animal

Advanced optimum contribution selection as a tool to improve regional cattle breeds: a feasibility study for Vorderwald cattle

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In the middle of the 20th century, increasing inbreeding rates were identified as a threat to livestock breeding. Consequences include reduced fertility, fitness and phenotypic expression of lethal alleles. An important step in mitigating this inbreeding was the introduction of optimum contribution selection (OCS). OCS facilitates the simultaneous management of genetic gain and inbreeding rates. However, using a standard OCS methodology for regional breeds with historical introgression for upgrading reasons could lead to reinforced selection on introgressed genetic material since those alleles improve the rate of genetic gain and reduce the average kinship in the population. Consequently, regional breeds may become genetically extinct if a standard OCS approach is used. Thus, the advanced OCS (aOCS) approach takes introgressed genetic material into account. The major goals of this study were to (i) gather key information on the feasibility of aOCS under practical conditions of the actual breeding scheme of Vorderwald cattle, (ii) identify superior strategies for implementing the actual scheme and (iii) examine whether historical breeding decisions to increase genetic gain by introgression from commercial breeds could have been avoided by using aOCS. Stochastic simulations were designed in this study to create populations from the historical gene pool by using aOCS. Simultaneously, all practical constraints of a breeding scheme were met. Thus, the simulated populations were comparable with real data. The annual genetic gain was higher in reality (1.56) than in the simulation scenarios (1.12–1.40). The introgressed genetic material increased to 61.3% in reality but was conserved at a final value of 15.3% (±0.78) across simulations. The classical rate of inbreeding and rate of native inbreeding were constrained to 0.092% on an annual basis. This value is equal to an effective population size of 100. The observed values for rates of inbreeding were 0.082–0.087% and 0.087–0.088% for classical and native kinship, respectively. The corresponding figures in reality were 0.067% and 0.184%, respectively. This study suggests that aOCS is feasible for Vorderwald cattle. Strategies for implementation are identified. Finally, we conclude that historical breeding decisions could have been avoided by using aOCS. The genetic gain would have been reduced by at least 12.2%, but the introgressed genetic material, genetic diversity and native genetic diversity would have been more desirable for a breed under conservation.

Keywords: migrant contribution, native contribution, native kinship, stochastic simulation, regional breed

Implications

Vorderwald cattle have an extremely high proportion of introgressed genetic material (61.3%). The breeding organization of Vorderwald cattle is aware of this characteristic and wants to conserve the remaining native genetic material and consolidate the breed. Economical disadvantages of a breed contribute to its probability of extinction. Thus, advanced OCS seems to be the method of choice to retain native genetic material, genetic diversity and native genetic diversity while achieving a moderate rate of genetic gain to reduce the risk of extinction.

Introduction

In the middle of the 20th century, increasing inbreeding rates (ΔF) were identified as a threat to livestock breeding. The inbreeding rates were almost unsupervised, while the main aim was to maximize the genetic gain (ΔG) in most breeds. Consequences include reduced fertility and fitness as well as phenotypic expression of lethal alleles. Management of the

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ΔF and possibilities for its reduction have been widely discussed. Since its invention, optimum contribution selection (**OCS**) has been the gold standard for maximizing the ΔG while restricting the ΔF to a predefined level (Meuwissen, 1997; Meuwissen and Sonesson, 1998). Several authors have confirmed the superiority of OCS over truncation selection (Sonesson and Meuwissen, 2000; Weigel, 2001; Avendaño et al., 2003; Kearney et al., 2004; Koenig and Simianer, 2006; Gandini et al., 2014). Other authors have shown that introgression from commercial breeds endangers the originality of regional breeds (Hartwig et al., 2014). In breeds with historical introgression, a standard OCS approach would lead to reinforced selection on introgressed alleles since carriers of introgressed alleles are less related to the population and superior in terms of breeding values (Wellmann et al., 2012). Consequently, regional breeds may become genetically extinct if a standard OCS method is used. Thus, Wellmann et al. (2012) developed an advanced OCS (**aOCS**) method. aOCS facilitates the simultaneous management of the ΔG, ΔF, rate of native inbreeding (ΔF_{nat}) (Wellmann et al., 2012) and introgressed genetic material, that is, the migrant contribution (**MC**). In breeds under conservation, the major goals are originality, genetic diversity and uniqueness. At the same time, these breeds have economic disadvantages compared to commercial breeds. However, the profitability of a breed will contribute to its chances of conservation (Meuwissen, 2009). Therefore, aOCS is of great interest for breeds under conservation. Basic research on the appropriate exploitation of aOCS procedures has already been carried out (Wellmann et al., 2012; Wang et al., 2017a and 2017b). Thus, this study will examine the possibilities of implementing aOCS in the actual breeding scheme of Vorderwald cattle, a model population with historical introgression. Our aim was a comparison with real data. Hence, a simulation study was carried out based on a breeding population that was actually available in the past. Advanced OCS was designed to maximize the ΔG under side constraints. A young sire breeding scheme was adopted for stochastic simulations. Similar schemes have been modeled by Gandini et al. (2014). Various annual flows of replacement of proven sires (**FoR** *strategy*) will be examined, assuming that this factor will have an impact on the ΔG (Gandini et al., 2014). Additionally, we tested whether the extent of progeny testing of mature bulls (**PT** *strategy*) impacts the ΔG (Gandini et al., 2014) when applying aOCS. All simulation scenarios were carried out for overlapping generations. The major goals of this study were to (i) gather key information on the feasibility of aOCS under practical conditions of the actual breeding scheme of Vorderwald cattle, (ii) identify a superior *FoR strategy* and *PT strategy* combination that can be used in the actual scheme and (iii) examine whether historical breeding decisions to increase the ΔG by introgression from commercial breeds could have been avoided by using aOCS.

Material and methods

Base population
The raw data set, provided by the State Agency for Spatial Information and Rural Development Baden-Württemberg, consisted of 348 020 individuals with information on sex, breed, date of birth and estimated breeding values (**EBVs**) for the total merit index (**TMI**). In Germany, EBVs are standardized with a mean of 100 and a genetic SD of 12. We processed the raw data set for individuals with known EBVs and at least three equivalent complete generations (MacCluer et al., 1983). Pruning the raw data set for these individuals resulted in a pedigree of 94 457 individuals born between 1938 and 2014. Individuals with an unknown pedigree and born before 1970 were defined as native founders with an MC of 0%. Individuals from foreign breeds or with an unknown pedigree and born after 1970 were defined as migrant founders with an MC of 100%. This assumption is based on the results of Hartwig et al. (2014). The authors' results show that extensive introgression from foreign breeds to Vorderwald cattle started in 1970. After defining native and migrant founders, the MC was calculated with *optiSel* (Wellmann, 2019) for all individuals included in the pedigree. The resulting pedigree was used for population analyses of the real population. To start the simulation process with the breeding population that was available in 1984, the real pedigree was cropped at that point in time.

General simulation process
The simulation process is visualized in Figure 1. Birth cohorts from 1985 to 2014 consisted of 3512 individuals on average. Thus, the simulation process was modeled with 3512 progeny per iteration to create a comparable population. The simulation process was carried out for 30 iterations to reflect 30 years. In Iterations 1 and 2, there was a lack of male descendants for restocking of proven sires (Figure 1). The cropped pedigree included solely proven sires, and the first fictitious male descendants could not be assumed to be mature. Thus, we subdivided the process into two stages. *Stage 1* was carried out for two iterations to create fictitious male descendants. Fictitious males of the first iteration were assumed to be mature in Iteration 3 (Iteration 1 – pregnancy of dam; Iteration 2 – rearing). Hence, *Stage 2* comprised an additional section to visualize the selection of mature bulls and subsequent progeny testing. *Stage 2* was carried out for the 28 missing iterations. Both stages were carried out for overlapping generations. Each step in the iterative simulation procedure will be described in a separate section below (cf. Figure 1).

