

The maintenance of genetic diversity in a local cattle breed through optimum contribution selection

Nadia Guzzo¹, Cristina Sartori^{2*}, Enrico Mancin², Roberto Mantovani²

¹ University of Padova, Department of Comparative Biomedicine and Food Science, Viale dell'Università 16, 35020 Legnaro (PD), Italy

² University of Padova, Department of Agronomy, Food, Natural resources, Animals and Environment, Viale dell'Università 16, 35020 Legnaro (PD), Italy



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The present study aimed to evaluate the effects of optimum contribution selection (OCS) in a small native cattle breed. In practical animal breeding, the genetic improvement is often accompanied by an increase of inbreeding level due to the preferential use of closely related animals, particularly in small populations. This may lead to a reduction of genetic variability and to detrimental effects on some traits. The OCS maximizes the genetic merit of newborns while putting a restriction on the average relationship of the current generation. Despite the benefits, OCS has not been widely applied in practical breeding plans yet. This study considered the effects of OCS in the dual-purpose Rendena cattle, by applying different penalties to the average relationship of current generation (from 0 to -100,000). The OCS was applied on the candidate bull-dams and bull-sires for the years 2014 to 2019, and compared with simulations of random mating, traditional selection and mating system used by the breeders association. Considering the mating of 2014 and 2015, OCS allowed to obtain a predicted offspring with lower genetic merit than in traditional selection, but also with a lower inbreeding. When OCS was routinely introduced in the breed, in 2016, a reduction in genetic merit but also a consistent reduction in the average relatedness and inbreeding rate were observed. Subsequent years showed the actual effects of the OCS program: after the introduction of the optimization, the inbreeding rate did not increase over years. Moreover, the traditional mating system results were suboptimal in respect to OCS simulations. The study confirmed the benefit of OCS as effective tool for long-term preservation of small local breeds under selection, which is important for biodiversity and sustainable use of the genetic resources.

Keywords: optimal contribution selection, native cattle, small population, inbreeding, Rendena

1 Introduction

The practice of maximizing the genetic gain without accounting for the increase in inbreeding rate (ΔF) was recognized in middle 1990s as a threat to livestock breeding. Inbreeding depression is expressed as reduced fitness (fertility, longevity) as well as the phenotypic expression of lethal alleles (Leroy, 2014). Management of the ΔF and the chances for its reduction have been widely investigated. Over time, optimum contribution selection (OCS) has been identified as the best choice to maximize the genetic gain while restricting the ΔF (Meuwissen, 1997; Kohl et al., 2020). Several authors have confirmed the superiority of OCS over truncation selection (e.g., Sonesson and Meuwissen, 2000; Gandini et al., 2014). In the last decades, various OCS selection methods have been developed, introducing, e.g., a penalty for inbreeding, or maintaining a pre-defined ΔF , or allowing a simultaneous management of the genetic gain, ΔF and introgressed genetic material (e.g., Wray and Goddard, 1994; Meuwissen, 1997; Wellmann et al., 2012).

* **Corresponding Author:** Cristina Sartori. Department of Agronomy, Food, Natural resources, Animals and Environment (DAFNAE), University of Padova, Viale dell'Università 16, 35020 Legnaro (PD), Italy. E-mail: cristina.sartori@unipd.it. ORCID: <http://orcid.org/0000-0002-2091-2280>

Nowadays, the OCS is routinely applied in an increasing number of livestock species such as sheep, horse and pigs (Gourdine et al., 2012; Kjetså, 2016; Kettunen and Berg, 2017), due to its efficacy in terms of counteracting the increasing ΔF . About cattle, the application of OCS has been investigated both in highly specialized cosmopolitan breeds, like Holstein (Sørensen et al., 2008), and in small local populations, like German Angler and Vorderwald cattle (Wang et al., 2017). The first applications of OCS were done in northern countries (e.g., in Denmark; Sørensen et al., 2008), but this practice has received an increased interest worldwide (Biscarini et al., 2015). Also, an increasing number of programs aimed at optimizing the mating and maintaining the genetic diversity have been developed over years (e.g., Berg et al., 2006; Gorjanc and Hickey, 2018; Kohl et al., 2020), also introducing the possibility to account for genomic information (Clark et al., 2013).

