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Most of the long-term genetic gains from optimum-contribution selection can be realised with restrictions imposed

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ABSTRACT: We reasoned that optimum-contribution selection (OCS) with restrictions imposed during optimisation will realise most of the long-term genetic gains realised by OCS without restrictions. We used stochastic simulation to estimate long-term rates of genetic gain realised by breeding schemes using OCS without and with restrictions imposed during optimisation. In all but a few exceptions, the long-term rates of genetic gain realised by OCS with restrictions was 95-100% of the rates realised by OCS without restrictions. It was only when the restrictions became overly strict that we began to lose gain. We also present evidence from the Danish pig-breeding scheme for Duroc that practical implementation of OCS with restrictions increases genetic gains and decreases rates of inbreeding. OCS has gone from a selection method that was difficult to apply in practice, to one that is readily applicable to most breeding schemes.
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Introduction

Optimum-contribution selection (OCS) can be difficult to implement in practical breeding schemes. The main reason is that the optimum number of matings, as defined by OCS, cannot be allocated to all of the selection candidates because of biological and logistical restrictions. One way to make OCS more practical is to impose restrictions on OCS during optimisation. Not only would this make OCS decisions readily applicable to individual breeding schemes, it may even realise most, if not all, of the long-term genetic gains realised by OCS without restrictions for two reasons. First, in most OCS-analyses, there are many ways to allocate matings to the selection candidates (i.e., many possible solutions in the parameter space) (Kinghorn (2011)). It is likely that many solutions lie at, or near, the optimum solution. Imposing restrictions on OCS merely removes some of the solutions from the parameter space, so solutions can still exist near the optimal solution. Second, OCS is able to correct for selection decisions made at earlier times. It does so by taking into accounting that some selection candidates and ancestral animals have already generated offspring (Meuwissen and Sonesson (1998); Grundy et al. (2000)). Based on this line of reasoning, we hypothesised that OCS with restrictions imposed during optimisation will realise most of the long-term genetic gains realised by OCS without restrictions. We tested this hypothesis by stochastic simulation of breeding schemes that resembled those used for pigs. We also present estimated trends of genetic gain and inbreeding realised before and after OCS with restrictions was implemented in the Danish pig-breeding scheme for Duroc.

Materials and Methods

Simulation. We used stochastic simulation to estimate long-term rates of genetic gain realised by OCS without and with restrictions imposed during optimisation. We did this by simulating breeding schemes that loosely resembled those used for pigs. We also simulated two schemes with truncation selection. In all schemes, BLUP-breeding values were used as the indicator of genetic merit.

The breeding scheme that applied OCS without restrictions was *unrestricted OCS*. A total of 300 matings were allocated to approximately 2250 male and 2250 female selection candidates by OCS to generate a new cohort of animals. Males were candidates for selection from times t_i+3 to t_i+5, where t_i is the birth time of the *i*th animal and each time represents a female reproductive cycle. There was no upper limit for the number of matings that could be allocated to each male. Females were candidates from times t_i+4 to t_i+6. Females could not be allocated more than one mating at each time (i.e., 0 or 1 mating per female).

OCS was carried out by applying a penalty to the average relationship of the current generation, which included the new cohort (Sørensen et al. (2008)). The average relationship was calculated using an additive-relationship matrix that included male and female selection candidates, immature offspring that were too young to be candidates for selection, and all ancestors traced back from these animals. The penalties applied were 5, 10, 20, 50, 100, 200, 500, 1000, and 5000. The 300 sire and dam matings were paired randomly. Each dam produced five offspring, resulting in 300 full-sib families and 1500 offspring. Offspring were assigned as males and females with a probability of 0.5.

Restrictions imposed on *unrestricted OCS* were:

- *Unrestricted OCS of sires*. OCS was only applied to male candidates. Females were truncation selected. A total of 300 dams were truncation selected at each time and each selected dam was allocated one mating. OCS of sires was carried out with an additive-relationship matrix that included male selection candidates, truncation-selected dams, immature offspring, and all ancestral animals traced back from these animals.

