Monte Carlo Simulation to Assess the Impact of Adult MOET Schemes in Somba Cattle

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Summary

Monte Carlo simulations were carried out in order to assess the impact of multiple ovulation and embryo transfer (MOET) on the dairy performance of Somba cattle. Adult MOET-nucleus schemes were simulated over 20 generations of selection, assuming a fixed test capacity of 512 milk recorded females, a success rate of transfer of 70%, a survival rate of 70% and various sibship sizes (n_D = 4, 8, 16). Selection criteria were the BLUP estimates of the true additive genetic values of candidates using the reduced animal model. For different combinations of number of donors (D = 64, 128, 256) and number of sires (S = 4, 8, 16) to be selected, the simulated genetic response in milk yield ranged from 0.088 to 0.127 phenotypic standard deviation units (SU) per year. These figures corresponded to a genetic progress of 2.2 to 3.2% of the population mean per year (coefficient of variation in milk yield is 25% for Somba cattle). For all alternatives with regard to population structure, the simulated rate of inbreeding ranged from 1.32 to 2.93% per year, while the expected one ranged from 0.83 to 3.32%. Compared to the rate of inbreeding commonly admitted in a conventional progeny-testing scheme (0.1 to 0.2% per year), the rates of inbreeding expected from the simulated adult MOET schemes were quite high and could be a cause of concern. Strategies to reduce inbreeding in short or medium terms were examined.

■ INTRODUCTION

The Somba breed has been described as belonging to the group of trypanotolerant West African Shorthorn (WAS) savannah type (20). The breed enjoys a particularly high reputation for its adaptability to marginal environments characterized by limited feed resources, high climatic stress and disease challenge. Its native area lies between lat. 9°45' and 10°45' N, and long. 0°45' and 1°45' E. This corresponds to the area stretching from the Atacora Mountain chain to the valley formed by the Tapiongo Mountain, the frontier between Benin and Togo, the Nattiwah Mountain and the Keran River. The number of Somba cattle has steadily declined during the last decade, decreasing from 58 000 head in 1987 to 25 000 head

in 1995 (9). This negative trend in population size is due mainly to the high culling rate of young bulls for religious purposes and to the extensive crossbreeding with zebu stocks in order to obtain heavier animals for draft or better milkers. Concern about the risk of loss of the Somba breed was first expressed by FAO (6), who stressed the need for conservatory measures to prevent its further erosion. Recent achievements in non-surgical recovery of embryos from super-ovulated Somba cows (5), though modest (about two transferable embryos per cow), are significant for the feasibility of embryo transfer (ET) in this breed. ET is in turn a prerequisite for multiple ovulation and embryo transfer (MOET) breeding programs. The advantages of MOET schemes are: increased reproductive rates of donors, increased efficiency of selection in females and acceleration of genetic progress. MOET schemes should be especially useful for conservation of endangered breeds, as they can help both to compensate the handicap of small populations and to decide farmers to stick to their local breeds. This seems to be only possible by improving productivity of the latter (14). The purpose of this work was to assess the impact of adult MOET schemes on genetic progress in dairy performance in Somba cattle.

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■ MATERIALS AND METHODS

A Monte Carlo simulation was used to design adult MOET-nucleus breeding schemes, similar to that proposed by Nicholas and Smith (15) with minor adaptations. Candidates of each sex were selected at 34 months of age, when females have completed their first lactation, so that the generation interval was 3.7 years. Parameters and symbols used are presented in table I.

Generation 0

Generation 0 consisted of founder animals. D dams were randomly sired by S bulls with a mating ratio of M according to a hierarchical family structure. Founder animals were assumed to be unrelated.

Generation 1

Generation 1 consisted of MOET offspring of the founder population. Assuming that the total number of transferable embryos obtained from D females (donors) is T, the total number of MOET progeny of each sex surviving at selection will be $n_o / 2 = svT / 2$, where s is the success rate of transfer and v the survival rate of calves. This corresponds to a MOET sibship size of $n_D = svT / D$ with a sex ratio of 50%. When female offspring completed their first lactation, they were selected on individual and sib records, while male offspring were selected on full and half sib records. S out of $n_o / 2$ test bulls and D out of $n_o / 2$ test dams were selected to form the next generation.

Generation 2 to t

Test animals in generation t were offspring of selected animals in generation t − 1. In these generations, individual records and sib records, plus all available pedigree information were used for

selection in females. For selection in males, sisters' performance plus all available pedigree information were used.