The use of OCS for routinely breeding plans can be of main importance in small local breeds under selection, often showing a limited effective population size and therefore a pretty high ΔF (Gandini et al., 2014). Nevertheless, the introduction of OCS in breeding plans is just at its beginning in many contexts, such as in local cattle breeds of Italy. Among Italian cattle, OCS has been recently introduced for mating plans of Valdostana cattle, Rendena, Alpine Grey, and Reggiana. In most of the other breeds, a great attention is paid to avoid mating among relatives, but without realizing an optimum selection policy, and therefore theoretically falling under the so called "frontier line". This line represents the OCS realizing when different penalties for the increase in average relationship (ar) of candidates, and therefore of the predicted ΔF , are considered. Moving from these considerations, the present study aimed to evaluate the application of OCS in Rendena local cattle breed, considering some years of transition from traditional selection method to OCS. Specifically, OCS was evaluated on candidate bull-dams and bull-sires for the years 2014 to 2019, in comparison with: i) random mating and ii) the traditional selection method (assignment of a given mating percentage to each bull-sire).

2 Material and methods

2.1 Rendena local breed

Rendena cattle is a rustic breed native from Rendena Valley (Trento Province, Italy) and currently reared both in plains and in alpine mountain farms (Guzzo et al., 2018). This breed shows a great adaptation to harsh environment such as alpine pastures and marginal mountain areas, and its rusticity confers to the breed appreciable levels of fertility and longevity. Rendena is a dual-purpose breed (milk and meat), with a selective preference for milk. Indeed, the current selection index (ILQCM) includes milk quality (65% of economic weight), udder conformation (10%), muscularity (10%), average daily gain (4.5%), and *in vivo* carcass evaluation (10.5%) (Sartori et al., 2018). Most of milk produced by this breed is converted into typical Sprezza and Grana Padano cheeses. The selection process has been always carried out considering the risk of inbreeding. In fact, the traditional genetic improvement aims to minimize ΔF by avoiding mating between relatives up to the third generation. Optimum contribution selection was introduced in 2016 after a couple of years of study. The current population size, updated at 2018, comprises 6,842 animals, including 37 bulls and 3,619 cows, and the local risk status reported in the FAO database is "vulnerable" (www.fao.org/dad-is/).

2.2 Data

The pedigree of Rendena breed from 1952 to 2019, including 58,933 animals, was provided by the National Breeders Association of the Rendena breed (ANARE, Trento, Italy). The candidate bull-sires (minimum $n=16$ /year) and bull-dams (minimum $n=350$ /year) for the years 2014 to 2019 were considered for calculating optimal mating plans using an OCS algorithm. These years were selected since they showed the transition from traditional method to OCS in the breed. The individual genetic merit (EBV) for the ILQCM of the candidate bull-sires and bull-dams were calculated in collaboration with ANARE separately for each target year and merged from time to time to the pedigree of the breed. Therefore, 6 datasets were built from the pedigree and used for analysis. The number of candidate bull-sires and bull-dams, as well as the number of individuals in pedigree and the average EBV of bull-sires for each target year is reported in Table 1.

2.3 Optimum contribution selection (OCS) analysis

For each target year, that is, from 2014 to 2019, individual inbreeding was calculated following a traditional algorithm (Meuwissen and Luo, 1992) implemented in the software EVA, v. 3.0 (Berg et al., 2006). Additionally, a comparison of annual average EBV and ar for the newborns of each target year was obtained by applying an OCS algorithm in EVA. By applying an evolutionary algorithm, this software is able to describe inbreeding in a population and to predict the genetic contribution to

maximize response to selection. This is done giving either a penalty on ΔF or on ar , this last option used in the present study. Specifically, the response to selection is maximized by assigning a penalty weight (w) on the ar of candidate parents (inbreeding is half the relationship between parents). Weights may be changed depending on the desired restrictions on inbreeding: the higher the penalty (e.g., $w = -100,000$), the less related are the animals chosen for mating. An amount of 15 different penalties on ar were applied for realising the OCS of each target year ($w = 0; -5; -10; -25; -50; -75; -100; -250; -500; -750; -1,000; -2,500; -5,000; -10,000; -100,000$). As additional constraint, a maximum number of mating was allowed for each candidate bull-sires, i.e., a maximum 10% of bull-dams bred by each bull-sire. In addition, annual average EBV and ar for the new-borns were calculated by assuming a situation of random mating that is a full conservation policy. Moreover, the traditional selection method was also considered, i.e., to avoid mating between relatives up to the third generation and to account for the number of mating decided by ANARE for each bull-sire. All the combinations of EBV and ar were reported in graph representing the decision space on short term (Berg et al., 2006).

