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Genetic parameters of measures and population-wide infrared predictions of 92 traits describing the fine composition and technological properties of milk in Italian Simmental cattle

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ABSTRACT

The objectives of this study were to estimate, for the Italian Simmental cattle population, genetic parameters for 92 traits and their infrared predictions (IP) and to investigate the genetic relationship between measured traits (MT) and IP. Data for milk fat fatty acid composition (n = 1,040), detailed protein composition (n = 3,337), lactoferrin (n = 558), pH (n = 3,438), coagulation properties (n = 3,266), curd yield and composition obtained by a micro-cheese making procedure (n = 1,177), and content of Ca, P, Mg, and K (n = 689) were obtained using reference laboratory analysis. Infrared prediction for all the investigated traits was performed using 143,198 spectra records belonging to 17,619 Italian Simmental cows. (Co)variance components for MT and their IP were estimated in a set of bivariate animal model REML analyses and genetic correlations between MT and IP were estimated using all IP obtained at the population level. A significant positive relationship was observed between the coefficient of determination of the infrared prediction models and the phenotypic and genetic variation of the IP. The decrease in the estimated genetic variance of IP compared with MT was on average 64%. For traits exhibiting calibration models with coefficients of determination in cross-validation (R^2_{CV}) greater than 0.9, the decrease in the genetic variance ranged from approximately 20 to 50%. Most traits (88 out of 92) exhibited lower heritability estimates for IP than for the corresponding MT. The estimated genetic correlations between IP and MT (r_a) were in general very high. A positive relationship (r = 0.57) between R^2_{CV} of calibration models and the estimated r_a has been detected. For calibration models exhibiting R^2_{CV} higher than 0.75, r_a were greater than 0.9. The variability in the estimated correlations increased when R^2_{CV} decreased, and for calibration models of moderate predictive ability, estimates of r_a ranged from 0.2 to 1. Genetic parameter estimates suggested that IP can be used as indicator traits in breeding programs for the enhancement of fine composition and technological properties of milk. The genetic gain achievable selecting for IP is expected to be high for fatty acid composition, minerals, and for technological properties of milk, whereas it will be low for casein and whey protein composition and for the content of lactoferrin.

Key words: infrared spectra, fatty acid, protein fraction, genetic parameter

INTRODUCTION

Interest in high-throughput methods for routine phenotyping of dairy cows is rapidly growing, and mid-infrared spectroscopy (**MIR**) is recognized as a powerful tool to collect individual data for traditional and innovative milk traits on a large scale. The MIR predictions of milk fat, protein, casein, and lactose content have replaced measures provided by gold standard methods used for analyzing samples collected in milk recording programs (ICAR, 2012). Besides traditional traits, MIR has been used to predict several milk characteristics, albeit integrations of such predictions in routine milk analysis are still scarce and have been accomplished only for major fatty acids, coagulation properties (**MCP**), lactoferrin (**LF**), and hyperketonemia (De Marchi et al., 2014). Depending on the predictive ability of models, infrared predictions (**IP**) may be adopted in payment systems to reward or penalize producers or in monitoring metabolic status of cows (Gengler et al., 2016). In addition, literature estimates of genetic parameters for IP suggest a role of predictions as indicator traits in breeding programs for dairy cattle populations (Gengler et al., 2016). The potential of MIR calibrations to provide novel phenotypes usable in indirect selective breeding relies on the heritability of IP and the genetic correlation between IP and the measured trait (**MT**). Although the predictive ability of

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MIR is moderate for some traits, the genetic response achievable using IP as indicator traits may be equal to or slightly lower than the response achievable when direct measurements of traits are performed (Cecchinato et al., 2009; Rutten et al., 2010).

For most novel traits, information on the potential use of IP in selective breeding is still limited. Genetic correlations between MT and IP have never been estimated for a large number of traits comprehensively describing fine milk composition or including predictions obtained at the population level. To date, estimates of genetic correlations between MT and IP have been obtained using IP for the reference data only (i.e., IP of samples used to build calibration models). This resulted in large standard errors for the estimated correlations and in inaccurate estimates of genetic parameters for IP (Cecchinato et al., 2009; Bittante et al., 2014).

The objectives of this study are to estimate, for the Italian Simmental cattle population, genetic parameters of 92 traits and their IP, describing the fine composition and technological properties of milk, and to investigate the genetic relationship between MT and IP, using predictions obtained at the population level, to assess the potential role of IP as indicator traits for dairy cattle breeding.

MATERIALS AND METHODS

Measured Traits, Spectral Data, and Calibration Models

A large database of fine milk composition and technological traits, including a total of 3,438 individual records of Italian Simmental cows, was available. Data for milk fat fatty acid composition, detailed protein composition and LF were available for 1,040, 3,337, and 558 samples, respectively. Milk fat was separated using an accelerated extraction method and fatty acids were analyzed by 2-D gas chromatography. Of the 1,040 samples having a measure of fatty acid profile, 1,008 samples had also a measure of total fat content (i.e., the infrared prediction derived from herd test data), which was used to compute the content (g/dL) of individual fatty acids. Contents of the major casein (α_{S1}-CN, α_{S2}-CN, β-CN, γ-CN, glycosylated and unglycosylated κ-CN), and whey protein (β-LG, and α-LA) fractions were measured by RP-HPLC. Lactoferrin was measured by ELISA. Measures of pH and MCP obtained by a computerized renneting meter over a 60-min analysis were available for 3,438 and 3,266 samples, respectively. Curd yield and composition were measured for 1,177 samples using a micro-cheese making procedure performed on 25 mL of milk. Mineral content (Ca, P, Mg, and K) was measured in 689 samples by inductively coupled plasma optical emission spectrometry. Details on methods used to obtain the MT can be found in Bonfatti et al. (2016).

The MIR absorption spectra were available for all Simmental cows farmed in the Friuli Venezia Giulia region (Italy) and enrolled in the national milk recording program from January 2013 to June 2015. Spectra were routinely collected using a MilkoScan FT6000 instrument (Foss Electric A/S, Hillerød, Denmark) by the Friuli Venezia Giulia Milk Recording Agency laboratory (Codroipo, Italy). Infrared predictions were obtained for all the investigated traits using a total of 143,198 spectra records of 17,619 Italian Simmental cows reared in 356 herds. Average, minimum, and maximum number of spectra records per cow were 8.1, 1, and 19, respectively. Predictions were obtained using calibration models developed by Bonfatti et al. (2016).

Depending on the trait, either all records (for minerals, LF, fatty acids, cheese yield traits) or part of the records (1,240 for protein fractions, 1,430 for pH and MCP) with MT had also spectral information, and as a consequence, IP traits. Both for MT and IP, values greater than 3 SD or lower than −3 SD were considered outliers and discarded. The final number of samples is reported in Appendix Table A1.

Estimates of (Co)variance Components and Genetic Parameters

Pedigree information was supplied by the Italian Simmental Cattle Breeders Association (ANAPRI, Udine, Italy) and included all animals having spectral data or a phenotypic record for at least one MT and their ancestors. Ancestors were traced back for as many generations as possible. The ultimate pedigree file included a total of 72,365 animals and the minimum number of generations of known ancestors for a cow with phenotypic record was 3. The total number of sires was 9,234. Of these, 1,302 had progeny with IP records. The average number of daughter per sire was 11.9.

(Co)variance components for MT and their IP were estimated in a set of bivariate animal model REML analyses using VCE software (version 6.0; Groeneveld et al., 2010). Each bivariate analysis included one MT and its population-wide IP. For MT, the model included the fixed effect of parity (first, second, third, and fourth and later parities), the fixed effect of the DIM class (12 classes of 30-d intervals with the exception of the last class including samples collected at DIM ≥360), the random effect of the herd-test day (**HTD**; from 11 to 70 levels depending on the trait), and the random additive genetic effect of the animal. For IP, the model in-

cluded the fixed effect of parity × DIM class (48 levels), the random effects of HTD (4,840 levels), the random permanent environmental (cow) effect, and the random additive genetic effect of the animal. The HTD effects, permanent environmental effects, and residuals were assumed to be uncorrelated in the bivariate analysis Ratios of additive genetic, permanent environmental, HTD, and residual variance to total variance were calculated. The ratio of additive genetic variance $\left(\sigma_a^2\right)$ to the total variance was used as an estimate of heritability. The difference in additive genetic, HTD and residual variance estimates between IP and MT was computed as a percentage of the MT variance estimate. For each trait, the genetic correlation between IP and MT ($\mathbf{r_a}$) was estimated.

