Climatic Factors and Secondary Sex Ratio in Dairy Cows

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ABSTRACT

The hypothesis for this study was that the prevailing climate around the time of conception was associated with changes in the secondary sex ratio (SSR) in grazing, seasonally bred dairy cattle. Calving date, parity, cow breed, and calf sex were obtained for 8,621 lactations (with single births only) from 1,897 cows between 1970 and 2003 (inclusive). Conception date was estimated by subtracting a gestation length of 282 d from the date at calving. Climatic factors, including maximum and minimum ambient temperature, relative humidity, rainfall, sunlight hours, and evaporation rate, were averaged across the week immediately prior to conception for all lactations. Sun radiation data were available after 1976. Generalized estimating equations, with cow included as a repeated effect, were used to determine the effect of climate around the time of conception on the logit of the probability of a male calf. Breed of cow, year of conception, and parity at conception did not affect the SSR. The odds of a male calf being born were 3.74 times greater when the immediately previous calf born was male. A male calf was more likely to be born following periods of elevated air temperature, greater evaporation, or both. A 1°C increase in average maximum air temperature from the average (18.3°C), during the week immediately prior to conception, was associated with a 1-percentage unit increase in the probability of a male calf being born (i.e., from 52 to 53%). A corresponding 1°C increase in average minimum air temperature was reflected in a 0.5-percentage unit increase in the probability of a male calf being born. The probability of a male calf being born increased by 2.9 percentage units with each additional millimeter of evaporation per day. Results indicate that climatic factors associated with elevated temperatures and greater evaporation may influence the SSR in dairy cattle.

Key words: sex ratio, climate, weather

INTRODUCTION

Probability theory dictates that the secondary sex ratio (SSR, i.e., the proportion of male to female offspring born) should be 50:50 in situations of evolutionary equilibrium. However, substantial evidence exists that both the primary sex ratio (male-to-female ratio at the time of conception) and the SSR can be strikingly skewed from this balance (Rosenfeld and Roberts, 2004). Skjervold and James (1979) summarized a body of work showing a primary sex ratio in dairy cattle in excess of 60%, with the greatest early embryonic mortality and number of abortions occurring in cows carrying males. Support for the previous summary is based on reports of the SSR in dairy cattle being skewed toward males (Foote, 1977; Skjervold and James, 1979; Roche et al., 2006). Furthermore, studies in humans (Crawford et al., 1987; Chacon-Puignau and Jaffe, 1996), bison (Wolff, 1988; Green and Rothstein, 1991), dairy cattle (Roche et al., 2006), sheep (Kent, 1995), horses (Cameron et al., 1999), reindeer (Kojola and Eloranta, 1989), rodents (Meikle and Thornton, 1995), birds (Alonso-Alvarez and Velando, 2003), and sea mammals (Wiley and Clapham, 1993) indicate that various factors are associated with a change in the SSR. Such factors (examples) include the BCS, BW, and change in the BCS and BW of the dam near conception (Cameron, 2004; Roche et al., 2006), maternal age (Jacobsen et al., 1999), previous reproductive performance (Kojola and Eloranta, 1989), sex of previous offspring (Roche et al., 2006; Jacobsen et al., 1999), latitude (Grech et al., 2000), diet (Lyster, 1972; Meikle and Thornton, 1995), and social dominance (Grant, 1996).

Nevertheless, results have been inconsistent. For example, many studies have reported an effect for season of the year on the SSR in various species (Skjervold, 1979; Braza et al., 1988; Zuleta and Bilenca, 1992; Lerchl, 1998; Cagnacci et al., 2003), whereas other equally comprehensive studies have reported no such association (Foote, 1977; Havelka and Millar, 1997). Others have reported an effect of environmental conditions but have noted that the effect is dependent on the season of the year (Myers et al., 1985). In a review by Cameron (2004), the number of studies reporting an effect for season was approximately equal to those reporting no effect.

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The effect of maternal body condition on the SSR also has been the subject of much debate because of inconsistencies in the published results. Trivers and Willard (1973) hypothesized that in species in which reproductive success varies more among one sex than the other, mothers in better physiological condition would gain an advantage by investing more heavily in the more variable sex (Trivers and Willard, 1973). Similarly, mothers with limited resources would gain an advantage by investing in the more reproductively stable sex, thereby ensuring a continuation of the genetic line. Although many studies have reported support for this hypothesis (Cameron, 2004; Sheldon and West, 2004; Roche et al., 2006) approximately 50% have shown no effect on the SSR of any maternal condition factor investigated, and 8.5% of the studies reviewed by Cameron (2004) showed results contrary to this hypothesis. Cameron (2004) claimed that much of this inconsistency was because of differences in the definition of maternal condition, and found overwhelming support for the hypothesis (92% of studies) when maternal condition was defined as BCS. Recent results by Roche et al. (2006) confirmed this positive effect of maternal BCS on the SSR in dairy cows, indicating that despite domestication of the species, they conform to the Trivers–Willard hypothesis.