Genetic values and selection criteria

An infinitesimal model was assumed, i.e. the inheritance of the trait under consideration was determined by a large number of loci, each with a small and additive effect. The true genetic value of an individual was expressed in terms of gametic contributions of its parents plus a Mendelian sampling term:

$$a_i = 0.5a_s + 0.5a_d + \phi_i \quad (1)$$

where a_s and a_d are the genetic values of the sire and dam of animal i, and ϕ_i the Mendelian sampling term.

$$\phi_i \sim N\left(0; 0.5\,(1 - \overline{F_i})\,\sigma_a^2\right)$$

$\overline{F_i}$ is the average inbreeding coefficient of the parents of animal i and σ_a^2 the additive genetic variance of the milk yield.

Considered as deviations from population mean, the additive genetic values of founder animals were generated as random normal distributed numbers:

$$a_i \sim N\left(0, \sigma_a^2\right)$$

Selection criteria were the BLUP estimates of true additive genetic values of candidates, using the reduced animal model (RAM) (11, 16).

Phenotypic records were also generated as follows:

$$Y_i = \mu + 0.5a_s + 0.5a_d + \phi_i + e_i \quad (2)$$

where μ is the population mean and e_i the random environmental effect.

$$e_i \sim N\left(0, \sigma_e^2\right)$$

In matrix notation, the reduced animal model can be written as:

$$Y_o = Xb + Za_p + e^* \quad (3)$$

with $e^* = \phi + e$ and where Y_o is the vector of observations on offspring, b the vector of fixed effects, a_p the vector of breeding values of parents, φ the vector of the Mendelian sampling terms, e the vector of random environmental effects, X the design matrix of fixed effects, and Z an incidence matrix of 0's and ½'s identifying the parents of the animals for each record.

Using the computational approach proposed by Kennedy et al. (12), estimates of breeding values of offspring were derived from the following equation:

$$\hat{a}_o = 0.5(\hat{a}_s + \hat{a}_d) + h_w^2 \left[Y - \hat{\mu} - (0.5\hat{a}_s + 0.5\hat{a}_d)\right] \quad (4)$$

where $\hat{a}_o$ is the estimate of the breeding value of the candidate, $\hat{a}_s$ and $\hat{a}_d$ are the estimated breeding values of sires and dams of the candidate,

$h_w^2 = 0.5(1 - \overline{F})h^2 / [0.5(1 - \overline{F_i})h^2 + (1 - h^2)]$ is the within family heritability, and h^2 is the heritability coefficient of the milk yield.

The estimates of the breeding values of parents $\hat{a}_s$ and $\hat{a}_d$ are solutions of the following mixed model equation:

$$\begin{bmatrix} X'\,R^{-1}\,X & X'\,R^{-1}\,S \\ S'\,R^{-1}\,X & S'\,R^{-1}\,S + A_p^{-1}/\sigma_a^2 \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a}_p \end{bmatrix} = \begin{bmatrix} X'\,R^{-1}\,Y \\ S'\,R^{-1}\,Y \end{bmatrix} \quad (5)$$

with $S = \begin{bmatrix} I \\ Z \end{bmatrix}$ and $R = \begin{bmatrix} I\,\sigma_e^2 & 0 \\ 0 & D \end{bmatrix}$

and where I is the pxp identity matrix, D a $n_o \times n_o$ diagonal matrix with $D_{ii} = 0.5(1 - \overline{F_i})\sigma_a^2 + \sigma_e^2$, and A_p is the pxp numerator relationship matrix among parents.

Table I

Parameters and symbols used for the simulated adult MOET breeding schemes

Parameter	Symbol	Value
Num. of transferable embryos recovered	T	
Success rate of transfer	s	70 %
Survival rate of MOET progeny	v	70 %
Num. of breeding sires per generation	S	
Num. of female donors per male	M	
Sex ratio	r	50 %
Num. of donors per generation	D = SM	
Num. of MOET progeny at selection	$n_o = svT$	
Breeding goal is the daily milk yield	MY	
Heritability	h^2	0.25
Coefficient of variation	cv	0.25
Evaluation method of bulls and dams	BLUP (RAM)	
Selection criterion	Estimated breeding value	
Generation interval	L	3.5 years
Num. of replicates	R	100
Num. of test bulls (dams)	$t_B = t_D = svT / 2$	

Genetic response

The simulated average genetic response per generation was computed by the regression of the cumulated responses $\Sigma\Delta G_t$ on the generation number t, and compared to the expected response obtained from the formula of Rendel and Robertson (17):

$$\Delta G_E = (\rho_{AI_M} i_M + \rho_{AI_F} i_F)\, \sigma_a^2 / 2 \quad (6)$$

where ΔG_E is the expected response to selection, ρ_{AI_M} and ρ_{AI_F} are the correlation between true and estimated breeding values of males and females, respectively, i_M and i_F are the standardized selection differentials for males and females, respectively, while σ_a^2 is the additive genetic variance.