RESULTS AND DISCUSSION

Descriptive statistics of all investigated MT and IP can be found in Appendix Table A1.

Fatty Acid Composition

Estimates of variance components, as percentages of total variance, for measured and predicted milk fatty acid contents (g/dL) are reported in Table 1. For contents of fatty acids and groups of fatty acids, heritability (σ_a^2 as a % of the total variance) was low or moderate for MT, ranging from 6 (CLA) to 36% (C10:0). In general, SFA had greater σ_a^2 estimates than UFA. Heritability was 0.15 or less for unsaturated long-chain fatty acids. Large heritability for contents of short- and medium-chain fatty acids relative to that of long-chain fatty acids has been reported also in previous studies (Stoop et al., 2008; Bastin et al., 2011; Bilal et al., 2014) and can be explained by the origin of milk fatty acid. Bovine milk fatty acid originate from 2 major sources: de novo synthesis and dietary uptake of preformed fatty acid. Almost all fatty acids from C4:0 to C14:0 and approximately half of C16:0 fatty acids are synthesized de novo in the mammary gland, whereas the remaining half of C16:0 and C18 or longer carbon chain fatty acids derive mainly from the diet. Hence, for the latter group, influence of genetic factors affecting variation in fatty acid milk content is limited (Bauman and Griinari, 2003). In agreement with Bilal et al. (2014), C14:1, which originates to a large extent from C14:0 as a result of stearoyl-CoA desaturase activity, C16:1 and C18:1 exhibited the largest heritability estimates among the UFA under study. Heritability estimates obtained for percentages of fatty acids in milk fat (Table 2) were lower than those for fatty acid milk contents and consistent with literature results (Stoop et al., 2008; Bilal et al., 2014).

In comparison with MT, total variance in IP was low for both fatty acid contents and percentages. For IP of fatty acid percentages, the estimated heritability was from 2 to 3 times lower than the estimate for the corresponding MT. Heritability estimates for fatty acid reported by Rutten et al. (2010) were generally lower for IP than for MT, but there were traits (e.g., C18:0) for which the IP were more heritable than the MT.

The lower heritability of IP compared with MT is to be attributed to a marked decrease in the estimated σ_a^2, which was, on average, −52% for fatty acid contents and −69% for percentages of fatty acids in fat (Δ variance; Tables 1 and 2). For fatty acids, the decrease in σ_a^2 was related to the coefficient of determination in cross-validation of the calibration model ($\mathbf{R^2_{CV}}$): the lower the reliability of the calibration model, the larger the decrease ($r = 0.75$; $P < 0.01$).

Despite the decreased σ_a^2 and heritability relative to MT, most IP for fatty acid contents were highly genetically correlated with the corresponding MT. The weakest correlation ($r_a = 0.57$) was obtained for C18:3n-3. Of 25 traits measuring fatty acid contents in milk, 18 traits exhibited additive genetic correlations between IP and MT greater than 0.85 and for 12 traits the estimated genetic correlation was greater than 0.95. In agreement with Rutten et al. (2010), very high r_a values were also observed for fatty acid percentages, although the R^2_{CV} for fatty acid percentages were, on average, 10% lower than those obtained for fatty acid milk contents and the decrease in the σ_a^2 ranged from 54 to 85% of the MT genetic variance (Table 2).

Protein Composition

Variance component estimates for MT and IP of milk protein content (g/L), protein fraction contents (g/L), and protein composition (% of each protein fraction in milk protein) are reported in Table 3. Heritability values for MT of protein fraction contents ranged from 0.09 (γ-CN) to 0.64 (unglycosylated κ-CN). For major protein fractions, such estimates were either greater or lower than those obtained by Bonfatti et al. (2011), whereas heritability values of κ-CN fractions were in line with results reported by Bonfatti et al. (2014) for the same population. Inconsistencies between studies might be caused by the different sample used or by the different sample handling conditions: in Bonfatti et al. (2011), samples were frozen right after milking, whereas in the current study samples were refrigerated.

Table 1. Cross-validation coefficient of determination of the calibration model used for infrared prediction (R^2_{CV}) and estimates of variance components and related parameters for measures (MT) and infrared predictions (IP) of fatty acid contents (g/dL of milk)[1]

		IP (n = 143,198)					MT (n = 1,008)				IP − MT difference in variance[3]					
			% of σ^2_p					% of σ^2_p			%				r_a	
Trait[2]	R^2_{CV}	σ_a	σ^2_a	σ^2_{pe}	σ^2_{htd}	σ^2_e	σ_a	σ^2_a	σ^2_{htd}	σ^2_e	σ^2_p	σ^2_a	σ^2_{htd}	σ^2_e	Estimate	SE
SFA	0.97	0.264	28	1	19	51	0.299	34	19	47	−5	−22	−2	4	0.995	0.002
MUFA	0.93	0.064	11	3	29	58	0.078	16	28	57	−3	−34	0	−1	0.992	0.008
PUFA	0.75	0.009	6	3	60	30	0.016	17	54	29	−18	−69	−9	−16	0.847	0.040
Short-chain fatty acids	0.90	0.065	24	4	28	43	0.077	30	31	39	−9	−28	−16	1	0.996	0.005
Medium-chain fatty acids	0.95	0.179	25	3	26	47	0.214	33	25	42	−7	−30	−5	2	0.994	0.004
Long-chain fatty acids	0.77	0.023	11	5	41	43	0.038	23	31	45	−24	−64	−1	−28	0.928	0.031
n-6	0.75	0.005	5	3	67	25	0.009	10	68	22	−19	−63	−21	−6	0.879	0.050
n-3	0.72	0.001	4	3	76	18	0.003	13	61	25	−19	−78	0	−41	0.711	0.077
C10:0	0.88	0.017	25	5	27	43	0.021	36	25	39	−10	−36	0	−2	0.999	0.006
C12:0	0.90	0.022	25	4	31	40	0.026	33	31	36	−8	−30	−8	1	0.996	0.005
C14:0	0.90	0.048	25	5	25	45	0.056	32	23	45	−8	−27	−2	−7	0.985	0.008
C16:0	0.92	0.130	25	4	28	43	0.158	34	27	40	−9	−32	−4	−1	0.993	0.005
C18:0	0.78	0.021	10	5	43	42	0.035	23	33	44	−22	−66	−1	−25	0.958	0.031
ΣC14:1	0.64	0.004	15	8	38	38	0.007	29	29	41	−24	−60	0	−29	0.691	0.054
ΣC16:1	0.73	0.008	14	4	27	55	0.012	23	23	55	−26	−53	−13	−25	0.917	0.035
ΣUnsaturated C18	0.91	0.056	8	3	35	54	0.078	16	31	53	−1	−48	10	0	0.977	0.011
ΣC18:1	0.90	0.049	8	3	33	55	0.068	15	31	53	−3	−48	3	1	0.980	0.011
ΣC18:1 *trans*	0.67	0.003	4	4	61	30	0.006	13	56	31	−28	−75	−22	−30	0.894	0.052
C18:1n-7 *cis*-9	0.90	0.044	8	3	33	56	0.061	14	32	53	−4	−49	−1	0	0.986	0.015
C18:1n-7 *trans*-9	0.67	0.003	4	4	63	29	0.006	11	63	26	−31	−75	−32	−22	0.809	0.048
ΣC18:2	0.76	0.007	5	2	64	29	0.011	13	62	26	−13	−62	−9	−4	0.879	0.040
C18:2n-6	0.75	0.004	3	2	72	23	0.008	8	75	17	−21	−67	−24	8	0.889	0.047
ΣCLA	0.61	0.001	3	2	73	22	0.002	6	60	34	−18	−56	0	−47	0.773	0.089
C18:2 *cis*-9,*trans*-11, CLA	0.65	0.001	5	3	60	32	0.001	10	47	43	−21	−59	0	−41	0.805	0.083
C18:3n-3	0.29	0.001	5	3	66	26	0.002	14	52	34	−26	−74	−5	−43	0.566	0.077

[1]σ_a = additive genetic standard deviation; σ^2_a = additive genetic variance; σ^2_{htd} = herd-test date variance; σ^2_{pe} = permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; r_a = additive genetic correlation between IP and MT. Standard error of σ^2_a as a percentage of σ^2_p ranged from 0.008 to 0.04, for MT, and from 0.002 to 0.006, for IP.