- *Dams unknown*. As for *unrestricted OCS of sires* with the added restriction that truncation-selected dams were not included in the additive-relationship matrix used in OCS of sires.
- *One-chance OCS of sires*. As for *unrestricted OCS of sires* with the added restriction that males were only candidates for OCS at age t_i+3.
- *Pre-selection of sires*. As for *unrestricted OCS of sires* with the added restriction that 0.5, 1, 5, 10, and 25% of the male selection candidates were pre-selected by truncation selection before OCS. Males that were not pre-selected were not candidates for OCS.
- *Sire multiples*. As for *unrestricted OCS of sires* with the added restriction that matings were allocated to male selection candidates in multiples of 5, 10, 20, 50, and 100. For example, when matings were allocated in multiples of 5, sires could only be allocated 0, 5, 10, … , 300 matings.
- *No offspring*. As for *unrestricted OCS of sires* with the added restriction that immature offspring were excluded from the additive-relationship matrix used in OCS of sires. The additive-relationship matrix only included male-selection candidates, truncation-selected dams, and ancestral animals traced back from these animals.
- *Multiple restrictions*. Several of the restrictions were imposed simultaneously, namely *unrestricted OCS of sires*, *dams unknown*, *one-chance OCS of sires*, *pre-selection of sires 5%*, and *sire multiples* 10.

The two schemes with truncation selection were:

- *Truncation selection intense*. Ten sires and 300 dams were truncation selected at each time. Each sire was randomly mated with 30 dams and each dam produced five offspring, resulting in 300 full-sib families and 1500 offspring.
- *Truncation selection less intense*. Sixty sires and 300 dams were truncation selected. Each sire was randomly mated with 5 dams and each dam produced five offspring, resulting in 300 full-sib families and 1500 offspring. This scheme realised similar rates of inbreeding as *unrestricted OCS* at the penalty that maximised long-term genetic gains.

Selection was for a single trait (h^2=0.2) that was observed on all selection candidates prior to selection. The trait was assumed to be normally-distributed and genetically controlled by the infinitesimal model of additive genetic effects.

Schemes were run for 100 time steps (approx. 25 generations). They were initiated by sampling an unrelated base population of 20 sires and 600 dams. In the first 20 time steps, truncation selection was carried out by applying *truncation selection intense*. OCS was applied at times 21,…, 100. Each breeding scheme was replicated 100 times.

The long-term rate of genetic gain presented for each scheme was at the penalty that maximised long-term gains for the trait under selection. Long-term rates of genetic gain were calculated as the linear regression of S_t on t, where S_t is the average true breeding value of animals born in time t (t = 91, … , 100). The rates were scaled by setting to 100 the long-term rates of genetic gain realised by *unrestricted OCS* at the penalty that maximised long-term rate of genetic gain. The scaled rates are presented as means (± s.d.) of the 100 replicates. Differences between the means were tested for significance by Tukey's test assuming variance homogeneity. The *p*-value for significance was 0.05.

The schemes were simulated using ADAM (Pedersen et al. (2009)), the breeding values were predicted by DMU6 (Madsen et al. (2006)), and OCS was carried out by EVA (Berg et al. (2006)).

Practical implication. OCS with restrictions was implemented in the Danish pig-breeding scheme for Duroc. The first pigs from parents selected by OCS were born in January 2013. Pigs born before January 2013 were from parents selected by truncation selection. We present average monthly indices and inbreeding coefficients for pigs born over a six-year period: five years before and one year after OCS was implemented. Rates of genetic gain and inbreeding before and after OCS was implemented were estimated using linear regression.

Results

Simulation. OCS with restrictions imposed during optimisation realised most of the long-term genetic gain realised by OCS without restrictions (Table 1). In all but a few exceptions, the maximum long-term rate of genetic gain realised by OCS with each restriction was 95-100% of the maximum long-term rate of genetic gain realised by *unrestricted OCS* during time steps 91-100. Even *multiple restrictions*, where several restrictions were imposed simultaneously, did not decrease long-term gains significantly. The exceptions were *pre-selection of sires* 0.5%, *sire multiples* 50 and 100, and *no offspring*. Imposing these restrictions realised only 83-92% of the *maximum* long-term rate of genetic gain realised by *unrestricted OCS*.

