thermal tolerances than cattle in warmer climates where  
542 most work was undertaken.

543

544 Climate change models predict that temperatures will get warmer this century,  
545 leading to an increased incidence of heat stress. The statistical estimates presented  
546 here can be used in conjunction with UK Climate Projections to model the economic  
547 costs (or benefits) of climate change to milk yield and quality over the 21<sup>st</sup> century  
548 under different emissions scenarios. Such predictions about future productivity can  
549 be an important tool for informing policy. In addition, climate change is expected to  
550 bring further changes, such as a longer growing season, wetter soils and a higher  
551 incidence of disease (Gauly *et al.*, 2013), and these should also be considered.

552 Potential decreases in productivity may be offset through changes in farming  
553 practices (adaptation), such as diet, housing or selective breeding. Future studies  
554 should investigate how genetic merit influences the effects of weather on  
555 performance.

556

## 557 **Conclusions**

558 Milk yield and composition were affected by extremes of THI under conditions  
559 currently experienced in Scotland, and the shape of the relationship depended on  
560 whether animals were inside or outside. Solar radiation also impacted productivity,  
561 while moderate winds helped to alleviate heat stress. Metrics summarising weather  
562 across the week preceding the test day usually explained milk traits better than  
563 shorter-term summaries. A limitation to this study is that food intake and quality can  
564 depend on weather, and animals consumed different diets when they were indoors

565 and outdoors. However, diet and management system are associated under typical  
566 farming practices, so this does not reduce the practical relevance of these findings.

567 **Acknowledgements**

568 Scotland's Rural College (SRUC) receives grant-in-aid from the Scottish  
569 Government. This research was funded by the Scottish Government Rural Affairs  
570 and the Environment Portfolio Strategic Research Programme 2011-2016  
571 (Environmental Change Programme and the Climate Change Centre of Expertise,  
572 ClimateXChange). The authors wish to thank the farm staff and data managers at  
573 the Dairy Cattle Research Centre for collecting and maintaining such excellent  
574 records. The authors are grateful to Prof. Mike Coffey and two anonymous referees  
575 for helpful comments on the manuscript.

576

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691 **Table 1** Weather data collected by Meteorological Office stations near research Farms 1 (1990 to 2002) and 2 (2003 to 2011). Descriptive  
 692 statistics are provided for each farm, and weather between the two farms is compared using separate Generalized Least Squares models fit by  
 693 REML. Averages for  $THI_1$  and  $THI_2$ , which we calculated from Meteorological Office data using Equations 1 and 2 respectively, are also given

Weather			Farm 1 (4177 daily records)			Farm 2 (2896 daily records)			Farm 1 vs 2	
element/index	Recording regime	Accuracy	Mean±s.e.m	Min	Max	Mean±s.e.m	Min	Max	<i>t</i>	<i>P</i>
Precipitation (ppt)	Total over 24h (0900-0900)	0.1mm	2.5±0.08	0	56.0	3.1±0.11	0	55.8	3.27	**
	PS	0.1°C	8.2±0.08	-13.0	22.4	9.7±0.10	-8.9	25.2	3.81	***
Dry bulb temperature ( $T_{db}$ )	Minimum over 24h (0900-0900)	0.1°C	4.6±0.07	-14.6	17.1	6.0±0.09	-13.0	18.4	10.70	***
	Maximum over 24h (0900-0900)	0.1°C	11.5±0.08	-3.1	28.3	13.1±0.10	-4.1	30.7	9.64	***
Wet bulb temperature ( $T_{wb}$ )	PS	0.1°C	6.9±0.07	-13.0	19.9	8.2±0.09	-9.3	21.3	8.95	***
$THI_1$	See $T_{db}$ and $T_{wb}$		51.5±0.11	21.9	70.8	53.6±0.14	27.5	73.9	9.85	***
$THI_2$	See $T_{db}$ and RH		47.7±0.13	11.9	70.2	50.4±0.16	20.8	73.9	11.46	***
Grass temperature	Minimum over 24h (0900-	0.1°C	2.5±0.08	-17.4	16.1	2.8±0.10	-16.0	17.5	2.47	*

