FACTORS ASSOCIATED WITH INBREEDING IN CHAROLLAISLAMBS

K. Sercombe and M.J. Bell

The University of Nottingham, School of Biosciences, Sutton Bonington Campus, Loughborough LE12 5RD, UK

ABSTRACT

Inbreeding within sheep populations is a relatively understudied area due to limited pedigree information. This study assessed the level of inbreeding within a Charollais sheep population. Data were obtained from35,220 Charollais lambs between the years2000 to 2018 from performance-recorded flocks in the UK. Differences among flocks, study years, lamb eight-week body weight categories and if embryo transfer lambs were assessed. Mean inbreeding value for Charollaislambswas2.8% (s.e. $\pm$ 0.1), with a range of 0% to 31%. While the proportion of lambs with an inbreeding value of >7% has been relatively stable at 0.1 or less since 2006, the general trend is an increasing mean inbreeding coefficient for the population in recent years. After adjusting lamb inbreeding coefficient for fixed and random effects, the average inbreeding coefficient was found to be lower for lambs in the heavier eight-week body weight category (>32kg), for certain flocks (mean ranged from 0.4% to 14.6%), and for embryo transfer lambs. Monitoring of inbreeding and approaches used for genetic selection in flocks can help minimise poor lamb performance(i.e. potentially lower growth and body weight) associated with inbreeding.

Keywords: Sheep, inbreeding, offspring, population, trends.

1. INTRODUCTION

Charollais Sheep were first introduced into the UK in 1977, after being imported from the Charolais region of France.[1] The population of Charollaisbreeding ewes in the UK is relatively small at about 0.4% of the total sheep population of 16 million ewes.[1] [2]However, the Charollais breed is popular as a terminal sire and represents about 8.4% of sires used on commercial farms[1] [2],with the breed known for traits such as ease of lambing, growth and carcase composition. Inbreeding within sheep populations is a relatively understudied area, with little research assessing the level of inbreeding in commercial sheep populations due to limited pedigree information.

The intensive use of a few related animals (i.e. inbreeding), particularly where the selection intensity is high, can result in deleterious effects on animal performance such as a reduction in productivity (e.g. growth and development) and fitness performance (e.g. survival, reproduction and disease resistance).[3] [4]Inbreeding has been defined as the mating of individuals whose relatedness between them is greater than the average degree of relationship existing in the population.[5]In a finite population, inbreeding is inevitable. A high inbreeding coefficient exceeds 7% and the point when genetic merit is considered to decrease as inbreeding depression

increases.[6]Selvaggi*et al.*[7] highlighted that heterozygosity and allelic diversities can be lost from small, closed, selected populations at a rapid rate. In addition, having closed flocks and populations makes it increasingly difficult to control and reduce the levels of inbreeding due to the lack of unrelated individuals being available and introduced. In recent decades, the increased rate of inbreeding in dairy cows has been considerable(i.e. 0.2 to 0.3% per year) with average levels of inbreeding reaching 3-5% in different developed countries.[4]The main attributing factors are the use of fewer Holstein sires and dams through artificial insemination (AI), selection for fewer traits and genetic selection techniques such as BLUP,estimated breeding values (EBV's), and multiple ovulation embryo transfer (MOET)i.e. increasing section intensity.[3][4]It is therefore important that other livestock breeding programmes using similar approaches for genetic selection monitor inbreeding and adopt approaches to minimise inbreeding depression. In the UK, only about 2% of breeding females and 0.5% of breeding sires within the Charollais sheep breed arein a performance recording scheme with detailed pedigree information describing the relationship between individual animals for several generations. Therefore, pedigree information and inbreeding coefficients for sheep are not widely recorded by farms and studied. Drobik and Martyniuk[8]studied Polish Olkuska sheep with a highlevel of inbreeding at 10%, which was found to reduce the body weight of offspring at birth and at eight-weeks of age.

The objective of this study was to assess the level of inbreeding within the UKCharollais sheep population using performance recording data to assess differences in the mean inbreeding coefficient among flocks, study years, lamb eight-week body weight categories and lambsconceived by embryo transfer.

2. MATERIALS AND METHODS

The use of producer performance recording data was approved by Signet, Charollais Sheep Society and the local ethics committee at The University of Nottingham.

