Extent and implications of incorrect offspring-sire relationships in pastoral production system in Kajiado District, Kenya

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Abstract

The aim of this study was to evaluate accuracy of farmer's paternity identification which determines success of future breed selection and hence genetic gain. Paternity of 269 Orma/zebu and Sahiwal/zebu calves was evaluated using genetic markers and the likelihood based method.

Results indicate that only 6.7% farmer alleged paternities were confirmed, 88% parent-offspring relationships were rejected and 18% parent-offspring relationships were undetermined. However, 82% of offsprings were assigned at least 80% confident paternities to one of the sampled candidate males.

These results suggest that there is need to institute proper breeding program in the pastoral area if farmers are to benefit from their current efforts of breed improvement.

Key words: breed improvement, pastoralists cattle, paternity determination

Introduction

Correct pedigree information is paramount in a successful breeding program and its importance has increased with the introduction in 1990 of individual animal models for national genetic evaluations. Even though pedigree assignments are generally not questioned, several studies have shown that the proportion of errors in sire identification varies from a few percent to as much as 22% (Christensen et al 1982, Geldermann et al 1986, Bovenhuis and van Arendonk 1991, Ron et al 1996, Visscher et al 2002). These mistakes reduce the rate of genetic progress (Van Vleck 1970a and b, Israel and Weller 2000, Banos et al 2001, Visscher et al 2002). Various studies have estimated the effect of pedigree mistakes on the rate of genetic gain and found an annual reduction rate of 2-15% (Banos et al 2001, Geldermann et al 1986, Israel and Weller 2000, Visscher et al 2002).

Deviation of a population from Hardy-Weinburg equilibrium results in evolution. The rules of Mendelian inheritance require that, barring mutation, each parent and progeny should share at least one common allele. DNA microsatellites can be efficiently used to determine incorrect paternity attribution of cattle based on exclusion probabilities and likelihood odds ratio (Heyen et al 1997). Discrepancies between the calve and putative sire genotypes may be due to mutation, genotyping error, null alleles and error in paternity allegation and leads to exclusion of a candidate sire (Ron et al 2004). The use of a likelihood approach in CERVUS® 2.0 accounts for potential imperfections in the data (Marshall et al 1998).

Bos indicus cattle types in Kenya are divided into either the small or large East African zebu which can further be divided into different breeds and strains (Rege and Tawah 1999, Rege et al 2001). A recent genetic study revealed that the Kenyan Zebu populations were fairly outbred and apart from the Kenyan Boran were at Hardy Weinberg Equilibrium. This suggests that there has been little or no systematic selective breeding in these populations (Rege et al 2001). In Kajiado district, the Maasai zebu (MZ) breed has declined in the 20th century due to outcrossing with improved Kenyan boran (KB) and Sahiwal (SW) breeds (Maichomo et al 2001). This pastoral population uses natural service in a communal grazing set-up and attempts to keep off “visiting bulls” from a farmers breeding herd is ineffective due to lack of physical barriers. Besides, farmers do not keep conventional records on basic breeding practices. In an earlier study, 11 Orma boran (OB) bulls were crossed with the Sahiwal/zebu (S/Z) (crosses between the MZ and SW breeds) cows in an attempt to breed for large sized trypanotolerant Orma/zebu (O/Z) crosses. The aim of this study was to verify the farmer alleged paternities by confirming, rejecting or failing to determine the sire-offspring relationship in the pastoral communal setting.

Objectives of the study

The objectives of this study were to:
1. Establish paternity of O/Z and S/Z calves from a pastoral communal setting using genetic markers.
2. Based on paternity verification, hypothesize the effect of current pastoral cattle breeding structure on expected genetic gain.

