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Phenotypic and genetic parameter estimates for early growth, growth rate and growth efficiency-related traits of Fogera cattle in Ethiopia

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Abstract

Background: Understanding the phenotypic and genetic parameter estimates of growth traits is important for an effective livestock genetic improvement programme.

Objectives: In this study, we evaluated the phenotypic performances and estimated genetic parameters for birthweight (BWT), weaning weight (WWT), pre-weaning average daily gain (PADG), pre-weaning Kleiber ratio (PKR), pre-weaning growth efficiency (PGE) and pre-weaning relative growth rate (PRGR) of Fogera cattle in Ethiopia.

Methods: Growth data collected from 2000 to 2018 in Andassa Livestock Research Center were used for the study. General linear model of SAS 9.1 was used to estimate the least squares mean (LSM) ± standard error (SE) for phenotypic performances, and AI-REML of Wombat software combined with a series of five single-trait animal models to estimate phenotypic variance and its direct, maternal and residual components. Calf sex, calf birth season and calf birth year were the fixed effects considered.

Results: The overall LSM ± SE BWT, WWT, PADG, PKR, PGE and PRGR were 21.28 ± 0.05 kg, 97.99 ± 0.67 kg, 320.29 ± 2.79 g, 10.10 ± 0.04, 3.51 ± 0.35 and 1.95 ± 0.00, respectively. All the fixed effects considered significantly ($p < 0.001$) affected all the traits. The direct heritability estimates for BWT, WWT, PADG, PKR, PGE and PRGR were 0.21 ± 0.07, 0.26 ± 0.01, 0.55 ± 0.19, 0.53 ± 0.18, 0.33 ± 0.00 and 0.50 ± 0.00, respectively. The genetic correlations among the traits ranged from negative (−0.20 ± 0.04; BWT-PKR) to positive (0.99 ± 0.00; BW-PGE, BW-GR, WWT-PGE, WWT-PGR, ADG-PGR, PKR-PGR, PKR-PGE and PGE-PGR). Similarly, the phenotypic correlations ranged from −0.03 ± 0.20 to 0.99 ± 0.01; BWT-PGE, BWT-PRGR, WWT-PGE, WWT-PRGR, PKR-PGE, PKR-PRGR and PGE-PRGR).

Conclusion: The positive and larger phenotypic and genetic correlations between most of the traits implied that selection based on one trait could improve the other traits. However, the negative phenotypic and genetic correlation between BWT-PKRA

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implies that selection of Fogera calves based on either of the traits has an adverse effect on the other. Therefore, caution should be taken when designing the selection criteria for growth improvement.

KEYWORDS
Fogera cattle, genetic parameter estimates, growth efficiency, growth performance, Klieber ratio

1 | INTRODUCTION

Growth performance traits, primarily expressed and described by body weight and growth rate (Menale et al., 2011), are important factors that need to be considered in any breed improvement programme (Kumar et al., 2017; Pires et al., 2016). The growth performance of cattle determines the profitability of a farm which, in turn, is influenced by genetic and environmental factors. Accurate estimation of genetic parameters is critically important to implement sound breeding programmes and to assess the progress of ongoing genetic improvement programmes (Demeke et al., 2004). Similar to the genetics of the animal, management (feeding, health care) plays a determinant role on the performance of cattle.

The early growth rate of cattle has a strong implication on both reproductive and production performances (Zeleke et al., 2016). Early growth performance traits such as birthweight (BWT) and weaning weight (WWT) are the basis for selection in genetic improvement programmes for meat production due to their strong association with each other and mature body weight (Pires et al., 2016; Tesfa & Garikipati 2014). Thus, evaluation of the growth performances of indigenous cattle breeds is essential to ascertain the potential of the breeds and design genetic improvement programmes for a particular purpose. Moreover, growth rate and efficiency-related traits including Kleiber ratio (KR), growth efficiency (GE) and relative growth rate (RGR) are very important for their indirect evaluation of growth. KR, defined as the weight gain per unit of metabolic body weight (Kleiber, 1961), is an important measure of GE (Kleiber, 1947; Köster et al., 1994). KR has an association with growth traits so that it can also be used as selection criteria for growth traits (Abegaz et al., 2005; Köster et al., 1994; Shoja & Sarain, 2016). GE-related traits are economically important for genetic improvement programmes in the tropics (Mokhtari et al., 2019). Similar to KR, GE and RGR have a strong positive genetic correlation with growth traits (Ghafouri-Kesbi & Gholizadeh 2017), and therefore, selection for better GE traits could improve the growth performance of the breed.

Fogera cattle are among the Zenga cattle of Ethiopia adapted to the belt area of Lake Tana, north-western Ethiopia. The breed is known for its adaptation to the waterlogged marshy grazing areas of Lake Tana wetlands, better resistance to internal parasites and flies infestations, and for its traction power in marshy fields (Tesfa et al., 2016). Moreover, meat and milk production, and the high draught power of the breed are traits perceived by Fogera breed keepers in the belt (Bitew et al., 2010; Tesfa et al., 2016).