The effect of climate on the SSR is less well known. It is possible that environmental conditions (climate) near conception may influence the SSR, either through alterations in the internal milieu or psychological feedback mechanisms associating climate with the future feed supply. Others (Myers et al., 1985; Havelka and Millar, 1997) have reported an effect for climate on the SSR in deer mice. Lerchl (1998) reported a bimodal seasonal distribution of the SSR in humans born approximately 6 mo apart, indicating that the human SSR may be influenced by some climatic variables. Tomar et al. (1976) reported no effect of climate on the SSR in cattle, although the numbers of observations studied may have been too small ($n = 964$) to detect a difference, if one existed. Failure to detect a significant difference in the SSR when the male:female ratio was 53.5:46.5 indicates that the sample size was insufficient. Post et al. (1999) reported a positive effect of winter temperature on the SSR in deer. The objective of the present study was to investigate the association between climate near the time of conception and the SSR in grazing dairy cattle.

MATERIALS AND METHODS

Data

Data on cow breed, parity, calving date, BW immediately postcalving, sex of the calf, and incidence of multi-

ple births were available for 8,716 lactations from 1,897 cows between the years 1970 and 2003 (inclusive). Records of BCS at calving were available for cows only from 1976 onward. All cows resided at the No. 2 dairy farm, Dexcel, Hamilton, New Zealand. This farm was used for multiyear farm systems-based research, and during the period in question, research was also conducted comparing the profitability of Holstein-Friesian and Jersey heifers under grazing systems, different pasture species and cultivars, different grazing rotation lengths, systems that optimized the use of nitrogen fertilizer and supplementary feeds, and the most profitable stocking rate for dairy cow grazing systems (Macdonald, 1997). Breeds represented in the present study were Jersey, Holstein-Friesian, and Holstein-Friesian–Jersey crosses.

The system of milk production was seasonal, with cows calving and being bred during a 12-wk period. Cows were inseminated during the first 6 wk, with bulls being used exclusively thereafter. On average, 81% of cows conceived following AI. Within the study, 95 cases of multiple births were removed before analysis. Conception date was obtained by subtracting the assumed gestation length (282 d; Macmillan and Curnow, 1976) from the recorded calving date. Week of the year at conception was derived as the number of weeks between the start of the year and the date of conception within the year. Cows having more than 5 calves were grouped into the same class. Roche et al. (2006) reported a significant effect of calving BCS on the sex of the calf at the subsequent calving. Therefore, BCS at the previous calving as well as BW immediately postcalving were also retained and were set to “missing” in heifers or those that had no previous calving record in the study. Sex of the immediately previous calf born to each cow also was recorded and was allocated a separate code when no information on the previous calf’s gender was available, including those calving for the first time.

Daily climatic data were obtained for the years 1969 to 2002 (inclusive) from the Ruakura Climatological Station located <1 km northwest of the experimental farm. The climatic variables measured included maximum screen temperature (°C), minimum screen temperature (°C), relative humidity (%), daily sunlight hours, radiation intensity (MJ/m^2), evaporation rate (mm), and rainfall (mm). Radiation intensity data were available only from 1987 onward.

Means for each climatic variable during the 7, 14, and 30 d immediately preceding conception were calculated for each conception date represented in the study. A change in climate immediately preceding conception was calculated as the difference in the averages of the climatic variables from 2 wk to 1 wk before conception.

Climatic and cow data were merged by climatic date and date of conception. Only dates with both climate and conception records were retained. After data were merged, 8,621 lactation–conception dates had corresponding climatic information. Number of cow-conceptions per day varied from 1 to 31, with 1,920 different dates across 34 yr represented in the study.

The density function of all the climatic variables resembled a normal distribution, with the exception of rainfall, which was positively skewed. Each of the average climatic variables during the 7, 14, or 30 d before conception was subdivided across all years into deciles, with the exception of rainfall. Zero rainfall was coded into one class, with the subsequent amounts of rainfall divided into deciles; hence, 11 classes were present for rainfall. Changes in all climatic variables were treated as continuous variables.