Materials and methods

Study area, study population and determination of paternity by farmers

This study was conducted in Olkiramatian and Shompole group ranches of Kajiado district, South Western Kenya, which is a semi-arid area inhabited by Maasai pastoralists. A total of 269 (162 O/Z and 107 S/Z) cross calves allegedly sired by OB and SW bulls respectively from 11 herds of 4-47 individuals were sampled between October 2003 and October 2004. These animals were listed as progeny of 21 sires (11 OB, 10 SW). The mating system used was natural service. The criteria used to appraise offspring's paternity by the pastoral farmers was inherited physical features and color, dominant bull in the herd at the time of conception, and observed actual mounting. Date of birth, body weight at birth and unique dam identification number were recorded for each calf at birth.

Genotyping methods

Five to twenty milliliters of blood samples were collected from the jugular vein of calves and their alleged sires using vacutainer tubes with heparin anticoagulant (Becton Dickinson). High molecular weight DNA was extracted from blood by the mini salt-out procedure (Sambrook et al 1989, Ma et al 1996, Ron et al 2004) adapted at International Livestock Research Institute (Nairobi, Kenya). The concentration of DNA samples (genomic DNA) was determined using the Gene Quant Pro® spectrophotometer by measuring absorbance at 230nm, 260nm, 280nm. Genomic DNA samples with a concentration of more than 100ng/µl were diluted to 20ng/µl by adding the appropriate amount of TE. Primer solutions for regular use were diluted to 200ng/µl.

The PCR protocols for DNA isolated from blood cells were as described by Ron et al (1995) using a DNA engine thermocycler (GeneAmp®, PCR system 9700, ABI). PCR was performed using cattle step-down method 5955 to amplify and fluorescently label alleles present at 15 bovine microsatellite loci using markers/primers (ABI) shown in Table 1.

Table 1. Size range and dye colour of markers used for allele detection in the O/Z and S/Z cross calves

Primer panel	Marker[1]	Dye	Range (bp)
1	AGLA293	Blue	190-260
	ILSTS023	Red	150-310
	HEL1	Green	75-150
	ETH225*	Yellow	115-190
2	ILSTS006	Blue	250-340
	INRA032	Red	130-230
	TGLA122*	Green	110-200
	MGTG4B	Yellow	85-170
3	ETH152	Blue	155-240
	INRA035	Red	75-150
	BM2113*	Green	100-175
	ILSTS50	Yellow	140-210
4	ILSTS005	Blue	150-225
	INRA005	Green	115-175
	CSSM66	Yellow	150-240

[1]*Markers denoted with an asterisk are included in the International Society for Animal Genetics (ISAG) standard panel for pedigree confirmation (Bredbacka and Koskinen 1999).*

Agarose Gel Electrophoresis was performed to check the quantity and quality of PCR products and since all the products were concentrated, they were diluted 1:30 with a Hydra Robotic dispenser (Robbins scientific). LIZ formamide standard was used as reference for allele size calling. Fifteen (15) FAO microsatellite markers chosen for this analysis were: *AGLA 293, BM2113, CSSM66, ETH152, ETH225, HEL1, ILSTS005, ILSTS006, ILSTS023, ILSTS50, INRA005, INRA032, INRA035, MGTG4B and TGLA122* (http://sol.marc.usda.gov/genome/cattle/cattle.html) (Table 1).

Electrophoresis was performed in an ABI-3730s DNA analyzer (Applied Biosystems). Automated fragment analysis, size calling and binning for measurement of microsatellite length polymorphism were then used by Genemapper™ (Ver. 3.7) genetic software (Applied Biosystems) to identify the alleles of each of the microsatellite loci. Defined peaks in basic mode were detected and examined in the electropherogram. Lengths of fluorescently labeled amplicons were determined by comparison to the internal lane size standard, LIZ™ (ABI, UK). Least-square 3rd-order method was used for size calling whereby known standard and the amplified fragments were used to produce a best-fit least squares sizing curve based on multiple linear regression. Consensus based allele-calling algorithms involving envelope detection, optimization of parametric models and rule-based system were eventually utilized for allele calling. Only good quality alleles were used for further genotype information. A second quality check of the genotype data was performed manually by an independent worker.