Sampling of breeding candidates
Each iteration of the simulation process started with the sampling of additional individuals to be labeled as deceased. This process was modeled to facilitate a realistic deployment of females. Sampling depended on an age distribution that reflected the demography of a cattle population and was carried out for discrete birth cohorts of 1 year. Birth cohort B_t
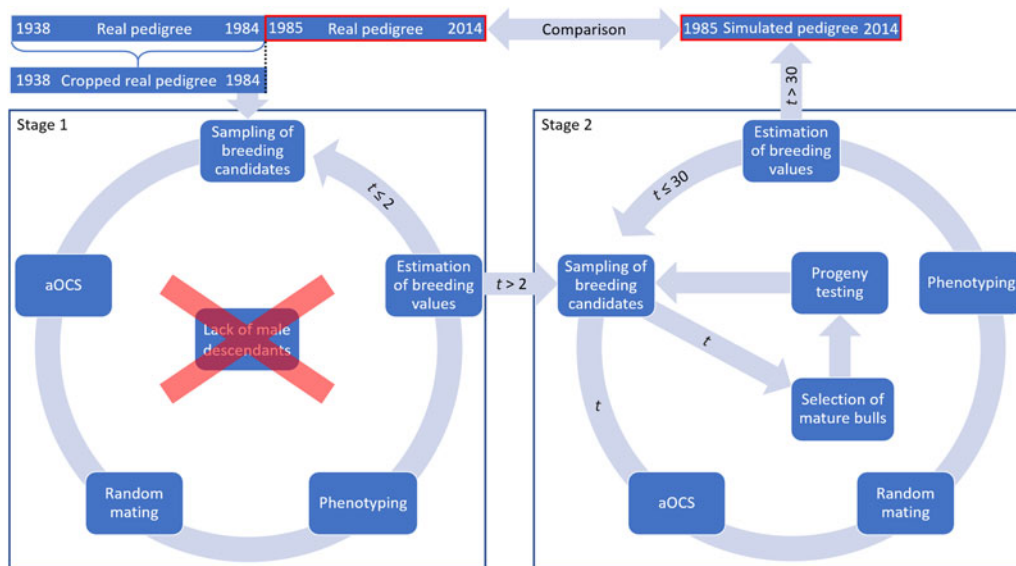
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Figure 1 (Colour online) Schematic structure of the simulation process to create Vorderwald cattle populations comparable to real data – to start the simulation process, the available base population in 1984 was derived by cropping the real pedigree at that point in time. The simulation process was carried out for 30 iterations, equaling 1 year in reality. Thus, a fictitious pedigree was created by using aOCS that was comparable to real data. aOCS=advanced optimum contribution selection.

consisted of all individuals born in the latest iteration t. Sampled living females belonged to birth cohorts $B_t - B_{t-8}$. Subsequently, dams were defined as breeding candidates in birth cohorts $B_{t-1} - B_{t-8}$. Available proven sires belonged to birth cohorts $B_{t-3} - B_{t-14}$, assuming that they were progeny tested and produced semen before deployment in the breeding population.

Advanced optimum contribution selection
Advanced OCS is implemented in the open-source *R package optiSel* (Wellmann, 2019) and allows for simultaneous management of the ΔG, ΔF, ΔF_{nat} and *MC* (Wang *et al.*, 2017a; Wellmann *et al.*, 2012). Advanced OCS was used solely for the selection of proven sires for deployment in the breeding population. The result of an aOCS approach for overlapping generations is a vector c with genetic contributions c_{it} of each individual i to the next birth cohort t. The genetic contribution of each individual i cannot be negative, that is, $c_{it} \geq 0$. This is a general constraint of OCS approaches. As a second constraint, the genetic contributions of each sex equal 0.5 since the proportion of genes of diploid species originates half from sires and half from dams, that is, $c_t's = 0.5$ and $c_t'd = 0.5$, where s and d are vectors indicative of sex (0 / 1). Due to the limited number of progeny per cow and year, the female contributions were forced to be equal, that is, $c_t'd_1 = c_t'd_2 = \ldots = c_t'd_n$. Since we chose a breeding scheme with a substantial amount of natural service (50.2%), the maximum genetic contribution per sire and year was forced not to exceed 0.05, that is, $c_{it} \leq 0.05$. As a result, the aOCS procedure selected at least 10 sires per year (i.e., $c_t's/10 = 0.05$) to satisfy the population under natural mating. According to the absolute number of progeny per birth cohort, a single sire could service a maximum of 351 females on an annual basis ($3512/10 \approx 351$). As an objective

function, aOCS was designed to maximize the ΔG by maximizing $c_{it}'EBV$, where *EBV* is a vector of *EBVs* of selection candidates. The maximization of $c_{it}'EBV$ was performed under constraints. Effective population sizes of 50–100 have been suggested in the literature to keep a breed vital in the long term (Meuwissen, 2009). Thus, we chose an N_e and a native effective population size ($N_{e(nat)}$; (Wellmann, 2019)) of 100 to restrict the ΔF. We calculated the ΔF for overlapping generations per year as

$$\Delta F = \frac{1}{2 * N_e * L} = 0.092\%$$

where L is the generation interval of 5.41 (Hartwig *et al.*, 2013). The first constraint of the aOCS procedure was defined as an upper bound for the average classical kinship in birth cohort $t+1$:

$$ub.classKin_{t+1} = \emptyset classKin + (t - 1983) * \Delta F$$

where $\emptyset classKin$ is the average classical kinship of living individuals in 1984 (0.017), sampled from the age distribution of the simulation process, and t is the year of optimization. We calculated the ΔF_{nat} for overlapping generations per year as

$$\Delta F_{nat} = \frac{1}{2 * N_{e(nat)} * L} = 0.092\%$$

The second constraint of the aOCS procedure was defined as an upper bound for the kinship of native alleles in birth cohort $t+1$:

$$ub.natKin_{t+1} = \emptyset natKin + (t - 1983) * \Delta F_{nat}$$

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where $\emptyset natKin$ is the average kinship of native alleles of living individuals in 1984 (0.019). Based on pedigree data, the MC is the expected percentage of introgressed alleles carried by an individual i. The MC was managed by introducing an additional upper bound for the average MC of the next birth cohort t+1:

$$ub.MC_{t+1} \leq \emptyset MC_t,$$

where $\emptyset MC_t$ is the average MC of breeding candidates in year t. Computation of the genetic parameters MC, $classKin$ and $natKin$ was carried out by $optiSel$. The estimated optimum contributions of sires were allocated randomly across females (cf. Figure 1; 'Random mating') since selection of dams is a key competence of breeders.

