

Estimation Genetic Parameters of Semen Quality Traits in Iranian Holstein Bulls

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Abstract: For the design of any successful breeding program, knowledge about semen quality traits is greatly important and per-required. Reproductive performance is of paramount economic importance in the livestock industry, including dairy cattle production. Despite the importance of the quality of semen used in artificial insemination to the reproductive success of dairy herds, few studies have estimated the extent of genetic variability in semen quality traits. In this study, records collected by Jahed (station 1) and Sheykh Hasan (station 2) breeder centers from 1991 to 2013, were used to estimate variance components, heritability, and repeatability for sperm quality traits. Records information was analyzed by wombat software. Data were analyzed by using the repeatability model in three models, first by year-season-station, secondary by station, and third by year. In the first model, maximum heritability and repeatability (0.9755) estimated the total number of sperm in milt ejaculation trait. In the second model, maximum heritability (0.96), that was in Jahed center, estimated for total number sperm in milt ejaculation, maximum repeatability (1), that was in Jahed center, too, estimated for sperm volume and maximum repeatability (1), that was in both breeding centers, estimated for motility to post-thaw motile ratio trait. In the third model, maximum heritability and repeatability (0.54), estimated for (liveafmil) trait. Maximum heritability and repeatability estimates for the total number of post-thaw motile sperm per milt ejaculation trait were 0.19 and 0.32, respectively. The objectives of this study were to estimate genetic parameters of semen quality traits using data from routine semen collection in the Iranian Holstein.

Keywords: Genetic Parameters, Traits Quantitative and Qualitative, Holstein Cows, Semen

1. Introduction

Holstein is the main cattle breed used in Iran, being the largest commercial herd in the world. Beyond the importance of male reproductive efficiency for farm profit, the use of reproductive techniques, mainly artificial insemination, makes evaluating male reproductive traits even more important. Estimation of genetic parameters increases the knowledge on traits variances and allows envisaging the possibility of the inclusion of new traits as the selection criterion.

Artificial insemination (AI) plays an important role in dairy cattle because it is directly related to fertility. It is the main reproductive tool used for genetic improvement by introducing genes from superior sires into herds. Semen traits are important for the widespread use of superior bulls.

The quality of the semen depends on different factors such as the number of motile spermatozoa, sperm motility, sperm viability, abnormal spermatozooids, and also some genetic

factors associated with the bull.

In addition to the importance of semen quality for fertility, sperm production of bulls in AI studs needs to be optimized for economic reasons, especially because the demand for some AI sires are very high [1].

Genetic parameters need to be estimated between all the involved traits to optimize management and selection for both conception rate and sperm production. These parameters can indicate which traits can be efficiently selected, which traits have high repeatability (for which successive records can be predicted with high precision), etc.

Semen traits such as progressive sperm motility (SM) and ejaculate volume (VE) are complex and affected by genetic factors [2] as well as by non-genetic factors such as handler, season, the interval between ejaculations, and age [3]. For the design of any successful breeding program, knowledge about semen quality traits is greatly important and per-required. Because of the critical role of bulls through artificial

insemination in the knowledge about semen characteristics, genetic improvement of the dairy cattle herds, and genetic factors, which affect semen parameters, is essential. In addition, semen with poor fertility requires more units of semen to establish a successful pregnancy and produce live offspring. Nonetheless, both impacts are economically important factors that the producers consider, leading to the rejection of bulls with poor semen quality and investing mainly in highly fertile sires. The summary of previous literature highlights semen traits and their key roles in cows' upcoming fertility and pregnancy within herds [4].

Additionally, previous reports supported a low heritability scenario of semen characteristics in livestock species [5].

Reproductive performance is of paramount economic importance in the livestock industry, including dairy cattle production. Several studies in dairy and beef cattle have explored the genetic parameters of female fertility [6]. However, few have investigated the genetics of service sire fertility and its association with semen characteristics. Low semen quality and quantity have been shown to contribute to a significant percentage of reproductive failures in AI dairy cattle [7].

Semen quality traits are routinely recorded at AI centers for production and marketing decisions. Thus, large-scale data on these traits are available and can be an important source of correlated information to improve traditional fertility traits registered in females. Traditional female fertility traits, in general, tend to have low heritability in different cattle breeds [8]. Previous studies on genetic parameters of semen quality traits indicate moderate heritability estimates [9]. Given that the pregnancy rate for males is significantly affected by semen quality [7] and that it is highly genetically correlated with

pregnancy rate in females [10], selection for semen quality traits could potentially lead to improvement in pregnancy rate, not only for males but also for females [8].