Phenotypic performance evaluation (Bekele et al., 2016; Menale et al., 2011; Tesfa et al., 2016) and genetic parameter estimates for growth traits (Bekele et al., 2016) for Fogera cattle have been carried out at Andassa Livestock Research Center (ALRC) and Metekel Fogera cattle ranch. Both genetic parameter estimates and phenotypic performance traits are imperative in determining the method of selection and formulating any suitable breeding plan (Goshu et al., 2014; Kumar et al., 2017; Pires et al., 2016) and need to be worked out and updated every time. In this study, we used additional data and additional traits including pre-weaning average daily gain (PADG), pre-weaning KR (PKR), pre-weaning GE (PGE) and pre-weaning RGR (PRGR). With this regard, there is a dearth of information on PADG, PKR, PGE and PRGR traits and their associations with other growth traits of indigenous cattle in Ethiopia. Therefore, the objective of this study was to estimate the genetic parameters, phenotypic performances and phenotypic & genotypic correlations of growth and efficiency-related traits of Fogera cattle at ALRC.

2 | MATERIAL AND METHODS

2.1 | Description of ALRC

Growth data collected from Fogera cattle maintained at ALRC were used in this study. ALRC is found at 587 km away from Addis Ababa, which is the capital city of Ethiopia, and 22 km from Bahir Dar city, the capital of Amhara regional state, on the way to the Blue Nile Falls. Its geographic location is 11^{O} 29′ North and 37^{O} 29′ East. ALRC has an elevation of 1730 m above sea level. The centre receives an average annual rainfall of 1150 mm, and temperature ranging from 6.5to 30°C.

ALRC owns a total of 365 hectares of land of which 310 hectares are covered with natural pastureland. Offices, bushes, animal housing and other infrastructures occupy the remaining 55 hectares. The centre has a topography ranging from a gentle slope to flat. Andassa River, a big and year-round flowing river, crosses the centre. As the soil is predominantly characterised as vertisol, it holds water during the rainy season, and it cracks during the dry season when it dries. The main grass species found in the natural pastureland of the centre include Cynodon, Cetaria, Hyperhenia, Elusin, Andropogon, Paspalum, Eragrostis, Sporobulus and Trifolium species (Denekew et al., 2005).

TABLE 1 Descriptive statistics of the data set used for the analysis

Traits analysed	*N*	Mean	SD	Minimum	Maximum	Range
Birthweight, kg	1475	21.3	3.07	12	33	21
Weaning weight, kg	1154	98.0	22.9	33	170	137
Pre weaning average daily weight gain, g	1154	320	94.9	50	608	558
Kleiber ratio	1154	10.1	1.38	3.63	13.4	9.76
Growth efficiency	900	35.1	1.05	1.08	7.46	6.38
Relative growth rate	900	1.94	0.09	1.69	2.01	0.32

TABLE 2 Information related to pedigree, traits analysed and sample sizes

	Number of observation in each trait					
Animals	BWT	WWT	PADG	PKR	PGE	PRGR
Number of animals	1475	1154	900	900	900	900
Number of sires	54	48	48	48	48	48
Numbers of dams	683	581	581	581	581	581
No of animals with unknown dams	71	71	71	71	71	71
No of animals with unknown sire	152	6	218	218	218	218
Dam with records and progeny	270	156	156	156	156	156
Animals with unknown sire with records	3	6	5	5	5	5
Animals with unknown dam with records	247	247	247	247	247	247
Animals with both parents unknown	3	3	2	2	2	2
Progeny per sire	21	19	19	19	19	19
Progeny per dam	2	2	2	2	2	2
Animals with paternal grand sire	161	79	78	78	78	78
Animals with paternal grand dam	114	79	78	78	78	78
Animals with maternal grand sire	245	211	210	210	210	210
Animals with maternal grand dam	190	151	153	153	153	153

2.2 | Herd management at Andassa Livestock Research Center

The research centre, on average, owns more than 530 Fogera cattle of which about 300 are breeding cows. Natural mating is the major breeding system implemented in the centre. For this purpose, the cowherd is divided into groups of about 40–50 cows, and one bull is assigned to each group considering pedigree information to avoid the mating of closely (Son to Dam, and Sire to Daughter) related animals.

The general cattle management system at the centre is semi-intensive. During the dry season, in addition to grazing, cattle are supplemented with hay harvested from the natural pasture and are rarely supplemented with concentrate during the mid-dry season, January–May. Seasons are grouped into wet season (June–September) and dry season (October–May) (Bitew et al., 2010). The herd's water source is from the Andassa River. However, tape water is provided for young and sick indoor animals. Health management practices focus on prevention through vaccination. Vaccination for major prevalent diseases including blackleg, anthrax and pasteurellosis are provided to the entire herd once every 6–8 months. Internal and external parasite control measures are also provided twice a year, at the start and end of the rainy season. Calves suckle their dams for the first 4 days to ensure enough colostrum consumption. After 4 days, calves are separated from their dams during the day- and night-time. During milking time in the morning and evening, calves partially suckle (two teats) their dams until weaning age of 8 months.

2.3 | Data source and management

Data and traits (BWT and WWT) collected and recorded in a herd book from 2000 to 2018 were used for this study. The data were entered, filtered, cleaned and organised using MS excel software and arranged for analysis (Table 1). Information related to pedigree, traits analysed and sample sizes are presented in Table 2. After cleaning, growth rate and efficiency-related traits: PADG, PKR, PGE and PRGR were calculated from BWT and WWT data for each individual animal record.