Phenotyping

Phenotypes were allocated to females belonging to birth cohort B_{t-2}, assuming a performance test at their first lactation. The phenotype of female i was defined as its true breeding value TBV_i, plus an environmental effect. As the $TBVs$ are unknown in reality, we assumed the $EBVs$ in 1984 to be true ($EBV_{1984} = TBV_{1984}$, where EBV_{1984} is a vector of $EBVs$ of individuals in 1984 and TBV_{1984} is a corresponding vector of $TBVs$):

$$Phenotype_i = TBV_i + E_i$$

The environmental effect followed a normal distribution:

$$E_i \sim N\left(0, VA_t * \left(\frac{1-h^2}{h^2}\right)\right)$$

with VA_t being the additive genetic variance assessed through the mean inbreeding of the population at time t ($\emptyset Ft$):

$$VA_t = \emptyset F_t * 12^2$$

Vorderwald cattle are a dual-purpose breed with an emphasis on milk yield and fitness. The actual breeding objective comprises performance traits, equaling 44%, 44% and 12% for milk yield, fitness and meat production, respectively. According to documentation of historical breeding decisions in Vorderwald cattle (Brodauf, 1996), we derived the historical breeding objective. In 1965, this objective comprised solely performance in milk yield and meat production. For 1996, the objective was 5000 kg of milk per cow and year, 4.0% milk fat and 3.6% milk protein (Brodauf, 1996). In comparison with the actual breeding objective, the direction of selection was amended toward fitness to the disadvantage of meat production. We hypothesized a TMI based on an individual's performance, which is equivalent to a simulated trait with a heritability of $h^2 = 0.25$. This value should be similar to the h^2 in reality since the historical breeding objective comprised no fitness traits. Fitness traits are known to be less heritable than

performance traits in the meat production of cattle (Knapp and Nordskog, 1946; Utrera, 2004; Andersen-Ranberg et al., 2005). The $TBVs$ of individuals in ongoing iterations were estimated with the following equation:

$$TBV_i = 0.5TBV_{Sire\,i} + 0.5TBV_{Dam\,i} + MS_i$$

where TBV_{Sirei} is the true breeding value of the sire and TBV_{Dami} is the true breeding value of the dam of individual i. MS_i represents the Mendelian sampling term of individual i, chosen from a normal distribution:

$$MS_i \sim N(0, 0.5 * VA_t)$$

Estimation of breeding values

Estimation of breeding values was carried out with $ASReml$-R (Butler et al. 2009). The mixed linear model was as follows:

$$y_i = \mu + a_i + e_i$$

where y_i is the phenotype of individual i; μ is the intercept, modeled as a fixed effect; a_i is the random animal effect, which equals the TBV of individual i; and e_i is the environmental effect for individual i. Breeding value estimation was incorporated into simulations to enable changes in $EBVs$ due to increasing accuracies ($\dot{r}$) over time. Otherwise, the results would be incomparable with real data.

Selection of bull calves (exclusively Stage 2)

Bull calves were selected as candidates for progeny testing in birth cohort B_t. Selection was limited to male descendants of 10 sires with the greatest optimum contributions in iteration $t-1$. Selection was performed by truncating the best 1, 3 or 5 half brothers per sire on the basis of $EBVs$. In this part, aOCS was omitted as discussed later on (cf. Discussion – aOCS scenarios). As a result, we examined three FoR strategies with 10, 30 or 50 young sires for annual restocking (FoR10, FoR30 and FoR50 strategies, respectively).

Progeny testing (exclusively Stage 2)

We assumed that bull calves became mature at the end of B_t. Thus, the calves were progeny tested in B_{t-1}. Matings for progeny testing were allocated randomly across female candidates belonging to $B_{t-2}-B_{t-8}$. We examined three strategies for annual progeny testing of young bulls with 300, 600 or 900 matings for progeny testing in total (PT300, PT600 and PT900 strategies, respectively). Combining FoR strategies and PT strategies resulted in nine different scenarios of the simulation process, as shown in Table 1. Subsequently, young sires became available for deployment in the breeding population when they belonged to B_{t-3}.

Genetic gain

To compare the simulation scenarios and reality, we defined ΔG as the average annual improvement in the mean $EBVs$ of birth cohorts within a given time period of n years:

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Table 1 *Different simulation scenarios are defined by combinations of the flow of replacement of sires (FoR strategy) and extent of progeny testing of young sires (PT strategy) of Vorderwald cattle*

Scenarios	FoR[a]	PT[b]	PT/YS	n	ΔG[c]	ΔF	ΔF_nat	MC_{2014}	ØSires
Reality	≈2–3[d]	≈250–300	≈50–60[e]	1	1.56	0.067	0.184	61.3	77.9 ± 30.2
FoR10 + PT300	10	300	30	5	1.12[A] ± 0.06	0.084 ± 0.002	0.088 ± 0.0003	14.3 ± 0.8	60.3 ± 11.5
FoR10 + PT600	10	600	60	5	1.15[A] ± 0.07	0.087 ± 0.004	0.088 ± 0.0003	15.4 ± 1.8	53.6 ± 10.7
FoR10 + PT900	10	900	90	5	1.18[A] ± 0.05	0.086 ± 0.002	0.088 ± 0.0004	16.5 ± 1.0	53.2 ± 10.3
FoR30 + PT300	30	300	10	5	1.35[B] ± 0.03	0.082 ± 0.001	0.087 ± 0.0005	13.2 ± 0.7	67.9 ± 14.0
FoR30 + PT600	30	600	20	5	1.37[B] ± 0.04	0.084 ± 0.001	0.087 ± 0.0002	15.2 ± 0.7	66.2 ± 13.5
FoR30 + PT900	30	900	30	5	1.36[B] ± 0.05	0.084 ± 0.001	0.087 ± 0.0002	16.1 ± 0.7	57.1 ± 13.5
FoR50 + PT300	50	300	6	5	1.35[B] ± 0.06	0.085 ± 0.001	0.087 ± 0.0001	13.7 ± 0.5	72.7 ± 18.3
FoR50 + PT600	50	600	12	5	1.40[B] ± 0.05	0.085 ± 0.002	0.087 ± 0.0003	14.8 ± 0.8	64.4 ± 14.5
FoR50 + PT900	50	900	18	5	1.37[B] ± 0.06	0.085 ± 0.002	0.087 ± 0.0001	15.4 ± 0.8	56.9 ± 13.1

Scenarios=different scenarios consisting of combinations of the *FoR strategy* and *PT strategy*; *FoR*=annual flow of replacement of sires; *PT*=extent of progeny testing of young sires; *PT/YS*=matings for progeny testing per young sire; *n*=replicates per scenario; *ΔG*=annual genetic gain, measured as the improvement in mean estimated breeding values (*EBVs*) for the total merit index (*TMI*) among birth cohorts B_{1984}–B_{2014}; *ΔF*=rate of inbreeding for overlapping generations (in %); *ΔF_{nat}*=rate of native inbreeding for overlapping generations (in %); *MC_{2014}*=average migrant contribution of birth cohort 2014 as a final value; *ØSires*=average number of deployed sires per iteration among birth cohorts B_{1984}–B_{2013}.
[a] Three different *FoR strategies* were examined with 10, 30 or 50 young sires for restocking of proven sires per year.
[b] Three different *PT strategies* were examined. These strategies included 300, 600 or 900 matings for progeny testing of all young sires in total.
[c] Genetic gain was defined as the annual improvement in the mean *EBV* of birth cohorts.
[d] According to personal communication (Dr Franz Maus, 22 February 2018).
[e] According to (Hartwig *et al.* 2013).
[A,B] Different superscripts indicate significantly different values ($P < 0.01$) between the *FoR strategies*.

$$\Delta G_{t-(t+n)} = \frac{\text{Ø}EBV_{t+n} - \text{Ø}EBV_t}{n}$$

where $\text{Ø}EBV_t$ is the average *EBV* of a given birth cohort *t* averaged over five replicates. To verify the average value differences, we performed a *two-factorial ANOVA* and *Tukey's Honestly Significant Difference (HSD) test*. The response variable was $\Delta G_{1984-2014}$. We included the *FoR strategy* and *PT strategy* as factor variables.