Farm data

Data were obtained from 35,220individual Charollaislamb recordsbetween the years of 2000 to 2018 (Table 1). The dataset consisted of 146 commercialflocksthat were using performance recording in the UK. The records available included the identification of individual lambs and their dam, sire, date of birth, eight-week body weight, if conceived by embryo transfer(MOET), and the lamb's calculated inbreeding coefficient. The population studied had complete pedigree information for at least three generations (parents, grandparents and great grandparents) in order to derive individual lamb inbreeding coefficients. The data represented a subset of the current total UK Charollais sheep population of about 67 thousand breeding ewes and 34 thousand sires at 2% of breeding ewes and 0.5% of breeding sires of UK origin (Table 1).

Inbreeding coefficient

The inbreeding coefficient was determined using methodology of Meuwissen and Luo[9]. This was based on the decomposition of the additive genetic relationship matrix A, as described by Henderson[10]:

$$A = LDL \qquad \text{Equation 1}$$

Where L is the lower triangular matrix containing the fraction of genes that animals derive from their ancestors and D is the diagonal matric containing the within family additive genetic variances of the animal. L is calculated row by row in the algorithm[11]. This assumes that each individual receives half its genetic merit from both parents equally. However, the accuracy of an individual's inbreeding coefficient will be greater if the depth of pedigree has been recorded over a larger number of generations. Hence, at least three generations of pedigreerecords per lamb were used to derive their inbreeding coefficient.

Statistical analysis

Data from the most recent 10 years of the study period (from 2009 to 2018)were analysed using a linear mixed model in Genstat Version 19.1 (Lawes Agricultural Trust, 2012) to assess differences in the mean inbreeding coefficient amongflocks, study years, lamb eight-week body weight categories and embryo transfer lambs. This subset of data allowed assessment of recent trends across 102 pedigree flocks and20,103 individual Charollais lambs. Individual lamb eight-week body weights were categorised into four quartiles:<23 kg, 23-27.5 kg, 27.6-32 kg and >32 kg respectively. The following model was used for the analysis:

$$Y_{ijklm} = \mu + F_{i} + B_{j} + W_{k} + E_{l} + S_{m} + e_{ijklm} \qquad \text{Equation 2}$$

where Y_{ijklm} is the dependant variable of lamb inbreeding coefficient;μ is the overall mean;F_i is the fixed effect of individual flock number; B_j is the fixed effect of yearof birth for each lamb where i = year 2009 to 2018;W_k is the fixed effect of eight-week body weight category where k = quartile 1 to 4; E_l is the fixed effect of birth using embryo transfer where l = 0 or 1;S_m is the random effect of lamb sire;$e_{ijklm}$is the residual error term.

Significance was attributed at P<0.05. High levels of inbreeding were attributed to coefficients >7%.[6]

3. RESULTS

Historical trends in inbreeding coefficient since the year 2000

The inbreeding coefficient for lambs ranged from 0% to 31.4% during the study period (figure 1). Categorising inbreeding coefficients into four quartiles of <1.2%, 1.2-2.0%, 2.1-3.6% and >3.6% showed that the proportion of lambs with an inbreeding coefficient of <1.2% has been reducing since about 2012 and the proportion of lambs above 2% has generally been increasing (figure 2).

However, the proportion of lambs with a high inbreeding coefficient >7% has consistently been at 0.1 or less since the year 2006 (figure 3).

Effect of flock, year, body weight category and embryo transfer onlamb inbreeding coefficient

The predicted mean inbreeding coefficient for lambs across farms between 2009 and 2018 was 2.8 (s.e. ± 0.1). There were differences in the mean inbreeding coefficient for farms studied (df = 101, F statistic = 5.7, P<0.001; figure 4), with the lowest value for flock 24 at 0.4% and highest for flock 37 at 14.6%. The mean inbreeding coefficient was greater than 7% for four out of the 102 farms studied between 2009 and 2018.

The mean inbreeding coefficient of lambs has increased in recent years from about 2% in 2010 and 2011 to 3.4% in 2017 and 2018 (df = 9, F statistic = 17.6, P<0.001;figure 5).Lambs with an eight-week body weight>32kg had a lower mean inbreeding coefficient (df= 3, F statistic = 8.1, P<0.001; figure 6) compared to lighter body weight lambs. Lambs with an eight-week body weight <23kg had a higher inbreeding coefficient than heavier lambs. Embryo transfer lambs had a lower mean inbreeding coefficient(df = 1, F statistic = 4.9, P<0.05; figure 7) compared to non-embryo transfer lambs.