Paternity simulation in CERVUS® 2.0 program

The expected frequency of heterozygotes and probability of exclusion for markers were calculated as described by Ron et al (1996) and Marshall et al (1998). Since the exclusionary approach was found inadequate for this data when multiple candidate parents remained non-excluded, the likelihood approach (LOD score) was used to confirm paternity. Simulations were used to calculate LOD score, Delta statistic (Δ) as well as assess the significance of Δ values (Marshall et al 1998). Assuming Hardy–Weinberg equilibrium, a maternal genotype and a paternal genotype were generated from allele frequencies observed in the study population, and an offspring genotype derived by Mendelian sampling of the parental alleles. Genotypes were also generated for a number of unrelated candidate males. The genotypic data for all individuals were then altered to reflect the existence of unsampled males, missing loci and incorrectly typed loci, according to the values of the parameters described in Table 2. Next, each candidate male was considered in turn as the alleged father, beginning with the father predicted by the farmer. The likelihood that the alleged father was the true father (H_1) was evaluated relative to the likelihood that the alleged father was an unrelated individual selected at random from the population (H_2), written as $L(H_1,H_2| g_a, g_o)$:

Where:

g_a and g_o represent the genotypes of alleged father and offspring, respectively, at a given locus,

$T(g_o|g_a)$, the probability of the offspring's genotype given the genotypes of the alleged father, and

$P(g_o)$, is the frequency of the offspring's genotype.

Once all males were considered, the most-likely and second-most-likely males were identified and the male with the highest score was considered as the putative father. The statistical confidence of this estimate was measured by the difference between LOD scores of the male with the highest score and the male with the second highest score. Like Marshall et al (1998), an LOD score of zero was used as a threshold. Computer simulation was used to estimate critical value of Δ to be used to establish statistical confidence so that 99% of the values above critical Δ were correct assignments.

Table 2. The parameters used in simulation of paternity inference for 269 Orma/zebu and Sahiwal/zebu calves in Kajiado District

Parameter	Value used
Number of candidate males	21
Proportion of candidate males sampled	0.8
Proportion of loci typed	1
Rate of typing error	0.01
Number of tests	10,000
Relaxed confidence level	80%
Strict confidence level	95%

Candidate males were ranked such that $LOD_i \geq LOD_{i+1}$ for $1 \leq i < n$ and Δ was defined as: $n \geq 2, \Delta = LOD_1 - LOD_2; n = 1, \Delta = LOD_1; n = 0, \Delta$ *undefined.* Based on this information, alleged paternities were either confirmed, rejected or undetermined. All 95% confident paternities were nested within the 80% confident paternities.

Results

Details of loci used

A total of 189 alleles were detected with an average of 12.6 alleles per locus (MNA) (range 6-20). The estimated mean observed (Ho) and expected (He) heterozygosity were 0.739 and 0.753 respectively. Combined exclusion probability of the 15 markers was 0.999463 with confidence level of 95%. The frequency of the most common microsatellite allele ranged from 0.21 to 0.68. Most loci had at least one allele that was present in only a single individual. The mean frequency of heterozygotes over all markers was 0.74, and the difference between the observed and expected heterozygosity ranged from –0.009 to 0.058, with a mean of -0.0138. Of the 15 markers genotyped, some were more prone to genotyping mistakes than others. The frequencies of offspring with at least single discrepancies among all animals genotyped for each of the 15 markers are listed in Table 3. Assuming that all known parent-offspring pairs were equally

independent, mean observed error rate across loci was 0.326, and average rate of at least single discrepancies was 0.25.

