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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 21st 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 ≥75% Holstein Friesian (mean 93.0±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±10.68) for milk yield and 3-129 (mean

166   73.2±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 ≤14.4km 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 $\textbf{\textit{T}}_{\textbf{\textit{db}}}$ was dry bulb air temperature (°C) and $\textbf{\textit{T}}_{\textbf{\textit{wb}}}$ was wet bulb temperature (°C),

185 and THI_2:

186 **Equation 2**

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

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

9

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**

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

229

230 where y was the response variable (milk yield, fat or protein content, all normally

231 distributed), μ was the overall mean and w was a single weather metric or weather

232 metric plus weather metric × 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 ε 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_2, based upon Exploratory Factor Analysis (psych package;

262   Revelle, 2013), correlation coefficients (≤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_2, 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 (β) 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 <1h sunshine over 24h on 2343 days (33.4%) and >9h 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_1:

296    $\beta = 0.17\pm0.04$, $t = 4.34$, $P<0.001$; THI_2: $\beta = 0.13\pm0.04$, $t = 2.95$, $P = 0.003$), but did

297   not change over the 8 years at Farm 2 (THI_1: $\beta = -0.11\pm0.07$, $t = 1.63$, $P = 0.103$;

298   THI_2: $\beta = 0.13\pm0.08$, $t = 1.64$, $P = 0.101$). The number of hours of sunshine

299   increased over the study period at Farm 1 ($\beta = 0.09\pm0.02$, $t = 4.85$, $P< 0.001$), but

300   did not change over the years of the study at Farm 2 ($\beta = -0.02\pm0.04$, $t = 0.47$, $P =$

301   0.636). WS decreased over the time at Farm 1 ($\beta = -0.21\pm0.05$, $t = 3.90$, $P<0.001$),

302   but did not change at Farm 2 ($\beta = 0.12\pm0.07$, $t = 1.80$, $P = 0.072$). Precipitation did

303   not change over the study period at Farm 1 ($\beta = 0.02\pm0.03$, $t = 0.49$, $P = 0.625$) or at

304   Farm 2 ($\beta = 0.10\pm0.06$, $t = 1.55$, $P = 0.122$). Daily maximum temperatures exceeded

305   point samples measured at 0900 h by 3.3°C ($t6919 = 120.6$, $P<0.001$), and daily

306   minimum temperatures were 3.7°C cooler than point samples ($t6919 = 123.0$,

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_1, THI_2 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 12th, 11th and 13th across all 3 milk traits).

316   Models testing for direct measures of temperature (T_s, THI_2, T_{db}, THI_1, 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_2 showed a better fit to the data than

319   THI_1 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 (7th) and RH (8th) 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_{db}, THI_1,

327   T_{wb} and snow on protein content) not significantly worse than models without the

328   interaction term. In all but one case (TD T_s), 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_{db}, 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_2 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: $\beta = 4.64\pm0.31$, $t =$

368   14.74, $P<0.001$; effect of genetic group in LF animals: $\beta = 4.45\pm0.49$, $t = 9.00$,

369    $P<0.001$) animals, and in LF than HF animals (effect of feed group in C animals: $\beta =$

370   1.75 ± 0.03, $t = 51.39$, $P<0.001$; effect of feed group in S animals: $\beta = 2.21\pm0.03$, $t =$

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: $\beta = 0.09\pm0.03$, $t = 2.77$, $P = 0.006$); effect of

392   genetic group in LF animals: $\beta = 0.16\pm0.04$, $t = 4.17$, $P<0.001$) and in HF than LF

393   animals (effect of feed group in C cows: β = -0.24±0.01, t = 18.36, P<0.001; effect of

394   feed group in S cows: β =-0.24±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_2 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 (β =

408   0.002±0.001, t = 1.80, P = 0.072), but there was no effect of ppt (β = -

409   0.0001±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: β =0.05±0.01 , t = 3.48, P<0.001; effect of

416   genetic group in LF animals: β = 0.10±0.02, t = 5.79, P<0.001) and in HF than in LF

417   cattle (effect of feed group in C animals: β = 0.04±0.01, t = 7.58, P<0.001; effect of

418   feed group in S animals: β = 0.06±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_2, 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   Rodriquez *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 21st 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**

576 **Reference List**

577

578 Agnew RE, Yan T and Gordon FJ 1998. Nutrition of the high genetic merit dairy cow-energy
579 metabolism studies. In Recent Advances in Animal Nutrition (eds PC Garnsworthy & J
580 Wiseman), pp. 181-208. Nottingham University Press, Nottingham, UK.