Rates of inbreeding

For a better understanding of time-specific developments, we defined the ΔF and ΔF_{nat} in a given time period of *n* years, averaged over five replicates, as

$$\Delta F_{t-(t+n)} = \frac{\text{Ø}classKin_{t+n} - \text{Ø}classKin_t}{n}$$

and

$$\Delta F_{nat(t-(t+n))} = \frac{\text{Ø}natKin_{t+n} - \text{Ø}natKin_t}{n}$$

Migrant contribution

Furthermore, we defined the ΔMC as the average annual increase in the mean *MC* of birth cohorts within a given time period of *n* years:

$$\Delta MC_{t-(t+n)} = \frac{\text{Ø}MC_{t+n} - \text{Ø}MC_t}{n}$$

where $\text{Ø}MC_t$ is the average *MC* of a given birth cohort *t* averaged over five replicates.

Number of deployed sires

Since natural service is the dominant reproductive mode in Vorderwald cattle, the number of annually deployed sires will influence the feasibility of a breeding scheme. Thus, we chose an average number of annually deployed sires for each scenario as

$$\text{Ø}Sires_{1984-2013} = \frac{\sum_{1984}^{2013} \text{Ø}Sires_t}{29},$$

where $\text{Ø}Sires_t$ is the average number of deployed sires in a given year *t* averaged over five replicates.

Results

Restricted parameters

With regard to a feasibility study that considers practical conditions, there was marginal variation in the values of the constraint parameters *MC*, *classKin* and *natKin* (cf. Table 1 for *SDs*). Hence, the results will be visualized exemplarily for scenario *For30 + PT300*. The development of the mean *MC* in birth cohorts is shown in Figure 2. In reality, $\Delta MC_{1984-1996}$, $\Delta MC_{1996-2005}$, $\Delta MC_{2005-2014}$ and $\Delta MC_{1984-2014}$ were 0.73%, 2.0%, 0.88% and 1.15%, respectively. Between 1984 and 2005, the *MC* increased by 27.3%, since $\Delta MC_{1996-2005}$ was 2.7- and 2.3-fold higher than $\Delta MC_{1984-1996}$ and $\Delta MC_{2005-2014}$, respectively. In the simulation scenarios, $\Delta MC_{1984-1985}$ was −14.8% (±0.0004) across all scenarios, reducing MC_{1985} to 11.8% (±0.0004). Subsequently, the *MC* was conserved at a final value of 15.3% (±0.78) (cf. Table 1 for values of specific scenarios). As a result, $\Delta MC_{1984-2014}$ was −0.38%. The development
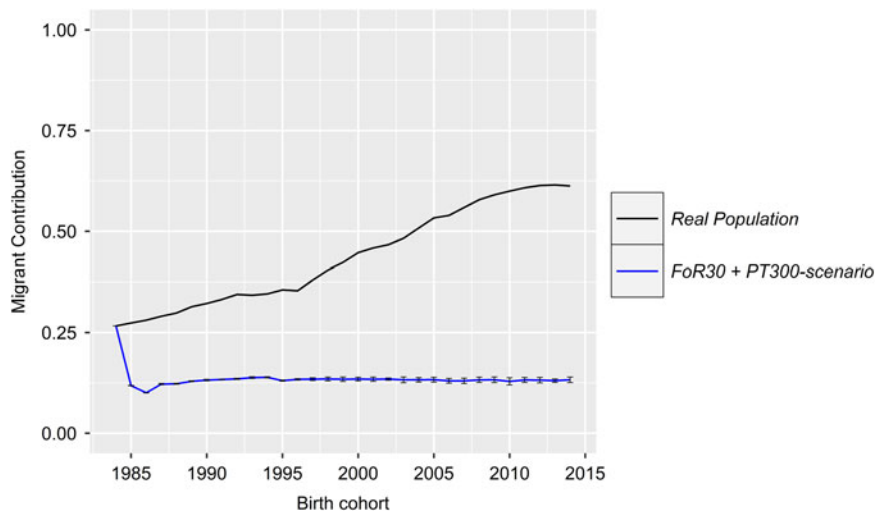
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Figure 2 (Colour online) Development of the MC in the birth cohorts of the real and the simulated Vorderwald cattle populations – we examined nine different scenarios. The scenarios consisted of combinations of strategies for the flow of replacement of sires (FoR strategy) and number of matings to test young sires for restocking (PT strategy). The presented graphs visualize the mean MC of birth cohorts in the real population (black) and simulated populations averaged over five replicates with the SD (blue). Variation in the development of the MC was virtually negligible across the simulation scenarios (Table 1). Thus, the results are presented exemplarily for the FoR30 + PT300 scenario (30 young sires for restocking with 300 matings for annual progeny testing) for clarity. MC=migrant contribution.
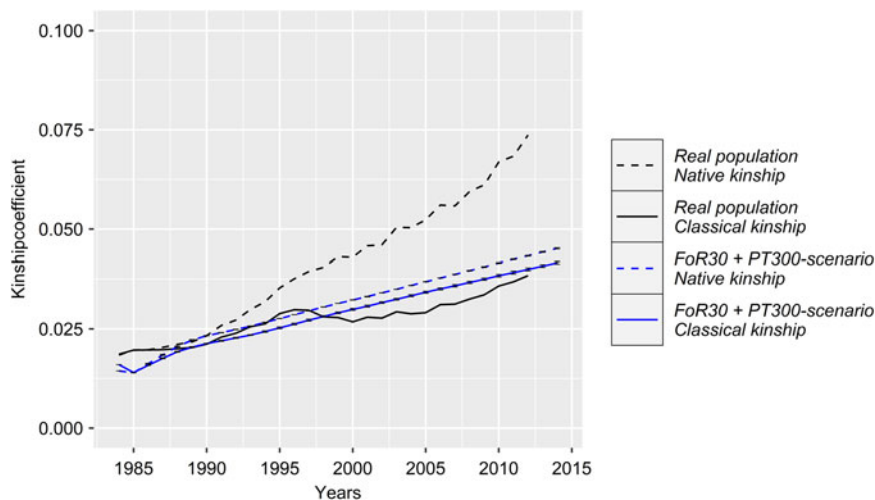

Figure 3 (Colour online) Development of the classical and native kinship of the real and the simulated Vorderwald cattle populations – we examined nine different scenarios. These scenarios consisted of combinations of strategies for the flow of replacement of sires (FoR strategy) and number of matings to test young sires for restocking (PT strategy). The graphs present the mean classical kinship coefficient (classKin, solid lines) and native kinship coefficient (natKin, dashed lines) of birth cohorts in the real population (black) and simulated populations averaged over five replicates with the SD (blue). Variation in the development of classKin and natKin was virtually negligible across simulation scenarios (Table 1). Thus, the results are presented exemplarily for scenario FoR30 + PT300 (30 young sires for restocking with 300 matings for annual progeny testing) for clarity.

of the *classKin* and *natKin* is visualized in Figure 3. *ClassKin* developed with an irregular pattern in the real population; $\Delta F_{1984-1996}$, $\Delta F_{1996-2005}$ and $\Delta F_{2005-2014}$ were 0.09%, −0.008% and 0.13%, respectively. Overall, $\Delta F_{1984-2014}$ was 0.067%. In contrast, the *natKin* increased steadily, with a $\Delta F_{nat(1984-2014)}$ of 0.184%. Across all simulation scenarios, the *classKin* and *natKin* decreased in 1985 with a $\Delta F_{1984-1985}$ of −0.2% and a $\Delta F_{nat(1984-1985)}$ of −0.05%. In subsequent iterations, both values increased linearly, with a $\Delta F_{1984-2014}$ of 0.082−0.087% and a $\Delta F_{nat(1984-2014)}$ of 0.087−0.088%. The constraints on inbreeding rates (*ub.classKin* and *ub.natKin*) and

corresponding developments in the *classKin* and *natKin* in the simulation scenarios are visualized in Figure 4. Generally, $\Delta F_{nat(1984-2014)}$ (0.087−0.088%) approximated *ub.natKin* (0.092%). However, $\Delta F_{1984-2014}$ was lower (0.082−0.087%) across all scenarios and constrained to the same value (*ub.classKin* = 0.092%).