[2]Short-chain fatty acids = fatty acids from C4 to C10; medium-chain fatty acids = fatty acids from C12 to C16; long-chain fatty acids = fatty acids from C18 to C24; Σ = sum of fatty acids.

[3]Computed by relating the difference in variance between IP and MT to the MT variance.

Table 2. Cross-validation coefficient of determination of the calibration model used for infrared prediction (R^2_{CV}) and estimates of variance components and related parameters for measures (MT) and infrared predictions (IP) of fatty acid percentages (g/100 g of fat)[1]

		IP (n = 143,198)					MT (n = 1,040)				IP − MT difference in variance[3]					
			% of σ^2_p					% of σ^2_p			%				r_a	
Trait[2]	R^2_{CV}	σ_a	σ^2_a	σ^2_{pe}	σ^2_{htd}	σ^2_e	σ_a	σ^2_a	σ^2_{htd}	σ^2_e	σ^2_p	σ^2_a	σ^2_{htd}	σ^2_e	Estimate	SE
SFA	0.81	1.283	11	6	48	36	2.044	23	46	31	−13	−61	−11	2	0.993	0.010
MUFA	0.78	1.075	10	6	45	39	1.777	22	45	33	−19	−63	−18	−4	0.986	0.013
PUFA	0.70	0.185	5	3	75	17	0.364	14	72	14	−21	−74	−18	−1	0.893	0.040
Short-chain fatty acids	0.69	0.658	11	6	44	39	0.988	19	46	34	−22	−56	−26	−12	0.991	0.022
Medium-chain fatty acids	0.75	1.113	7	6	61	26	2.052	20	54	27	−17	−71	−6	−18	0.972	0.021
Long-chain fatty acids	0.72	0.383	6	4	64	25	0.756	18	52	30	−24	−74	−6	−38	0.952	0.045
n-6	0.71	0.116	4	3	72	20	0.209	12	75	13	−21	−69	−24	24	0.903	0.042
n-3	0.64	0.026	3	2	84	11	0.066	13	73	14	−30	−85	−19	−45	0.717	0.062
C10:0	0.73	0.239	15	6	36	43	0.355	28	34	39	−19	−55	−13	−9	0.997	0.027
C12:0	0.77	0.304	15	6	36	43	0.450	28	34	37	−16	−54	−11	−3	1.000	0.001
C14:0	0.66	0.421	10	5	44	40	0.739	24	37	39	−21	−68	−5	−17	0.939	0.031
C16:0	0.70	1.050	13	8	49	30	1.800	29	43	28	−23	−66	−13	−17	0.978	0.017
C18:0	0.72	0.346	5	4	70	21	0.691	15	57	28	−22	−75	−4	−40	0.966	0.049
ΣC14:1	0.47	0.070	13	6	49	32	0.170	38	24	39	−51	−83	2	−59	0.638	0.051
ΣC16:1	0.53	0.122	10	5	52	33	0.218	19	37	43	−37	−69	−13	−51	0.881	0.052
ΣUnsaturated C18	0.82	1.197	10	6	48	37	1.901	22	48	30	−14	−60	−14	4	0.984	0.014
ΣC18:1	0.81	1.030	9	6	46	39	1.660	20	48	32	−13	−61	−16	6	0.984	0.013
ΣC18:1 *trans*	0.52	0.083	3	2	81	14	0.167	8	79	12	−30	−75	−28	−22	0.803	0.050
C18:1n-7 *cis*-9	0.81	0.916	8	5	47	40	1.548	20	47	33	−11	−65	−11	6	0.988	0.015
C18:1n-7 *trans*-9	0.51	0.083	3	2	81	13	0.164	8	80	12	−31	−75	−30	−24	0.795	0.052
ΣC18:2	0.70	0.159	4	3	77	15	0.281	11	78	11	−21	−68	−22	12	0.913	0.027
C18:2n-6	0.71	0.107	4	3	73	20	0.185	10	78	12	−21	−67	−27	36	0.896	0.042
ΣCLA	0.44	0.025	3	2	80	15	0.050	9	66	25	−31	−75	−17	−58	0.790	0.077
C18:2 *cis*-9,*trans*-11, CLA	0.54	0.021	6	4	64	26	0.037	13	52	35	−35	−69	−19	−52	0.767	0.086
C18:3n-3	0.66	0.021	3	3	79	15	0.046	12	73	15	−22	−79	−15	−19	0.827	0.057

[1]σ_a = additive genetic standard deviation; σ^2_a = additive genetic variance; σ^2_{htd} = herd-test date variance; σ^2_{pe} = permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; r_a = additive genetic correlation between IP and MT. Standard error of σ^2_a as a percentage of σ^2_p ranged from 0.013 to 0.051, for MT, and from 0.001 to 0.006, for IP.

[2]Short-chain fatty acids = fatty acids from C4 to C10; medium-chain fatty acids = fatty acids from C12 to C16; long-chain fatty acids = fatty acids from C18 to C24; Σ = sum of fatty acids.

[3]Computed by relating the difference in variance between IP and MT to the MT variance.

Table 3. Cross-validation coefficient of determination of the calibration model used for infrared prediction (R^2_{CV}) and estimates of variance components and related parameters for measures (MT) and infrared predictions (IP) of protein fractions (g/L of milk and g/100 g of protein)[1]

		IP (n = 143,198)					MT (n = 3,337)				IP − MT difference in variance[3]					
			% of σ^2_p					% of σ^2_p			%				r_a	
Trait[2]	R^2_{CV}	σ_a	σ^2_a	σ_a	σ^2_{htd}	σ^2_e	σ_a	σ^2_a	σ^2_{htd}	σ^2_e	σ^2_p	σ^2_a	σ^2_{htd}	σ^2_e	Estimate	SE
Protein	0.81	1.77	31	8	26	34	2.37	33	24	42	−40	−44	−35	−52	0.978	0.010
Protein fraction, g/L																
Casein	0.80	1.51	29	8	30	33	2.10	32	29	40	−44	−48	−40	−53	0.969	0.010
α_{S1}-CN	0.74	0.61	20	7	47	26	0.92	33	34	34	−27	−55	2	−42	0.944	0.014
α_{S2}-CN	0.49	0.21	17	7	50	25	0.37	30	28	42	−43	−68	2	−66	0.869	0.028
β-CN	0.58	0.46	17	9	49	25	1.14	25	50	24	−76	−84	−77	−76	0.628	0.037
γ-CN	0.33	0.05	10	10	50	30	0.17	9	61	30	−93	−92	−94	−93	0.552	0.074
Total κ-CN	0.39	0.27	21	6	39	34	0.63	59	10	31	−48	−81	104	−44	0.898	0.019
Glycosylated κ-CN	0.46	0.17	16	7	42	35	0.32	43	8	49	−31	−74	252	−50	0.843	0.030
Unglycosylated κ-CN	0.22	0.14	21	7	35	37	0.45	64	7	28	−70	−91	41	−61	0.831	0.024
Whey protein	0.53	0.22	14	8	53	25	0.36	24	38	38	−38	−62	−13	−60	0.830	0.038
α-LA	0.24	0.05	7	4	69	20	0.08	12	38	50	−44	−67	1	−77	0.566	0.072
β-LG	0.48	0.19	15	8	54	24	0.33	26	33	40	−40	−67	−3	−65	0.769	0.040
Protein fraction, g/100 g of protein																
Casein	0.53	0.24	4	1	86	9	0.65	15	59	26	−40	−86	−12	−79	0.440	0.051
α_{S1}-CN	0.26	0.27	3	2	87	8	1.60	24	64	12	−77	−97	−68	−85	0.231	0.044
α_{S2}-CN	0.28	0.29	4	3	78	15	0.77	30	31	40	−3	−86	145	−63	0.797	0.038
β-CN	0.43	0.58	6	4	65	24	2.14	29	58	13	−68	−93	−63	−41	0.552	0.036
γ-CN	0.30	0.15	11	11	52	27	0.39	7	59	34	−90	−85	−92	−93	0.666	0.079
Total κ-CN	0.25	0.60	21	7	40	32	1.60	78	10	12	−49	−86	110	33	0.822	0.021
Glycosylated κ-CN	0.38	0.42	15	6	50	29	0.80	48	15	37	−14	−73	180	−32	0.903	0.021
Unglycosylated κ-CN	0.21	0.29	18	7	32	43	1.04	69	5	26	−71	−92	101	−52	0.725	0.027
α-LA	0.27	0.10	8	4	63	25	0.23	16	36	48	−64	−80	−37	−81	0.525	0.060
β-LG	0.40	0.18	3	1	87	9	0.63	19	51	30	−49	−92	−12	−85	0.310	0.051