4. DISCUSSION

Few studies around the worldhave evaluated the level of inbreeding within sheep populations. This is presumably due partly to a lack of pedigree information available for individual sheep, the fragmented nature of the industry and the perceived need to monitor inbreeding coefficients in sheep populations. Pedigree information allows monitoring of the genetic relationship among animals to prevent breeding with related animals, and inbreeding. While the mean inbreeding coefficient for the Charollais lamb population in the current studywas 2.8% between the years 2009 to 2018,the range of inbreeding values for lambs was considerable from 0% to 31%, and notably higher in a selection of performance recorded flocks. The present study would support the belief that it is important to monitor levels of inbreeding within sheep flocks. A few flocks studied had mean inbreeding coefficients far exceeding the mean across flocks (the highest being 14.6%). Thesefarmers may be unaware of any potential impact on the performance of their flock(as observed in cows i.e. Kearney et al.[4]; Howard et al.[3]), and availability of inbreeding coefficients may help future breeding decisions. The Charollaissheep breed is a popular terminal sire (8.4% of the UK sire population) for lamb meat producing enterprises based on growth and carcase traits of offspring. However, as seen in the current study and found by others[7 8 12], lambs with a high inbreeding coefficient are particularly known to have poorer growth and body weights.Gholizadeh and Ghafouri-Kesbi[13] found a significant effect on body weight at inbreeding coefficients greater than 5%.

Although the proportion of lambs with an inbreeding coefficient greater than 7% has stayed at 0.1 or less since 2006, the mean inbreeding coefficient has increased in recent years from 2% to 3.4%. This increase may reflect adoption of EBV's and AI, particularly when selecting sires on a range of traits such as growth rate, body muscle depth,body fat depth and body weight within performance recorded flocks. Reproductive technologies (e.g. AI and embryo transfer) can increase the rate of inbreeding due to an increase in selection intensity.[14]Inbreeding is primarily a function of selection intensity rather than population size.[15]Awareness of changing levels of inbreeding within flocks using pedigree information may help inform breeding decisions for desirable traits of growth, body composition and body weight, whilst balancing the potential risk of inbreeding. The most recent coefficient of 3.4% in 2018 for Charollais lambsis similar to the

Holstein dairy cow population in the UK (at about 3%), where a rapid increase in the rate of inbreeding occurred in recent decades due to the intensity of genetic selection and the adoption of breeding methods(i.e. AI, selection using few traits and sires etc.[4]). Goyache*et al.*[16] found that the higher the average relatedness of sires, the level of inbreeding will increase quickly in sheep populations. The level of inbreeding in UK Charollais sheep was generally higher than in most other studies on different sheep breeds, with 1.5% found in Xalda[16], 1.6% in Baluchi[13], 2.3% in Santa Ines[17], 2.9% in Moghani[18] and 10% in Polish Olkuska sheep.[8]Genetic technologies that are commonly used in more intensive livestock systems (e.g. dairy and pigs) are becoming more widely used in sheep breeding, such as AI and embryo transfer. These approaches have benefits associated with more controlled management of genetic selection and no management of sires or minimising the potential risk of diseases being introduced to a closed flock from purchased sires.

The introduction of new unrelated individuals can be used to reduce the levels of inbreeding in a closed population, which is often the case for pedigree sheep flocks.The current study found that embryo transfer lambs had a lower mean inbreeding coefficient. This may reflect the popularity of the Charollais and the numbercommercially available, with about 10 dams per sire on average seen in the data used in the current study, and also the breeding of unrelated animals based on known genetic background (for several generations). Increasing the number of sires per dam with known genetic background can minimise inbreeding without compromising genetic gain.[15]Embryo transfer may help small populations minimise the risks of inbreeding depression by introducing new genetic lines if they are available. Van Wyk*et al.*[12]showed that the addition of 3 outside sires to a population of Elseburg Dormer sheep reduced inbreeding to acceptable levels.