Table 1 Number of bull-sires and bull-dams considered in the study, and pedigree size by target year. The number of bulls that were used only in the target year is also reported in parentheses, as well as the average genetic merit (EBV) of bull sires \pm standard deviation, and the percentage of use of bull-sires in the traditional selection method of the national breeders association (ANARE)

Year	Bull-sires	EBV bull sires	% use, traditional method	Bull-dams	Pedigree
2014	16 (16) ¹	1278.1 \pm 130.4	6.25 (5 to 10)	358	51,511
2015	18 (14)	1332.7 \pm 107.2	5.56 (5 to 10)	359	52,913
2016	16 (8)	1225.3 \pm 116.5	6.25 (5 to 10)	350	54,281
2017	16 (10)	1242.6 \pm 96.4	6.25 (5 to 10)	350	55,817
2018	16 (11)	1109.3 \pm 126.2	6.25 (5 to 10)	350	57,338
2019	20 (12)	1132.9 \pm 101	5 (5 to 5)	350	58,932

¹Information on bull-sires before 2014 that could be shared with bull sires of 2014 was not available

3 Results and discussion

3.1 Descriptive statistics and inbreeding information

An average of 17 bulls/year were used in the study (Table 1) and about 64% were used as sires only in the target year (this calculation was done excluding bulls of 2014 since we did not have information about previous years). A slight decrease in the average EBV of bull sires was observed over years. In the traditional selection method of ANARE, considered in the current study to calculate the annual average EBV and ar for the newborns, each bull sired from 5% to 10% of the bull-dams available for each target year (353 dams/year), for an average of 21 mating for each bull-sire.

The percentage of inbred animals in pedigree for each target year, as well as the average and the maximum inbreeding values for individuals in the pedigree are reported in Table 2.

Table 2 Pedigree inbreeding (average level by year, and percentage of inbred animals), and average relationships among bull-sires and bull-dams (excluding the ones with themselves)

Year	Pedigree inbreeding (F)		Average relationships of bull-sires and bull-dams			
	Inbred animals (%)	Average F ¹	Males-males	Males-females	Females-females	Average SD
2014	69.7	0.026	0.151	0.145	0.141	0.018
2015	71.4	0.027	0.159	0.158	0.151	0.017
2016	66.2	0.026	0.149	0.154	0.152	0.017
2017	66.9	0.027	0.159	0.159	0.149	0.017
2018	67.6	0.028	0.168	0.165	0.157	0.019
2019	68.2	0.029	0.171	0.166	0.158	0.020
Average	68.3	0.027	0.160	0.158	0.151	0.018

¹In all the target years, the maximum level of inbreeding was 0.375; SD – standard deviation

On average, the inbreeding in the Rendena breed was 0.027, and 68.3% of individuals in the pedigree were inbred. Table 2 also reports the ar occurring among the bull-sires and bull-dams, with higher values (of about 0.01) for relationships within the bull-sires group than within the bull-dams.

3.2 Optimum contribution selection (OCS) analysis

Figure 1 to 4 report the results of the OCS simulation applied to candidate bull-sires and bull-dams of Rendena breed from 2014 to 2019, as well as some results about the simulation of a random mating among candidates and of the mating obtained using the same selection criteria applied by ANARE in each target year.

Figure 1 shows the number of bulls used for the OCS simulation in each target year. From 10 to 15 candidate bull-sires were used for breeding over years, depending on the penalty for the ar of candidate bull-sires and bull-dams applied. When inbreeding was not considered ($w = 0$), and the mating was decided only looking at EBV of the parents, just 10 sires were chosen in each year by OCS simulation to optimize the breeding decisions. The number of bulls increased when the importance (“penalty”) of inbreeding increased. In years 2014 and 2016 just 12 bulls were used for OCS at the strongest penalty for inbreeding, likely due to the fact that the ar among bull-sires and between bull-sires and bull-dams were the lowest in the target years (Table 2). Contrariwise, the years with the highest values of ar (2018 and 2019) required a greatest number of bull-sires (15) for the optimization. Over years, the ar increased, and therefore also the number of bull-sires required to minimize the increase in inbreeding.