[1]σ_a = additive genetic standard deviation; σ^2_a = additive genetic variance; σ^2_{htd} = herd-test date variance; σ^2_{pe} = permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; r_a = additive genetic correlation between IP and MT. Standard error of σ^2_a as a percentage of σ^2_p ranged from 0.015 to 0.036, for MT, and from 0.002 to 0.008, for IP.

[2]Protein = casein + whey protein; casein = α_{S1}-CN + α_{S2}-CN + β-CN + γ-CN + κ-CN; κ-CN = glycosylated κ-CN + unglycosylated κ-CN; whey protein = α-LA + β-LG.

[3]Computed by relating the difference in variance between IP and MT to the MT variance.

Like for fatty acid profile, heritability estimates for IP of protein fraction contents were lower than those for MT as a result of considerable decreases (−70% on average) in the estimated σ_a^2. In particular, heritability for IP of κ-CN and fractions thereof (glycosylated and unglycosylated) was approximately one-third of the estimate obtained for the corresponding MT. For IP of protein fraction percentages, heritability was always below 0.11 except for κ-CN fractions and σ_a^2 was 10% of the estimate obtained for MT.

In general, estimates of r_a were high (0.57–0.98) for protein fraction contents, whereas r_a for percentages was on average 0.58. These results are in contrast with those reported by Rutten et al. (2011) who, for MT and IP of milk protein composition, estimated greater heritability and r_a than those obtained in our study. Such inconsistencies might be ascribed to the different populations investigated (Holstein vs. Italian Simmental) or to the different methods used for MT assessment (capillary electrophoresis vs. HPLC).

Technological Properties

Variance components estimates for MT and IP of technological traits are reported in Table 4. Heritability estimates observed for MT of pH, RCT, k20, and a30 were consistent with the literature (Bittante et al., 2012). For t20 (the time interval from rennet addition to a curd firmness of 20 mm), a45, and a60, heritability was 0.29, 0.11, and 0.11, respectively. To our knowledge, these are the first estimates of genetic parameters for such traits. Heritability estimates for MT of curd yield traits ranged from 0.11 (water curd yield) to 0.32 (DM curd yield) and were similar to previous estimates (Bittante et al., 2014), whereas for curd composition, all heritabilities of MT were lower than 0.12.

For MCP, a considerable decrease in both the genetic and the residual variance was observed for IP in comparison with MT. As a consequence, heritabilities for IP were similar to or even greater than those for MT, with the only exception of RCT for which heritability decreased from 0.48 to 0.29. Conversely, Cecchinato et al. (2009) reported that heritability for the IP of RCT was higher than the estimates for the MT.

As for fatty acid contents, r_a for MCP were very high (>0.9). These results are in agreement with Cecchinato et al. (2009), who obtained estimates greater than 0.9 for r_a between Fourier transform infrared-predicted and measured RCT, and using different subsets of data, ranging from 0.71 to 0.87 for r_a between MT and IP of a30.

Contrary to estimates for fatty acid contents, protein composition, pH, and RCT, heritabilities for IP of curd yield traits and curd composition were equal or very similar to estimates for MT, whereas r_a was greater than 0.94 for curd yield traits and greater than 0.9 for traits related to curd composition. For such traits, Bittante et al. (2014) also estimated similar heritability for IP and MT, although they estimated slightly lower r_a values. Those authors detected also a smaller difference in the σ_a^2 estimated for IP and MT, albeit the predictive ability of calibration models was comparable to the one of our study. Such inconsistency may be explained by the exclusive use, in the estimation process of that study, of samples for which both MT and IP were available.

Lactoferrin and Minerals

Studies investigating genetic parameters of contents of LF and minerals are scarce and comparisons between variation or genetic parameters for MT and IP have never been reported for such traits. Heritability for MT of LF (Table 4) was in agreement with findings of previous studies (Klobasa et al., 1977; Gaunt et al., 1980), whereas heritability values estimated for Ca, P, Mg, and K contents were lower than previous studies (van Hulzen et al., 2009).

For LF, the decrease in the estimated σ_a^2 of IP was −83% of the MT estimate and heritability of IP (0.14) was lower than literature estimates. All previous estimates of heritability for LF were from studies on Holstein cows and ranged from 0.2 (Soyeurt et al., 2007) to 0.37 (Leclercq et al., 2013). However, in those studies, HTD was included in the statistical models as a fixed effect, and as a consequence, higher heritability values, compared with our estimates, are expected.

Unlike what was observed for fatty acid and LF, heritabilities for IP of mineral contents were very similar to those obtained for MT, although lower than those reported by Soyeurt et al. (2008). The higher heritability estimates obtained for IP of LF and minerals obtained by Soyeurt et al. (2007) and (2008), respectively, might have been due to the higher predictive ability of calibration models.

For P content, predictions were more heritable than measurements (h^2: 0.25 vs. 0.16). Although all variance estimates for IP of mineral contents were low relative to MT, for P content the decrease in the estimated σ_a^2 was small relative to the decrease in the HTD and residual variance. Although r_a was relatively low (0.61) for LF, it was very large (>0.89) for minerals, suggesting that IP of mineral concentrations may play a role in selective breeding addressed to modify the content of major minerals in milk.

Table 4. Cross-validation coefficient of determination of the calibration model used for infrared prediction (R^2_{CV}) and estimates of variance components and related parameters for measures (MT) and infrared predictions (IP) of technological traits, lactoferrin, and mineral contents[1]

		IP (n = 143,198)					MT[3]				IP − MT difference in variance[4]					
			% of σ^2_p					% of σ^2_p			%				r_a	
Trait[2]	R^2_{CV}	σ_a	σ^2_a	σ^2_{pe}	σ^2_{htd}	σ^2_e	σ_a	σ^2_a	σ^2_{htd}	σ^2_e	σ^2_p	σ^2_a	σ^2_{htd}	σ^2_e	Estimate	SE
pH	0.79	0.034	18	6	56	20	0.048	30	42	27	−12	−48	15	−35	0.979	0.009
Coagulation property																
RCT, min	0.69	2.629	29	18	15	38	3.610	48	13	40	−14	−47	3	−17	0.948	0.013
k20, min	0.42	0.333	26	17	20	38	0.597	7	76	17	−92	−69	−98	−82	0.970	0.023
t20, min	0.55	2.551	24	20	18	38	3.540	29	30	41	−38	−48	−64	−42	0.914	0.028
a30, mm	0.32	2.328	23	17	23	38	3.975	27	16	57	−59	−66	−41	−73	0.925	0.028
a45, mm	0.20	0.963	16	8	46	30	1.478	11	21	68	−71	−58	−36	−87	1.000	0.001
a60, mm	0.21	0.945	15	7	49	29	1.431	11	25	64	−69	−56	−40	−86	1.000	0.004
Curd yield, g/100 g of milk																
Overall	0.67	1.912	12	3	61	24	2.398	13	45	42	−29	−36	−4	−60	1.000	0.001
DM	0.85	0.503	27	6	25	43	0.605	32	21	47	−18	−31	−2	−26	0.998	0.012
Water	0.64	1.477	9	3	69	19	1.958	11	51	38	−31	−43	−7	−65	0.950	0.073
Protein	0.62	0.158	22	8	43	27	0.209	23	32	45	−42	−43	−21	−65	0.992	0.041
Fat	0.69	0.273	20	6	22	52	0.351	21	14	65	−35	−39	4	−48	0.935	0.048
Curd composition, %																
Moisture	0.61	0.672	3	2	88	7	1.154	7	64	29	−28	−66	−2	−83	0.929	0.107
Protein in DM	0.43	1.014	9	6	32	53	1.692	11	17	72	−56	−64	−14	−68	1.000	0.000
Fat in DM	0.35	1.130	8	5	33	54	1.851	8	16	76	−61	−63	−20	−72	0.904	0.144
Lactoferrin, log	0.42	0.203	14	12	32	42	0.493	36	27	37	−58	−83	−51	−52	0.611	0.074
Mineral, g/dL																
Ca	0.48	0.006	14	7	46	32	0.008	15	55	30	−40	−43	−50	−36	1.000	0.000
P	0.43	0.005	25	8	42	25	0.006	16	52	32	−52	−25	−62	−63	0.997	0.064
Mg	0.46	0.003	16	6	42	36	0.005	19	40	40	−39	−50	−37	−45	0.886	0.211
K	0.41	0.004	7	4	63	26	0.006	7	54	39	−50	−50	−41	−67	0.953	0.070