In conclusion, this study found the mean inbreeding coefficient of the UK Charollais sheep population studied to increase in recent years from 2% to 3.4%. The current mean inbreeding coefficient of 3.4% is comparable to other livestock industries that have increased the intensity of genetic selection. One genetic technology that reduced inbreeding levels in the Charollais sheep population was the use of embryo transfer, which may reflect targeted selection ofUK sire genetic lines when using MOET in with selected dams. A few flocks had particularly high levels of inbreeding. Lambs in the heavier weight category were associated with a lower average inbreeding coefficient. Further awareness and monitoring of inbreeding coefficients from genetic information on farms will improve flock productivity.

Acknowledgements

Funding and competing interests

REFERENCES

1. Charollais Society. The society. 2019. www.charollaissheep.com/about-us/ (accessed 11 February 2019).

2. Defra. Livestock numbers in England and the UK. 2019. www.gov.uk/government/statistical-data-sets/structure-of-the-livestock-industry-in-england-at-december (accessed 23 July 2019).

3. Howard J, Pryce J, Baes C, Maltecca C. Invited review: Inbreeding in the genomics era: Inbreeding, inbreeding depression, and management of genomic variability. *Journal of Dairy Science* 2017; 100:6009-6024. doi:10.3168/jds.2017-12787

4. Kearney J, Wall E, Villanueva B; Coffey M. Inbreeding trends and application of optimised selection in the UK Holstein population. *Journal of Dairy Science* 2004; 87:3503-3509.doi:10.3168/jds.S0022-0302(04)73485-2

5. Lush J. Animal breeding plans. Iowa: The Iowa State College Press, 1943.

6. Weigel KA**, Lin SW. Controlling inbreeding by constraining the average relationship between parents of young bulls entering AI progeny test programs**. *Journal of Dairy Science*2002; 85:2376-2383.doi:10.3168/jds.s0022-0302(02)74318-x

7. Selvaggi M, Dario C, Peretti V, Ciotola F, Carnicella D, Dario M. Inbreeding depression in Leccese sheep. *Small Ruminant Research* 2010; 89:42-46.doi:10.1016/j.smallrumres.2009.12.005

8. Drobik W,Martyniuk E. Inbreeding and its impact on the prolific Polish Olkuska sheep population. *Small Ruminant Research* 2016; 137: 28-33.doi:10.1016/j.smallrumres.2016.02.009

9. Meuwissen T, Luo Z. Computing inbreeding coefficients in large populations. *Genetics Selection Evolution* 1992; 24:305-312.doi:10.1186/1297-9686-24-4-305

10. Henderson C. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics* 1976; 32:69-83.

11. Roughsedge T, Brotherstone S,Visscher P. Quantifying genetic contributions to a dairy cattle population using pedigree analysis. *Livestock production science* 1999; 60:359-369.doi: 10.1016/S0301-6226(99)00106-2

12. Van Wyk J, Fair M,Cloete S. Case study: The effect of inbreeding on the production and reproduction traits in the Elseburg Dormer sheep stud. *Livestock Science* 2009; 120:218-224. doi:10.1016/j.livsci.2006.10.005

13. Gholizadeh M, Ghafouri-Kesbi F. Inbreeding depression in growth traits of Baluchi sheep. *Small Ruminant Research* 2016; 144:184-190.doi:10.1016/j.smallrumres.2016.09.012

14. Van der Werf J, Marshall K. Combining gene-based methods and reproductive technologies to enhance genetic improvement of livestock in developing countries. Applications of Gene-

Based Technologies for Improving Animal Production and Health in Developing Countries, pp.131-144, 2005.

15. Weigel KA.**Controlling inbreeding in modern breeding programs**. *Journal of Dairy Science*2001; 84:E177-E184.doi:10.3168/jds.S0022-0302(01)70213-5

16. Goyache F, Gutiérrez J,Fernández I. Using pedigree information to monitor genetic variability of endangered population: the Xalda sheep breed of Asturias as an example. *Animal Breeding and Genetics*2003; 120:95-105. doi:10.1046/j.1439-0388.2003.00378.x

17. Pedrosa V, Santana M, Oliveira P, Eler J, Ferraz J. Population structure and inbreeding effects on growth traits of Santa Ines sheep in Brazil. *Small Ruminant Research* 93; 135-139.doi:10.1016/j.smallrumres.2010.05.012