Table 3. Average heterozygosity, mean number of alleles and exclusion probability of 15 microsatellite loci used

Locus	Number scored	H_O	H_E	Allelic frequency	PIC[1]	PE[2]	Heterozygosity obs – ex[3]	Freq of discrepancy[4]	Estimated error rate e_l
AGLA293	289	0.685	0.723	14	0.695	0.343	-0.038	0.20	0.295
BM2113	291	0.732	0.738	10	0.706	0.351	-0.006	0.16	0.228
CSSM66	291	0.845	0.858	12	0.840	0.550	-0.013	0.33	0.297
ETH152	290	0.483	0.507	9	0.475	0.14	-0.024	0.12	0.425
ETH225	287	0.725	0.709	9	0.675	0.313	0.016	0.16	0.254
HEL1	290	0.745	0.738	8	0.701	0.342	0.007	0.19	0.279
ILSTS005	291	0.766	0.767	6	0.727	0.365	-0.001	0.26	0.351
ILSTS006	291	0.694	0.767	15	0.733	0.385	-0.073	0.25	0.329
ILSTS023	290	0.697	0.775	20	0.754	0.422	-0.078	0.39	0.464
ILSTS050	291	0.777	0.784	8	0.749	0.400	-0.007	0.27	0.339
INRA005	291	0.729	0.730	9	0.685	0.319	-0.001	0.23	0.355
INRA032	291	0.797	0.806	19	0.781	0.454	-0.009	0.25	0.274
INRA035	291	0.742	0.684	15	0.648	0.292	0.058	0.18	0.312
MGTG4B	291	0.852	0.860	16	0.843	0.556	-0.008	0.38	0.341
TGLA122	291	0.818	0.848	19	0.833	0.546	-0.03	0.37	0.341
Mean	291	0.739	0.753	12.6	0.723	0.385	-0.0138	0.25	0.326

[1] *Polymorphic Information Content*
[2] *Probability of Exclusion*
[3] *Difference between the observed and expected frequencies of heterozygotes, based on the Hardy-Weinberg equilibrium*
[4] *Frequency of observing at least a single conflict/discrepancy between offspring and candidate sire genotype*

Assignment of paternity

Due to observed high error rate, paternity was assigned to the most likely male based on the observed genotypes, LOD and delta scores. Critical delta values of 1.7 and 0 were used to award paternity with 95% and 80% confidence respectively. Only 6.7% farmer alleged paternities were confirmed at 80% confidence to a most likely candidate male with LOD and delta scores ranging from 0.0529 to 9.2, and 0.0037 to 9.2 respectively. Less than half of the 80% confident paternities (2.6% of all tests) were secure at 95% confidence (Table 4). Regardless of confidence level, more S/Z calves (11.7%) had their paternities confirmed relative to the O/Z (3.6%). The biological parents of 221 offsprings were established from the 21 candidate fathers. The percentage of father–offspring relationships in which 80% and 95% confidence paternities were assigned is 82% and 31% respectively. The success of paternity inference in O/Z and S/Z calves was in close agreement with the predictions of the simulation at 80% confidence (82% vs. 84%) compared with 95% confidence (31% vs. 93%). Fewer paternities were secure at 95% confidence than at 80% confidence.

More than 88% alleged paternities were rejected and none of the calves genetically matched haplotypically at all loci to only one of the 21 candidate sires. Finally, all alleged sires were excluded from the paternity of 18% of offsprings, probably due to the existence of a non-

sampled male in the studied population. Considering the breed aspect, confirmation was slightly higher, being 35.4% and 46.1% for the O/Z and S/Z respectively.

Table 4. Proportion of confirmed, rejected and unresolved 80% and 95% confident paternities of 269 calves

Breed*	Sample size	Confidence level	Confirmed		Rejected		Unresolved
			Breed	Paternity	Breed	Paternity	
O/Z	167	95%	18(10.8%)	3(1.8%)	108(65%)	161(96%)	27(16%)
		80%	41(24.6%)	3(1.8%)			
S/Z	102	95%	19(18.6%)	4(3.9%)	55(54%)	90(88%)	21(21%)
		80%	28(27.5%	8(7.8%)			