Genetic gain
The development of the ΔG is visualized in Figure 5. Differences in ΔG were not significant across *PT strategies* ($P = 0.29$). Thus, the ΔG is exclusively visualized for scenarios with the fewest number of matings for progeny testing (i.e.,
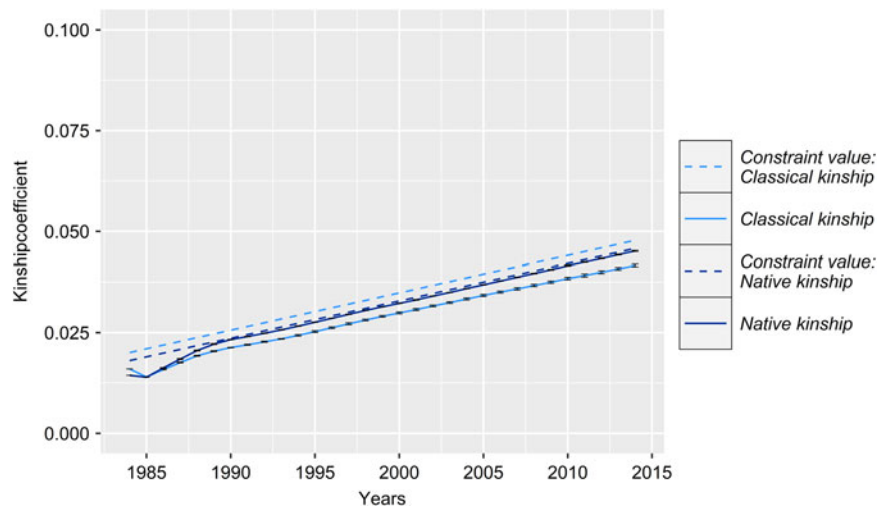
Figure 4 (Colour online) Development of the classical and native kinship with corresponding upper bounds of the real and the simulated Vorderwald cattle populations – average classical kinship coefficient (*classKin*, light blue) and native kinship coefficient (*natKin*, dark blue). Dashed lines represent corresponding upper bounds in respective iterations. Variation in the development of *classKin* and *natKin* was virtually negligible across simulation scenarios (Table 1). Thus, the results are presented exemplarily for scenario *FoR30 + PT300* (30 young sires for restocking with 300 matings for annual progeny testing) for clarity.
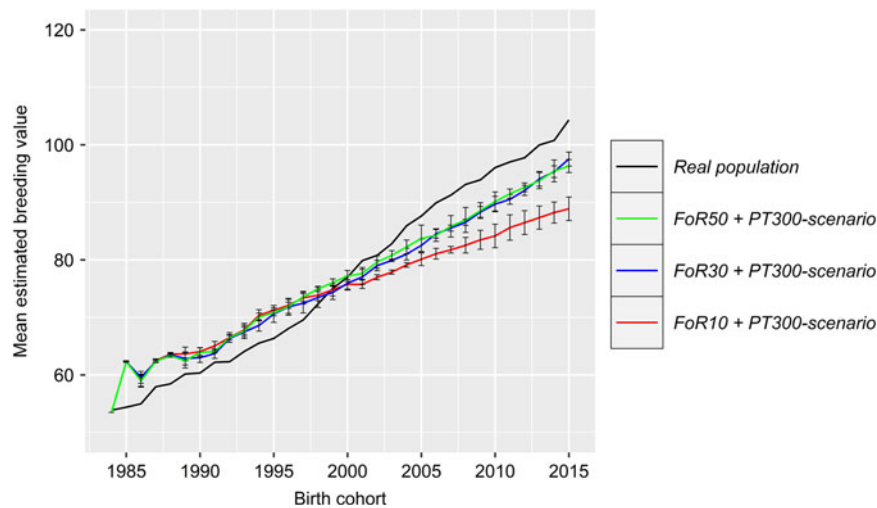

Figure 5 (Colour online) Development of the genetic gain of the real and the simulated Vorderwald cattle populations – we examined nine different scenarios. These scenarios consisted of combinations of strategies for the flow of replacement of sires (FoR strategy) and number of matings to test young sires for restocking (PT strategy). Graphs present the development of the mean EBV for the TMI of birth cohorts. Differences were not significant across PT strategies (Table 1). Thus, graphs are presented for scenarios with the smallest number of matings for progeny testing (300 in total) but various numbers of young sires for annual restocking of proven sires (50, 30 or 10; FoR50, FoR30 and FoR10, respectively; colored) and the real population (black). The results were averaged over five replicates. The graphs include SDs. EBV=estimated breeding value ; TMI=total merit index.

the *PT300 strategy*). In reality, $\Delta G_{1984–2014}$ was highest (1.56), with $\Delta G_{1984–1997}$, $\Delta G_{1997–2006}$ and $\Delta G_{2006–2014}$ equaling 1.21, 2.26 and 1.36, respectively. All scenarios of the simulation show a strong increase in $\Delta G_{1984–1985}$ (8.8 ± 0.1). Thereafter, the ΔG develops almost linearly. Values for the $\Delta G_{1984–2014}$ (1.12–1.40) of specific scenarios are presented in Table 1. The impact of *FoR strategies* on the ΔG is significant at $P = 3 \times 10^{-16}$. The results of *Tukey's HSD test* on *FoR strategies* averaged over *PT strategies* are visualized in Figure 6 and presented in Table 1. The $\Delta G_{1984–2014}$ of the

FoR10 scenarios (1.12–1.18) was significantly lower ($P = 0.05$) than that of the *FoR30 scenarios* (1.35–1.37) and *FoR50 scenarios* (1.35–1.40).