To account for finite population size, order statistics of Becker (1) were used for standardized selection differentials.

Inbreeding

The rate of inbreeding per generation was derived from the regression of logarithm of $1 - F_t$ on generation number t, where F_t is the average inbreeding coefficient of the population at generation t. Inbreeding coefficients per generation were obtained from the numerator relationship matrix constructed by the technique of Hudson et al. (11). The simulated rate of inbreeding per generation was compared to those expected assuming a Poisson distribution of family size (21).

$$\Delta F_E = \frac{1}{2Ne} = \frac{1}{8}\left(\frac{1}{S} + \frac{1}{D}\right) \quad (7)$$

where ΔF_E is the theoretical rate of inbreeding per generation, Ne is the corresponding effective population size, and S and D are the number of sires and dams selected per generation.

■ RESULTS AND DISCUSSION

Table II shows the simulated and expected genetic responses per year in closed adult MOET-nucleus schemes with alternative designs of selected populations and a constant test capacity of 512 milk recorded females, assuming one batch of 1024 successful transfers, a success rate of transfer of 70%, a survival rate of 70% and variable sizes of MOET sibship. For different combinations of number of donors (D = 64, 128, 256), number of selected sires (S = 4, 8, 16) and number of MOET offspring per donor (n_D = 4, 8, 16), the simulated genetic response in milk yield ranged from 0.088 to 0.127 phenotypic standard deviation units (SU). These figures correspond to rates of genetic change of 2.2 to 3.2% of the population mean per year, the coefficient of variation in milk yield being 0.25 for Somba cattle (4).

These results showed that the adult MOET nucleus schemes studied had the potential to increase genetic response in milk yield by about 10 to 59% more than a well-organized progeny testing scheme could. The conventional progeny-testing scheme used as base for comparison is referred to by Nicholas and Smith (15) as the one with the maximum impact on genetic change (equilibrium genetic change is 0.1 SU per year).

Results also showed that the smaller was the number of donors needed to generate the assumed number of candidates, the higher were the simulated and expected genetic changes. With 256 donors selected to breed the test population of 512 candidates of each sex, the simulated genetic response per year was 0.088 SU. With 128 donors needed to breed the same test population, the simulated genetic response increased to 0.2 SU per year.

The expected genetic changes showed the same tendency, the corresponding values being 0.096, 0.12 and 0.14 SU per year for 256, 128 and 64 donors, respectively, to be selected. On the other hand, the number of MOET offspring to be produced by a donor, given the constant test population assumed, was inversely proportional to the size of the donor population. For example, 256 donors would be selected, if four MOET offspring per donor were produced. With eight MOET progeny per donor, the number of donors needed would be 128, and so on. In other words, the efficiency of selection, coupled with the intensity of selection on the females to breed female (FF) and females to breed male (FM) paths depended on the capacity of donors to produce more MOET offspring. Similarly, accuracy and intensity of selection on the males to breed male (MM) and males to breed female (MF) paths became greater with a decreasing number of sires used or with an increasing mating ratio, given a fixed number of donors used to breed the test population. Consequently, the simulated genetic response increased from 0.115 SU to 0.116 SU and to 0.118 SU as the number of bulls used to sire the donor population decreased from 16 to 8 and 4 (mating ratio = 8, 16, 32), respectively.