Weather affects milk yield and composition

( <b>T<sub>g</sub></b> )	0900)										
Soil temperature	PS, 30cm below the	0.1°C	8.8±0.08	0.8	19.1	10.5±0.09	1.2	20.4	9.79	***	
( <b>T<sub>s</sub></b> )	surface										
Wind speed ( <b>WS</b> )	0850-0900 mean, 10m above ground	1 knot	9.4±0.12	0	44.0	5.6±0.10	0	52.0	15.60	***	
Visibility	PS	1m	1394.1±16.78	4	4000.0	1060.4±18.29	10.0	4000.0	8.94	***	
Snow depth	PS	1cm	0.3±0.03	0	25.0	0.1±0.01	0	9.0	2.48	*	
Sunshine	No. hours over 24h (0000- 2359); measured using Campbell-Stokes recorder	0.1 h	3.5±0.05	0	15.4	3.8±0.07	0	14.7	1.83	0.068	
Air pressure, mean sea level ( <b>P<sub>MSL</sub></b> )	PS	0.1 hpa	1012.5±0.20	965.1	1047.5	1013.6±0.23	962.4	1045.1	1.05	0.294	
<b>RH</b>	PS	0.1%	83.0±0.18	26.7	100	80.7±0.22	28.1	100	6.48	***	

694 Recording regime indicates whether values are point-samples (PS) taken at 0900 h or 24h summaries (mean, minimum, maximum, total).



695 **Table 2** *The best models for each weather element or index for milk yield, fat content and protein content based on an information-theoretic*  
 696 *comparison of 521 Maximum Likelihood models per response variable (Supplementary Table S2 shows the full set of models compared)*

Weather element	Milk yield		Fat content		Protein content	
	Rank	Unique term in best model	Rank	Unique term in best model	Rank	Unique term in best model
T <sub>s</sub>	a	TD × m	a	Weekly mean × m	e	TD × m†
THI <sub>2</sub>	b	Weekly mean × m	b	Weekly mean × m	cd	3 day mean × m†
T <sub>db</sub>	c	Weekly mean × m	b	Weekly mean × m	d	TD†
THI <sub>1</sub>	d	Weekly mean × m	b	Weekly mean × m	de	TD†
T <sub>wb</sub>	e	Weekly mean × m	c	Weekly mean × m	e	TD†
T <sub>g</sub>	f	Weekly min × m	d	Weekly min × m	c	3 day min × m
sun	g	Weekly max × m	e	Weekly min × m†	b	Weekly max × m†
RH	h	Weekly mean × m	e	TD × m†	c	Weekly mean × m†
visibility	i	Weekly mean × m	f	Weekly mean × m	g	Weekly mean × m
WS	j	Weekly mean × m	g	TD†	a	Weekly mean × m
P <sub>MSL</sub>	k	Weekly mean × m	gh	Weekly mean × m†	f	3 day mean × m†
ppt	l	Weekly max × m	hi	3 day max × m†	g	Weekly mean × m†
snow	m	Weekly mean × m	i	TD presence/absence†	h	TD-1 presence/absence†

697 All 521 models were based on Equation 3 and a single dataset of 659918 records (1357 individuals) for milk yield or 77178 records (1212  
698 individuals) for fat and protein content. Each model differed from the others in a single weather metric, the presence or absence of the weather  
699 metric  $\times$  management interaction (indicated by  $\times$  m) or order of polynomial term for the weather metric. Polynomial terms and AIC values are  
700 given in Supplementary Table S3. Models are ranked from best to worst (lowest to highest AIC) for each weather element or index (see Table 1  
701 for abbreviations); 'a' represents the highest rank, and different lower case letters indicate meaningful differences ( $\geq 7$  AIC units) in rank. †  
702 indicates that more than one model had equal support for a given weather variable; equally ranked models are listed in Supplementary Table  
703 S3. TD (test day) is the day that the cow was milked; TD-1 is the day before milking.