[1]σ_a = additive genetic standard deviation; σ^2_a = additive genetic variance; σ^2_{htd} = herd-test date variance; σ^2_{pe} = permanent environmental variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; r_a = additive genetic correlation between IP and MT. Standard error of σ^2_a as a percentage of σ^2_p ranged from 0.012 to 0.078, for MT, and from 0.002 to 0.012, for IP.

[2]RCT = rennet coagulation time; k20 = curd firming time; t20 = time from rennet addition to k20; a30 = curd firmness at 30 min from rennet addition; a45 = curd firmness at 45 min from rennet addition; a60 = curd firmness at 60 min from rennet addition.

[3]Measures of pH and milk coagulation properties were available for 3,438 and 3,266 samples, respectively; curd yield and composition were available for 1,177 samples; the contents of lactoferrin and minerals were available for 558 and 689 samples, respectively.

[4]Computed by relating the difference in variance between IP and MT to the MT variance.

Effect of Reliability of Calibrations on the Estimated Additive Genetic Variation in Infrared Predictions

The relationship between the reliability of calibrations, as measured by R^2_{CV}, and the decrease in the phenotypic variance of IP compared with the one estimated for MT is shown in Figure 1a. As expected, a significant correlation (r = 0.78; $P < 0.01$) was present between the predictive ability of calibration models and the estimated variation in IP. A decreased phenotypic variation is inherent when predictions are used in place of original measures of traits of concern. For the 92 traits investigated in our study, the average decrease in total variance of IP compared with the variance of MT was approximately 35%, but it was lower than 10% for traits predicted from calibration models exhibiting R^2_{CV} greater than 0.9. Within the different components of phenotypic variance, the greatest decreases in the estimated variances for IP, compared with the ones for MT, were observed for the σ^2_a. Also the decrease in the IP σ^2_a was related to the reliability of calibration models, albeit the relationship was weaker (r = 0.61; $P < 0.01$; Figure 1b) than that observed for the phenotypic variance. The decrease in σ^2_a was on average 64%, ranging from 22 (for the content of SFA measured on a milk basis) to 97% (for the content of α_{S1}-CN expressed on a protein basis). For traits exhibiting R^2_{CV} greater than 0.9, the decrease in σ^2_a ranged from approximately 20 to 50%. A negative relationship between the phenotypic, genetic, or residual variance and the predictive ability of calibration models was also detected in a study using a small number of beef quality traits predicted by near infrared spectroscopy (Cecchinato et al., 2011).

Differences in HTD variance between IP and MT were generally small (−9% on average) and not related to the R^2_{CV} of calibration models (data not reported). In a previous study on MCP variation, the HTD variance estimated for IP did not decrease when compared with the one for MT of RCT, but it was nearly halved for IP of a30 (Cecchinato et al., 2009). Conversely, Bittante et al. (2014) reported that the HTD component of the IP variance decreased more than the other variance components did, leading to slightly increased estimates of across-herd heritability of IP in comparison with estimates of intra-herd heritability.

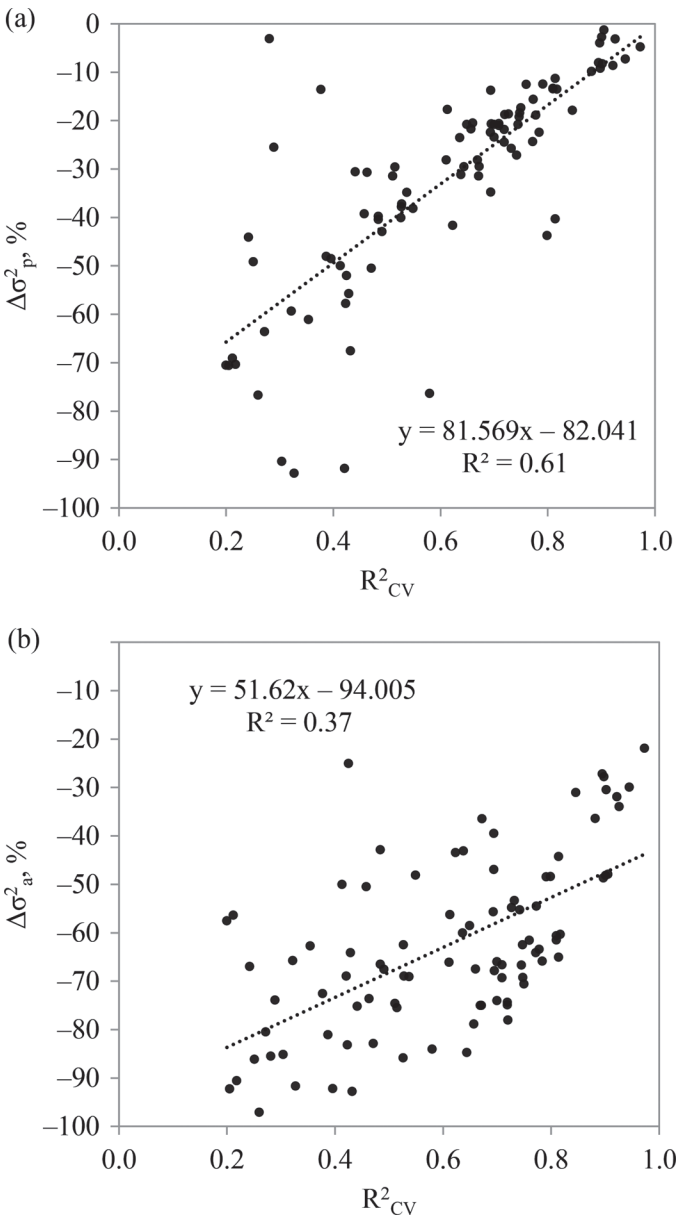

Figure 1. Relationship between the coefficient of determination in cross-validation (R^2_{CV}) of the calibration model used for infrared prediction and the decrease (a) in phenotypic variance $\left(\Delta\sigma^2_p\right)$ and (b) in additive genetic variance $\left(\Delta\sigma^2_a\right)$ estimates of infrared predictions compared with the measured traits.

Heritability of Measured and Predicted Traits

In our study, 88 out of 92 traits exhibited lower heritability estimates for IP than for the corresponding MT. Increased heritability estimates for IP relative to MT were observed for k20 and P, and to a lower extent, for a45 and a60 (Table 4). For technological properties of milk (MCP, curd yield, and composition) and mineral contents, heritability of IP was very similar to the estimate obtained for MT. In the majority of previous investigations conducted on milk technological properties, heritability estimates for IP were greater than those for MT because the decreased σ^2_a estimated for IP relative to MT also corresponded to a decrease in the estimated residual variance, particularly for traits with

low R^2_{CV} in calibration (Cecchinato et al., 2009; Bittante et al., 2014). This is in contrast with findings of our study. However, a common feature of all previous studies comparing estimates of variance components or genetic parameters for MT and IP was the use of IP obtained for the same set of data exploited, as a whole (Bittante et al., 2014) or split in different subsets (Cecchinato et al., 2009; Bittante et al., 2014), in calibration. To our knowledge, the present study is the first investigation where genetic parameters of MT and IP have been estimated for a large number of traits (92) using IP obtained at the population level and not focusing exclusively on the reference set of data used to develop calibration models.