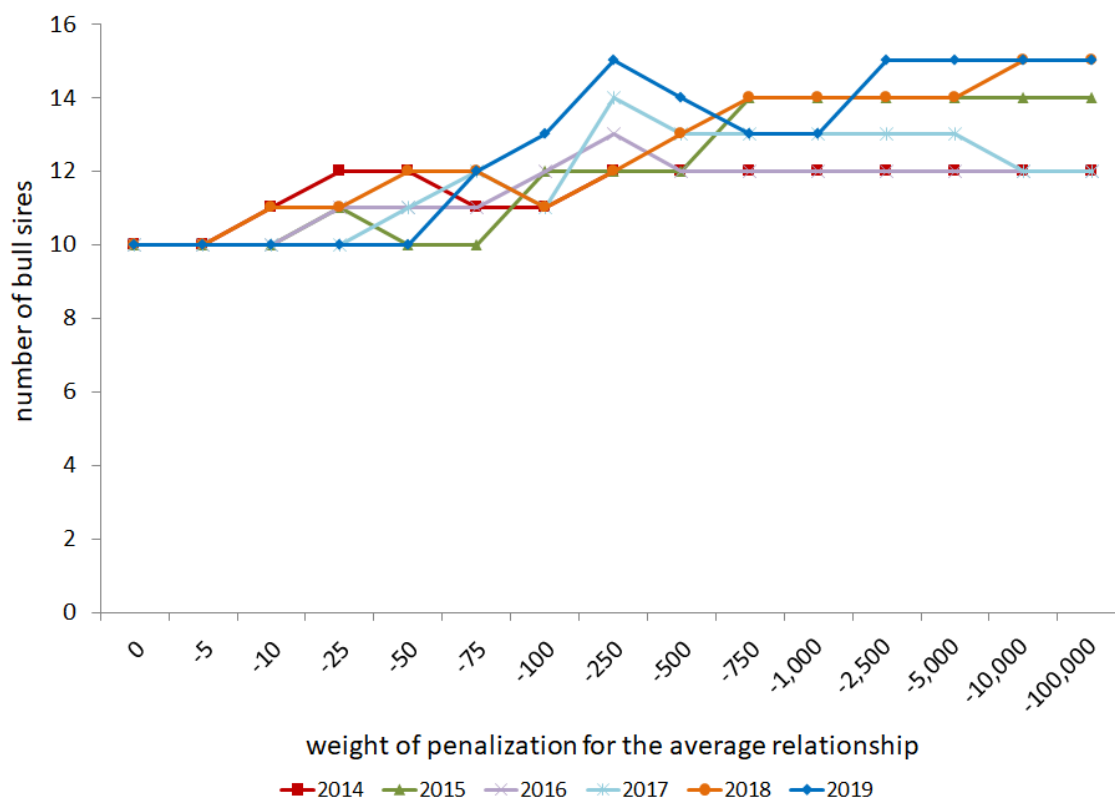


Figure 1 Number of bulls used for optimum contribution selection simulation in the target years, depending on the different weight of penalization (from 0 to -100,000, the latter being the strongest penalty) for the average relationship of bull-sires and bull-dams

The relationship between the variation of the EBV and ar of bull-sires and bull-dams under different penalties w for the ar by year is depicted in Figure 2. Here, for each target year the so called “frontier line” for OCS decision has been drawn looking at the coordinate pairs of EBV and ar for the different w applied. Moving from the weakest ($w = 0$) to the strongest penalty ($w = -100,000$) for ar , both EBV and ar decreased following the path of the frontier line. When breeding decisions are made, if the

coordinates of EBV and ar are on the frontier line, then optimization of mating has occurred (with different importance for inbreeding). Otherwise, if the coordinates of EBV and ar fall under this frontier line (it is not possible to fall over), then suboptimal values for the mating occur (Berg et al., 2006). Figure 2 shows that all the random mating that occurred in target years are under the frontier line (and therefore are suboptimal choice), as well as the mating decisions taken by applying the same percentages for the use of bull-sires that ANARE establishes each year. It is possible to note that the routinely decisions of ANARE have produced nearly the same coordinates of the random mating. Looking at the values obtained in different years using all the mating criteria considered (OCS, random mating and ANARE decisions), a tendency to an increase of ar has been observed over time, even if with different magnitudes.