704 **Table 3** LMMs to test the effect of weather and prevailing management group (indoors or outdoors) on milk yield in 1362 Holstein Friesian cows  
 705 (752674 records), fat content in 1220 cows (85134 records) and protein content in 1220 cows (87446 records) between the years 1990-2011

Fixed effects	Milk yield (kg)				Fat (%)				Protein (%)			
	$\beta$	SE	t	P	$\beta$	SE	t	P	$\beta$	SE	t	P
Intercept	24.770	0.265	93.44	***	3.919	0.030	132.13	***	3.115	0.013	243.38	<0.001
THI <sub>2</sub>	0.042	0.006	6.80	***	-0.005	0.002	-2.85	**	-0.001	0.001	-1.56	0.120
THI <sub>2</sub> (^2)	0.015	0.001	20.48	***	-0.001	<0.001	-6.12	***	<0.001	<0.001	-0.39	0.696
THI <sub>2</sub> (^3)	<0.001	<0.001	-1.53	0.127	<0.001	<0.001	-1.90	0.058	<0.001	<0.001	-1.55	0.122
THI <sub>2</sub> (^4)	<0.001	<0.001	-9.83	***	<0.001	<0.001	2.14	*	<0.001	<0.001	-0.09	0.928
ppt	-0.008	0.003	-2.92	**	-0.001	0.001	-1.53	0.127	0.001	0.001	1.05	0.296
Sun	-0.049	0.015	-3.22	**	0.040	0.020	2.01	*	-0.007	0.001	-5.65	***
Sun (^2)	0.029	0.005	5.77	***	-0.015	0.014	-1.09	0.277	-0.001	<0.001	-2.61	**
Sun (^3)	<0.001	<0.001	1.07	0.284	0.002	0.002	1.14	0.256	<0.001	<0.001	-0.53	0.595
Sun (^4)	<0.001	<0.001	-4.13	***	<0.001	0.001	0.47	0.638	<0.001	<0.001	-0.54	0.587
WS	0.085	0.013	6.78	***	0.009	0.002	3.79	***	0.002	0.002	1.30	0.195
WS (^2)	-0.014	0.002	-8.53	***	<0.001	<0.001	0.20	0.840	<0.001	<0.001	0.02	0.985
WS (^3)	0.001	<0.001	1.46	0.146	<0.001	<0.001	-2.53	*	<0.001	<0.001	-0.15	0.881

Weather affects milk yield and composition

WS (^4)	<0.001	<0.001	0.52	0.606	<0.001	<0.001	3.30	**	<0.001	<0.001	-0.09	0.931
Diet group (LF)	1.852	0.033	55.79	***	-0.306	0.012	-25.14	***	0.052	0.004	13.84	***
Genetic group (S)	4.440	0.309	14.36	***	0.091	0.028	3.28	**	0.073	0.012	6.17	***
Farm (1)	0.774	0.119	6.49	***	0.304	0.028	11.02	***	0.093	0.013	7.22	***
Management (out)	-0.714	0.030	-23.54	***	-0.027	0.009	-2.91	**	0.009	0.004	2.27	*
Lactation number (^2)	4.985	0.016	308.06	***	0.023	0.004	5.18	***	0.033	0.002	17.04	***
Lactation number (^3)	-1.320	0.010	-126.56	***	0.005	0.003	1.72	0.086	-0.026	0.001	-19.43	***
Days in milk	-0.041	<0.001	-512.92	***	0.001	<0.001	41.74	***	0.002	<0.001	151.37	***
Days in milk (^2)	<0.001	<0.001	-89.74	***	<0.001	<0.001	66.50	***	<0.001	<0.001	63.15	***
Management x THI <sub>2</sub>	0.021	0.004	5.20	***	-0.014	0.001	-9.70	***	0.002	0.001	2.16	*
Management x THI <sub>2</sub> (^2)	-0.020	0.001	-40.32	***	<0.001	<0.001	1.21	0.228	<0.001	<0.001	0.26	0.795
Management x THI <sub>2</sub> (^3)	<0.001	<0.001	-9.68	***	<0.001	<0.001	3.04	**	<0.001	<0.001	-3.07	**
Management x THI <sub>2</sub> (^4)	<0.001	<0.001	15.92	***	<0.001	<0.001	-1.78	0.076	<0.001	<0.001	2.53	*
Management x ppt	-0.020	0.002	-13.32	***	0.001	0.001	1.60	0.110	0.003	0.001	4.04	***
Management x sun	0.249	0.009	27.21	***	-0.057	0.011	-5.39	***	0.001	0.001	0.82	0.411
Management x sun (^2)	-0.036	0.003	-11.43	***	0.027	0.007	3.89	***	<0.001	<0.001	0.07	0.947
Management x sun (^3)	-0.004	<0.001	-14.63	***	-0.003	0.001	-4.02	***	<0.001	<0.001	-0.80	0.427

