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Recent Updates on Production and Reproduction Traits of Buffalo: A Review

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Abstract

In many South Asian and Mediterranean countries, buffaloes are an important livestock resource, contributing milk, meat, skins, and draft power for agricultural operations, which are essential for the overall development of society. Various recent high-throughput technologies, such as molecular markers, genomic selection (GS) and genome-wide association studies (GWASs), provide an extensive range of whole-genome data and high coverage of genomic, transcriptomic and proteomic data. This review highlights these high-throughput technologies linked to the production and reproduction traits of buffaloes. The availability of recent high-quality reference genome and genotyping marker panels for buffaloes have supported many genome-based studies and provided valuable information for understanding the genetic basis of growth, functional traits, and performance traits. In conclusion, high-throughput technologies provide an opportunity to detect important markers and genomic regions associated with performance traits and also present the possibility of genomic selection as a promising strategy in buffalo breeding programs to accelerate genetic gain.

Keywords: Buffalo, reproduction traits, production traits

Among the livestock species, domestic Asian water buffalo (*Bubalus bubalis*) plays a crucial role in the production of milk and meat (as a high-quality animal protein), dung (as a fuel and organic fertilizer), draught power and transportation (contributes to crop productivity), and hides (as a raw material for the industry) in various countries (FAO, 2000; Naveena and Kiran, 2014). Indian buffaloes contribute 67.12% of the world's buffalo milk production (FAOSTAT, 2019) and about 49.2% of total milk production in India (DAHD, 2018).

Unquestionably, the performance of various production and reproduction traits is of utmost importance in determining the profitability and sustainability of a buffalo dairy farm. Important production traits are milk yield, fat yield, lactation length, SNF percentage, dry period, etc. Similarly, some important reproduction traits are age of maturity, age at first calving, service period, conception rate, calving interval, etc. These traits of each breed and animal within a breed vary due to feeding and management conditions, environment, animal genetic makeup, and location specificity (Dahiya *et al.,* 1994; Singh *et al.,* 2000; Chitra *et al.,* 2018). Buffaloes also exhibit several known reproductive problems such as late onset of puberty, poor oestrus signs, longer postpartum ovarian activities, low conception rates, etc., which affect their performance.

Current developments in high-throughput technologies, such as whole-genome sequencing (WGS), genome-wide association study (GWAS), transcriptome analysis, next-generation sequencing(DNA), RNA-seq, candidate gene approaches, and genome-wide CHIP-seq scanning, provide

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opportunities to identify potential genetic variants and study gene regulation, gene function, and single nucleotide polymorphism (SNP) ordering resources. Fewer GWAS studies have been conducted in buffaloes compared to cattle, covering all aspects of production and reproduction performance. This may be due to the limitations of the costs incurred and the lack of systematized large-scale genotyping programs (Vohra *et al.,* 2021).

Therefore, the objective of this review was to examine the overall developments in the buffalo production system. This review highlights the molecular markers, candi- date genes, transcriptome studies, genomic selection (GS), and genome-wide association studies (GWASs) associated with production, fertility, and reproduction traits in buffalos.

Production traits

The breeding worth of an animal cannot always be determined by its physical appearance, as appearance is an inherited characteristic from the parents and depends on the environment in which the animal is raised. Therefore, it is important to utilize production traits to increase the accuracy of selection when estimating the breeding worth of an animal. The production status, however, may vary depending on the agro-climatic and management conditions. Milk yield is an economically important quantitative trait that directly contributes to the value of animals to farmers or livestock owners, and it is measurable at the individual level. Production traits of farm animals are generally influenced by many genes, whose expression in a particular animal also reflects environmental influences. Milk productivity varies between breeds of buffalo and their locations. Differences in milk production among the Murrah, Mediterranean, Mestizo, and Jafarabadi water buffalo genetic groups have been reported as 1651.4, 1592.2, 1578.3, and 1135.5 kg, respectively (Ramos *et al.,* 2007). Various studies have been conducted to ascertain the relation- ship between phenotypic characteristics and behaviour with milk production. The results of these studies show that black-colored water buffalo cows produce more milk than dark brown-colored females (2195±34 vs. 1863±30 kg). Additionally, no significant differences in milk production were observed between buffalo cows with different shapes and sizes of horns. Observations also indicate that docile animals produce more milk (2120±27 kg) than nervous (1829±49 kg) or aggressive (1743±147 kg) animals (Bharadwaj *et al.,*2007). It has been reported that the contents of milk are also affected during the lactation period in buffaloes. In one study, buffalo milk was found to contain 8.4% fat and 4.6% protein (Borghese, 2010). Another study reported an average milk production of 8.64 kg/head/day, with 47.71 g/kg of protein and 87.08 g/kg of fat (Bartocci *et al.,*2002). Primiparous Mediter-