Statistical Analyses

A generalized estimating equations approach with a logit link function was adopted, using PROC GENMOD (SAS Institute, 2005) to account for the binary nature of the SSR as well as the repeated calving records per cow. A first-order autoregressive correlation structure was assumed among records within cow. Empirical model solutions and standard errors are reported in the present study. In all cases, the logit of the probability of a male calf being born was modeled.

Initially, univariate analyses were undertaken in which the independent variables investigated included breed of cow, year of conception, parity at conception, BCS at the previous calving, sex of the previous calf by the same cow, and calendar week of the year at conception, as well as the average climatic variables averaged for the immediate 7, 14, or 30 d before conception and the climate change in the 2 wk preceding conception. Breed of cow, year of conception, parity at conception, and sex of the previous calf were treated as class variables, whereas week of the year at conception and BCS at the previous calving were treated as continuous variables, with higher-order polynomials of the continuous variables also tested for significance in the model. Climatic variables were treated as class variables when included as deciles. Otherwise, climatic variables were treated as continuous variables, with the exception of rainfall, which was treated as a class variable only because of its skewed distribution. Climate-change variables were treated as continuous variables. A multivariate analysis also was carried out using PROC GENMOD (SAS Institute, 2005), in which the variables included in the model were chosen based on a stepwise forward–backward algorithm with entry

and stay significance levels of $P < 0.25$ and $P < 0.05$, respectively.

The probability of a male calf being born was estimated using the results from the individual univariate analyses as follows:

$$P(X) = (1 + e^{-(\hat{\alpha} + \hat{\beta}X)})^{-1},$$

where $P(X)$ equals the probability of a male calf, $\hat{\alpha}$ is the predicted intercept of the model, and $\hat{\beta}$ is the predicted regression coefficient for independent variable X (Kleinbaum and Klein, 2002). Odds ratios were calculated as the exponent of the model solutions.

RESULTS

Cow Factors

The SSR averaged 52% and was not affected by breed of cow, year of conception, parity at conception, or BW immediately postcalving. However, sex of the previous calf born to the same cow, BCS of the cow at the calving immediately preceding conception, and week of the year at conception were all associated ($P < 0.05$) with the sex of the subsequent calf. The odds of a male calf being born were 3.74 times [95% confidence interval (CI): 3.34 to 4.12; intercept = -0.70] greater when the calf born in the calving immediately prior to the conception being investigated was male compared with female. The odds ratio for BCS at the calving immediately prior to the conception being investigated was 0.63 (95% CI: 0.44 to 0.89; intercept = 1.52). Hence, a change in BCS at calving from the average of 3.08 to 4.08 decreased the probability of a male calf being born from 52 to 41%. The odds ratio for week of the year at conception was 1.03 (95% CI: 1.01 to 1.06; intercept = -1.33). For example, using the model solutions, the predicted probabilities of a male calf being born following conception in wk 41, 42, and 43 of the year were 51, 52, and 53%, respectively.

Climatic Factors

The range in climatic variables during the study is summarized in Table 1. A substantial range existed in all climatic variables measured, with rainfall varying from 0 to 54.9 mm/d, and maximum and minimum ambient temperatures varying by 18.2 and 20.0°C, respectively. Similar statements could be made regarding the range in the other weather variables measured.

The P -values and solutions describing the effect of pre-conception climatic variables on the SSR were similar, irrespective of whether climate was averaged over the 7, 14, or 30 d before conception. Therefore, only solutions relating to the average climate during the 7

Table 1. Intercept of the model, odds ratio, 95% odds ratio confidence interval (CI), and *P*-values for the range of climatic variables investigated in the univariate analyses¹

Climatic variable	Range	Intercept	Odds ratio	95% CI	<i>P</i> -value
Maximum air temperature, °C	10.1–28.3	–0.643	1.04	1.013–1.078	<0.01
Minimum air temperature, °C	–1.3–18.7	–0.114	1.02	1.000–1.048	<0.05
Relative humidity, %	47.0–100.0	0.457	1.00	0.986–1.005	0.31
Sunlight, h/d	0.0–14.4	0.051	1.01	0.977–1.034	0.73
Radiation, MJ/m ²	1.4–30.9	–0.220	1.02	0.993–1.050	0.15
Evaporation, mm/d	0.0–10.7	–0.278	1.12	1.046–1.207	<0.001

¹Range of climatic variables during the week preceding conception.

d before conception are reported (Table 1). In addition, the *P*-values and the general trend of the solutions were similar, irrespective of the category of variables (continuous or class). Therefore, solutions obtained when the climatic variables were treated as continuous are reported, with the exception of rainfall, which was included in the model only as a class variable. Changes in any of the climatic variables from wk 2 before conception to the week of conception did not significantly affect the SSR and are not discussed further.