18. Hossein-Zadeh N. Inbreeding effects on body weight traits of Iranian Moghani sheep. *Archives of Animal Breeding* 2012; 55:171-178.doi:10.5194/aab-55-171-2012

Table 1. Number of flocks, lambs, sires, dams, embryo transfer lambs and average eight-week body weight (mean +-s.d.) of lambs during the study period from 2000 to 2018

| Year	Flock	Lambs	Sire	Dam	Embryo transfer No	Embryo transfer Yes	Body weight (kg)
2000	10	110	14	65	110	0	22.4 (6.5)
2001	16	150	22	91	150	0	25.1 (6.2)
2002	22	316	32	177	316	0	25.5 (7.2)
2003	31	583	53	313	565	18	27.4 (7.4)
2004	41	863	67	454	788	75	27.1 (7.4)
2005	50	1191	80	658	1156	35	29.0 (7.7)
2006	54	1644	102	867	1641	3	27.1 (6.6)
2007	55	1678	90	906	1631	47	27.6 (8.4)
2008	64	1787	97	859	1687	100	27.1 (6.3)
2009	64	1656	121	874	1525	131	27.6 (7.4)
2010	68	2569	141	1186	2313	256	27.8 (6.9)
2011	74	2858	165	1356	2549	309	27.9 (7.1)
2012	74	2516	151	1198	2205	311	28.7 (6.4)
2013	60	2659	35	1282	2413	246	28.7 (6.8)
2014	67	3125	152	1540	2889	236	27.5 (6.4)
2015	64	3745	166	1833	3595	150	27.8 (6.6)
2016	59	3202	151	1548	2930	272	26.6 (6.3)
2017	53	2914	157	1446	2711	203	27.7 (6.2)
2018	41	1525	95	847	1440	85	25.2 (5.7)
Total records	146	35220	928	9443	32743	2477	
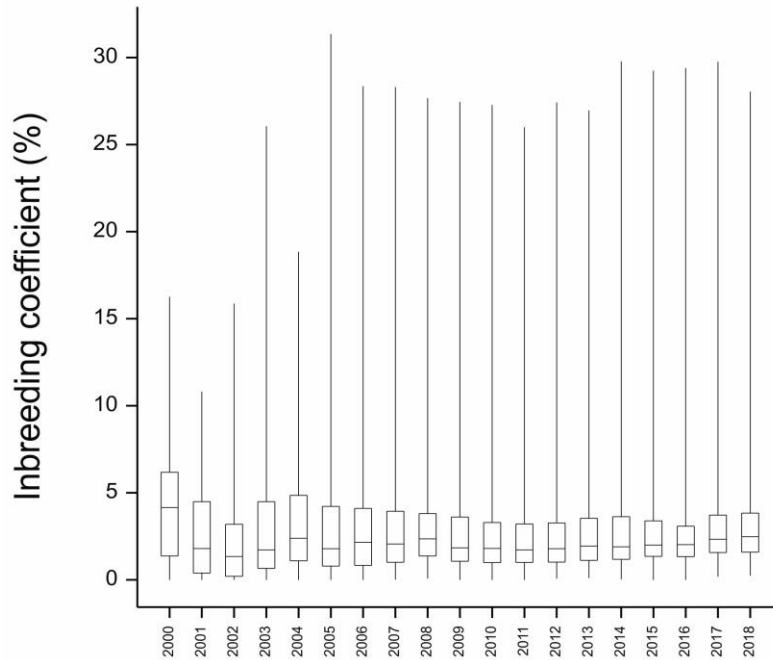
Figure 1.A box and whisker diagram showing minimum, lower quartile, median, upper quartile and maximum for the inbreeding coefficient across lambs during the years 2000 to 2018.
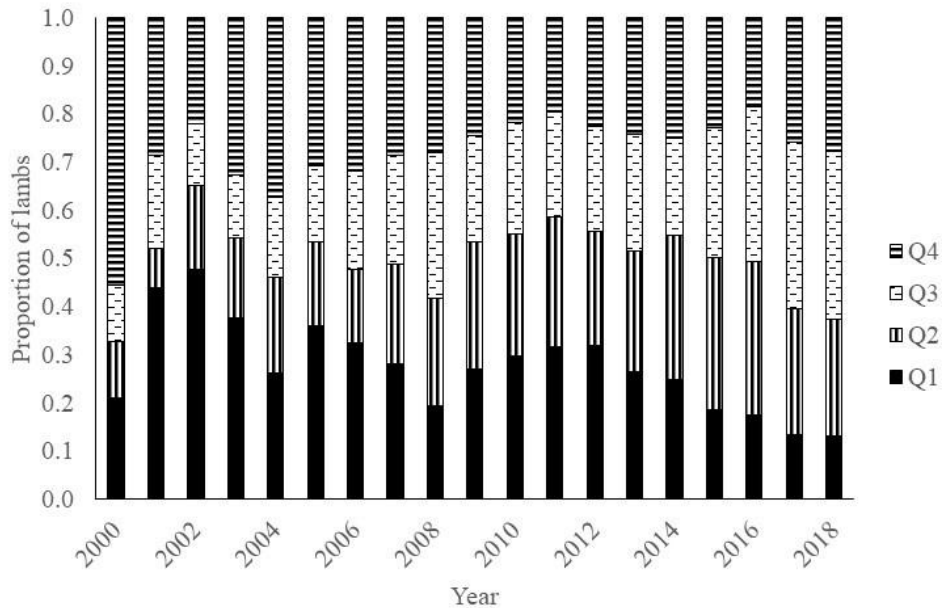