PADG is growth rate to weaning age, calculated as PADG = (WWT – BWT)/240, where 240 is the number of days between birth and weaning.

PKR is the ratio of PADG to the metabolic body weight to a certain period. Here, we calculated to WWT at 8 months of age (240 days). PKR is calculated as PKR = PADG/WWT$^{0.75}$ (Kleiber, 1947).

PGE is an indirect measure of GE, calculated as PGE = (WWT−BWT/BWT) × 100 (Ghafouri-Kesbi & Gholizadeh, 2017).

PRGR = Log (WWT) – Log (BWT)/240, for 8 months (240 days) of weaning age (Ghafouri-Kesbi & Eskandarinasab, 2018; Ghafouri-Kesbi & Gholizadeh, 2017).

2.4 | Data analysis

Phenotypic data were analysed using the general linear model (GLM) procedures of the statistical analysis system, SAS 9.1 (SAS, 2002). The fixed effects used in the model included calf birth year (2000–2018), calf birth season (dry, wet) and calf sex (male, female). Tukey Cramer test was used to separate significantly different means. The traits analysed were BWT, WWT, PADG, PKR, PGE and PRGR.

The statistical model used for the analysis of variances of fixed effects was:

$$Y_{ijk} = \mu + Y_i + S_j + Q_k + e_{ijk},$$

where Y_{ijk} = the observation on BWT, WWT, PADG, PKR, PGE and PRGR; μ = overall mean, Y_i = fixed effect of the ith birth year (2000–2018), S_j = fixed effect of the jth birth season (dry, wet), Q_k = fixed effect of the kth calf sex (male, female), e_{ijk} = residual associated with each observation.

The genetic parameters were estimated with single-trait animal models using an average information restricted maximum likelihood (AI-REML) method in WOMBAT software (Meyer, 2012). The log-likelihood ratio test was performed to determine significant random effects and consequently the most appropriate model for each trait. Genetic and phenotypic correlations between the traits were estimated using pairwise trait analyses.

The statistical models for BWT, WWT, PADG, PKR, PGE and PRGR were:

$$\text{Model 1} : y = Xb + Z_1a + e$$

$$\text{Model 2} : y = Xb + Z_1a + Z_2m + e(\text{cov}_{a,m} = 0)$$

$$\text{Model 3} : y = Xb + Z_1a + Z_2m + e(\text{cov}_{a,m} \neq 0)$$

$$\text{Model 4} : y = Xb + Z_1a + Z_2m + Z_3c + e(\text{cov}_{a,m} = 0)$$

$$\text{Model 5} : y = Xb + Z_1a + Z_2m + Z_3c + e(\text{cov}_{a,m} \neq 0)$$

where y is the vector of records; b is the vector of fixed effects; X is an incidence matrix of fixed effects; a is a vector of direct additive genetic effect; m is a vector of maternal additive genetic effects; c is a vector of permanent environmental effects; Z_1 is an incidence matrix of direct additive genetic effects; Z_2 is an incidence matrix of maternal additive genetic effects; Z_3 is an incidence matrix of permanent environmental effects; e is a vector of residuals.

The heritabilities, genetic correlations and phenotypic correlations were estimated as $h^2 = \sigma^2{}_a/\sigma^2{}_p$, $r_G = \sigma_{aij}\ \sqrt{\sigma^2{}_{ai}\sigma^2{}_{aj}}$ and $r_P = \sigma_{pij}/\sqrt{\sigma^2{}_{pi}\sigma^2{}_{pj}}$, respectively, where h^2 is heritability, r_G is genetic correlations, r_P is phenotypic correlations, $\sigma^2{}_a$ is the additive genetic variance, $\sigma^2{}_p$ is the total phenotypic variance, σ_{aij} is the additive genetic covariance between traits i and j, σ_{pij} is the phenotypic covariance between traits i and j, $\sigma^2{}_{ai}$ is the additive genetic variance for trait i, $\sigma^2{}_{aj}$ is the additive genetic variance for trait j, $\sigma^2{}_{pi}$ is the phenotypic variance for trait i and $\sigma^2{}_{pj}$ is the phenotypic variance for trait j.

3 | RESULTS

3.1 | Growth performance

The overall mean BWT of Fogera calves at ALRC is presented in Table 3. The mean BWT (21.3 ± 0.05 kg) was significantly affected ($p < 0.001$) by calf sex; male Fogera calves were heavier than their female counterparts. Similarly, calf birth season significantly affected ($p < 0.001$) the BWT of Fogera calves; calves born during the wet season outweighed those born in the dry season. Calf birth year also affected ($p < 0.001$) the BWT of calves. The heaviest calves were born in 2006, whereas the smallest BWT was recorded in the year 2008.

The overall mean WWT was 98.0 ± 0.67 kg (Table 3). The mean WWT of female Fogera calves was greater than the WWT of their male counterparts (104 vs. 98.5 kg). The effect of calf birth season on the WWT of Fogera calves in this study was significant ($p < 0.001$); calves born in the wet season were heavier than those born in the dry season (105 ± 1.15 vs. 95.3 ± 0.82). Calf's birth year significantly ($p < 0.001$) affected the WWT of Fogera calves; the smallest WWT was recorded in 2016, and the largest was in 2011.