From a practical, industry-oriented perspective, it is obvious that semen quality traits play a key role in dairy cattle breeding. Based on the results of recent studies, it is now evident that semen quality reveals a considerable genetic component, both through moderate heritability estimated by models assuming an infinitesimal model of inheritance as well as through several candidate genes identified through genome-wide association studies. As many traits describing semen quality undergo routine recording, it is tempting to consider including the phenotypes in genetic evaluation.

The objectives of this study were to estimate genetic parameters of semen quality traits using data from routine semen collection in the Iranian Holstein.

2. Materials and Methods

Pedigree information:

For this study, 309 bulls were selected from two breeding stations in the Northwest of Iran (91 bulls, station 2) and the National Livestock Improvement Center (218 bulls, station 1), which were in the sperm production stage between 1991- 2013.

Pedigree information included after initial editing removal of animals whose parents were not identified and did not breed was used. Preliminary studies on this pedigree showed that the information of the imported sperm pedigrees was incomplete, and in most cases, the ancestral information they are limited. Also, Descriptive statistics of measured traits are presented in Table 1.

Table 1. Statistical summary of various studied traits.

Trait	Number of records	mean	Standard deviation	minimum	Maximum
Sperm volume per ml of ejaculation	9399	5/69	1/56	0/50	12/70
Sperm concentration per ml of ejaculation	9206	1117/31	320/87	9	2492
Mobility ratio before and after ejaculation	8610	1/72	0/33	0/77	3
Percentage of mobility after thawing	8839	38/78	10/66	5	89
Percentage of motility after ejaculation	9395	64/42	12/49	22/50	95
Number of live sperm per ml	9112	4020/81	1593/96	11/25	9509/71
Ejaculation in fresh semen					
Total number of live sperm in the ejaculation	8749	2412/08	1002/67	146/25	6299/41
Total number of live sperm per	9144	718/84	249/96	4/50	1591/20
MI ejaculation after thawing					
Total number of sperm in the ejaculation	9167	6261/51	2230/93	4/50	14597/01
Number of live sperm per ml	8748	430/44	163/64	24/72	1009/43
Ejaculation after thawing					
Number of production payot	8872	193/27	85/29	20/01	500

Traits measured:

In this regard, several related traits of semen quality were considered, including sperm volume, sperm concentration (sp), motility to the post-thaw motile ratio (moveper), post-thaw motility (moaen), motility (mo), the number of fresh motile sperm per milliliter in fresh semen (livetobef), the total number of motile sperm in milt ejaculation (totsp), the total number of post-thaw motile sperm per milt ejaculation (liveafmil), the number of post-thaw motile sperm per milt ejaculation, and the number of produced payot, traits.

Software used:

To edit data from Excel and Fox Pro (version 9). And to analyze the preparations and modeling of SAS and also genetic parameters were analyzed by wombat software.

Statistical Analysis:

At first, a least-squares analysis was conducted using the PROC GLM procedure of the SAS software to determine the significant environmental effects to be included in the model.

Data were analyzed using the repeatability model in three models: first by year-season-station, secondary by station,

and third by year.

The first model:

$$Y_{ijnm} = \mu + y_{ssti} + a_j + pm + \sum b_n x_n + e_{ijnm}$$

where μ , overall mean of population;

Y_{ijnm} , each observation;

y_{ssti} , fixed effect of year-season-station i ;

a_j , random effect of animal

pm , permanent environment effect

b_n , vector of fixed regression coefficients

x_n , is the incidence matrix associating phenotypic records to fixed effects

e_{ijnm} , residual effects

The second model:

$$Y_{ijkmn} = \mu + y_i + s_j + a_k + pm + \sum b_n x_n + e_{ijkmn}$$

μ , overall mean of population;

Y_{ijkmn} , each observation;

y_i , fixed effect of year i ;

s_j , fixed effect of season j ;

a_k , random effect of animal k ;

pm , permanent environment effect;

b_n , vector of fixed regression coefficients

x_n , is the incidence matrix associating phenotypic records to fixed effects

e_{ijkmn} , residual effects

The third model:

$$Y_{ijkmn} = \mu + s_i + s_j + a_n + pm + \sum b_k x_k + e_{ijkmn}$$

μ , overall mean of a population;