In a preliminary analysis, we have estimated variance components for IP and MT of the 92 traits analyzing only data belonging to the calibration set (n = 1,230). For many traits, the estimated σ^2_a for MT were much lower than that obtained when predictions were performed using all spectral data available at the population level and included in the bivariate analysis. As a consequence, many MT had also lower heritability estimates than those obtained when IP of the entire population were included in the analysis. In agreement with previous studies (Cecchinato et al., 2009; Bittante et al., 2014), the analysis carried out on the calibration set led to small differences in the σ^2_a between IP and MT and also to similar or slightly higher heritability estimates for IP compared with MT.

For the 92 investigated traits, the additive genetic covariance between MT and IP obtained analyzing only data belonging to the calibration set was on average 74% of that obtained when predictions were performed using all spectral data available at the population level. In particular, the genetic covariance was 46% of that obtained analyzing the population spectra for fatty acid contents, 81% for the percentage of fatty acid in total fat, 82% for minerals, 31% for LF, 93% for contents of protein fractions, 120% for percentage of protein fractions in total protein, 41% for pH and MCP traits, and 79% for cheese yield traits and curd composition.

When all the available spectral data were considered, the additive genetic covariance between MT and IP, as well as the additive genetic relationships between animals in the calibration set and those in the population, enhanced the estimation of σ^2_a for MT and led to increased estimates of σ^2_a for most traits. This occurred especially for MCP, curd yield, curd composition, and minerals, and to a lesser extent, for fatty acids.

For protein composition, estimates of variance components and genetic correlations between MT and IP were not influenced by the use of either the reference data set or the population data. For protein fractions, heritability of IP was always lower than heritability of the MT, as observed also by Rutten et al. (2011).

In agreement with previous studies (Rutten et al., 2010; Cecchinato et al., 2011), the magnitude of heritability estimates for IP was not related to the R^2_{CV} of calibration models (data not reported). Hence, R^2_{CV} of calibration models, the estimated heritability for IP, the decrease in σ^2_a of IP relative to MT, as well as the genetic covariance and correlation between MT and IP are all key factors affecting the potential usefulness of IP for selective breeding programs.

Effect of Reliability of Calibrations on the Estimated Genetic Correlation Between Measured and Infrared-Predicted Traits

The utility of calibration models for practical applications is evaluated on the basis of the R^2_{CV}, which is a measure of the relationship between MT and IP. According to Soyeurt et al. (2011), equations with R^2_{CV} greater than 0.95 are useful in milk payment systems and equations with R^2_{CV} greater than 0.75 can be used for selective breeding purposes. For selection, the usefulness of calibrations relies on the relative genetic gain achievable using IP, as indicator traits, in place of MT, which often are not available at the population level or cannot be acquired routinely. The achievable genetic gain is affected by the heritability of IP, the magnitude of the additive genetic correlation between MT and IP, and the additive genetic variation in MT (Falconer and Mackay, 1996).

Consistent with Rutten et al. (2010), a positive relationship ($r = 0.55$; $P < 0.01$) between R^2_{CV} and the estimated r_a between MT and IP has been detected for the traits investigated in this study (Figure 2). When the predictive ability of calibrations is very high, differences between IP and MT are small. As a consequence, the estimation of genetic parameters for IP yields estimates approximately identical to those for MT. When the reliability of calibrations is low, differences in estimates between IP and MT get larger. In our study, for calibration models exhibiting R^2_{CV} higher than 0.75, r_a between IP and MT were greater than 0.9. However, the variability in the estimated correlations increased when R^2_{CV} decreased, and for calibration models of moderate predictive ability, estimates of r_a ranged from 0.2 to 1.

Such results are consistent with the relationship between the coefficient of determination in validation and the estimated genetic correlation between MT and IP described by Rutten et al. (2010) and with findings by Cecchinato et al. (2009) and Bittante et al. (2014), who reported that the variation in the estimated genetic

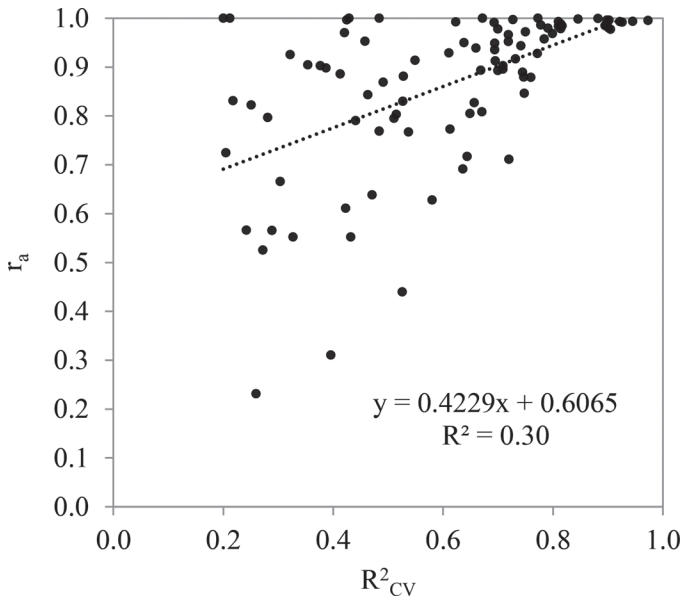

Figure 2. Relationship between the coefficient of determination in cross-validation (R^2_{CV}) of the calibration model used for infrared prediction and the estimated additive genetic correlation (r_a) between measured and infrared predicted traits.

parameters for IP and genetic correlations between IP and MT was greater for traits exhibiting low R^2_{CV} in calibration. When the r_a between IP and MT is large, even calibrations showing low predictive performance may be used in selective breeding, especially considering that multiple predictions per animal will be available.

In agreement with results of previous investigations (Cecchinato et al., 2009, 2011; Rutten et al., 2010, 2011; Bittante et al., 2014), the estimated r_a between IP and MT obtained in our study were very high, albeit most calibration models were of moderate predictive ability. The r_a between MT and IP was on average 0.83 when predictions were obtained from the calibration set only and 0.85 when all the available spectra were included in the analysis.

A large positive relationship ($r = 0.69$; $P < 0.01$) between r_a and the decrease in the estimated σ^2_a of IP compared with MT has been detected (Figure 3). From a theoretical point of view, for IP traits estimated very accurately ($R^2_{CV} = 1$), the value of σ^2_a is expected to be identical to that of MT and $r_a = 1$. This would be true if calibration models having $R^2_{CV} = 1$ had actually $R^2 = 1$ for data not included in the calibration set (i.e., external validation), but the coefficient of determination in external validation is usually lower than the one in cross-validation and our IP are obtained for the entire population, i.e., on a very large number of samples that are not included in the calibration set. As evidenced from our results, values of estimated σ^2_a for IP, when R^2_{CV} is close to 1, were lower than the ones of MT (i.e., lower than expected). When bivariate analyses between IP and MT were performed, on the calibration set only, the differences in σ^2_a between IP and MT were greatly reduced (results not reported in tables). This suggests that the true coefficient of determination between MT and IP in population is lower than the R^2_{CV}.

Infrared predictions with reduced σ^2_a compared with MT are those that are more likely predicted with a low accuracy and are more likely to exhibit a low r_a value. However, it is worth noting that even though σ^2_a of IP is reduced compared with MT, for a group of traits (e.g., contents of fatty acid) the r_a is very close to 1. This might be due to the fact that σ^2_a of IP is part of the denominator in the calculation of r_a. Consequently, a reduction in σ^2_a can increase the estimates of r_a.