The overall mean PADG of Fogera calves in this study was 320 ± 2.79 (Table 3). The study showed that sex significantly ($p < 0.001$) affected the PADG of Fogera calves. The mean PADG of female calves was greater than for male calves (334 vs. 317 g). The effect of calf birth season on PADG of Fogera calves in this study was significant ($p < 0.001$). Calves born in the wet season had larger PADG than those born in the dry season (347 ± 3.41 vs. 304 ± 4.78). Similarly, calf birth year showed a significant effect on the PADG of Fogera calves.

The overall mean PKR of Fogera calves in this study (10.1 ± 0.04; Table 3) was affected by the sex of calf ($p < 0.001$), calf birth season ($p < 0.001$) and calf birth year ($p < 0.001$). Female calves and calves born during the wet season had superior PKR.

The overall mean PGE was 3.51 ± 0.35. Male calves and calves born in the wet season had higher ($p < 0.001$) PGE than female and dry season born calves, respectively. Year of birth has also affected PGE; the

TABLE 3 Least squares means and standard errors (LSM ± SE) of growth traits of Fogera calves at Andassa Livestock Research Center, Ethiopia

	BWT (kg)		WWT (kg)		PADG (g/day)		PKR		PGE		PRGR	
Factors	N	LSM ± SE	N	LSM ± SE	N	LSM ± SE	N	LSM ± SE	N	LSM ± SE	N	LSM ± SE
Overall	1475	21.3 ± 0.05	1154	98.0 ± 0.67	1154	320 ± 2.79	1154	10.1 ± 0.04	900	3.51 ± 0.35	900	1.95 ± 0.00
Sex of calf		***		***		***		***		***		***
Male	675	21.7 ± 0.12	536	97.8 ± 1.05	536	317 ± 4.36	536	10.0 ± 0.06	417	3.73 ± 0.47	483	1.97 ± 5.61
Female	800	20.9 ± 0.10	618	101 ± 0.85	618	334 ± 3.53	618	10.3 ± 0.05	483	3.26 ± 0.51	417	1.94 ± 6.59
Birth Season		***		***		***		***		***		NS
Dry	584	21.0 ± 0.13	438	94.3 ± 1.15	438	304 ± 4.78	438	9.85 ± 0.06	326	3.46 ± 0.59	326	1.93 ± 5.02
Wet	891	21.7 ± 0.09	716	104 ± 0.82	716	347 ± 3.41	716	10.5 ± 0.05	574	3.54 ± 0.44	574	1.94 ± 6.13
Birth Year		***		***		***		***		***		***
2000	147	20.7 ± 0.24^{ed}	137	95.1 ± 1.87^{e}	137	310 ± 7.54^{f}	137	10.0 ± 0.11^{de}	114	3.61 ± 0.09^{d}	114	1.96 ± 0.00^{fg}
2001	79	21.9 ± 0.25^{cd}	68	102 ± 2.37^{de}	68	335 ± 9.75^{def}	68	10.3 ± 0.12^{cd}	49	3.56 ± 0.11^{de}	49	1.98 ± 0.01^{defg}
2002	119	21.3 ± 0.20^{cd}	80	112 ± 2.23^{abc}	80	376 ± 9.26^{bc}	80	10.8 ± 0.10^{b}	60	3.90 ± 0.09^{cd}	60	2.01 ± 0.00^{bcd}
2003	98	22.0 ± 0.16^{cd}	93	$84.7 \pm 1.80f^{g}$	93	261 ± 7.47^{gh}	93	9.21 ± 0.12^{f}	80	2.84 ± 0.08^{g}	80	1.91 ± 0.00^{h}
2004	122	22.0 ± 0.13^{bc}	112	87.6 ± 2.48^{f}	112	274 ± 10.3^{g}	112	9.24 ± 0.17^{f}	73	2.72 ± 0.10^{g}	73	1.89 ± 0.01^{h}
2005	58	24.2 ± 0.22^{a}	45	104 ± 3.41^{d}	45	332 ± 14.1^{def}	45	10.1 ± 0.18^{de}	37	3.20 ± 0.13^{ef}	37	1.99 ± 0.01^{cdef}
2006	75	24.4 ± 0.21^{a}	34	118 ± 2.99^{ab}	34	392 ± 12.5^{b}	34	10.9 ± 0.14^{b}	19	3.53 ± 0.12^{de}	19	2.04 ± 0.00^{ab}
2007	45	21.9 ± 0.50^{bc}	25	99.4 ± 3.40^{de}	25	325 ± 13.8^{ef}	25	10.2 ± 0.19^{cd}	20	3.55 ± 0.19^{de}	20	1.97 ± 0.01^{efg}
2008	66	16.9 ± 0.44^{h}	61	78.7 ± 1.99^{g}	61	258 ± 7.64^{gh}	61	9.67 ± 0.11^{e}	54	3.84 ± 0.12^{cd}	54	1.88 ± 0.01^{h}
2009	108	19.5 ± 0.18^{gf}	95	103 ± 2.72^{bcd}	95	349 ± 11.5^{cde}	95	10.6 ± 0.14^{bc}	55	3.73 ± 0.14^{d}	55	1.95 ± 0.01^{g}
2010	67	20.0 ± 0.30^{efg}	54	101 ± 1.29^{de}	54	339 ± 5.21^{def}	54	10.6 ± 0.07^{bc}	51	4.15 ± 0.09^{c}	51	1.99 ± 0.00^{cde}
2011	64	19.4 ± 0.29^{fg}	64	124 ± 1.94^{a}	64	438 ± 8.13^{a}	64	11.7 ± 0.08^{a}	38	4.99 ± 0.15^{a}	38	2.05 ± 0.01^{a}
2012	66	19.0 ± 0.17^{g}	97	106 ± 0.85^{cd}	97	365 ± 3.34^{bcd}	97	11.0 ± 0.03^{b}	82	4.58 ± 0.04^{b}	81	2.01 ± 0.00^{bc}
2016	113	24.4 ± 0.27^{a}	83	101 ± 2.28^{de}	83	319 ± 9.39^{ef}	83	9.86 ± 0.12^{de}	71	2.94 ± 0.08^{fg}	71	1.97 ± 0.00^{efg}
2017	68	21.9 ± 0.41^{bc}	63	80.8 ± 1.64^{fg}	63	245 ± 6.70^{hg}	63	9.00 ± 0.11^{f}	56	2.74 ± 0.10^{g}	56	1.89 ± 0.00^{h}
2018	120	21.2 ± 0.23^{cd}	43	80.0 ± 2.32^{g}	43	241 ± 10.3^{h}	43	8.89 ± 0.19^{f}	41	2.71 ± 0.15^{g}	41	1.88 ± 0.012^{h}