However, the magnitude of the increase in genetic change resulting from the increased mating ratio was less than that obtained by increasing the number of MOET offspring per donor. Similar results were also reported by Kosgey et al. (13). These results indicated that the relative contribution of both FF and FM paths to the genetic response was higher than that of the MM and MF paths. Simulated genetic responses were about 0.9 to 13.4% lower than those expected. The discrepancy between simulated and expected genetic change was probably caused by the reduction in selection differentials due to the intra-class correlations between estimated breeding values (10). This discrepancy became greater as the number of half-sib families and the sibship size increased. Similar results have been previously reported by Ruane and Thompson (18). Another reason that could account for the discrepancy between simulated und estimated genetic changes was the depletion of genetic variance due to the negative linkage disequilibrium, the so-called Bulmer effect (2). The classical formula of Rendel

Table II

Simulated and expected genetic response
in milk yield[1,2]

Num. of MOET progeny[3] per donor	Num. of donors	Num. of sires	Genetic response	
			Simulated	Expected
n_D	D	S	ΔG_S	ΔG_E
4	256	16	89	91
		8	88	101
8	128	16	115	116
		8	116	120
		4	118	127
16	64	8	116	134
		4	127	143

[1] Simulated and expected genetic response in milk yield (x10³ standard deviation units) per year in adult MOET-nucleus breeding schemes with alternative designs of selected populations, assuming a batch of 1024 successful transfers, a success rate of 70%, a survival rate of 70% and variable sizes of MOET sibship
[2] $h^2 = 0.25$; $\sigma_a^2 = 1$
[3] Number of MOET progeny living at selection

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and Robertson to predict genetic response did not account for reduction in selection differential and changes in additive genetic variance in subsequent cycles of selection. Therefore, the expected genetic gains obtained in the present study should be considered as the upper bounds of the predictable ones.

The simulated and expected rates of inbreeding per year are given in table III. For all alternatives with regard to the population structure, the simulated rates of inbreeding ranged from 1.32 to 2.93%, while those expected ranged from 0.83 to 3.32% per year.

These results showed that, in general, the inbreeding rates were underestimated by the theoretical formula of Wright (21) under the assumption of Poisson distribution of family size. It should be noticed here that the formula of Wright (1931) (21) does not account for the effect of selection differentials and that of the correlations between selection criteria on the rates of inbreeding. The approach of Burrows (3) does account for these parameters but is inappropriate to the hierarchical family structures as it is to repeated cycles of selection. With a constant mating ratio, the rate of inbreeding increased as the number of MOET offspring per donor increased (table III). On the other hand, the rate of inbreeding increased with increasing mating ratio, given a fixed number of MOET progeny per donor and a constant test capacity. As a result, the rate of inbreeding increased, when the selection pressure and the accuracy of selection on any of the four paths of gene transmission increased.

Compared to the rate of inbreeding commonly admitted in a conventional progeny testing scheme of 0.1 to 0.2% per year, the rates of inbreeding expected from the simulated adult MOET schemes were quite high and could be a cause of concern, if realized in practice as pointed out by Ruane and Thompson (18). To reduce the rates of inbreeding by MOET, the latter suggested the opening of the nucleus to outstanding animals or to run the MOET scheme under the regime of overlapping generations.

Other attempts to reduce inbreeding in short or medium term could be the avoidance of mating close relatives, and, as importantly, to apply some restrictions on family structure, i.e. select the best bull out of the half-sibs and/or the best dam out of the full-sibs. The price to pay for such selection strategies is the reduction in selection differentials and hence in the genetic response.

Results in the present study showed that the MOET technique can be valuable to increase potential rates of genetic progress in Somba cattle. As argued by Nicholas and Smith (15), a greater control over breeding, performance recording and selection can be exercised because of the small number of animals involved in the nucleus. The costs of embryo transfer are prohibitive in developing countries due to the required importation of inputs (19). However the actual embryo transfer service or technology may be quite low, if the number of calves produced is high (7). These services and management facilities can be provided by a government, a cooperative or a breeders association.

■ CONCLUSION

Results from this study confirm the finding that substantial improvements in genetic response can be achieved by adult MOET-nucleus schemes. There are also good reasons to use MOET through a utilizationist approach of conservation (8) of the Somba population. Since the number of MOET offspring per donor living at selection is the major biological parameter that promotes efficiency of breeding work by MOET, the capability of Somba cows to produce more MOET offspring than possible today will be determinant for the implementation of a MOET scheme involving the Somba breed in its native tract. Further progress in the application of the MOET biotechnology to the Somba cattle is also worthwhile. The Achilles heel of closed MOET-nucleus schemes is the high rate of inbreeding, if selection has to be efficient. Open nucleus schemes or schemes with overlapping generations, among other strategies, might be useful to overcome this difficulty to a higher or lesser extent.