Y_{ijkmn} , each observation;

s_i , fixed effect of season i ;

s_j , fixed effect of station j

a_n , random effect of animal n

pm , permanent environment effect

b_n , vector of fixed regression coefficients

x_n , is the incidence matrix associating phenotypic records to fixed effects

e_{ijnm} , residual effects

3. Results and Discussion

In the first model, maximum heritability and repeatability (0.9755) were estimated for the total number of sperm in the milt ejaculation trait. In the second model, maximum heritability (0.96), that was in Jahed center, estimated for total number sperm in milt ejaculation, maximum repeatability (1), that was in Jahed center, too, estimated for sperm volume and maximum repeatability (1), that was in both breeding centers, estimated for motility to post-thaw motile ratio trait. In the third model, maximum heritability and repeatability (0.54), estimated for (liveafmil) trait. Maximum heritability and repeatability estimates for the total number of post-thaw motile sperm per milt ejaculation trait were 0.19 and 0.32, respectively.

Estimates of phenotypic variance, heritability, and repeatability in the semen quality traits for the first model (year-season-station) are presented in Table 4. Also, estimates of phenotypic variance, heritability, and repeatability in the semen quality traits for the third model (station) are presented in Table 3.

Table 2 presents an estimation of the heritability and repeatability of qualitative and quantitative traits of sperm of Iranian Holstein bulls during 1991-2013.

Table 2. Estimation of heritability and repeatability of qualitative and quantitative traits of sperm of Iranian Holstein bulls during 1991-2013.

Number of records	year	sperm volume		sperm concentration		total number of sperm in milt ejaculation		Total number of live sperm		Sperm motility ratio before and after thawing	
		r	h ²	r	h ²	r	h ²	r	h ²	r	h ²
45	1991	0/0003	0/0001	0/1100	0/0430	0/2232	0/2231	0/3016	0/2644	0/1434	0/1334
138	1992	0/07	0/0699	0/2895	0/1993	0/9117	0/7335	0/0858	0/0584	0/6461	0/4659
170	1993	0/25	0/2135	0/1844	0/1800	0/9330	0/9332	0/1216	0/0539	0/4159	0/0018
285	1994	0/15	0/1586	0/1478	0/0277	0/9351	0/9351	0/2438	0/0089	0/0417	0/0001
344	1995	0/64	0/4034	0/0569	0/0013	0/9417	0/1826	0/3784	0/2658	0/0308	0/0242
456	1996	0/1398	0/0000	0/0935	0/0395	0/9817	0/9771	0/0776	0/0246	0/6777	0/6179
600	1997	0/1532	0/1494	0/1381	0/0877	0/9477	0/8517	0/1711	0/1284	1	0/2732
578	1998	0/1031	0/0239	0/0284	0/0238	0/9480	0/8228	0/0259	0/0259	0/9334	0/5391
632	1999	0/6313	0/2340	0/1403	0/1269	0/9714	0/7588	0/0292	0/0213	0/1030	0/0846
633	2000	0/1945	0/1450	0/1577	0/0355	0/9350	0/9350	0/0272	0/0030	0/0278	0/0116
506	2001	0/1477	0/0001	0/1597	0/1386	0/9518	0/8293	0/0285	0/0000	0/9972	0/8303
384	2002	0/1073	0/0706	0/0204	0/0051	0/9263	0/8164	0/0828	0/0224	0/9369	0/2508
330	2003	0/0693	0/0003	0/0462	0/0004	0/9307	0/9293	0/0356	0/0356	0/0046	0/0023
345	2004	0/0959	0/0968	0/0842	0/0099	0/9434	0/8934	0/0816	0/0221	1	0/6183
438	2005	0/2295	0/2036	0/0053	0/0001	0/9731	0/9730	0/0562	0/0558	0/2212	0/1155
472	2006	0/0500	0/0500	0/1691	0/1181	0/9600	0/9575	0/1270	0/1108	0/0952	0/0000
571	2007	0/9464	0/9464	0/0792	0/0753	0/9697	0/8758	0/0658	0/0060	1	0/5507
483	2008	0/2223	0/0289	0/3103	0/1349	0/9832	0/9709	0/1441	0/0891	0/8076	0/4467
121	2009	0/2186	0/0247	0/0763	0/0452	0/9103	0/6021	0/0269	0/0095	0/3809	0/0701
137	2010	0/1185	0/1158	0/0009	0/0007	0/9725	0/4705	0/0158	0/0116	0/2273	0/0519
174	2011	0/7249	0/5406	0/0146	0/0071	0/9851	0/7131	0/0482	0/0092	1	0/6369
40	2012	0/2364	0/2364	0/2955	0/1457	0/5220	0/000	0/0830	0/0491	0/9723	0/0748