N: number of observations.

***$p < 0.001$: means within the same column and effect with different letters are significantly different.

Abbreviations: BWT, birthweight of calves; LSM, Least squares mean, NS, non-significant; PADG, pre-weaning average daily body weight gain of calves; PGE, pre-weaning growth efficiency; PKR, pre-weaning Kleiber ratio; PRGR, pre-weaning relative growth rate; SE, standard error; WWT, weaning weight of calves.

highest and lowest PGEs were observed in 2011 and 2018 (4.99 ± 0.15 vs. 2.71 ± 0.15), respectively.

The overall mean PRGR (1.95 ± 0.00) is presented in Table 3. Sex of calf and birth year had a significant effect on PRGR. Female calves had a higher RGR than males and the highest and the lowest PRGR of Fogera calves were recorded in 2011 and 2018 (2.05 ± 0.01 vs. 21.9 ± 0.012), respectively.

3.2 | Genetic parameter estimates

Co(variance) components and heritabilities of Fogera cattle estimated using five animal models for BWT, WWT, PADG, PKR, PGE and PRGR are presented in Table 4. Based on the log-likelihood ratio tests applied to choose the most appropriate model for each of the traits (Meyer, 2012), Model 2 was appropriate for estimating the heritability of BWT. In Model 2, the direct additive genetic and maternal genetic effects had a significant impact on BWT. The direct heritability of BWT for Fogera calves obtained in this study (0.21 ± 0.07; Table 4) was higher when the maternal effect was removed from the model.

The model that included the direct additive and maternal genetic effects with non-zero covariance between direct and maternal effects ($\text{cov}_{a,\ m} \neq 0$), Model 3, was appropriate to explain the variation in WWT. Accordingly, the direct additive heritability value of WWT for Fogera cattle was 0.27 ± 0.00 (Table 4). The direct genetic heritability estimates obtained in this study were higher than the corresponding maternal heritabilities. The inclusion of maternal and permanent environmental effects in the model reduced the heritability of WWT from 0.39 ± 0.09 to 0.27 ± 0.00. The direct maternal genetic correlation (0.72 ± 0.02) was high and positive.

Models 5 and 3 were appropriate to estimate the heritability of PADG and PKR, respectively. Accordingly, the estimates of direct heritability (h^2_a) for ADG and PKR were 0.55 ± 0.18 and 0.53 ± 0.17, respectively.

Model 2, which included random direct additive and maternal genetic effects, had the highest log-likelihood value for PGE, whereas Model 4, which included random direct additive, maternal additive genetic and permanent environmental effects, was selected as the most appropriate model for PRGR. The direct heritability estimates for PGE and PRGR were 0.33 ± 0.00 and 0.12 ± 0.00, respectively.

3.3 | Phenotypic and genetic correlations

Phenotypic and genetic correlations estimated from a bivariate animal model are presented in Table 5. Small and negative (−0.20 ± 0.04: BWT-PKR) to large and positive (0.99 ± 0.00: BWT-PGE, BWT-PRGR, WWT-PGE, WWT-PRGR, PKR- PGE, PKR-PRGR and PGE-PRGR) genetic correlations were found in this study. The genetic correlations between BWT-ADG, WWT-PADG, PGE-PADG and PRGR-PADG were moderate and positive. Similar to genetic correlations, small and negative (−0.03 ± 0.20: BWT-PKR) to large and positive (0.99 ± 0.00: BWT-PGE, BWT-PRGR, WWT-PGE, WWT-PRGR, PKR-PGE, PKR-PRGR and PGE-PRGR) phenotypic correlations were found. The phenotypic correlations between BWT-WWT, BWT-PADG, WWT-PADG and PADG-PGE traits were moderate and positive.