Deployed proven sires
The numbers for *øSires$_{1984–2013}$* are presented in Table 1. Across all simulations, *øSires$_{1984–2013}$* varies between 53.2 and 72.7. In reality, 77.9 ± 30.2 sires were deployed annually.
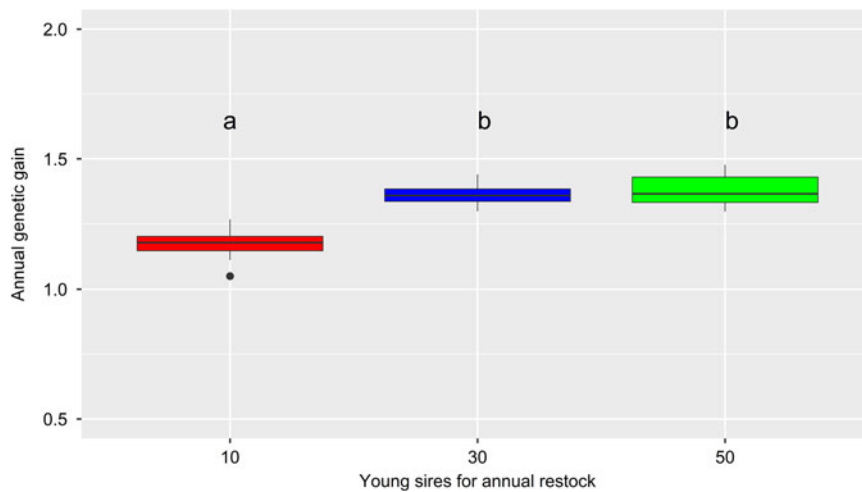
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Figure 6 (Colour online) Average annual genetic gain of different simulated Vorderwald cattle populations over 30 iterations of the simulation process – box plot of annual genetic gain, measured as the improvement in mean EBVs for the TMI between pairs of birth cohorts from B_{1984} (starting point of the simulation) to B_{2014} (end point of the simulation). Different colors indicate different flows of replacement of proven sires, with levels of 10, 30 or 50 young sires for annual restocking (FoR10, FoR30 and FoR50 strategies, respectively). Additionally, three strategies for progeny testing of young sires were examined, with levels of 300, 600 or 900 matings for progeny testing in total (PT300, PT600 and PT900 strategies, respectively). The results of different FoR strategies were averaged over PT strategies, with five replicates per strategy combination. Different letters indicate significant differences at $P < 0.01$. EBV=estimated breeding value; TMI=total merit index.
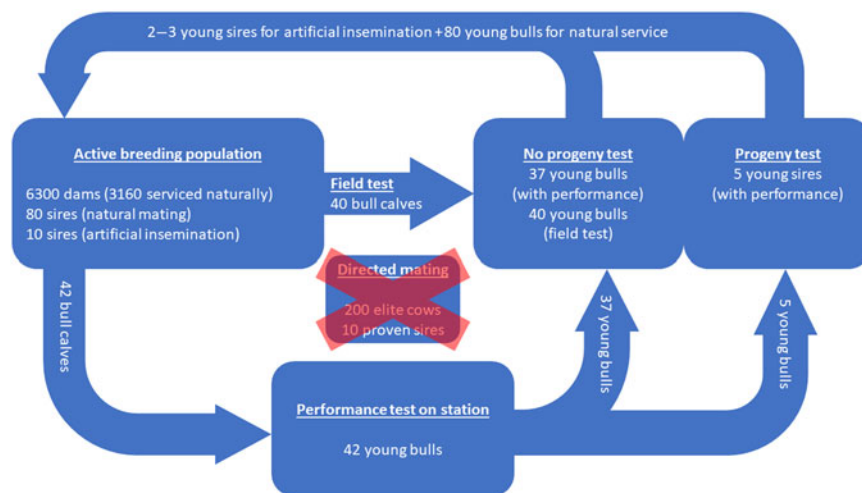

Figure 7 (Colour online) Actual breeding scheme of Vorderwald cattle – the presented figures are long-term averages (10 years) and presented on an annual basis (Dr Franz Maus, personal communication, 22 February 2018). A total of 6300 dams are available; therefore, 3160 dams are serviced naturally. Forty-two bull calves are selected from the breeding population for a performance test on station. Thirty-seven of those calves will restock sires for natural mating without passing a progeny test. The missing 40 bull calves for restocking of sires for natural mating originate from field tests. Five young bulls successfully pass the performance test on station and are subsequently progeny tested. A total of two to three bulls pass the progeny test successfully and will restock proven sires for artificial insemination. Directed mating is planned but has not yet been introduced.

Discussion

This discussion will provide an analysis of the performance and limitations of the given aOCS procedure in connection with the designed young sire breeding scheme. Subsequently, simulation scenarios will be compared in terms of the ΔG, MC, classKin and natKin. First, ideas for improvements in the actual breeding scheme of Vorderwald cattle will be derived. Furthermore, a comparison of simulation scenarios with real data will identify opportunities and limitations of the implementation of aOCS and clarify whether historical breeding decisions

could have been avoided. Subsequently, we will select superior scenarios and provide ideas for practical implementation in a young sire breeding scheme. Finally, we will discuss efforts to add genomic information to optiSel. The SDs of all parameters (MC, ΔG, ΔF and ΔF_{nat}) were marginal. Thus, our study was based on merely five replicates per scenario.

Breeding schemes
The actual breeding scheme of Vorderwald cattle is illustrated in Figure 7. All figures are long-term averages from

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the last 10 years (Dr Franz Maus, personal communication, 22 February 2018). The active breeding population consists of 6300 dams in total. However, 3160 dams are serviced naturally by 80 unproven sires, and 3140 dams are serviced by artificial insemination by 10 proven sires. Thus, assuming an even distribution of born males and females, 3150 bull calves are born in the breeding population. Of these 3150 bull calves, 42 bull calves are selected for a performance test on station. Selection is performed by the breeding director on the basis of pedigree-based *EBVs* (Dr Franz Maus, personal communication, 26 February 2019). Subsequently, 37 of the 42 young bulls do not have sufficient performance to justify a progeny test. However, the bulls replace the sires for natural mating without passing a progeny test. Additionally, 40 young bulls for replacement of sires for natural mating originate from field testing. Field testing involves the measurement of daily gain and a rating of conformation. As a result, five young bulls have sufficient performance on station to justify a progeny test. Subsequently, two to three of these five young bulls successfully pass the progeny test and become available for restocking of proven sires for artificial insemination in the breeding population. A time frame of usage of proven sires for artificial insemination is not clearly defined. Young sires that do not pass the progeny test successfully (2–3) will be used to restock sires for natural mating. Directed mating is planned but has not yet been introduced. Gandini *et al*. (2014) carried out stochastic simulations of young sire breeding schemes and similar population sizes (500–6000 dams) 'according to criteria of the European Commission' (Gandini *et al*., 2004) on 'population sizes of local dairy cattle breeds designated as endangered'. Their simulations were carried out by implementing a standard OCS strategy. The breeding scheme for stochastic simulations in our study was based on the actual Vorderwald cattle population and used the young sire breeding schemes of Gandini *et al*. (2014) as a template. The first major difference between the modeled schemes is the existence of progeny testing of young bulls in our study. This testing reportedly has an impact on the ΔG (Meuwissen and Sonesson, 1998). Additionally, *FoR strategies* should have an impact on the ΔG (Gandini *et al*., 2014). Thus, we examined three *FoR strategies* in combination with three *PT strategies*. Furthermore, Gandini *et al*. (2014) did not consider reasonable amounts of natural service. In comparison to the actual breeding scheme, the scheme in this study omitted performance records as an additional selection criterion for young bulls. Finally, progeny testing of all selected mature bulls was a major difference since sires for natural mating in the actual scheme did not pass a progeny test.

The introduction of subsidies for registered breeding animals of Vorderwald cattle has led to heavy registration in the herdbook in recent years. Thus, a breeding population of 6300 dams (Figure 7) was established. Since all dams are registered breeding animals, a nucleus is non-existent. Therefore, we did not consider a breeding scheme based on a nucleus.