Table I. Candidate genes or genomic regions affecting milk production traits in buffaloes

Sl.No	Name of the trait(s)	Associated gene(s)	Reference(s)
1	Fat production	KCTD8, FOXO4, SSTR3 and ESRRG, A2M, GHRL,*P1M 1, CHST9, CIB3, FAM32A, HSH2D, RAB8A,* and *TPM4*	Camargo *et al.* (2015); Du *et al.*(2019); Lazaro *et al.* (2021)
2	Fat Percentage	A2M, DGAT1, GHRL, LEP, MC4R, PRL, SCD, SREBF1, STAT1 and TG	Du *et al.*(2019)
3	Protein production	CCND3, ADRA1A, A2M, CSN1S1, DGAT1, GHRL, INSIG2, MC4R, MTNR1A, PRL and SPP1	Camargo *et al.* (2015); Du *et al.*(2019)
4	Milk production traits	MFSD14A, SLC35A3, RGS22, VPS13B, PALMD, BTN1A1, INSIG2, LALBA, LEP, MC4R, OXT, PRL, SCD, SREBF1, STAT1, STAT5A, GRIA3, GRIK2, DAPK2, TCERG1, CCDC34, ANKRD44 LRRC34, *IL23A, MIP, APOF, CNPY2 and GLS2*	Liu *et al.* (2018); Du *et al.*(2019), Vohra et al. (2021);Lazaro *et al.* (2021)
5	Lactose percentage	TPD52, ZBTB10, AADAT, GALNT6, COL8A1 and PLOD2.	Du *et al.*(2019); Awad *et al.* (2020)

ranean buffalo cows produced 12% less milk compared to multiparous females (Salari *et al.,*2013). The same study also reported that milk production increased between days 16 and 60 (11.35 kg/per head) and that the fat content was higher at the end of the peak production period (8.64 %). Additionally, protein levels were higher at the beginning and end of lactation (4.84 vs. 4.93 %). Finally, Yilmaz *et al.* (2012) reported milk yields of 24-26 liters per day over a lactation period of 225±6 days. Total milk solids were 17.7 ±0.3 %, protein was 4.2±0.1 %, and fat was 8.1±0.2 %. Taking all of these factors into account, buffalo milk yields are 40% higher than those of bovine milk (Andrade *et al.,* 2009).

Genes affecting production traits in buffalo

Identification of genomic regions and candidate genes associated with milk production traits will help in the genetic improvement of buffaloes via selective breeding. In a study, 19 candidate genes containing 47 mutations related to milk production traits have been identified in buffaloes. These candidate genes are classified into four major groups: milk yield, fat yield, fat percentage, and protein percentage (Du *et al.,* 2019; Table I). Vohra *et al.* (2012) have reported a significant association of alpha-lactoglobulin with milk yield, fat percentage, total fat yield, and SNF% in Murrah and Surti buffaloes, whereas beta-lactoglobulin showed a significant effect on milk yield in Murrah, Bhadawari and Mehsana buffalo breed. In Murrah buffaloes, genetic polymorphism in the A2M gene was associated with fat and protein percentages (Freitas *et al.,* 2016).A significant association of FASN, SCAP and PRL genes with milk production and its composition traits has been reported by various researchers (Kumar *et al.,* 2017;Deng *et al.,* 2018; El-Magd *et al.,*2021; Ye *et al.,* 2021). It has been reported that the SCAP gene as a candidate gene associated with milk production traits in buffalo (Deng *et al.,*2018). Ahmadzadeh *et al.* (2019) identified the significant genotypic frequency differences in GH, GHR and Pit1 genes in low and high-milk yielding buffaloes. The significant association of the PPARGC1A gene with milk production and quality traits was identified in Italian Mediterranean buffaloes (Hosseini *et al.,* 2021). Hao *et al.* (2022) used the pGBLUP method to integrate milk-related QTL information from cows into the genomic prediction of buffalo milk traits. They discovered that certain QTLs associated with cattle milk production also significantly influenced buffalo milk production traits.