**O/Z – Orma/Zebu, S/Z – Sahiwal/Zebu*

Discussion

Microsatellite loci and null alleles

The loci used in this study were highly polymorphic, had high exclusionary power, were within the expected heterozygosity as predicted under Hardy-Weinberg conditions, but high frequency of discrepancies and error rate were noted. The high error rate increased the probability of observing erroneous genotypes reflected as genotypic mismatches, making it harder to dismiss an unrelated male's genotype as unlikely (Kalinowski et al 2006). Definitely this has associated costs as described by Morrissey and Wilson (2005). All loci in this study showed presence of null alleles which resulted in presence of many homozygote-homozygote mismatches between cervus-assigned father and offspring. However, some true father–calf mismatches are inevitable especially when screening a large number of markers (Pemberton et al 1995).

Paternity estimation and confidence

The PE value from this study (0.385) was lower than reports from other studies of 0.85 to 0.99 hence it could not be used for paternity confirmation (Ron et al 1996). Thus, while PE is an excellent measure for comparing alternatives in test development, its usefulness is limited for predicting the number of offspring unambiguously assigned to their true sires in this population. Using likelihood approach, biological fathers of 82% of the offsprings were identified from among the 21 sires. Some calves were identified with sires other than those alleged by the farmers, belonging to herds located more than 30km apart, and perhaps such mating occurred at watering points or distant grazing areas.

This study used critical delta of 1.7 and >0 to award paternity at 95% and 80% confidence compared to 3.15 used by Marshall et al (1998) and 4 used by Foltz and Hoogland (1981) at 95% confidence. Due to differences in production systems (extensive versus dairy), the critical delta of 1.7 and >0 used in this study may be acceptable. Reliability of observed LOD scores was derived from the observation of Kalinowski et al (2007) that the male with the highest likelihood of being the father was in fact usually the actual father. Marshall et al (1998) also ascertains that paternities assigned with 80% confidence were more accurate than can be achieved by direct observation, and are also better than would be obtained by a purely exclusionary approach,

where confidence in paternity of non-excluded males is generally unknown. Although very low paternity confirmations were achieved in this study (6.7%), the number of markers used (11) was higher than for most published studies, thus yielding results with higher confidence in line with current recommendations (Morrissey and Wilson 2005, Kalinowski et al 2007).

Paternity failure and its implications on breeding strategies in Kajiado District

The 88% frequency of rejected paternity determinations in this study was higher than most previous studies of 5.2% to 20% on other populations (Beechinor and Kelly 1987, Bovenhuis and van Arendonk 1991, Christensen et al 1982, Geldermann et al 1986, Ron et al 1996, Visscher et al 2002). Low paternity confirmations observed may be a reflection of the farmer's inaccurate prediction based on phenotypic characteristics, coupled with absolute lack of record keeping. Perhaps more paternities could have been assigned, or confidence in existing paternities increased, by sampling a larger number of candidate males and obtaining the mothers genotypes. Breed confirmation of more than 30% in this study was however higher for the S/Z than O/Z and shows fast experience on ability to match phenotypic characteristics of the S/Z which farmers have long experience with.

Paternity failure of 18% observed in this study is fairly high even for extensively managed beef cattle compared to 7.6% for cows in communal herds in Israel (Weller et al 2004). Generally, non-paternity is attributed to the combined effects of null alleles, intrusion of an unidentified and therefore untyped sire and existence of a non-sampled male in the studied population, factors that could have been at work in this population. Scrutiny of obtained genotype data suggests that the most likely reason for high failure rate would have been non sampled sires since complete sampling would have required massive resources.

Conclusion and recommendations

Despite the low paternity confirmations achieved, the simulation appears to be a useful predictive tool. These results suggest poor genetic gain and point to the importance of instituting a proper breeding program within the constraints of pastoral production system in Kajiado District. Castration of unwanted bulls and keeping of basic breeding records are some of the practices that can assist in appropriate sire identification. Annual genotyping of a portion of pedigree sires to reduce misidentification rate in order to increase productivity can be perhaps viable within Kenyan commercial ranches but costs are currently prohibitive for pastoral systems.

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