Management × sun (^4)	0.001	<0.001	8.65	***	<0.001	0.001	-0.88	<i>0.377</i>	<0.001	<0.001	-1.59	<i>0.111</i>
Management × WS	0.015	0.007	2.13	*	-0.001	0.001	-1.52	<i>0.128</i>	-0.016	0.001	-15.06	***
Management × WS (^2)	-0.005	0.001	-4.91	***	<0.001	<0.001	-0.56	<i>0.577</i>	<0.001	<0.001	-0.34	0.735
Management × WS (^3)	0.001	<0.001	3.08	**	<0.001	<0.001	-0.14	<i>0.888</i>	<0.001	<0.001	5.10	***
Management × WS (^4)	<0.001	<0.001	-3.39	***	<0.001	<0.001	0.76	<i>0.445</i>	<0.001	<0.001	-4.62	***
Diet group × genetic group	0.557	0.039	14.11	***	0.101	0.015	6.96	***	0.011	0.006	1.74	<i>0.082</i>
<b>Random intercepts</b>	<b>%σ</b>				<b>%σ</b>				<b>%σ</b>			
Animal identity	55.4				48.2				46.3			
Ordinal calving date	7.9				1.3				4.9			
Test date	5.4				8.9				10.6			
Residual variance	31.3				41.5				38.2			

706 Linear, quadratic (^2), cubic (^3) and quartic (^4) effects were tested for where indicated. Non-significant effects that were not components of  
707 significant interactions were removed from the final models; their estimates are italicised. WS is wind speed and ppt is precipitation

708 **Table 4** Means  $\pm$  standard errors (s.e.m) with the numbers of records and unique individuals for milk yield and fat and protein content.

709 Significant differences between levels are indicated in Table 3

		Milk yield (kg)				Fat content (%)				Protein content (%)		
		mean	s.e.m	records	cows	mean	s.e.m	records	cows	mean	s.e.m	records
Diet group	HF	23.8	0.17	435074	1026	4.2	0.02	45592	865	3.3	0.01	46865
	LF	29.4	0.24	317600	923	3.9	0.02	39542	707	3.3	0.01	40582
Genetic group	S	29.2	0.22	412594	742	4.1	0.02	44338	654	3.3	0.01	45418
	C	24.8	0.25	340080	620	3.9	0.02	40796	566	3.2	0.01	42418
Prevailing management	in	28.8	0.18	499575	1346	4.0	0.02	58625	1192	3.2	0.01	60131
	out	22.2	0.17	253099	971	4.2	0.02	26509	836	3.3	0.01	27315
Farm	1	25.5	0.27	421620	742	4.2	0.03	40025	601	3.2	0.01	39993
	2	24.8	0.27	331054	667	3.9	0.03	45109	664	3.1	0.01	47453
Lactation no.	1	20.7	0.27	327348	1300	4.0	0.03	38503	1145	3.1	0.01	39480
	2	25.9	0.27	244721	985	4.1	0.03	27273	855	3.2	0.01	28088
	3	27.8	0.26	180605	723	4.1	0.03	19358	606	3.2	0.01	19878
Overall		27.2	0.17	752674	1362	4.0	0.02	85134	1220	3.2	0.01	87446

710 The number of animals used for analyses of protein content was the same as for analyses of fat content

711 **Figure 1** The effect of i) THI, ii) wind speed ('WS') and iii) sunshine on a) daily milk yield ( $N = 752674$  records from 1362 cows), b)  
712 milk fat ( $N = 85134$  records from 1220 cows) and c) milk protein ( $N = 87446$  records from 1220 cows) in a herd of dairy cattle on two  
713 research farms in Scotland depended on whether the animals were indoors (thin unbroken line) or outdoors (thick line), except  
714 where both groups of cattle are represented by a single broken line. Weather values were recorded from the closest outdoor  
715 weather station to each farm for each element. All plots are adjusted for the terms in Equation 3, and statistical estimates for the  
716 effects presented here are provided in Table 3. Note that plots are truncated to exclude the highest and lowest 0.5% of weather  
717 records due to small samples for extreme weather events.