The odds ratios presented in Table 1 indicate positive associations between minimum air temperature ($P < 0.05$), maximum air temperature ($P < 0.01$), and evaporation rate ($P < 0.001$), and the likelihood of a male calf subsequently being born. The increase in odds as the pre-conception temperature increased was equivalent to a 1-percentage unit increase in the probability of a male calf being born when the maximum temperature increased by 1°C (i.e., from 52 to 53% males as the maximum air temperature increased from 18.3 to 19.3°C). A corresponding 1°C increase in the average minimum temperature was reflected in a 0.5 percentage unit increase in the probability of a male calf being born, indicating a greater association between the maximum air temperature and SSR.

Similarly, an increase in evaporation rate of 1 mm/d increased the odds of a male calf being born by 1.12. This is equivalent to a 2.9-percentage unit increase in the SSR for each additional millimeter of evaporation per day. A trend ($P = 0.15$) was detected for a greater SSR with greater solar radiation, with each unit increase in radiation intensity increasing the SSR by 0.8 percentage units. This trend became stronger ($P = 0.08$) when the average radiation during the 14 d before conception was included in a univariate analysis. Average rainfall during the week immediately preceding conception was not associated with a change in the SSR. No significant quadratic effect of any of the climatic variables was observed.

Based on the stepwise significance criteria imposed in the multivariate analysis, inclusion of sex of the previous calf and week of the year at conception precluded

the inclusion of other effects such as BCS at calving, air temperature (both minimum and maximum), and evaporation rate, which were previously significant in the univariate analyses.

DISCUSSION

These results present support for our initial hypothesis that a significant association exists between climate during the month before conception and the sex ratio of the subsequent progeny. Across the entire study, the ratio of male to female calves was 52:48, corroborating previously reported ratios in dairy cattle (Foote, 1977; Skjervold and James, 1979; Roche et al., 2006). The male-to-female ratio increased with greater temperatures and greater rates of evaporation in the period preceding conception. Sex of the previous calf, BCS at calving, and week of the year at conception also significantly influenced the sex of the calf.

Known sexually dimorphic physiological characteristics in the embryo provide a potential mechanism for gender selection. For example, there is sexual dimorphism in both the embryo metabolic rate (Ray et al., 1995; Dumoulin et al., 2005) and in the expression of IFN- γ (Kimura et al., 2004), indicating sex-differential signaling of the dam. Evidence also exists that the nutrient content of the growth medium can play a large part in determining the survival of either the male or female blastocyst (Larson et al., 2001). It is therefore plausible that factors influencing, but external to, the dam could potentially affect both the primary sex ratio and the SSR.

Effect of Climate

Despite the short breeding seasons observed in the present study (annual range of 90 to 113 d), a significant association existed between week of the year at conception and the SSR. This is consistent with reported effects of season of conception on the SSR in sheep (Skjervold, 1979), deer (Braza et al., 1988; Post et al., 1999), mice (Myers et al., 1985; Zuleta and Bilenca, 1992; Ha-

velka and Millar, 1997), and humans (Lyster and Bishop, 1965; Lerchl, 1998). The effect of season on the SSR in dairy cattle is not clear. Skjervold and James (1979) reported an effect of season of calving on the SSR, but only in primiparous cows. In contrast, others (Tomar et al., 1976; Foote, 1977) reported no such association. The univariate analysis results presented here show significant positive associations between the SSR and ambient temperature (both maximum and minimum) and evaporation during the month before conception, and a trend toward an increase in male offspring with increased radiation. The lack of a significant effect for climatic variables on SSR in the multivariate analysis, when week of the year was already included in the model, is most likely attributable to the temporal patterns in climate across the year in New Zealand (D. P. Berry and J. R. Roche, unpublished data). This cannot be said with certainty, however. Although a human-assigned calendar date is unlikely to have affected the SSR, other factors associated with calendar date that might have influenced the association between calendar date and SSR include days postpartum and associated BCS at mating (Roche et al., 2006) or the hierarchy of dominant females being mated first (in natural breeding). The reason for the inconsistent effects of season or climate in previous studies is unclear but may have resulted from large differences in climate within season masking any potential effect of climate.