Recently, a genome-wide association study identified a genomic region in buffalo related to milk production traits (El-Halawa- ny *et al.,* 2017; Herrara *et al.,* 2018; Vohra *et al.,* 2021.). A total of 1,562 SNP markers have been found to affect the production and/ or quality of buffalo milk using a high-density bovine Bead Chip (Venturini *et al.,* 2014). Camargo *et al.* (2015) have carried out single- trait, single-SNP GWAS using a 90K Axiom Buffalo Genotyping chip for milk production and composition traits in dairy buffalo. They reported various genes significantly associ- ated with various traits as mentioned in the Table I. Liu *et al.* (2018) have identified a total of 4 SNPs in 2 genomic regions (Table I), which were located on the equivalent of *Bos taurus* autosomes and were reported to affect the milk production traits in dairy cattle. Similarly, the genomic regions associated with milk production and composition traits in Egyptian buffalo were studied by Abdel- Shafy *et al.* (2020) and reported a total of 47 SNPs located on 20 chromosomes. In a very recent study, Deng *et al.* (2024) conducted whole-genome resequencing on 387 buffalo

Table II. Physiologically classification of various reproduction traits in buffaloes

Categories	Traits
Ovulation	Ovulation rate and superovulation rate
Mating	Twinning rate and age of puberty
Calving-related traits	Age at first calving, non-return rate, pregnancy rate, calving interval (CI), days open (DO), calving difficulty and length of productive life

genomes from 29 diverse Asian breeds, including river, swamp, and crossbred buffaloes. They identified 36,548 copy number variants (CNVs) spanning 133.29 Mb of the genome and mapped 2,100 CNV regions (CNVRs), with 1,993 being common across buffalo types. The study utilized three methods to pinpoint candidate genes associated with milk production traits. Population differentia- tion revealed 11 CNVR-linked genes related to milk production, while expression quanti- tative trait loci (eQTL) analysis and GWAS identified additional relevant genes.

The double-digest restriction-site associated DNA sequencing of Egyptian and Chinese buffalo identified SNPs close to 29 genes that significantly differed in allelic frequencies in the two populations. A total of 9 genes including ADCY5, CREB1, INHBA, INHBB, CACNA1A, PLCB1, PRKCE, PIK3R1 and SMAD2, which are known to regulate lactation, were detected and considered as promising candidate genes associated with buffalo milk yield (Ye *et al.,* 2020). Lazaro *et al.* (2021) reported a total of 26 genomic regions associated with milk yield, 21 regions associated with fat yield, and 26 regions associated with protein yield across different lactations in water buffalo using the GWAS approach. Vohra *et al.* (2021) have also conducted a GWAS on the first two principal components of test-day records of milk yields, 305-day milk yield, fat percentages, and SNF percentages separately in Murrah buffalo. They observed a significant association of SNPs with the first principal component, which explained the maximum proportion of variation in buffalo milk yield (Table I).

Transcriptomic studies revealed higher expression of the CSN2, CSN1S1, CSN3, LALBA, SPP1, and TPT1 genes throughout lactation in Murrah buffalo (Arora *et al.,* 2019). 2019). Deng *et al.* (2019) have performed transcriptomics and identified several genes including *TUBA1C, C2CD4 B, MAP3K5, PDCD11, SRGAP1,DCP1B, GD PD5, BARX2, SCARA3, CTU,BNIPL,*and *RP L27A,* that are involved in multiple pathways related to milk production could be considered potential candidate genes for mammary gland functions in buffalo. Transcriptomic profiling of the water buffalo mammary gland revealed higher expression of CSN1S1, BTN1A1, LALBA, ALDH1L2, SCD, and MUC15 genes in high-fat yielding buffalo compared to low-fat yielding buffalo (Hao *et al.,*2021).