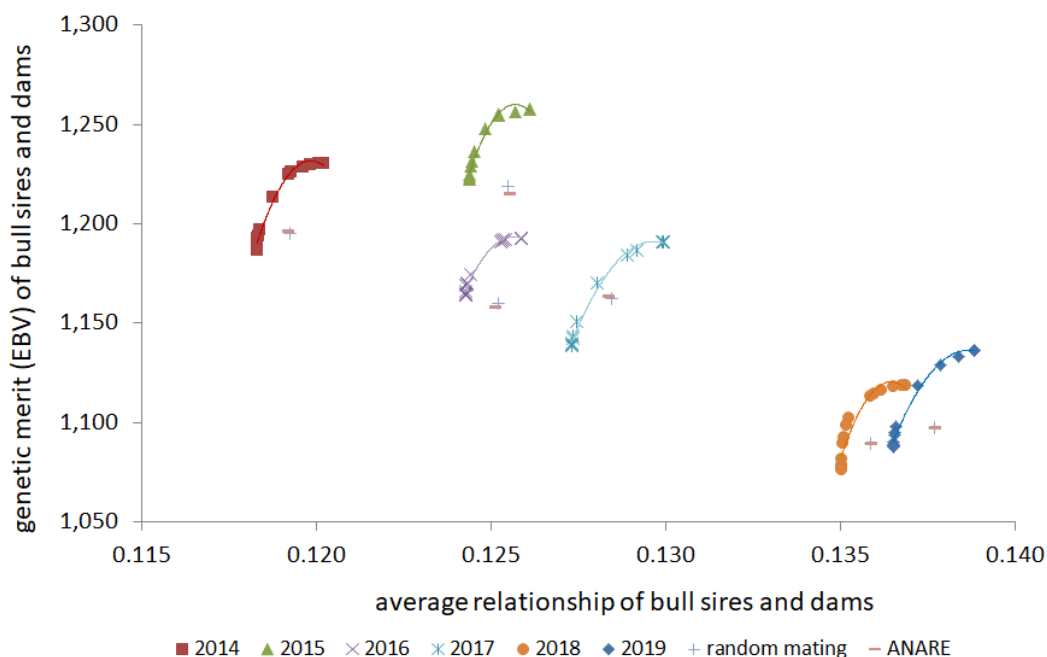


Figure 2 The “frontier line” obtained by the average relationship among bull-sires and bull-dams and the genetic merit (EBV) of bull-sires and bull-dams obtained for each target year by applying different penalties for the average relationship using the optimum contribution selection algorithm. The average relationship and the EBV obtained under random mating and following the traditional criteria of the national breeders association (ANARE) are also reported

The 2014 and 2015 were the first years in which the possibility of introducing OCS in Rendena was studied, but it was not applied in practice, and it is possible to note, from the first year to the second, higher values of both EBV and ar . In 2016 the OCS was introduced in mating plans, and in this year the average EBV decreased, and the ar did not increase (and therefore the inbreeding level), showing even slightly lower values than in 2015. In 2017, when OCS was used for mating, ar increased respect to 2016 but less than from 2014 to 2015; there was also a slight increase in average EBV. In 2018 a noteworthy increase of the ar among candidates was observed (Table 2), and so the frontier line also showed noteworthy higher values for ar and lower values for EBV respect to the previous year. This increase in the ar could be due to the fact that in 2018 the performance test for selecting the new candidate bulls was not realized, and the candidate bull-sires were chosen among the already proved young bulls, falling to choose on average more related individuals. Finally, in 2018 both ar and EBV slightly increased, but less than without applying an OCS in practice, as in 2014 and 2015.

Figure 3 shows the variation of the predicted average inbreeding of the newborns in target years under the different penalties for ar considered in the study. On its whole, predicted inbreeding varied from 0.0503 to 0.0623. Moving from the weakest to the strongest penalization for ar , the predicted inbreeding decreased, up to becoming roughly constant from a value of $w = -500$. Over years the predicted inbreeding increased, apart in 2016 that was when OCS was introduced as routinely criterion for mating choices in Rendena. Despite the noteworthy increase of ar in 2018 (Figure 2), the predicted inbreeding was pretty close to the values of 2017 and 2019. Figure 3 also reports the predicted ΔF using the selection criteria of ANARE in the target years. It is possible to note that

inbreeding always increased over years (from 0.0516 in 2014 to 0.0589 in 2019) and were close to the values found at intermediate levels of w using OCS.

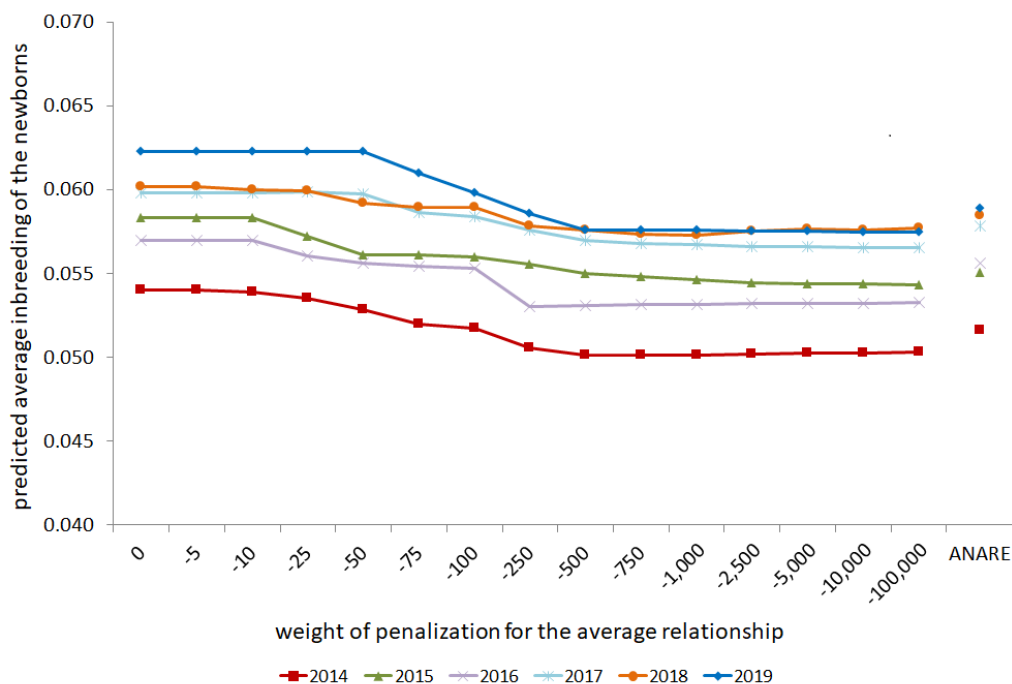


Figure 3 Predicted average inbreeding of the newborns obtained for each target year by applying a different penalty weight for the average relationship (from 0 to -100,000, the latter being the strongest penalty) of bull-sires and bull-dams, and by using the same criteria of the national breeders association (ANARE)