Advanced optimum contribution selection scenarios
All simulation scenarios showed a strong increase in $\Delta G_{1984–1985}$ (+8.8 ± 0.1) after the first iteration, while the *MC* was greatly reduced ($\Delta MC_{1984–1985} = -14.8\% \pm 0.0004$) (Figures 2 and 5). Additionally, the *classKin* and *natKin* decreased ($\Delta F_{1984–1985} = -0.2\%$ and $\Delta F_{nat(1984–1985)} = -0.05\%$) (Figure 4). This result might be explained by the identical base population of all simulation scenarios in combination with the optimization opportunities when aOCS is implemented for the first time. Deployed proven sires of the first iteration had an average *MC* of only 11.1% ± 0.2 (26.6% in the breeding population) and an average *EBV* of 71.3 ± 0.3 (53.5 in the breeding population) and were by chance not closely related across any scenarios (results not shown). In subsequent iterations, all simulation scenarios produced a final MC_{2014} value of 15.3% ± 0.78. This result was due to the lack of the upper bound for *MC*. The upper bound was expressed as $ub.MC_{t+t} \leq \emptyset MC_t$. Thus, the average *MC* of population $t + 1$ was constrained by the smallest value achieved at any given point of the simulation process since $ub.MC_{t+1} \geq ub.MC_{t+2} \geq ub.MC_{t+n}$. An *ub.MC* fixed to a starting value of 26.6% in the base population would have been preferable. However, aOCS roughly satisfied the upper bound for ΔF_{nat} (*ub.natKin* = 0.092%), at 0.087–0.088% across all scenarios. Simultaneously, *ub.classKin* (0.092%) was not fully exploited, with a ΔF of 0.082–0.087% across all scenarios (Table 1). Native alleles are a subset of all alleles in a given population. Assuming a closed population of Vorderwald cattle in former times, selection within native alleles (domestication and breeding) resulted in related individuals. As soon as foreign alleles (i.e., the *MC*) were introgressed, carriers of those alleles were less related to the population. As an artifact, the *classKin* will always be smaller than the *natKin*, and restricting the *natKin* by an upper bound will automatically restrict the *classKin* to a lower level. This finding is in line with the results of scenario *maxEBV.A.D.MC* of (Wang *et al*. 2017a). The constraint setting of the authors' simulation was the same as ours, with upper bounds for the *MC*, ΔF and ΔF_{nat}. We agree with Wang *et al*. (2017a) that restriction of the *classKin* can be omitted when the *MC* and *natKin* are restricted. Both parameters *classKin* and *natKin* show a linear and parallel increase across all scenarios (Figure 4). We conclude that aOCS can stop the increasing deviation of the *classKin* and *natKin* in the actual population and simultaneously conserve (or even reduce) the *MC*. Conserving or reducing the *MC* is of special interest for the actual population, with an MC_{2014} of 61.3% (Table 1). Since increasing the extent of progeny testing per mature bull positively influences the accuracies of *EBVs*, we assumed the *PT strategy* to have an impact on the ΔG. However, a significant impact was not observed ($P = 0.29$). The extent of progeny testing per mature bull varied between 6 (*FoR50 + PT300*) and 90 (*FoR10 + PT900*). Thus, the corresponding *r* was in the range of 0.4–0.75 across all scenarios (results not shown) when young sires were available for broad deployment in

B_{t-3}. At a population level, fluctuation of *EBVs* should be compensated for all deployed sires. This compensation might explain the non-significant impact of *PT strategies* on the ΔG. However, we must be aware of the realization of ΔG in single herds when deploying sires with $r \approx 0.5$. This consideration is analogous to the spread of risk in genomic breeding schemes. Optimally, this spread of risk might be transferred by deploying optimum contributions of sires in each herd (Kohl and Herold, 2017). However, the feasibility of this approach is questionable since $\emptyset Sires_{1984-2013}$ was 53.2–67.9 across all scenarios. Hence, we suggest implementing a sufficient spread of risk in single herds, even if the optimum contributions of sires cannot be completely transferred. Increasing the accuracy of breeding value estimation might be an added value since broader deployment of sires would result in enhanced approximation of herd effects. Furthermore, the $\Delta G_{1984-2014}$ in the *FoR30* and *FoR50 scenarios* was superior (1.36 ± 0.01 and 1.37 ± 0.03, respectively) to that in the *FoR10 scenarios* (1.15 ± 0.03). We conclude that the *FoR30* and *FoR50 strategies* are superior in terms of the ΔG with no drawbacks in terms of the *MC*, ΔF and ΔF_{nat}.

Prior to the actual simulation process, we performed various other procedures that tested for enhanced results by selecting bull calves for progeny testing with an additional aOCS approach. However, the results did not improve in any aspect and required approximately twice the computational time. The idea of the actual simulation process was to conserve the genetic diversity and uniqueness of the breed by selecting mature bulls for progeny testing across all deployed proven sires in every year. To ensure a sufficient ΔG, mature bulls were selected by truncation.

Comparison with real data

In reality, strong introgression of Montbéliard genetic material was carried out between 1995 and 2005 to upgrade the breed in terms of daily gain (Hartwig *et al.*, 2014). As a result, the ΔMC increased much faster than before (2.7-fold) and thereafter (2.3-fold), based on the $\Delta MC_{1984-1996}$, $\Delta MC_{1996-2005}$ and $\Delta MC_{2005-2014}$ values of 0.73%, 2.00% and 0.88%, respectively. Furthermore, introgression from Montbéliard is directly reflected in the development of the ΔG. During introgression, $\Delta G_{1996-2005}$ was 1.9- and 1.7-fold higher than $\Delta G_{1984-1996}$ and $\Delta G_{2005-2014}$, respectively. Additionally, introgression led to a decreasing *classKin* (with $\Delta F_{1996-2005} = -0.008\%$), as explained in the previous section. Simultaneously, the *natKin* strongly increased (with $\Delta F_{nat} = 0.184$) due to replacement of native alleles by the *MC* and subsequent directional selection within the remaining native gene variants. These two opposing trends led to a growing deviation between the *classKin* and *natKin* in reality. The ΔG was higher in reality (1.56) than in any scenario of the simulation (1.12–1.40, Table 1). Four aspects might have contributed to this outcome: (i) Since this is a feasibility study, it is based on the actual breeding scheme of Vorderwald cattle and is designed to meet all practical constraints. One of these constraints is the absence of selection in the dam path. This avoidance is a core competence of breeders. Deducting

this core competence would lead to the unwillingness of breeders to realize aOCS in their breeding scheme. However, breeders certainly select for superior dams. Such selection might have contributed to the higher rates of ΔG in reality. (ii) The ΔG increases as the heritabilities of traits increase (Gandini *et al.*, 2014). We assumed a *TMI*, based on an individual's own performance, equivalent to a simulated trait with an $h^2 = 0.25$. With respect to a historical breeding objective comprising solely performance traits, this value might have been too low. (iii) Inbreeding has not been supervised in reality. However, the low $\Delta F_{1984-2014}$ (0.067%) value compared to that obtained with simulations (0.082–0.087%) was due to the introgression of the *MC* since the real $\Delta F_{1996-2005}$ was −0.008%. Woolliams *et al.* (2015) suggested a comparison of ΔG values at equal ΔF values because a larger ΔF inefficiently turns genetic variance in ΔG and increases risks. Thus, a comparison of the real $\Delta F_{2005-2014}$ (0.13) and the $\Delta F_{1984-2014}$ of the simulations seems more appropriate since introgression was stopped in 2005 and the gene pool was again closed. This termination of introgression resulted in a 1.5-fold higher ΔF in reality. Additionally, replacement of native alleles by the *MC* is undesired in regional breeds under conservation. Thus, a further comparison of $\Delta F_{(nat)1984-2014}$ is advisable, with 0.184% and 0.087% in reality and across all simulations (2.1-fold higher), respectively. Hence, the ΔG in reality was achieved at the expense of genetic diversity and uniqueness. (iv) Introgression caused a larger ΔG in reality. Introgression from foreign breeds was avoided in the simulations. Additionally, the lack of $ub.MC_{t+1}$, as described in the preceding section, entailed a substantial decline in the *MC*. However, the *MC* is known to be positively correlated with ΔG (Wellmann *et al.*, 2012). Thus, simulation scenarios produced a ΔG out of the remaining 11.8% ± 0.0003 of the MC_{1985} (compared to 26.3% in reality) and inferior native gene variants. Our aim was to clarify whether historical breeding decisions to increase the ΔG by introgression of commercial breeds could have been avoided by using aOCS. Thus, a comparison of the ΔG in reality and that from superior simulation scenarios seems most appropriate. The ΔG in reality was superior to that in the *FoR30* and *FoR50 strategies* by 12.8% and 12.2%, respectively. However, a direct comparison was not possible because of the very large decline in MC_{1985}. A further comparison of ΔG was mandatory to demonstrate how poorly the *MC* was exploited after introgression was halted in 2005. The *MC* increased in reality by 27.3% in 1984–2005 (Figure 2). The additional *MC* resulted in a greater ΔG of only 12.4%, based on $\Delta G_{1984-1997}$ (1.21, before introgression) and $\Delta G_{2006-2014}$ (1.36, after introgression). Finally, the $\Delta G_{1984-2014}$ in the *FoR30* and *FoR50 scenarios* was superior to the $\Delta G_{2006-2014}$ in reality (including the exploitable *MC*), at 3.7% and 4.4%, respectively. The final values of MC_{2014} were 13.2–16.1% across the corresponding scenarios and 61.3% in reality. Therefore, historical breeding decisions could have been avoided with a loss of 12.2–12.8% in the ΔG but would have resulted in an almost unique breed of Vorderwald cattle.