Reproductive traits

In monotocous animals like buffalo, reproductive traits are economically important for farm profitability and sustainable food produc- tion. To better understand and utilize these traits in livestock and breeding programmes, they are physiologically classified into three categories (table 2; Cammack *et al.,* 2009).

Buffaloes typically reach puberty when they attain 60 % of their adult body weight (250 to 400 kg), but this can vary from 18 to 46 months (Jainudeen and Hafez, 1993). This is influenced by several factors such as genet- ics, feeding, management, climate, diseases, and breeds. In addition, estrus detection in buffaloes can also impair the determination of puberty. It can be achieved at 15 to 18 months in river buffaloes and 21 to 24 months in swamp buffaloes under optimal conditions (Borghese *et al.,* 2011). Late puberty consequently delays conception and other reproductive traits, resulting in low reproductive efficiency and a lengthening of the non-productive life. Good

Table III. Candidate genes or genomic regions affecting reproduction traits in buffaloes

Sl.No.	Name of the trait(s)	Associated gene(s)	Reference(s)
1	Age at first calving	IFNT, SLEP,ROCK, PMVK, GFP1, BMP10	Camargo *et al.* (2015); de Araujo Neto *et al.* (2020)
2	Calving interval	TPCN1,ADCY2, MAP2K6, GFP1, BMP10	Camargo *et al.* (2015); de Araujo Neto *et al.* (2020)
3	Number of services per conception	ABCC4	Camargo *et al.* (2015)

feeding and management conditions in the field may lead to early puberty. Delayed onset of puberty in pre-pubertal buffalo heifers is also partially influenced by low circulating thyroid hormone levels (Ghuman *et al.,*2011; Ingole *et al.,*2012), low body fat (Ghuman *et al.,*2011.), or the inherently suboptimal functioning of the hypothalamo-hypophyseal- gonadal axis and the resulting low circulating hormones (Kaur and Arora, 1982; Mondal and Prakash, 2007). The relationship between growth hormone and LHmay also affect the attainment of puberty (Saini *et al.,* 1998).

The estrous cycle duration in buffalo ranges from 17 to 26 days, with an average of around 21 days (Jainudeen and Hafez,1993). However, buffalo have more variability in estrous cycle length than cattle, and this could be attributed to a variety of factors, including poor nutrition, adverse environmental conditions, and irregularities in ovarian steroid hormone secretion (Kaur and Arora,1982). In buffalo, estrous behaviour and endocrinology show significant variations in reproductive endocrine activity without external signs of oestrus, which is known as silent heat (Singh *et al.,* 2000; Roy and Prakash, 2009). The low intensity of oestrus in buffaloes may be due to lower circulating levels of 17-oestradiol in comparison to dairy cattle (Seren *et al.,*1995). Tying up the animals, as well as high ambient temperatures (especially during the hot summer season), may increase the occurrence of silent heat in buffaloes (Marai and Habeeb, 2010; Warriach *et al.,*2015).

Wide variations in the age at first calving in buffalo heifers of different breeds have been reported by various researchers. As discussed earlier, puberty directly affects the age at first calving. The age at first calving is also influenced by many variables, being highest in rural buffaloes in India (Mangurkar and Desai, 1981; Gurung and Johar, 1982). Service period and CI traits are economi- cally important and tend to be prolonged in buffaloes compared to cattle, with significant variation across different breeds. These traits range from 85 to 224 days for the service period and 479 to 508 days for CI. Calving intervals in buffaloes are commonly considered to occur twice in three years. Generally, the service period and calving interval in Banni, Murrah and Nagpuri breeds of buffaloes at well-organized farms are much shorter compared to those observed in other breeds (Rao and Nagarcenkar, 1977; Bhat, 2010; Borghese *et al.,*2011.). It has been reported that Italian Mediterranean buffaloes, with better nutritional and breeding management, may have calving intervals as short as 400 days, which is shorter than the calving intervals observed in buffaloes elsewhere (Rao and Nagarcenkar, 1977; Bhat, 2010; Borghese,2010.; Borghese *et al.,* 2011). A large number of variables govern the calving intervals, including the season of resumption of postpartum ovarian activity, lactation yields and age at first calving (Shah *et al.,* 2007). The delay in the post-partum period in buffaloes is a foremost cause of economic loss for buffalo breeders (El-Wishy, 2007). Ratwan *et al.* (2019) examined the phenotypic correlations in large bovines, finding that 305-day milk yield (305-DMY), total milk yield (TMY), and lactation length (LL) were significantly and positively corre- lated with the interval between calving and first insemination (CFI), DO, and CI. This suggests that animals with higher milk production tend to experience longer intervals before first insemination, extended days open and longer calving intervals. These findings underscore the antagonistic relationship between production and reproduction traits. Similarly, numerous studies have examined the genetic variation of reproductive traits across various buffalo populations, revealing low heritability, particularly for AFC and CI, along with a negative correlation with produc- tive traits (Rathod *et al*., 2018). Addition- ally, the heritability of these traits differs significantly between breeds, highlighting the importance of evaluating each breed individu- ally.