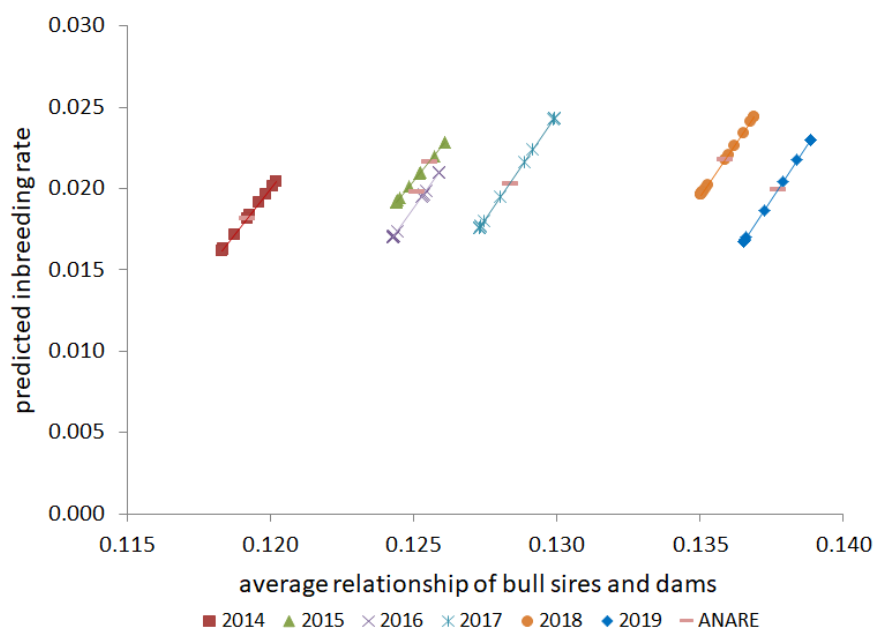


Figure 4 Average relationship among bull-sires and bull-dams and predicted rate of inbreeding in target years, obtained by applying different penalties for the average relationship using the optimum contribution selection algorithm, and by using the mating criteria of the national breeders association (ANARE)

Finally, Figure 4 shows the linear relationship between the ar of bull-sires and bull-dams and the predicted ΔF : increasing ar (that is, by reducing the penalization) resulted in ΔF increase, meaning that if ar increases by 1%, the ΔF increases by 2.46% (data not shown). Over years, after the introduction of the OCS in routinely practices (2016), the predicted ΔF did not increase over time under different penalization (Figure 4). The average value of the predicted ΔF increased indeed from 0.0178 in 2014 to 0.0205 in 2015, to remain around this average value in the subsequent years. Interestingly, higher values of ar were observed in 2019 under OCS respect to the previous year, but correspondingly ΔF was on average lower. Following the mating criteria of ANARE, ΔF increased since 2014 ($\Delta F = 0.018$), but in 2016 slightly decreased, as ar , after the routinely introduction of OCS, and in 2019 it was lower ($\Delta F = 0.02$) than in the previous year.

3.3 Discussion

The present study aimed to investigate how the EBV and ΔF changes depending on the penalization to assign to the average relationship among individuals, and therefore to inbreeding, when mating is planned. We considered the extreme situations of assigning no importance to inbreeding ($w = 0$) and of assigning maximum importance to inbreeding ($w = -100,000$), as in conservation policies. Obviously, the best choice for a breed under genetic improvement is to follow something in between, by choosing an intermediate weight for the penalization (e.g., $w = 100$), thus still realizing optimization.

The present study has shown as the OCS is able to provide better results in terms of EBV and ar of offspring respect to not-optimized mating choice, even if a breeder association pay attention to avoid mating among relatives. The introduction of OCS in Rendena breed has led to a reduction of the ar and ΔF of the newborns as soon as it was introduced, and has allowed maintaining the increase in inbreeding level a bit lower as it was realized without optimization. The OCS also allowed increasing the EBV, even if the immediate consequence of its introduction is to reduce the EBV of the newborns respect to the previous years in which optimization was not accounted for. However, this was expected, and in a medium-term perspective, EBV is still able to increase. Surely a long-term study considering many years of routine application of OCS could provide more interesting findings.