the number of produced payot		motility to post-thaw motile ratio		motility to post-ejaculation motile ratio		the number of fresh sperm per milliliter in fresh semen		total number of post-thaw motile sperm per milt ejaculation	
h^2	r	h^2	r	h^2	r	h^2	r	h^2	r
0/0528	0/0528	0/3590	0/3817	0/2695	0/2773	0/1601	0/1978	0/0274	0/0547
0/0042	0/0042	0/0000	0/2792	0/3564	0/5097	0/0107	0/0550	0/1312	0/2094
0/0006	0/0254	0/0097	0/3855	0/0024	0/3126	0.1151	0/1261	0/0367	0/0367
0/1021	0/1021	0/0000	0/0190	0/1785	0/1786	0/0988	0/3801	0/0003	0/0064
0/0312	0/0589	0/0091	0/0091	0/1944	0/2388	0/2512	0/4063	0/0000	0/0000
0/1033	0/1033	0.0866	0/0980	0/0000	0/1347	0/0324	0/0690	0.0111	0/0111
0/0217	0/0792	0/2502	0/5250	0.0003	0/2817	0/0001	0/0401	0/0473	0/0473
0/0008	0/1186	0/0000	0/0000	0/1216	0/3093	0/0382	0/0423	0/0020	0/1002
0/0000	0/0794	0/3334	0/3420	0/3804	0/3866	0/0039	0/0660	0/1184	0/1186
0/0380	0/0380	0/2070	0/4017	0/2504	0/3972	0/0139	0/0166	0/0000	0/1223
0/0030	0/1222	0/0136	0/4169	0/0574	0/0591	0/0678	0/3519	0/0000	0/0484
0/0000	0/1568	0/0672	0/7767	0/0001	0/0785	0/0498	0/0649	0/1257	0/1257
0/0000	0/0080	0/1340	0/1367	0/0000	0/1436	0.0765	0/0981	0/0007	0/0806
0/1376	0/1376	0/0187	0/0394	0/0000	0/0272	0/3051	0/3978	0/1890	0/1893
0/0673	0/0755	0/3394	0/3416	0/6690	0/9986	0/0587	0/2173	0/0022	0/0466
0/0709	0/0777	0/0154	0/0717	0/0788	0/1202	0/2367	0/2921	0/0001	0/0046
0/0230	0/0245	0/0215	0/0884	0/0633	0/0636	0/0497	0/0915	0/0108	0/2886
0/0054	0/0298	0/2493	0/2777	0/0248	0/1293	0/2794	0/4956	0/1947	0/1949
0/0445	0/0445	0/0000	0/0255	0/0000	0/0000	0/0040	0/0097	0/0001	0/0909
0/0738	0/0738	0/1834	0/1835	0/0000	0/0000	0/0466	0/0595	0/0263	0/0263
0/0027	0/0031	0/0176	0/1747	0/1636	0/1847	0/0826	0/2148	0/0000	0/0000
0/0058	0/0161	0/5953	0/5953	0/0215	0/0217	0/2051	0/4039	0/0046	0/3280

Table 3. Variance components and genetic parameters of different traits (station).