Truncation selection intense, where 10 sires and 300 dams were truncation selected at each time, realised only 85% of the maximum long-term rate of genetic gain realised by *unrestricted OCS*. *Truncation selection less intense*, where 60 sires and 300 dams were truncation selected, realised 93% of the maximum long-term rate of genetic gain.

Practical implication. The rate of genetic gain increased and the rate of inbreeding fell after OCS with restrictions was implemented in the Danish pig-breeding scheme for Duroc (Figure 1). The rate of genetic gain increased from 1.05 index-units per year for the five-year period before implementation to 1.27 index-units for the year after implementation. The annual rate of inbreeding fell from 0.51 to 0.14%.

Discussion

Our findings supported our hypothesis that OCS with restrictions imposed during optimisation realises most of the long-term genetic gain realised by OCS without restrictions. Realising more than 95% of the long-term genetic gains with most of our restrictions demonstrated that OCS is a robust selection method. This robustness was even evident with *multiple restrictions*, where several restrictions were imposed simultaneously. OCS with restrictions is worthwhile for two reasons. First, it enables OCS to be tailored to individual breeding schemes with the optimum number of matings readily allocable to available selection candidates. Second, breeding schemes using OCS with restrictions were more productive and are probably less prone to risk than truncation selection, the conventional method of selection. It was only when the restrictions became overly strict that we began to lose long-term genetic gain. Breeders must be encouraged by these findings because OCS has gone from a selection method that was difficult to apply in practice, to one that is readily applicable to most breeding schemes. A selection method that can make a major contribution to sustainable breeding schemes is now within reach. Therefore, provided the restrictions are not too strict, most of the benefits of OCS can be realised when restrictions are imposed during optimisation.

It was particularly encouraging to find that genetic gains increased and rate of inbreeding fell after OCS with restrictions was implemented in the Danish pig-breeding scheme for Duroc. These are prerequisites for increases in long-term genetic gains. However, we need to bear in mind that OCS has only been implemented for a year and we do not have direct evidence that OCS with restrictions will increase long-term genetic gains. So, although the initial signs indicate that OCS will increase long-term genetic gains in Duroc, an assessment of the level of increase must remain on hold until direct evidence becomes available.

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Table 1. Long-term rates of genetic gain realised by optimum-contribution selection (OCS) without and with restrictions[¥].

Scheme	Rate
Unrestricted OCS	100.0 ± 10.00
Unrestricted OCS of sires	98.4 ± 9.28
Dams unknown	98.0 ± 7.98
One chance OCS of sires	99.8 ± 8.22
Pre-selection of sires 25%	97.9 ± 9.85
Pre-selection of sires 10%	97.3 ± 8.21
Pre-selection of sires 5%	98.6 ± 7.56
Pre-selection of sires 1%	96.2 ± 9.05
Pre-selection of sires 0.5%	90.4 ± 10.12[*]
Sire multiples 5	98.0 ± 9.39
Sire multiples 10	97.2 ± 8.80
Sire multiples 20	95.0 ± 8.87
Sire multiples 50	91.7 ± 9.74[*]
Sire multiples 100	82.9 ± 12.02[*]
No offspring	89.4 ± 10.48[*]
Multiple restrictions	96.3 ± 9.33
Truncation selection intense	84.7 ± 9.12[*]
Truncation selection less intense	93.4 ± 5.77[*]

[§]Two scenarios with truncation selection are also presented, *truncation selection intense* and *truncation selection less intense*

[¥]Rates are scaled by setting to 100 the maximum long-term rate of genetic gain realised by *unrestricted OCS*

[*]Rates that are significantly different from *unrestricted OCS* (p<0.05)

Figure 1. Average monthly indices and inbreeding coefficients for pigs born before and after OCS with restrictions was implemented in the Danish pig-breeding scheme for Duroc