Another aspect that could be of interest but it has not be considered in the present study, is the investigation of OCS in the whole population, and not only in bull-sires and bull-dams, since the effectiveness of a breeding program should be measured in the whole population in which it is applied. The suggested mating for the whole population has been routinely published on the website of ANARE since 2017 (<http://www.anare.it/pagina/?82>). Similar information is also provided by the National Breeders Association of Valdostana cattle (<https://www.anaborava.it/servizinew.html>) and Alpine Grey (<http://www.grigioalpina.it/servizi/piani-di-accoppiamento/>). In all cases, suggested mating is provided both for candidate bull-sires and bull-dams and also for the whole population, and an evaluation of its effects in a medium-term perspective is thus feasible.

Looking at literature, one of the first application of the "frontier line" for OCS was shown by Sørensen et al. (2008) in Danish Holstein cattle. Here, different penalties for ar were applied ($w = 0$ to $-1,000$) in datasets differing for their completeness in inbreeding information. For each dataset, decreasing average EBVs but also decreasing average ar were found moving from the weakest to the strongest penalty for ar . Greater ar were also found in pedigrees with more complete information. The frontier line was also used by Henryon et al. (2015) to compare the short-term ΔF realized by breeding schemes using OCS with different kinds of biological or logical restrictions with the frontier line for OCS without restrictions (plotted using inbreeding instead of ar). Some of the restricted breeding schemes were able to overlap the frontier line representing optimization. The study was performed on simulated data and mimicking the typical breeding schemes of pigs. Considerations on the long-term response to selection were also provided. An application of OCS using penalties for ar was done on the small Sahiwal cow population in Kenya (Mwangi et al., 2020). Results showed that the current breeding nucleus should be expanded to prevent the ΔF per generation being higher than 1%. Different penalties were applied to the ΔF instead of ar to evaluate the feasibility of OCS in some horse populations, e.g. the Norwegian and North-Swedish cold-blooded trotters (Olsen et al., 2012) and Menorca horse (Solé et al., 2013). In pretty large populations, as Norwegian and North-Swedish trotters, the application of OCS allowed to select the best sires for optimal mating among the whole horse population. In local endangered population like Menorca horse, OCS was demonstrated to be a feasible approach to improve traits while maintaining the ΔF at an acceptable level, instead of applying a conservation policy only. A comparison of the results of an OCS theoretical scenario versus the real mating performed in a target year was done for Franches-Montagnes Swiss local horse (Hasler et al., 2011). When OCS was applied, lower inbreeding coefficients and ar , and increased EBV were found respect to the real situation. Specific considerations about how to apply OCS have to be done looking

at the specific characteristics, genetic variability and population history of each target breed. In a local cattle breed of small size but being not currently at high risk, the OCS may be surely a good approach to ensure genetic improvement by maintaining the genetic variability of the population.

4 Conclusions

This study has considered the implementation of optimum contribution selection in the small local Rendena cattle breed looking at the mating plans of bull-sires and bull-dams, and considering the simulations of OCS with different penalties for the *ar* of candidates and thus for the ΔF in a period of 6 years, during which OCS was routinely introduced in the breeding practice of the breed. The study has shown that OCS allows a maximization of genetic gain with a target restriction in inbreeding, in terms of better performances than those of random mating and traditional mating choice of the breeders organization. In a long-term period, OCS could be an effective tool for preserving local breeds under genetic improvement, as Rendena. This is important for maintaining biodiversity and for a sustainable use of the animal genetic resources.

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References

Berg, P., Nielsen, J. and Sørensen, M. K. (2006). EVA: Realized and predicted optimal genetic contributions. In Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Minas Gerais, Brazil, 13-18 August, 2006 (pp. 27-09). <http://www.wcgalp8.org.br>

Biscarini, F. et al. (2015). Challenges and opportunities in genetic improvement of local livestock breeds. *Frontiers in Genetics*, 6, 33. <https://doi.org/10.3389/fgene.2015.00033>

Clark, S. A. et al. (2013). The effect of genomic information on optimal contribution selection in livestock breeding programs. *Genetics Selection Evolution*, 45(1), 44. <https://doi.org/10.1186/1297-9686-45-44>

Gandini, G. et al. (2014). Selection with inbreeding control in simulated young bull schemes for local dairy cattle breeds. *Journal of Dairy Science*, 97(3), 1790-1798. <https://doi.org/10.3168/jds.2013-7184>

Gorjanc, G. and Hickey, J. M. (2018). AlphaMate: a program for optimizing selection, maintenance of diversity and mate allocation in breeding programs. *Bioinformatics*, 34(19), 3408-3411. <https://doi.org/10.1093/bioinformatics/bty375>