Genetic Gain

The additive genetic correlation between IP and MT is largely determining the relative amount of selection response that can be expected when using IP in place of MT in dairy cattle breeding schemes where progeny testing involves a large number of daughters per sire (Rutten et al., 2010). Rutten et al. (2010) reported that when exploiting IP of fatty acid, predicted by models showing coefficients of determination in validation between 0.53 and 0.77, the expected genetic gain

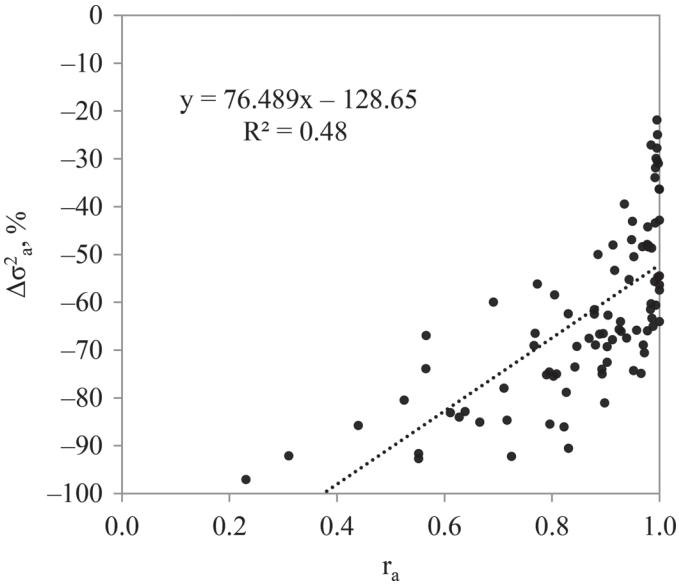

Figure 3. Relationship between the estimated additive genetic correlation (r_a) between measured and infrared predicted traits and the decrease in the estimated additive genetic variance $\left(\Delta\sigma^2_a\right)$ for infrared predictions compared with the one for measured traits.

was almost equal to the one achievable using fatty acid composition assessed by GC. Cecchinato et al. (2009) estimated that, using IP for RCT and a30 from calibration models exhibiting R^2_{CV} in the range between 0.46 and 0.69, the correlated genetic response in MT was 94 and 80%, respectively, of the one achievable when performing direct selection for MT. Following the same approach used by Rutten et al. (2010) to estimate the genetic gain (i.e., assuming a large number of daughters per sire), the genetic correlations estimated in this study indicate that the use of IP as indicator traits will yield, depending on the trait of choice, at least 57 and 55% of the potential genetic gain that might be achieved by direct selection of fatty acid and protein fraction contents, respectively. The genetic gain would be at least 93, 94, and 90% of the potential genetic gain achievable by direct selection for MCP, curd yield, and curd composition, respectively, 61% for LF, and at least 89% for minerals. Within the 92 investigated traits, protein fraction percentages and LF were the traits exhibiting the lowest estimated r_a between MT and IP, indicating that the genetic gain achievable using IP of such traits as indicator traits in selective breeding would be moderate relative to the one achievable for most traits investigated in this study.

Recent studies (Eskildsen et al., 2014, 2016) demonstrated that predictions of individual fatty acids, protein fractions, and MCP by infrared spectroscopy in milk are indirect and are based primarily on covariation between these traits and fat or protein content, suggesting that indirect models may not be useful in breeding programs because IP are providing information related to total fat or protein. In addition, indirect correlations responsible for successful predictions in a sample set may not be valid for samples of a different nature, meaning that calibration models may result in incorrect predictions in future samples. Hence, to fully evaluate the potential of using IP in selection programs, it is necessary to quantify the amount of additional information provided by these new traits compared with the one already provided by traits under selection.

CONCLUSIONS

Genetic parameters of 92 traits and their IP and the genetic correlations between MT and IP were estimated for the Italian Simmental cattle population. Results indicates that IP can be used as indicator traits in breeding programs for the enhancement of fine composition and technological properties of milk and that indirect selection for IP will be able to provide satisfactory responses. Calibration equations having high prediction accuracy would lead to faster genetic progress, but even less accurate equations might be successfully used for breeding purposes. Even when selective breeding for such traits is not of concern, availability of IP and estimated genetic parameters thereof is useful to monitor changes in milk fine composition and technological properties resulting, as a correlated response, from selection on breeding goal traits. Future studies are necessary to quantify the amount of additional information provided by the IP compared with the one already provided by traits under selection, such as protein and fat content.

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APPENDIX

Table A1. Descriptive statistics for measured and infrared predicted traits[1]

	Measure					Infrared prediction				
Trait	N	Mean	SD	Minimum	Maximum	N	Mean	SD	Minimum	Maximum
Fatty acid, g/dL										
SFA	1,007	2.879	0.517	1.551	4.659	143,194	2.918	0.517	0.826	4.983
MUFA	1,008	0.844	0.183	0.393	1.572	143,197	0.904	0.210	0.249	2.182
PUFA	1,006	0.149	0.037	0.073	0.300	140,759	0.150	0.036	0.070	0.336
Short-chain fatty acids	1,007	0.631	0.131	0.313	1.052	143,194	0.612	0.134	0.131	1.222
Medium-chain fatty acids	1,007	1.930	0.370	1.023	3.163	143,197	1.980	0.375	0.602	3.814
Long-chain fatty acids	1,007	0.253	0.085	0.066	0.599	143,189	0.269	0.070	0.041	0.644
n-6	1,008	0.081	0.024	0.037	0.188	142,702	0.083	0.025	0.005	0.199
n-3	1,004	0.021	0.007	0.005	0.043	143,145	0.022	0.006	0.004	0.053
C10:0	1,006	0.144	0.032	0.064	0.239	143,175	0.138	0.034	0.020	0.292
C12:0	1,005	0.172	0.041	0.067	0.299	143,142	0.167	0.046	0.020	0.379
C14:0	1,006	0.524	0.101	0.279	0.852	143,196	0.530	0.102	0.133	0.974
C16:0	1,004	1.295	0.256	0.673	2.070	143,194	1.346	0.266	0.315	2.597
C18:0	1,007	0.236	0.081	0.062	0.564	143,194	0.258	0.068	0.034	0.649
ΣC14:1	1,005	0.042	0.014	0.015	0.096	143,182	0.044	0.013	0.000	0.107
ΣC16:1	1,007	0.088	0.025	0.041	0.209	143,154	0.090	0.024	0.020	0.222
ΣUnsaturated C18	1,006	0.797	0.181	0.353	1.477	143,193	0.851	0.205	0.181	2.069
ΣC18:1	1,006	0.666	0.157	0.290	1.293	143,186	0.719	0.181	0.202	1.850
ΣC18:1 *trans*	1,006	0.052	0.014	0.021	0.116	142,060	0.052	0.015	0.020	0.162
C18:1n-7 *cis*-9	1,007	0.583	0.146	0.255	1.234	143,193	0.643	0.169	0.135	1.762
C18:1n-7 *trans*-9	1,007	0.050	0.014	0.020	0.126	142,140	0.050	0.015	0.020	0.149
ΣC18:2	1,001	0.111	0.027	0.056	0.193	142,882	0.115	0.031	0.010	0.290
C18:2n-6	1,008	0.069	0.021	0.031	0.164	142,703	0.076	0.025	0.010	0.198
ΣCLA	1,008	0.018	0.006	0.006	0.042	141,250	0.017	0.006	0.000	0.049
C18:2 *cis*-9,*trans*-11, CLA	1,008	0.014	0.005	0.005	0.035	141,960	0.013	0.004	0.003	0.037
C18:3 n-3	1,006	0.014	0.005	0.004	0.036	143,195	0.022	0.004	0.005	0.039
Fatty acid, g/100 g of fat										
SFA	1,039	74.28	3.50	61.52	82.75	143,191	73.65	4.00	49.19	88.81
MUFA	1,039	21.84	3.06	14.54	34.68	143,194	22.53	3.48	9.47	45.67
PUFA	1,037	3.86	0.79	2.20	6.50	143,182	3.91	0.85	0.11	7.45
Short-chain fatty acids	1,039	16.32	2.00	9.63	22.25	143,189	15.19	2.01	4.09	22.92
Medium-chain fatty acids	1,039	49.80	3.96	37.25	59.42	143,193	49.91	4.30	27.08	68.83
Long-chain fatty acids	1,039	6.54	1.86	2.01	13.44	143,179	7.10	1.66	1.00	14.89
n-6	1,040	2.11	0.55	1.10	3.98	142,943	2.09	0.54	0.20	4.80
n-3	1,038	0.54	0.16	0.15	1.06	143,192	0.56	0.15	0.07	1.30
C10:0	1,038	3.72	0.57	1.59	5.41	143,150	3.42	0.63	0.10	5.62
C12:0	1,037	4.44	0.76	1.74	6.78	143,029	4.05	0.82	0.10	6.99
C14:0	1,036	13.53	1.36	7.74	16.67	143,193	13.21	1.43	3.62	18.45
C16:0	1,039	33.49	3.07	26.05	41.47	143,195	33.42	2.98	19.05	48.90
C18:0	1,036	6.08	1.76	2.21	11.68	143,195	6.83	1.67	0.12	14.46
ΣC14:1	1,039	1.08	0.30	0.36	2.22	143,195	1.08	0.24	0.01	2.15
ΣC16:1	1,039	2.28	0.47	1.27	4.58	143,190	2.22	0.40	0.65	4.46
ΣUnsaturated C18	1,038	20.68	3.54	12.63	34.07	143,191	21.38	3.89	6.75	44.93
ΣC18:1	1,037	17.28	3.08	10.33	29.56	143,190	18.10	3.54	5.24	40.72
ΣC18:1 *trans*	1,037	1.35	0.31	0.72	3.11	143,198	1.29	0.48	−0.27	4.90
C18:1n-7 *cis*-9	1,036	15.09	2.90	8.19	27.11	143,198	16.15	3.35	2.83	40.17
C18:1n-7 *trans*-9	1,037	1.30	0.31	0.61	3.08	142,947	1.26	0.46	0.20	4.46
ΣC18:2	1,037	2.88	0.61	1.70	4.77	143,169	3.00	0.75	0.21	6.85
C18:2n-6	1,040	1.79	0.50	0.88	3.47	143,078	1.86	0.51	0.10	4.63
ΣCLA	1,038	0.46	0.13	0.19	0.94	141,374	0.42	0.14	0.01	1.11
C18:2 *cis*-9,*trans*-11, CLA	1,037	0.35	0.10	0.14	0.77	143,038	0.32	0.09	0.05	0.79
C18:3n-3	1,036	0.37	0.11	0.12	0.77	142,934	0.40	0.11	0.05	0.95
Protein, g/L	3,337	39.01	4.65	23.08	58.45	143,198	37.05	3.94	21.90	53.22
Protein fraction, g/L										
Casein	3,336	33.91	4.23	20.42	49.99	143,198	31.48	3.43	18.33	45.90
α_{S1}-CN	3,329	12.77	1.59	7.17	18.94	143,196	13.07	1.55	7.18	20.52
α_{S2}-CN	3,336	4.22	0.71	1.70	6.89	143,196	4.45	0.59	1.82	6.64
β-CN	3,336	11.95	2.48	5.38	20.95	143,198	9.82	1.29	5.13	15.17
γ-CN	3,334	1.31	0.59	0.23	3.39	143,184	0.66	0.18	0.00	1.45
Total κ-CN	3,335	3.63	0.83	1.05	6.88	143,197	3.74	0.64	0.74	6.79
Glycosylated κ-CN	3,324	1.63	0.55	0.58	4.74	143,173	1.82	0.47	0.11	4.31