Selecting the superior scenario

The *FoR30* and *FoR50 strategies* are superior to the *FoR10 strategy*. The *PT strategies* had no significant impact on the ΔG. In practical terms, the selection of bull calves as well as husbandry and progeny testing of mature bulls is a financial issue faced by the breeding organization. The actual breeding scheme selects 42 bull calves for a performance test on station (Figure 7). Subsequently, five of the calves passed the progeny test. The breeding scheme of Vorderwald cattle takes into account the *EBVs* of young sires on the basis of 25–30 daughters (Hartwig *et al.*, 2013). Expecting an even distribution of born males and females, at least 50–60 matings are required to test 5 young sires. Eventually, this process results in 250–300 matings in total. The *FoR30* and *FoR50 strategies* selected 30 and 50 bull calves for progeny testing, respectively. Since the differences in ΔG between the *FoR30* and *FoR50 strategies* were not significant, we recommend implementing the *FoR30 strategy* in combination with the *PT300 strategy*. As a result, the number of matings for progeny tests (300) is comparable to the actual numbers. This combination will cause the lowest costs in selection, husbandry and progeny testing while maximizing benefits (ΔG).

Improving the breeding scheme

The actual breeding scheme of Vorderwald cattle is confounded by three factors. (i) Sires for natural mating do not pass a progeny test. (ii) Only half of the sires have performance records. (iii) Directed mating has not yet been introduced. Therefore, bull calves have been selected from the breeding population of 6300 dams (Figure 7). This process is cost-effective, but the risk of losing promising young sires due to the immediate dropout of bull calves is high (sale and culling). Restructuring the breeding scheme might improve population parameters, even before introducing aOCS. Consequent selection of half brothers over sires, on the basis of *EBVs*, is new and organizationally challenging. To simplify this task, we recommend accelerating the implementation of directed mating. An additional aOCS approach could optimize and allocate matings among elite cows. This approach might result in further enhanced population parameters (Gandini *et al.*, 2014). As an added value, the risk of losing valuable genetic material due to the immediate dropout of bull calves would be minimized. However, the establishment of a nucleus is not possible at the moment. One assumption of the simulation process was that all female descendants of young sires reached the performance test. This assumption is unrealistic because some of these descendants will be unavailable. However, when applying the most cost-effective *FoR30 + PT300 scenario*, five daughters reached the performance test in the simulations. In combination with a realistic chance of survival of heifers of 72% (Wathes *et al.*, 2008), 14–15 matings are sufficient for progeny testing of mature bulls in reality. Thus, the absolute number of matings for progeny testing increases to 420–450 when the *FoR30 strategy* is implemented. The additional costs of extended progeny testing (420–450 compared to 250–300 in reality; cf. Table 1) might be compensated for fewer performance tests of bull calves on station (30 compared to 42 in reality, cf.

Table 1). In reality, 77.9 ± 30.2 sires were deployed on an annual basis. The *FoR30 + PT300 scenario* deployed 67.9 ± 14.0 sires. Thus, fewer sires will be available to naturally service 3160 dams. Additionally, realizing optimum contributions in the naturally serviced dam population is an obstacle to overcoming associated challenges (Kohl and Herold, 2017). Currently, sires for artificial insemination produce semen and are subsequently culled. However, it is mandatory to keep a sufficient proportion of sires to service dams naturally. As a solution, one half brother could be kept per half sibling group and year. The idea is to deploy a half brother if aOCS selects for a culled sire. In this way, at least the optimum contributions of the sire–sire path will be realized. From an organizational point of view, we recommend establishing a bull rotation program (Kohl and Herold, 2017) or re-establishing municipal husbandry of sires for natural mating.

Further studies

Following this study, we will examine the impact of applying identified superior strategies to the actual breeding population of Vorderwald cattle in combination with the designed young sire breeding scheme. We will clarify further possibilities of reducing the number of bull calves for the restocking of sires. Thus, the *FoR50 strategy* will be replaced by an *FoR20 strategy*. Additionally, we will test the effects of either equalizing or lowering the *MC* in the population. This test is of special interest, considering the alarming *MC* levels in the actual population. Finally, internal cost accounting and analyses of organizational efforts will clarify the financial issues associated with the breeding scheme.

Adding genomic data

Advanced OCS is available within the open-source *R package optisel*. Pedigree data are known to be biased (Oliehoek and Bijma, 2009). Thus, the estimation of the *classKin*, *natKin* and *MC* is impeded. Adding genomic information to *optiSel* facilitates the estimation of all parameters based on shared haplotype segments (runs of homozygosity) (Wang *et al.*, 2017b). As a result, estimates are realized values rather than expected values and reflect enhanced selection decisions by the aOCS procedure. However, genomic data are not currently available. There are impending projects that aim to genotype a subpopulation of Vorderwald cattle, but the applicability of genome-based methods is unforeseeable.

Conclusion

This study assumes purposive and economically optimal actions of all parties. In reality, this assumption is frequently not the case (Kohl and Herold, 2017). Conviction of breeders is essential for effectively implementing aOCS in a given breeding scheme of Vorderwald cattle. Developed strategies should be openly discussed. In this way, a personal commitment might be achieved (Kohl and Herold, 2017). Furthermore, this study suggests that aOCS with *optiSel* is feasible for Vorderwald cattle, given the designed young sire breeding scheme. Selection of 30 bull calves per year, with

subsequent progeny testing, was proposed for annual restocking of proven sires. Given the constraint setting of the aOCS procedure, a smaller ΔG arose in superior scenarios (1.35 ± 0.03 in *FoR30 + PT300*) than that observed in real data (1.56). However, there was a lack in the upper bound for the *MC*. Thus, MC_{2014} was greatly reduced to 15.3% ($\pm$ 0.78) across all simulation scenarios. In reality, MC_{2014} rose to an alarming level (61.3%). Genetic diversity was conserved at a $N_{e(nat)}$ of 100 with a ΔF_{nat} of 0.087% $\pm$ 0.0005 in the *FoR30 + PT300 scenario*. Hence, the upper bound of ΔF_{nat} was roughly satisfied (0.092%). Therefore, we conclude that historical breeding decisions could have been avoided by using aOCS with the *FoR30 + PT300 scenario*. As a result, ΔG would have been reduced by 12.2%, but the introgressed genetic material, genetic diversity and native genetic diversity would be more effective for a breed under conservation in safeguarding future changes in livestock breeding.

Acknowledgments

Declaration of interest
None.

Ethics statement
None.

Software and data repository resources
The data and the simulation code will be archived at the State Agency for Spatial Information and Rural Development Baden-Württemberg at Kornwestheim, Germany. Access might be given after a consultation with the Rinderunion Baden-Württemberg e.V. and the Breeding Value Estimation Team Baden-Württemberg.

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