Gourdine, J. L., Sørensen A. C. and Rydhmer, L. (2012). There is room for selection in a small local pig breed when using optimum contribution selection: a simulation study. *Journal of Animal Science*, 90(1), 76-84. <https://doi.org/10.2527/jas.2011-3898>

Guzzo, N., Sartori, C. and Mantovani, R. (2018). Heterogeneity of variance for milk, fat and protein yield in small cattle populations: The Rendena breed as a case study. *Livestock Science*, 213, 54-60. <https://doi.org/10.1016/j.livsci.2018.05.002>

Hasler, H. et al. (2011). Genetic diversity in an indigenous horse breed—implications for mating strategies and the control of future inbreeding. *Journal of Animal Breeding and Genetics*, 128(5), 394-406. <https://doi.org/10.1111/j.1439-0388.2011.00932.x>

Henryon, M. et al. (2015). Most of the long-term genetic gain from optimum-contribution selection can be realised with restrictions imposed during optimisation. *Genetics Selection Evolution*, 47(1), 21. <https://doi.org/10.1186/s12711-015-0107-7>

Kjetså, M. H. (2016). Optimal Contribution Selection Applied to the Norwegian Cheviot Sheep Population. Master's thesis, Norwegian University of Life Sciences, Ås, 2016. <http://hdl.handle.net/11250/2399694>

Kettunen, A. and Berg, P. (2017). Faroese Horse: Population status & conservation possibilities. [urn:nbn:se:norden:org:diva-5822](http://nbn:se:norden:org:diva-5822)

Kohl, S., Wellmann, R. and Herold, P. (2020). Advanced optimum contribution selection as a tool to improve regional cattle breeds: a feasibility study for Vorderwald cattle. *Animal*, 14(1), 1-12. <https://doi.org/10.1017/S1751731119001484>

Leroy, G. (2014). Inbreeding depression in livestock species: review and meta-analysis. *Animal Genetics*, 45(5), 618-628. <https://doi.org/10.1111/age.12178>

- Meuwissen, T. H. E. (1997). Maximizing the response of selection with a predefined rate of inbreeding. *Journal of Animal Science*, 75(4), 934-940. <https://doi.org/10.2527/1997.754934x>
- Meuwissen, T. H. E. and Luo, Z. (1992). Computing inbreeding coefficients in large populations. *Genetics Selection Evolution*, 24(4), 1-9. <https://doi.org/10.1186/1297-9686-24-4-305>
- Mwangi, S. I. et al. (2020). Effect of controlling future rate of inbreeding on expected genetic gain and genetic variability in small livestock populations. *Animal Production Science*. <https://doi.org/10.1071/AN19123>
- Olsen, H. F., Meuwissen, T. and Klemetsdal, G. (2013). Optimal contribution selection applied to the Norwegian and the North-Swedish cold-blooded trotter—a feasibility study. *Journal of Animal Breeding and Genetics*, 130(3), 170-177. <https://doi.org/10.1111/j.1439-0388.2012.01005.x>
- Sartori, C. et al. (2018). Genetic correlations among milk yield, morphology, performance test traits and somatic cells in dual-purpose Rendena breed. *Animal*, 12(5), 906-914. <https://doi.org/10.1017/S1751731117002543>
- Solé, M. et al. (2013). Implementation of Optimum Contributions Selection in endangered local breeds: the case of the Menorca Horse population. *Journal of Animal Breeding and Genetics*, 130(3), 218-226. <https://doi.org/10.1111/jbg.12023>
- Sonesson, A. K. and Meuwissen, T. H. (2000). Mating schemes for optimum contribution selection with constrained rates of inbreeding. *Genetics Selection Evolution*, 32(3), 231-248. <https://doi.org/10.1051/gse:2000116>
- Sørensen, M. K. et al. (2008). Optimal genetic contribution selection in Danish Holstein depends on pedigree quality. *Livestock Science*, 118(3), 212-222. <https://doi.org/10.1016/j.livsci.2008.01.027>
- Wang, Y., Bennewitz, J. and Wellmann, R. (2017). Novel optimum contribution selection methods accounting for conflicting objectives in breeding programs for livestock breeds with historical migration. *Genetics Selection Evolution*, 49(1), 45. <https://doi.org/10.1186/s12711-017-0320-7>
- Wellmann, R., Hartwig, S. and Bennewitz, J. (2012). Optimum contribution selection for conserved populations with historic migration. *Genetics Selection Evolution*, 44(1), 34. <https://doi.org/10.1186/1297-9686-44-34>
- Wray, N. R. and Goddard, M. E. (1994). Increasing long-term response to selection. *Genetics Selection Evolution*, 26(5), 1-21. <https://doi.org/10.1186/1297-9686-26-5-431>