4 | DISCUSSION

4.1 | Growth performance

The mean BWT found in this study (21.3 ± 0.08) is similar to previous reports for the same breed (Bekele et al., 2016; Bitew et al., 2010; Tesfa and Garikipati 2014), and Ogaden cattle by Mekuriaw et al. (2009). Nevertheless, it is smaller than the values reported for Ethiopian and Kenyan Boran and Barka cattle breeds (Demeke et al., 2003; Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b), and greater than the BWT of the same breed reported by Menale et al. (2011) and Horro cattle (Abera et al., 2012; Demeke et al., 2003).

A similar effect of calf sex on BWT was previously reported for Fogera and other Ethiopian cattle breeds (Bekele et al., 2016; Mekuriaw et al., 2009; Menale et al., 2011). The male superiority in BWT of calves may be attributed to hormonal differences. Male fetuses have higher androgen concentration than females, which, in turn, affects sex-based differences in skeletal muscles. Unlike the current study, Gunawan and Jakaria (2011) reported a non-significant effect of sex on the BWT of Bali Cattle.

Calf's birth season had a significant effect on the BWT of Fogera calves; calves born during the wet season outweighed those born in the dry season. Similar results were reported previously for the same breed (Bekele et al., 2016; Menale et al., 2011), and Bali cattle in Indonesia (Gunawan & Jakaria, 2011). This may be due to the reason that feed availability is better in the wet season than in the dry season, which helps cows to get better nutrition in the last trimester of their pregnancy. Better nutrition (protein) in the last trimester of pregnancy is indicated to improve the BWT of animals (Miguel-Pacheco et al., 2017). The significant effect of birth year on BWT of Fogera calves may be due to the fluctuation in rainfall patterns across years, in the country in general, which, in turn, affect feed availability. It may also indicate the inconsistent and subsistent cattle management and husbandry practices in the centre. Previously, several scholars reported the effect of birth year on calf BWT (Bekele et al., 2016; Bitew et al., 2010; Menale et al., 2011).

The mean WWT (98.0 ± 0.67) was greater than other findings elsewhere in Ethiopia and in the tropics (Bekele et al., 2016; Demeke et al., 2003; Gunawan & Jakaria, 2011; Mekuriaw et al., 2009; Menale et al., 2011; Praharani 2009; Sukmasari et al., 2002) (Table 6). The study confirmed that the mean WWT of female Fogera calves was greater than the WWT of male Fogera calves (104 vs. 98.5 kg). A similar effect of calf sex on the WWT of Fogera calves was reported by previous scholars (Bekele et al., 2016). However, in contrast to the current finding, Menale et al. (2011) reported a non-significant effect of calf sex on WWT. The unusual superiority in the WWT of Fogera female calves in this study may be due to the preferential treatment given to

TABLE 4 Estimates of variance components and heritability for growth traits of Fogera cattle at Andassa Livestock Research Center, Ethiopia