trait	station	Number of records	Genetic variance	Phenotypic variance	Permanent environment variance	Heritability	repeatability
Sperm volume per ml of ejaculation	1	6104	0/39	2/9	0/59	0/1355	0/3390
	2	2196	154220	338950	184720	0/4550	1
Sperm concentration per ml of ejaculate	1	6068	3781/3	9316/2	2255/6	0/4059	0/6480
	2	2232	24/68	52885	67877	0/0005	0/1289
Total sperm count in ejaculation	1	3032	2471/6	2640/0	120/61	0/9362	0/9819
	2	1109	2355/2	2442/2	22/45	0/9644	0/9736
Percentage of mobility after thawing	1	5888	2/21	51/16	2/59	0/0432	0/0941
	2	2144	73443	130620	57119	0/5622	0/9995
Mobility ratio before and after ejaculation	1	5754	58431	131930	73502	0/4429	1
	2	2128	8555/8	11745	3189/1	0/7285	1
Percentage of motility after ejaculation	1	6084	385/55	5476/6	5010/7	0/0701	0/9853
	2	2227	0/08	99/006	0/20	0/0008	0/0029
Total number of live sperm per Each ml after thawing	1	5889	11/60	929/81	2/83	0/0125	0/0155
	2	2067	0/003	919/45	12/21	0/0000	0/0133
Number of live sperm per Ml ejaculate in fresh semen	1	6072	3106/6	7584/8	2033/7	0/4096	0/6777
	2	2171	3643/4	12614	4278/7	0/2888	0/6280
Total number of live sperm in the ejaculation	1	5871	1613/6	9773/4	2188/1	0/1651	0/3890
	2	2086	0/02	62623	517/84	0	0/0081
Number of live sperm per Ml ejaculation after thawing	1	6091	50/45	1651/7	37/92	0/0305	0/0535
	2	2178	27/073	1701/1	2/18	0/0159	0/0172
Number of sperm doses produced	1	5824	2/33	2858/9	104/00	0/0008	0/0372
	2	2174	4/57	3539/2	126/69	0/0013	0/0371

Table 4. Variance components and genetic parameters of different traits (year-season-station).

Trait	Number of records	Genetic variance	Phenotypic variance	Permanent environment variance	Heritability	repeatability
Sperm volume per ml of the ejaculation	8300	0/655	4/85	0/000067	0/8002	0/8002
Sperm concentration per ml of the ejaculation	8300	5189/1	3980/1	3980/1	0/3792	0/6701
Total sperm count in ejaculation	4141	1784/0	1828/8	0/0021	0/9755	0/9755
Percentage of mobility after thawing	8032	35/43	72/57	4/06	0/4882	0/5442
Mobility ratio before and after ejaculation	7842	0/0065	0/36	0/30	0/0178	0/8415
Percentage of motility after ejaculation	8311	18/27	58/07	9/54	0/3147	0/4797
Total number of live sperm per Ml ejaculation after thawing	7956	4/76	877/42	8/48	0/0054	0/0151
Number of live sperm per ml	8243	3334/4	7813/6	2072/3	0/4267	0/6874

Trait	Number of records	Genetic variance	Phenotypic variance	Permanent environment variance	Heritability	repeatability
Ejaculation in fresh semen						
Total number of live sperm in the ejaculation	7957	5170/1	14804	4338/0	0/3492	0/6422
Number of live sperm per ml	8269	408/98	1663/1	234/35	0/2459	0/3868
Ejaculation after thawing						
Number of production payot	7998	165/38	2092/3	51/290	0/0790	0/1035

Our study indicates that measurements in semen quality traits from bulls at an early age might be volatile compared with measurements at later ages and that semen quality measurement tend to be higher with a bull's maturation. Bull age at ejaculate collection affects semen characteristics [11]; higher semen volume and quality were generally observed in mature bulls compared with younger ones [9].

In cattle, a commonly used definition of puberty is "the age at which an ejaculate contains 50 million spermatozoa with a minimum of 10% motility" because such an ejaculate can lead to pregnancy [12, 13].

Generally, the heritability values estimated for the Iranian Holstein bulls in this study were within the range of heritability estimates reported for semen quality traits in the literature [8, 9, 11]. The heritability of volume in our study was estimated to be 0.13 for the National Livestock Improvement Center (station 1), which is lower than the meta-analysis estimate of 0.20 [8], but between the heritability estimates found in 2 studies conducted by Mathevon etc. [11] analyzing performance test-station data for Holstein and French Montbeliarde bulls, respectively (0.24 and 0.08).

Our results generally indicated low to moderate heritability estimates for the semen quality traits, ranging from 0.0054 (sperm concentration post cryopreservation) to 0.97 (number of doses per ejaculate).

The lowest heritability estimate was reported for post cryopreservation sperm concentration. Therefore, management decisions underlie most of the variation in sperm concentration post cryopreservation rather than bull genetics; therefore, the observed low heritability in this trait is not unexpected. Our heritability estimate for fresh ejaculate volume in the Iranian Holstein was also comparable with estimates reported by Mathevon etc. [11] in Canadian Holstein bulls but higher than estimates reported in Chinese Holstein by Yin etc. [14], Norwegian Red by Olsen etc. [9], and US Hereford by Kealey etc. [15] bulls.