Genes affecting reproduction traits in buffalo

Identifying genomic regions associated with reproduction and fertility traits in buffalo is important in monotocous species such as buffalo, as these traits directly and greatly influence the genetic worth of an animal.

Reproductive parameters are complex traits regulated by many genes and QTLs. However, the genetic gains obtained for reproductive traits in buffaloes are low due to the low heritability estimates.

The candidate gene approaches have identified several genes associated with fertility, in both male and female buffaloes. The Follicle Stimulating Hormone Recep- tor (FSHR), luteinizing hormone receptor (LHR) and estrogen receptor- α (ERα) genes have been reported to be significantly associ- ated with fertility and reproduction traits in buffaloes (Jain *et al.,* 2016; Sosa *et al.,* 2016; Al-Mutar *et al.,* 2017; Othmanand Abdel-samad, 2019). The candidate gene approaches have also identified genes such as those in the transforming growth factor beta (TGFβ) superfamily, BMO15, GDF9, BMPR1B, SPAG11, IFN-TAU, ISG15, ghrelin, SERPINA14, SELP and MTRN1A, which are associated with various reproductive traits in buffaloes (Jain *et al.,*2012a; Kandasamy *et al.,* 2010, 2013; Gunwant *et al.,*2018;Rehman *et al.,* 2021; Deshmukh *et al.,* 2022)

Recently, various researchers have performed a genome-wide association study (GWAS) to identify casual genes associated with buffalo reproductive traits. Camargo *et al.* (2015) conducted a GWAS for four reproductive traits, including age at first calving, calving interval, open days and number of services per conception in Asian buffalo (Table III). Li *et al.* (2018a) identified a total of 80 SNPs associated with calving age, calving interval, the number of services per concep- tion and open days in buffalo using a 90K Affymetrix Buffalo SNP array. de Araujo Neto *et al.* (2020) conducted a GWAS on Murrah water buffalo and reported the association of various genes with different traits (Table III).

The transcriptomic study revealed that the *AKAP4, TSPAN6, RPL10* and *RPS4X* genes located on the sex chromosome have a significant correlation with the fertility rate and sperm kinetics in Murrah buffalo. Various genes associated with embryo survival during early pregnancy have been reported in the corpus luteum of buffalo (Jain *et al.,* 2012b; Jain and Mitra, 2012). Li *et al.* (2018b) reported higher expression of *the IGFBP7* gene in follicular granulosa cells in buffalo, highlighting its association with follicle growth. Several studies have associated the expression of cathepsins and GDF9 genes with developmental competence of oocytes in buffalo (Jain *et al.,* 2012c, d; Roy *et al.,* 2013). Recently, Paul *et al.* (2021) compared the transcriptomics of spermatozoa of high- and low-fertile buffalo bulls and found the lower expression of BX1, ORAI3, and TFAP2C genes in low fertility bulls, suggesting their significant role in buffalo bull fertility.

Conclusion

By using high-throughput technologies such as whole-genome sequencing, genome-wide association study (GWAS), next-generation sequencing (RNA and DNA), and genome-wide CHIP-seq scanning, various researchers have identified numerous genomic variants and correlated them with production and reproduction traits, disease resistance, and climate adaptation in buffaloes. There is ample scope for further development of buffaloes in Asia. The integration of these high-throughput technologies, combined with advancements in breeding, feeding, health and housing management practices, offers great prospects for the systematic improvement of buffaloes.

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