Trait	Models	σ^2_a	σ^2_m	cov $(_{a,\,m})$	σ^2_{pe}	σ^2_e	σ^2_p	h^2_a	m^2_a	r_{am}	c^2	Log *L*
BWT	1	0.16 ± 0.13	–	–	–	0.34 ± 0.12	0.51 ± 0.06	0.31 ± 0.25	–	–	–	−1746
	2	**1.21 ± 0.43**	**0.39 ± 0.21**	**–**	**–**	**4.11 ± 0.31**	**5.71 ± 0.25**	**0.21 ± 0.07**	**0.06 ± 0.04**	**–**	**–**	−1744
	3	1.18 ± 0.50	0.03 ± 0.33	0.026 ± 0.33	0.37 ± 0.32	4.12 ± 0.34	5.71 ± 0.25	0.21 ± 0.08	0.003 ± 0.05	0.04 ± 0.51	0.06 ± 0.3	−1744
	4	1.21 ± 0.44	0.38 ± 0.30	–	0.001 ± 0.29	4.11 ± 0.33	5.71 ± 0.25	0.21 ± 0.07	0.066 ± 0.05	–	0.07 ± 0.2	−1744
	5	1.18 ± 0.50	0.03 ± 0.30	0.26 ± 0.33	0.001 ± 0.29	4.12 ± 0.36	5.71 ± 0.25	0.21 ± 0.08	0.004 ± 0.06	0.04 ± 0.51	0.07 ± 0.3	−1744
WWT	1	93.4 ± 23.0	–	–	–	149 ± 18.0	242 ± 12.9	0.38 ± 0.08	–	–	–	2875
	2	95.2 ± 26.2	94.5 ± 12.4	–	–	147 ± 18.2	242.4 ± 13	0.39 ± 0.09	0.00 ± 0.05	–	–	−2874
	3	**1.10 ± 0.27**	**1.04 ± 0.03**	**0.77 ± 0.18**	**1.05 ± 0.02**	**3.98 ± 0.32**	**0.27 ± 0.01**	**0.26 ± 0.01**	**–**	**0.72 ± 0.02**	**3.89 ± 0.00**	−2866
	4	95.2 ± 26.2	0.00 ± 20.9	–	0.001 ± 21.1	147 ± 19.1	242 ± 13.1	0.39 ± 0.09	0.000 ± 0.09	–	4.13 ± 0.20	−2874
	5	222 ± 71.5	74.6 ± 45.5	122 ± 47	5.04 ± 24.0	82.7 ± 38.8	262 ± 20.1	0.18 ± 0.21	0.28 ± 0.16	−0.94 ± 0.13	0.01 ± 0.21	−2866
PADG	1	0.10 ± 0.00	–	–	–	0.20 ± 0.00	0.30 ± 0.00	0.33 ± 0.00	–	–	–	−20,026,444
	2	0.00 ± 0.00	0.10 ± 0.01	–	–	0.23 ± 0.00	0.51 ± 0.003	0.34 ± 0.13	0.193 ± 0.16	–	–	1246
	3	0.20 ± 0.00	0.10 ± 0.00	0.10 ± 0.001	–	0.202 ± 0.00	0.60 ± 0.00	0.33 ± 0.00	0.16 ± 0.00	0.71 ± 0.001	–	−37,449,745
	4	0.15 ± 0.00	0.2 ± 0.001	–	0.002 ± 0.12	0.20 ± 0.00	0.7 ± 0.00	0.20 ± 0.00	0.267 ± 0.00	–	0.33 ± 0.00	−32,095,9986
	5	**0.003 ± 0.01**	**0.002 ± 0.10**	**0.18 ± 0.01**	**0.001 ± 0.01**	**0.16 ± 0.01**	**0.006 ± 0.00**	**0.55 ± 0.19**	**0.32 ± 0.21**	**−0.70 ± 0.20**	**0.17 ± 0.01**	1948
PKR	1	0.10 ± 0.00	–	–	–	0.20 ± 0.00	0.30 ± 0.00	0.33 ± 0.00	–	–	–	−200,264,436
	2	0.002 ± 0.00	0.001 ± 0.00	–	–	0.001 ± 0.0	0.005 ± 0.004	0.33 ± 0.01	0.33 ± 0.01	–	–	−98,806
	3	**0.54 ± 0.20**	**0.30 ± 0.13**	**−0.35 ± 0.14**	**–**	**0.52 ± 0.11**	**1.02 ± 0.64**	**0.53 ± 0.18**	**0.30 ± 0.12**	**−0.30 ± 0.15**	**–**	−440
	4	0.01 ± 0.00	0.13 ± 0.00	–	0.014 ± 0.00	0.014 ± 0.00	0.053 ± 0.00	0.205 ± 0.01	0.25 ± 0.03	–	0.26 ± 0.00	−9327
	5	0.99 ± 0.02	0.06 ± 0.03	0.02 ± 0.01	–	0.15 ± 0.01	0.41 ± 0.016	0.24 ± 0.05	0.14 ± 0.07	0.24 ± 0.23	–	−792
PGE	1	0.23 ± 0.007	–	–	–	046 ± 0.005	0.7 ± 0.003	0.33 ± 00.01	–	–	–	−47,822
	2	**0.001 ± 0.00**	**0.001 ± 0.00**	**–**	**–**	**0.001 ± 0.00**	**0.003 ± 0.00**	**0.33 ± 0.00**	**0.33 ± 0.00**	**–**	**–**	−13,419,833
	3	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	–	0.02 ± 0.00	0.06 ± 0.00	0.33 ± 0.002	0.16 ± 0.00	0.7 ± 0.08	–	−648,328
	4	0.002 ± 0.00	0.002 ± 0.00	–	0.002 ± 0.01	0.002 ± 0.00	0.007 ± 0.04	0.28 ± 0.001	0.28 ± 0.01	–	0.28 ± 0.01	−6,027,690
	5	0.002 ± 0.07	0.002 ± 0.00	0.001 ± 0.00	0.002 ± 0.00	0.003 ± 0.05	0.01 ± 0.00	0.21 ± 0.01	0.15 ± 0.001	0.57 ± 0.04	0.2 ± 0.00	−4,458,638
PRGR	1	0.1 ± 0.00	–	–	–	0.3 ± 0.00	0.40 ± 0.00	0.25 ± 0.00	–	–	–	−16,764,024
	2	**0.01 ± 0.00**	**0.001 ± 0.00**	**–**	**–**	**0.01 ± 0.00**	**0.02 ± 0.00**	**0.50 ± 0.00**	**0.05 ± 0.00**	**–**	**–**	−1,645,196
	3	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	–	0.02 ± 0.00	0.06 ± 0.00	0.33 ± 0.00	0.17 ± 0.00	0.71 ± 0.01	–	−648,328
	4	0.001 ± 0.00	0.002 ± 0.00	–	0.002 ± 0.00	0.002 ± 0.00	0.008 ± 0.00	0.12 ± 0.00	0.25 ± 0.00	–	0.25 ± 0.00	−6,027,690
	5	0.002 ± 00	0.001 ± 0.00	0.001 ± 0.00	0.002 ± 0.00	0.003 ± 0.00	0.01 ± 0.00	0.20 ± 0.00	0.10 ± 0.00	0.58 ± 0.00	0.2 ± 0.00	−4,458,638

Abbreviations: σ^2_a, direct additive genetic variance; σ^2_m, maternal additive genetic variance; σ^2_{pe}, permanent maternal environmental variance; σ^2_e, residual variance; σ^2_p, phenotypic variance; h^2, direct additive heritability; m^2, maternal genetic heritability; c^2, the fraction of total variance to maternal permanent environmental effect; Log *L*, log-likelihood ratio.