581 Agnew RE and Yan T 2000. Impact of recent research on energy feeding systems for dairy
582 cattle. Livestock Production Science 66, 197-215.

583 Armstrong DV 1994. Heat Stress Interaction with Shade and Cooling. Journal of Dairy
584 Science 77, 2044-2050.

585 Bates D, Maechler M, Bolker B and Walker, S 2013. lme4: Linear mixed-effects models
586 using Eigen and S4. R package version 1.1-2. http://lme4.r-forge.r-project.org/

587 Bertocchi L, Vitali A, Lacetera N, Nardone A, Varisco G and Bernabucci U 2014. Seasonal
588 variations in the composition of Holstein cow's milk and temperature-humidity index
589 relationship. Animal 8, 667-674.

590 Bohmanova J, Misztal I and Cole J 2007. Temperature-humidity indices as indicators of milk
591 production losses due to heat stress. Journal of Dairy Science 90, 1947-1956.

592 Bouraoui R, Lahmar M, Majdoub A, Djemali M and Belyea R 2002. The relationship of
593 temperature-humidity index with milk production of dairy cows in a Mediterranean climate.
594 Animal Research 51, 479-491.

595 Bruegemann K, Gernand E, Koenig von Borstel U and Koenig S 2012. Defining and
596 evaluating heat stress thresholds in different dairy cow production systems. Archiv Tierzucht
597 55, 13-24

598 Bruegemann K, Gernand E, von Borstel U and Koenig S 2011. Genetic analyses of protein
599 yield in dairy cows applying random regression models with time-dependent and
600 temperature x humidity-dependent covariates. Journal of Dairy Science 94, 4129-4139.

601 Burnham KP and Anderson DR 2002. Information and Likelihood Theory: A Basis for Model
602 Selection and Inference. In Model Selection and Multimodel Inference: A Practical
603 Information-Theoretic Approach (eds KP Burnham and DR Anderson), pp. 49-97. Springer-
604 Verlag, New York, USA.

605 Burnham KP, Anderson DR and Huyvaert KP 2011. AIC model selection and multimodel
606 inference in behavioral ecology: some background, observations, and comparisons.
607 Behavioral Ecology and Sociobiology 65, 23-35.

608 Dikmen S and Hansen P 2009. Is the temperature-humidity index the best indicator of heat
609 stress in lactating dairy cows in a subtropical environment? Journal of Dairy Science 92,
610 109-116.

611 Dunn RJH, Mead NE, Willett KM and Parker DE 2014. Analysis of heat stress in UK dairy
612 cattle and impact on milk yields, Environmental Research Letters 9, 064006.

613 Gantner V, Mijic P, Kuterovac K, Solic D and Gantner R 2011. Temperature-humidity index
614 values and their significance on the daily production of dairy cattle. Mljekarstvo 61, 56-63.

615 Gauly M, Bollwein H, Breves G, Bruegemann K, Daenicke S, Das G, Demeler J, Hansen H,
616 Isselstein J, Koenig S, Lohoelter M, Martinsohn M, Meyer U, Potthoff M, Sanker C,
617 Schroeder B, Wrage N, Meibaum B, von Samson-Himmelstjerna G, Stinshoff H and
618 Wrenzycki C 2013. Future consequences and challenges for dairy cow production systems
619 arising from climate change in Central Europe - a review. Animal 7, 843-859.

620 Graunke KL, Schuster T and Lidfors LM 2011. Influence of weather on the behaviour of
621 outdoor-wintered beef cattle in Scandinavia. Livestock Science 136, 247-255.

622 Hammami H, Bormann J, M'hamdi N, Montaldo H and Gengler N 2013. Evaluation of heat
623 stress effects on production traits and somatic cell score of Holsteins in a temperate
624 environment. Journal of Dairy Science 96, 1844-1855.

625 Hansen PJ 2009. Effects of heat stress on mammalian reproduction. Philosophical
626 Transactions of the Royal Society B-Biological Sciences 364, 3341-3350.

627 Jenkins GJ, Murphy JM, Sexton DMH, Lowe JA, Jones P and Kilsby CG 2009. UK Climate
628 Projections: Briefing report. Exeter, UK,

629 Kadzere CT, Murphy MR, Silanikove N and Maltz E 2002. Heat stress in lactating dairy
630 cows: a review. Livestock Production Science 77, 59-91.