Table III

Simulated and expected rates of inbreeding (x100) per year in adult MOET-nucleus breeding schemes with alternative designs of selected populations

Num. of MOET progeny[3] per donor	Num. of donors	Num. of sires	Rate of inbreeding		
			Simulated	Expected	
n_D	D	S	ΔF_S	ΔF_E	
4	256	16	132	83	(63)
		8	174	161	(93)
8	128	16	175	88	(50)
		8	216	166	(77)
		4	254	322	(126)
16	64	8	263	180	(69)
		4	293	332	(113)

In parentheses is the ratio $\Delta F_E / \Delta F_S$ in percent

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Résumé

Senou M., Dempfle L. Simulation Monte-Carlo pour évaluer l'impact des schémas MOET adultes chez les bovins Somba

L'impact de la technique de superovulation et du transfert d'embryons (MOET) sur la performance de la race Somba a été évalué à l'aide de simulations du type Monte-Carlo. Des schémas MOET adultes en noyaux fermés ont été simulés et soumis à 20 générations consécutives de sélection en supposant une capacité fixe de testage de 512 femelles connues pour leurs performances laitières, un taux de succès de 70 p. 100 pour le transfert, un taux de survie de 70 p. 100 chez les embryons et des tailles variables de familles (n_D = 4, 8, 16). Les valeurs additives génétiques des candidats ont été estimées par la méthode BLUP utilisant le modèle animal réduit (RAM). Pour différents scénarios déterminés par le nombre de donneurs (D = 64, 128, 256) et le nombre de géniteurs (S = 4, 8, 16) à sélectionner, la réponse à la sélection a varié de 0,088 à 0,127 unités standard phénotypiques par an. Ces valeurs correspondaient à un progrès génétique annuel de 2,2 à 3,2 p. 100 par rapport à la moyenne de la population par an (le coefficient de variation de la performance laitière de la race Somba étant de 25 p. 100). Pour toutes les alternatives du point de vue de la structure de la population, le taux de consanguinité obtenu par simulation a varié de 1,32 à 2,93 p. 100 par an, contre une valeur estimée allant de 0,83 à 3,32 p. 100. Comparé au taux annuel de consanguinité de 0,1 à 0,2 p. 100 généralement admis pour le schéma conventionnel de testage sur descendance, les taux de consanguinité prédictibles pour les schémas MOET adultes ont été remarquablement élevés. Pour pallier ce handicap, des stratégies de réduction à court et à moyen terme du taux de consanguinité ont été examinées.

Mots-clés: Bovin Somba – Superovulation – Transfert embryonnaire – Gain génétique – Consanguinité – Bénin – Togo.

Resumen

Senou M., Dempfle L. Simulación de Monte Carlo para evaluar el impacto de esquemas MOET en el ganado Somba adulto

Se llevaron a cabo simulaciones de Monte Carlo, con el fin de evaluar el impacto de ovulaciones múltiples durante la transferencia de embriones (MOET), sobre el rendimiento del ganado Somba. Durante 20 generaciones de selección, se simularon esquemas de núcleo adulto-MOET, asumiendo una capacidad fija de prueba de 512 hembras lecheras registradas, una tasa de transferencia de 70% de éxito, una tasa de sobre vivencia de 70% y varios tamaños de sibship (n_D = 4, 8, 16). Los criterios de selección fueron las estimaciones del BLUP de los verdaderos valores genéticos adicionados de los candidatos, utilizando un modelo animal reducido. Para diferentes combinaciones de varios donadores (D = 64, 128, 256) y varios machos (S = 4, 8, 16) a seleccionar, la respuesta genética simulada en el rendimiento de leche fue de 0,088 a 0,127 unidades fenotípicas de desviación estándar por año. Estas figuras corresponden a un proceso genético de 2,2 a 3,2% del promedio de la población por año (el coeficiente de variación en el rendimiento de leche es de 25% para el ganado Somba). Para todas las alternativas relativas a la estructura de la población, la tasa simulada de endogamia varió de 1,32 a 2,93% por año, mientras que la esperada varió de 0,83 a 3,32%. En comparación con la tasa de endogamia comúnmente aceptada en un esquema de examen de la progenitura (0,1 a 0,2% por año), los esquemas fueron bastante altos y podrían ser preocupantes. Se examinan estrategias para reducir la endogamia a corto y mediano plazo.

Palabras clave: Ganado bovino Somba – Superovulación – Transferencia de embriones – Mejora genética – Endogamia – Benin – Togo.

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