Continued

Table A1 (Continued). Descriptive statistics for measured and infrared predicted traits[1]

	Measure					Infrared prediction				
Trait	N	Mean	SD	Minimum	Maximum	N	Mean	SD	Minimum	Maximum
Unglycosylated κ-CN	3,331	2.02	0.54	0.69	4.17	143,193	1.79	0.31	0.10	3.13
Whey protein	3,330	5.09	0.78	2.66	8.04	143,195	5.44	0.66	2.85	8.03
α-LA	3,328	1.28	0.23	0.63	2.24	143,198	1.26	0.18	0.42	1.96
β-LG	3,335	3.81	0.68	1.64	7.44	143,198	4.20	0.57	2.00	6.84
Protein fraction, g/100 g of protein										
Casein	3,331	86.89	1.74	80.02	90.96	143,196	85.22	1.28	80.48	89.68
α_{S1}-CN	3,332	32.91	3.32	25.07	42.63	143,198	34.99	1.68	29.04	42.98
α_{S2}-CN	3,333	10.83	1.36	5.67	15.94	143,193	11.96	1.40	6.51	16.86
β-CN	3,336	30.49	4.23	17.93	40.77	143,194	26.43	2.29	15.89	36.59
γ-CN	3,332	3.35	1.46	0.66	8.91	143,185	1.79	0.48	0.01	4.23
Total κ-CN	3,332	9.31	1.72	3.86	15.55	143,195	10.12	1.30	3.70	16.29
Glycosylated κ-CN	3,325	4.14	1.19	1.32	9.47	143,198	5.29	1.11	0.73	10.71
Unglycosylated κ-CN	3,329	5.17	1.23	1.59	8.77	143,190	4.80	0.73	0.67	8.34
α-LA	3,333	3.30	0.61	1.47	6.34	143,198	3.41	0.41	1.51	4.85
β-LG	3,335	9.80	1.51	5.30	16.36	143,197	11.35	1.04	7.77	15.30
pH	3,438	6.73	0.08	6.44	7.08	143,195	6.75	0.08	6.32	7.09
Coagulation property										
RCT, min	3,266	17.14	5.06	4.02	47.13	143,108	17.72	5.08	2.01	57.90
k20, min	3,006	4.54	2.32	0.77	15.20	143,196	6.94	0.67	4.12	11.65
t20, min	3,024	21.22	6.58	0.00	61.18	143,174	24.02	5.40	4.36	59.29
a30, mm	3,220	30.97	7.57	1.00	46.00	143,192	35.24	4.96	0.86	53.87
a45, mm	1,138	34.94	4.31	15.00	47.00	143,198	35.28	2.57	23.29	46.91
a60, mm	1,144	33.12	4.18	18.00	47.00	143,198	33.36	2.63	22.05	45.82
Curd yield, g/100 g of milk										
Overall	1,177	26.67	6.36	11.11	52.02	143,193	29.34	5.92	11.42	55.74
DM	1,058	7.57	1.12	4.21	11.36	143,198	7.83	1.09	3.93	12.45
Water	1,069	19.28	5.70	9.20	42.22	143,195	21.55	5.18	6.16	45.75
Protein	1,067	2.89	0.44	1.55	4.72	143,198	2.90	0.38	1.55	4.71
Fat	1,053	3.69	0.82	1.03	6.45	143,197	3.77	0.65	1.09	6.18
Curd composition, %										
Moisture	1,072	71.15	4.18	62.17	83.93	143,198	72.85	3.81	60.62	87.78
Protein in DM	1,065	38.59	5.20	26.98	64.44	143,195	37.25	3.38	23.76	54.04
Fat in DM	1,052	48.51	6.49	21.73	71.82	143,196	50.18	4.01	26.20	67.02
Lactoferrin, log	558	4.56	0.85	2.26	6.14	143,197	4.52	0.67	1.26	7.76
Mineral, g/dL										
Ca	689	0.121	0.019	0.074	0.185	143,197	0.133	0.017	0.076	0.229
P	688	0.101	0.014	0.061	0.139	143,197	0.106	0.012	0.062	0.164
Mg	689	0.010	0.002	0.005	0.015	143,198	0.011	0.001	0.005	0.019
K	689	0.159	0.023	0.091	0.217	143,198	0.168	0.017	0.093	0.244

[1]Short-chain fatty acids = fatty acids from C4 to C10; medium-chain fatty acids = fatty acids from C12 to C16; long-chain fatty acids = fatty acids from C18 to C24, protein = casein + whey protein; casein = α_{S1}-CN + α_{S2}-CN + β-CN + γ-CN + κ-CN; κ-CN = glycosylated κ-CN + unglycosylated κ-CN; whey protein = α-LA + β-LG; RCT = rennet coagulation time; k20 = curd firming time; t20 = time from rennet addition to k20; a30 = curd firmness at 30 min from rennet addition; a45 = curd firmness at 45 min from rennet addition; a60 = curd firmness at 60 min from rennet addition.