631 Knapp DM and Grummer RR 1991. Response of Lactating Dairy-Cows to Fat
632 Supplementation During Heat-Stress. Journal of Dairy Science 74, 2573-2579.

633 Kuznetsova A, Brockhoff, PB and Christensen, RHB 2014. lmerTest: Tests for random and
634 fixed effects for linear mixed effect models (lmer objects of lme4 package). R package
635 version 2.0-6. http://CRAN.R-project.org/package=lmerTest

636 Lambertz C, Sanker C and Gauly M 2014. Climatic effects on milk production traits and
637 somatic cell score in lactating Holstein-Friesian cows in different housing systems. Journal of
638 Dairy Science 97, 319-329.

639 National Research Council 1971. A guide to environmental research on animals. National
640 Academy of Science, Washington, DC, USA.

641 Pollott G and Coffey M 2008. The effect of genetic merit and production system on dairy cow
642 fertility, measured using progesterone profiles and on-farm recording. Journal of Dairy
643 Science 91, 3649-3660.

644 R Development Core Team 2013. R: A Language and Environment for Statistical
645 Computing. R Foundation for Statistical Computing, Vienna, Austria.

646 Ravagnolo O and Misztal I 2000. Genetic component of heat stress in dairy cattle, parameter
647 estimation. Journal of Dairy Science 83, 2126-2130.

648 Renaudeau D, Collin A, Yahav S, de Basilio V, Gourdine J and Collier R 2012. Adaptation to
649 hot climate and strategies to alleviate heat stress in livestock production. Animal 6, 707-728.

650 Ravagnolo O, Misztal I and Hoogenboom G 2000. Genetic component of heat stress in dairy
651 cattle, development of heat index function. Journal of Dairy Science 83, 2120-2125.

652 Revelle W 2013. Revelle, W. (2013) psych: Procedures for Personality and Psychological
653 Research, Version = 1.3.10. Northwestern University, Evanston, Illinois, USA,
654 http://CRAN.R-project.org/package=psych.

655 Rodriquez LA, Mekonnen G, Wilcox CJ, Martin FG and Krienke WA 1985. Effects of relative-
656 humidity, maximum and minimum temperature, pregnancy, and stage of lactation on milk-
657 composition and yield. Journal of Dairy Science 68, 973-978.

658 Sanker C, Lambertz C and Gauly M 2013. Climatic effects in Central Europe on the
659 frequency of medical treatments of dairy cows. Animal 7, 316-321.

660 Seedorf J, Hartung J, Schroder M, Linkert KH, Pedersen S, Takai H, Johnsen JO, Metz
661 JHM, Koerkamp PWGG, Uenk GH, Phillips VR, Holden MR, Sneath RW, Short JL, White RP
662 and Wathes CM 1998. Temperature and moisture conditions in livestock buildings in
663 Northern Europe. Journal of Agricultural Engineering Research 70, 49-57.

664 Smith D, Smith T, Rude B and Ward S 2013. Short communication: Comparison of the
665 effects of heat stress on milk and component yields and somatic cell score in Holstein and
666 Jersey cows. Journal of Dairy Science 96, 3028-3033.

667 St-Pierre NR, Cobanov B and Schnitkey G 2003. Economic losses from heat stress by US
668 livestock industries. Journal of Dairy Science 86, Supplement, E52-E77.

669 Stull C, Messam L, Collar C, Peterson N, Castillo A, Reed B, Andersen K and VerBoort W
670 2008. Precipitation and temperature effects on mortality and lactation parameters of dairy
671 cattle in California. Journal of Dairy Science 91, 4579-4591.

672 Thom EC 1959. The discomfort index. Weatherwise 12, 57-61.

673 UK Meteorological Office. 2012. Met Office Integrated Data Archive System (MIDAS) Land
674 and Marine Surface Stations Data (1853-present), NCAS British Atmospheric Data Centre.
675 http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_ukmo-midas

676 Veerkamp RF, Simm G and Oldham JD 1994. Effects of Interaction Between Genotype and
677 Feeding System on Milk-Production, Feed-Intake, Efficiency and Body Tissue Mobilization in
678 Dairy-Cows. Livestock Production Science 39, 229-241.

679 Vitali A, Segnalini M, Bertocchi L, Bernabucci U, Nardone A and Lacetera N 2009. Seasonal
680 pattern of mortality and relationships between mortality and temperature-humidity index in
681 dairy cows. Journal of Dairy Science 92, 3781-3790.