Figure 2. Proportion of lambs with an inbreeding coefficient of <1.2% (Q1), 1.2-2.0% (Q2), 2.1-3.6% (Q3) and >3.6% (Q4) during the years 2000 to 2018.
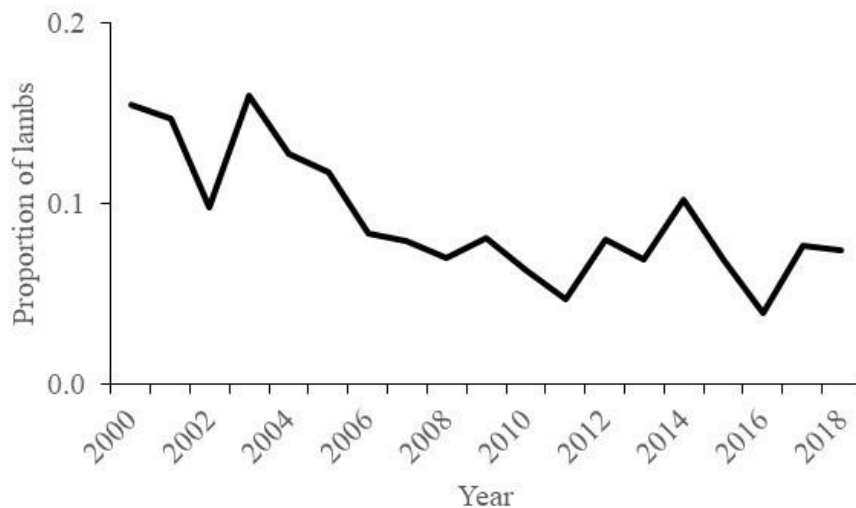