The physiology underpinning an effect of climate on the SSR adjustment is unknown. A number of physiological and endocrine traits can be influenced by environmental factors. Similarly, some psychological disorders have a pronounced annual rhythm (Lerchl, 1998), indicating climatic effects. In the current study, those weather factors positively associated with the SSR are also known to be the most influential in forage production (Mitchell, 1953; Silsbury, 1970). One could argue that the reported effect of climate is an evolutionary adaptation consistent with the Trivers–Willard hypothesis. This hypothesis indicates that in situations in which a mother will produce larger offspring, male offspring have an advantage in a species in which competition exists among males for a mate. Maternal BCS near conception (Cameron, 2004; Sheldon and West, 2004) and the energy balance of dairy cows pre-conception (Roche et al., 2006), as well as the BCS at calving in the current study, have been reported as being associated with changes in the SSR. The data analyzed were from pasture-based grazing cows, whose feed supply would be heavily dependent on climatic conditions. Therefore, it is possible that effects of climate in the present study are merely indicators of increased feed availability and the consequent improvement in energy balance and BCS change, factors previously reported

to increase the SSR (Cameron, 2004; Roche et al., 2006). Production and quality data for the pastures are not available to test this hypothesis further.

The theory of greater food availability would not explain the effect of climate in studies published on humans in developed countries (Slatis, 1953; Lyster and Bishop, 1965; Lyster, 1971; Lerchl, 1998). Body energy stores are unlikely to be related to climatic variation, and yet SSR was reported to be positively associated with ambient temperature. These results indicate an effect of climate beyond the immediate food supply, possibly indicating an innate evolutionary adaptation whereby climatic variables related to food supply also affect periconception selection of embryos based on their sex.

Determining the physiology underpinning the adjustment of SSR with variations in climate is not possible in the current study. Rosenfeld and Roberts (2004) proposed 2 possibilities: 1) elective fertilization (i.e., a change in the primary sex ratio) through either an effect on sperm motility or through selective fertilization at the ovum; or 2) increased early embryonic mortality of one sex or the other because of sexually dimorphic differences in the rate of blastocyst development or differences in blastocyst implantation because of differences in signaling pathways. It is not possible to determine whether the primary sex ratio or early embryonic mortality caused the SSR adjustment in the current study.

Cow Factors

The greater probability of a male calf being born when the previous calf born to the cow was male indicated that characteristics peculiar to the dam influence the sex of her offspring. In a review of the literature on variations in SSR in mammals, Cameron (2004) reported that only 25% of studies showed support for an effect of sex of the previous neonate on the SSR. The remaining 12 studies reviewed showed no such effect. Consistent with this finding, Roche et al. (2006) showed no effect of sex of the previous calf on the SSR in dairy cattle. However, Vandenberg and Huggett (1995) reported a greater SSR in rodents when dams were born between 2 males, an event possibly making females more masculine because of greater testosterone concentrations and thus more socially dominant as a result. Similarly, findings in humans indicate that female subjects with greater testosterone concentrations receive greater dominance scores and give birth to more boys than girls (Grant, 1996). Such a maternal effect would be expected to bias the SSR in all offspring of the dams under investigation, potentially resulting in an association with the SSR in successive pregnancies.

Increased odds of a male calf being born to cows with a low BCS in the calving preceding conception is consistent with the results of Roche et al. (2006), who investigated the effect of BCS-related variables on the SSR. Calving BCS is positively correlated with postcalving BCS loss, and therefore negatively correlated with BCS at conception, a factor reported to influence the SSR (Cameron, 2004). The lack of a parity effect on calf sex is consistent with previous findings in which no association between calf sex and dam age or parity was evident in dairy cows (Roche et al., 2006), American bison (Wolff, 1988), reindeer (Reimers and Lenvik, 1997), or humans (Jacobsen et al., 1999). However, the findings are not conclusive, with maternal age reported to positively influence the SSR in other studies (Skjervold and James, 1979; Kojola and Eloranta, 1989; Wauters et al., 1995; Trut, 1996; Oakwood, 2000; Côté and Festa-Bianchet, 2001).

In conclusion, a greater SSR was observed following periods of higher ambient temperature and greater evaporation rate before conception (from 1 wk to 1 mo pre-conception). Climatic changes during the 2 wk before conception were not associated with the SSR.

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