682 Webster JR, Stewart M, Rogers AR and Verkerk GA 2008. Assessment of welfare from
683 physiological and behavioural responses of New Zealand dairy cows exposed to cold and
684 wet conditions. Animal Welfare 17, 19-26.

685 West JW, Mullinix BG and Bernard JK 2003. Effects of hot, humid weather on milk
686 temperature, dry matter intake, and milk yield of lactating dairy cows. Journal of Dairy
687 Science 86, 232-242.

688 Wheelock JB, Rhoads RP, VanBaale MJ, Sanders SR and Baumgard LH 2010. Effects of
689 heat stress on energetic metabolism in lactating Holstein cows. Journal of Dairy Science 93,
690 644-655.

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 element/index	Recording regime	Accuracy	Farm 1 (4177 daily records)			Farm 2 (2896 daily records)			Farm 1 vs 2	
			Mean±s.e.m	Min	Max	Mean±s.e.m	Min	Max	t	P
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	*

(T_g)	0900)									
Soil temperature (T_s)	PS, 30cm below the surface	0.1°C	8.8±0.08	0.8	19.1	10.5±0.09	1.2	20.4	9.79	***
Wind speed (**WS**)	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 (P_{MSL})	PS	0.1 hpa	1012.5±0.20	965.1	1047.5	1013.6±0.23	962.4	1045.1	1.05	0.294
RH	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)*

	Milk yield			Fat content			Protein content	
Weather element	Rank	Unique term in best model	Rank	Unique term in best model	Rank	Unique term in best model		
T_s	a	TD × m	a	Weekly mean × m	e	TD × m†		
THI_2	b	Weekly mean × m	b	Weekly mean × m	cd	3 day mean × m†		
T_{db}	c	Weekly mean × m	b	Weekly mean × m	d	TD†		
THI_1	d	Weekly mean × m	b	Weekly mean × m	de	TD†		
T_{wb}	e	Weekly mean × m	c	Weekly mean × m	e	TD†		
T_g	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_{MSL}	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 × management interaction (indicated by × 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 (≥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 (%)			
	β	*SE*	*t*	*P*	*β*	*SE*	*t*	*P*	*β*	*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_2	0.042	0.006	6.80	***	-0.005	0.002	-2.85	**	-0.001	0.001	-1.56	0.120
THI_2 (^2)	0.015	0.001	20.48	***	-0.001	<0.001	-6.12	***	<0.001	<0.001	-0.39	0.696
THI_2 (^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_2 (^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

	Estimate	SE	t	p	Estimate	SE	t	p	Estimate	SE	t	p
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 × THI_2	0.021	0.004	5.20	***	-0.014	0.001	-9.70	***	0.002	0.001	2.16	*
Management × THI_2 (^2)	-0.020	0.001	-40.32	***	<0.001	<0.001	1.21	0.228	<0.001	<0.001	0.26	0.795
Management × THI_2 (^3)	<0.001	<0.001	-9.68	***	<0.001	<0.001	3.04	**	<0.001	<0.001	-3.07	**
Management × THI_2 (^4)	<0.001	<0.001	15.92	***	<0.001	<0.001	-1.78	*0.076*	<0.001	<0.001	2.53	*
Management × ppt	-0.020	0.002	-13.32	***	0.001	0.001	1.60	*0.110*	0.003	0.001	4.04	***
Management × sun	0.249	0.009	27.21	***	-0.057	0.011	-5.39	***	0.001	0.001	0.82	*0.411*
Management × sun (^2)	-0.036	0.003	-11.43	***	0.027	0.007	3.89	***	<0.001	<0.001	0.07	*0.947*
Management × 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	*0.377*	<0.001	<0.001	-1.59	*0.111*
Management × WS	0.015	0.007	2.13	*	-0.001	0.001	-1.52	*0.128*	-0.016	0.001	-15.06	***
Management × WS (^2)	-0.005	0.001	-4.91	***	<0.001	<0.001	-0.56	*0.577*	<0.001	<0.001	-0.34	0.735
Management × WS (^3)	0.001	<0.001	3.08	**	<0.001	<0.001	-0.14	*0.888*	<0.001	<0.001	5.10	***
Management × WS (^4)	<0.001	<0.001	-3.39	***	<0.001	<0.001	0.76	*0.445*	<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	*0.082*
Random intercepts	%σ				%σ				%σ			
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 ± 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.