The highest heritability value was estimated for the number of doses per ejaculate followed by ejaculate volume. It is observed that the results of the present study are in line with the results of others. Researchers do not match and are less in some traits and more in some traits. The number of data used, Location and conditions of data collection, a statistical method used, factors used in the statistical model, completeness Pedigree, and other factors can be the reason for the differences in the results reported by different researchers. To achieve more accurate results, it is better to use complete genealogies and carefully form basic populations.

Efficient production of high-quality semen is an important trait in dairy cattle breeding, due to the widespread use of artificial insemination; however, the genetic architecture (e.g., distributions of causal variants and their corresponding effects) underlying such semen quality traits remains unclear.

It is not easy to select animals directly, based on their semen phenotypes, due to the low to moderate heritability of these traits (0.04–0.30) [16, 17]. Therefore, many studies [18–20] have focused on identifying genes and genetic markers associated with bovine semen traits in order to understand their genetic architectures of these traits. Other species, such as boars and stallion, and several genome-wide association studies (GWAS) have been performed in recent years to detect functional genes for the semen traits [21, 22]. The low heritability of semen traits shows a substantial environmental influence that suggests potential environmental factors may influence semen quality, such as bull handler, season, and the interval between semen collections, need to be controlled carefully so that genetic differences are more accurately assessed. So, to improve semen quality and increase the number of superior bulls, environmental influences, such as seasons, bull handlers, and the interval of two continual semen collections for each bull should be optimized. Besides, other environmental effects that are not routinely recorded in AI stations, such as temperature, humidity, and feed, should be recorded. Studies on the candidate genes for semen traits and GWAS can be performed to select bulls with superior semen quality and quantity.

4. Conclusions

These differences in estimated genetic parameters of semen quality traits may be due to genetic backgrounds, different breeds, and different models used for parameter estimation.

This study indicated that the range of heritability values for the different semen quality characteristics are low to moderate, which may indicate that improvement of environmental factors is more effective than genetics basis.

Considering the hardships of understanding the genetic relationships between semen quality traits based on existing datasets (prospective studies), future efforts should be focused on experiments specifically designed to maximize control of the environmental factors influencing these traits.

These findings are according to a solid foundation for research into the genetic mechanism of semen traits and provide information for marker-assisted selection or genome selection for semen production traits in Holstein bulls. The

results provide valuable insights into the genetic basis of semen traits in the production period and should assist in designing selection programs to improve semen traits in Iranian Holstein bulls.

Disclosure Statement

All the authors do not have any possible conflicts of interest.

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Data Availability Statement

The original data are available upon request to the corresponding authors.