Figure 3. Proportion of lambs with an inbreeding coefficient >7% during the years 2000 to 2018.
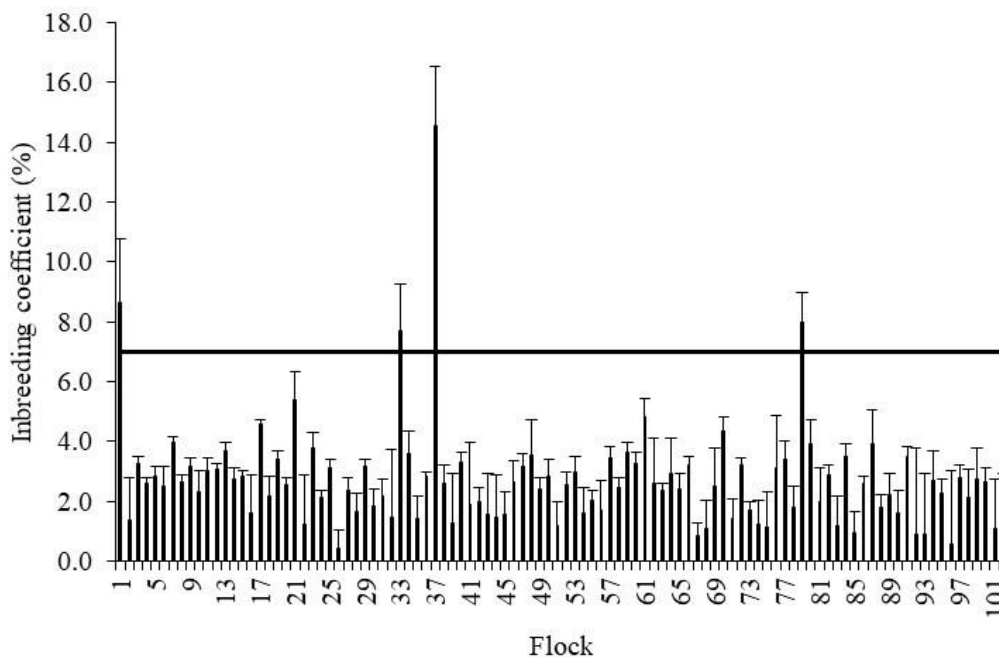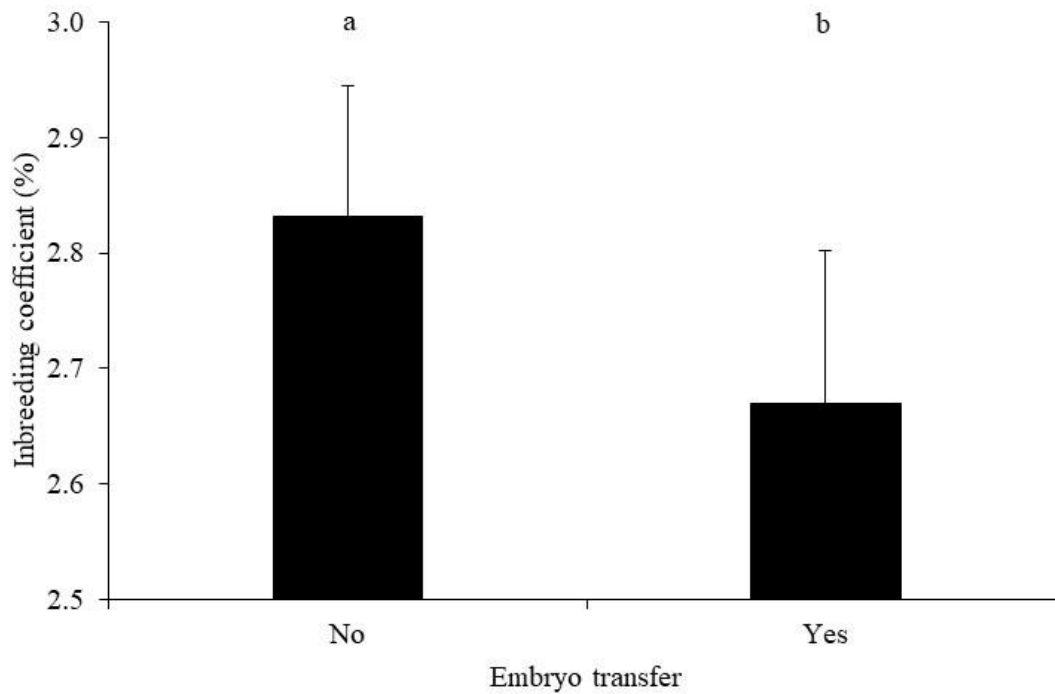

Figure 4. Predicted mean inbreeding coefficients for lambs in each flock adjusted for the effect of year of birth, eight-week body weight, embryo transfer and lamb sire. Standard error bars are shown. The solid black line represents an inbreeding coefficient of 7%.
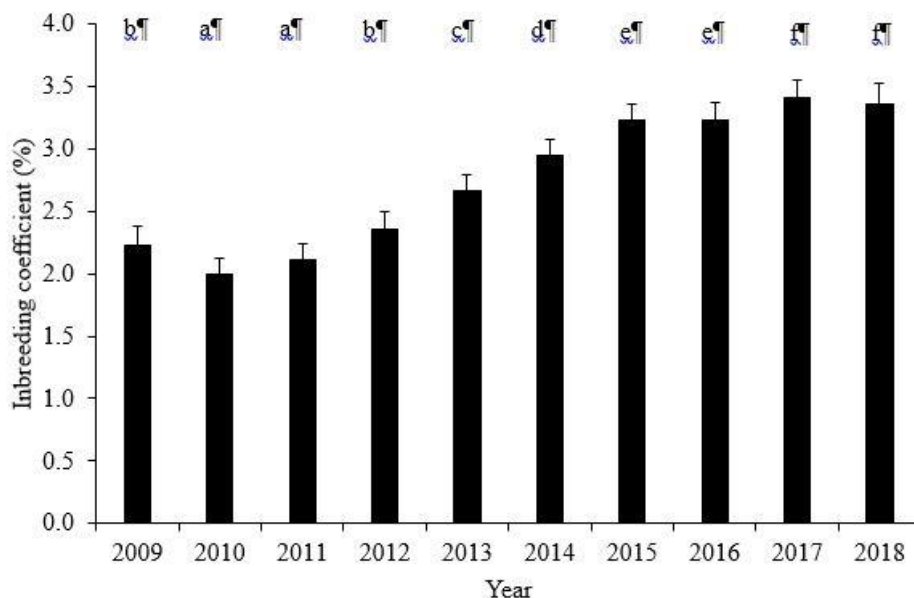
Figure 5. Predicted mean inbreeding coefficients for lambs during each year from 2009 to 2018 adjusted for the effect of eight-week body weight, embryo transfer, flock and lamb sire. Columns with different letters are significantly different at $P<0.05$. Standard error bars are shown.
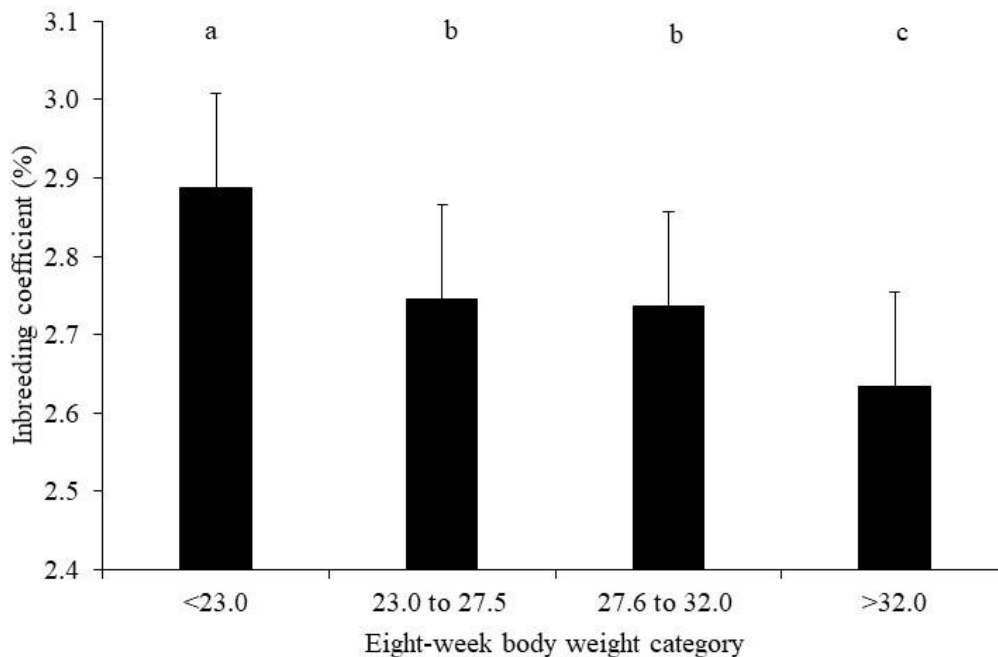
Figure 6. Predicted mean inbreeding coefficients for lambs in each eight-week body weight categories adjusted for the effect of year of birth, embryo transfer, flock and lamb sire. Columns with different letters are significantly different at $P<0.05$. Standard error bars are shown.

Figure 7. Predicted mean inbreeding coefficients for embryo transfer lambs or non-embryo transfer lambs (natural mating or AI) after adjusting for effects year of birth, eight-week body weight, flock and lamb sire. Columns with different letters are significantly different at P<0.05. Standard error bars are shown.