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References

- [1] Ducrocq V., Humblot P. (1995) Genetic characteristics and evolution of semen production of young Normande bulls. *Livest. Prod. Sci.*, 41, 1–10.
- [2] Sato, Y., Tajima, A., Sato, T., Nozawa, S., Yoshiike, M., Imoto, I., et al. (2018). Genome-wide association study identifies ERBB4 on 2q34 as a novel locus associated with sperm motility in Japanese men. *J. Med. Genet.* 55, 415–421. doi: 10.1136/jmedgenet-2017-104991.
- [3] Fuerst-Waltl, B., Schwarzenbacher, H., Perner, C., and Solkner, J. (2006). Effects of age and environmental factors on semen production and semen quality of Austrian Simmental bulls. *Anim. Reprod. Sci.* 95, 27–37. doi: 10.1016/j.anireprosci.2005.09.002.
- [4] Gacitua H and Arav A, 2005. Successful pregnancies with directional freezing of large volume buck semen. *Theriogenology* 63: 931-938.
- [5] England GC, Phillips L and Freeman SL, 2010. Heritability of semen characteristics in dogs. *Theriogenology* 74: 1136- 1140.
- [6] Berry, D. P., B. Eivers, G. Dunne, and S. McParland. 2019. Genetics of bull semen characteristics in a multi-breed cattle population. *Theriogenology* 123: 202–208. <https://doi.org/10.1016/j.theriogenology.2018.10.006>.
- [7] DeJarnette, J. M., C. E. Marshal, R. W. Lenz, D. R. Monke, W. H. Ayars, and C. G. Sattler. 2004. Sustaining the fertility of artificially inseminated dairy cattle: The role of the artificial insemination industry. *J. Dairy Sci.* 87 (E-Suppl.): 93–104. [https://doi.org/10.3168/jds.S0022-0302\(04\)70065-X](https://doi.org/10.3168/jds.S0022-0302(04)70065-X).
- [8] Berry, D. P., E. Wall, and J. E. Pryce. 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. *Animal* 8 (Suppl. 1): 105–121. <https://doi.org/10.1017/S1751731114000743>.
- [9] Olsen, H. B., B. Heringstad, and G. Klemetsdal. 2020. Genetic analysis of semen characteristic traits in young Norwegian Red bulls. *J. Dairy Sci.* 103: 545–555. <https://doi.org/10.3168/jds.2019-17291>
- [10] Berry, D. P., R. D. Evans, and S. McParland. 2011. Evaluation of bull fertility in dairy and beef cattle using cow field data. *Theriogenology* 75: 172–181.
- [11] Mathevon, M., M. M. Buhr, and J. C. M. Dekkers. 1998. Environmental, management, and genetic factors affecting semen production in Holstein bulls. *J. Dairy Sci.* 81: 3321–3330.
- [12] Evans, A. C. O., R. A. Pierson, A. Garcia, L. M. McDougall, F. Hrudka, and N. C. Rawlings. 1996. Changes in circulating hormone concentrations, testes histology and testes ultrasonography during sexual maturation in beef bulls. *Theriogenology* 46: 345–357. [https://doi.org/10.1016/0093-691x\(96\)00190-2](https://doi.org/10.1016/0093-691x(96)00190-2).
- [13] Thundathil, J. C., A. L. Dance, and J. P. Kastelic. 2016. Fertility management of bulls to improve beef cattle productivity. *Theriogenology* 86: 397–405. <https://doi.org/10.1016/j.theriogenology.2016.04.054>.
- [14] Yin, H., L. Fang, C. Qin, and S. Zhang. 2019. Estimation of the genetic parameters for semen traits in Chinese Holstein bulls. *BMC Genet.* 20. <https://doi.org/10.1186/s12863-019-0752-x>.
- [15] Kealey, C. G., M. D. MacNeil, M. W. Tess, T. W. Geary, and R. A. Bellows. 2006. Genetic parameter estimates for scrotal circumference and semen characteristics of line 1 Hereford bulls. *J. Anim. Sci.* 84: 283–290.
- [16] Gredler, B., Fuerst, C., Fuerst-Waltl, B., Schwarzenbacher, H., and Sölkner, J. (2007). Genetic parameters for semen production traits in austrian dual-purpose simmental bulls. *Reprod. Domestic Anim.* 42, 326–328. doi: 10.1111/j.1439-0531.2006.00778.x.
- [17] Druet, T., Fritz, S., Sellem, E., Basso, B., Gérard, O., Salas-Cortes, L., et al. (2009). Estimation of genetic parameters and genome scan for 15 semen characteristics traits of Holstein bulls. *J. Anim. Breed. Genet.* 126, 269–277. doi: 10.1111/j.1439-0388.2008.00788.x.
- [18] Hering, D. M., Olenski, K., and Kaminski, S. (2014a). Genome-wide association study for poor sperm motility in Holstein-Friesian bulls. *Anim. Reprod. Sci.* 146, 89–97. doi: 10.1016/j.anireprosci.2014.01.012.
- [19] Hering, D. M., Olenski, K., and Kaminski, S. (2014b). Genome-wide association study for sperm concentration in holstein-friesian bulls. *Reprod. Domestic Anim.* 49, 1008–1014. doi: 10.1111/rda.12423.
- [20] Qin, C., Yin, H., Zhang, X., Sun, D., Zhang, Q., Liu, J., et al. (2017). Genome-wide association study for semen traits of the bulls in Chinese Holstein. *Anim. Genet.* 48, 80–84. doi: 10.1111/age.12433.
- [21] Marques, D. B. D., Bastiaansen, J. W. M., Broekhuijsse, M., Lopes, M. S., Knol, E. F., Harlizius, B., et al. (2018). Weighted single-step GWAS and gene network analysis reveal new candidate genes for semen traits in pigs. *Genet. Sel. Evol.* 50, 14. doi: 10.1186/s12711-018-0412-z.

- [22] Gottschalk, M., Metzger, J., Martinsson, G., Sieme, H., and Distl, O. (2016). Genome-wide association study for semen quality traits in German Warmblood stallions. *Anim. Reprod. Sci.* 171, 81–86. doi: 10.1016/j.anireprosci.2016.06.002.