Note. Models in bold face are those models selected based on Log values.

TABLE 5 Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations between the studied traits

	BWT	WWT	PADG	PKR	GE	PRGR
BWT	***	0.22 ± 0.05	0.41 ± 0.01	−0.20 ± 0.04	0.99 ± 0.00	0.99 ± 0.00
WWT	0.49 ± 0.23	***	0.41 ± 0.00	0.27 ± 0.01	0.98 ± 001	0.99 ± 0.00
PADG	0.41 ± 0.01	0.41 ± 0.01	***	0.33 ± 0.02	0.40 ± 0.001	0.54 ± 0.07
PKR	−0.03 ± 0.20	0.27 ± 0.03	0.30 ± 0.10	***	0.99 ± 0.01	0.99 ± 0.01
GE	0.99 ± 0.00	0.99 ± 0.01	0.41 ± 0.005	0.99 ± 0.02	***	0.99 ± 0.01
PRGR	0.99 ± 0.00	0.99 ± 0.01	0.96 ± 0.00	0.99 ± 0.00	0.99 ± 0.02	***

Abbreviations: BWT, birthweight; PADG, pre-weaning average daily weight gain; PGE, pre-weaning growth efficiency; PKR, pre-weaning Kleiber ratio; PRGR, pre-weaning relative growth rate; WWT, weaning weight.

female calves in the centre considering them as future replacements for the herd.

The significant ($p < 0.001$) effect of calf birth season on the WWT of Fogera calves may be due to differences in feed availability. The better WWT of calves born during the wet season may be related to better grazing feed availability for cows that, in turn, affect milk availability for the calves at an early age. This result is similar to previous reports of Fogera cattle and elsewhere in Ethiopia as indicated in Table 6. Calf's birth year significantly ($p < 0.001$) affected the WWT of Fogera calves; the smallest WWT was recorded in 2016, and the largest was in 2011. This effect of birth year on calf WWT is in line with previous findings (Bekele et al., 2016; Menale et al., 2011). Similar to the BWT, the variation in WWT of calves across years may be related to the variable rainfall distribution, which, in turn, affects feed availability, and inconsistent cattle feeding management practices in the centre.

The mean PADG of Fogera cattle in this study (320 ± 2.79) was greater than the findings of the same breed in Ethiopia (Bekele et al., 2016; Menale et al., 2011). Similarly, the current result was lower than the results of Horro and Horro*Holstein Friesian crossbreeds (Abera et al., 2012; Demeke et al., 2003), respectively.

The study showed that sex significantly affected the PADG of Fogera cattle. The mean PADG of female Fogera calves was greater than for male Fogera calves (334 vs. 317 g). The current result is similar to the previous findings of (Abera et al., 2012). However, it differs from other reports (Bekele et al., 2016; Demeke et al., 2003; Menale et al., 2011; Wasike et al., 2006) (Table 6). Calf birth season affected PADG of Fogera calves; calves born in the wet season had larger PADG than those born in the dry season (347 ± 3.41 vs. 304 ± 4.78) which was in line with previous results (Bekele et al., 2016; Menale et al., 2011). Similarly, calf birth year showed a significant effect on the PADG of Fogera calves. The effect of birth year on calf WWT is in line with previous findings (Abera et al., 2012; Menale et al., 2011).

The mean PKR of Fogera cattle in this study (10.1 ± 0.04; Table 3) was affected by sex of calf, calf birth season and calf birth year. The effect of birth season and year may be associated with changes in climatic conditions, feeding and health management practices. Similar to this study, scholars reported the effect of year, season and sex of the animal on PKR in Herford cattle (Köster et al., 1994) and in sheep (Ghafouri-Kesbi & Gholizadeh, 2017).

The mean PGE (3.51 ± 0.35) was affected by the sex of calf and season of birth that female calves and calves born in the wet season had higher ($p < 0.001$) GE than male and dry season born calves, respectively. Even though female calves were superior for WWT and PADG, male superiority for PGE may be due to the fact that testosterone enhances better weight gain similar to growth hormone (Zung et al., 1999). Estrogen limits the growth of bones in female calves which finally affects growth rate and GE. Similarly, calves born in the wet season had higher GE than those born in the dry season which may be due to the effective utilisation of surplus feed available in the wet season. Year of birth also affected GE, and the highest and lowest PGEs were observed in 2011 and 2018 (4.99 ± 0.15 vs. 2.71 ± 0.15), respectively. Similar to the current study, the effect of sex of animals has been reported somewhere in the literature (Ghafouri-Kesbi & Gholizadeh 2017).

The mean PRGR (1.95 ± 0.00; Table 3) was significantly affected by the sex of calf and birth year. Female calves had a higher PRGR than males and the highest and the lowest PRGR of Fogera calves were recorded in 2011 and 2018 (2.05 ± 0.01 vs. 21.88 ± 0.012), respectively. Similar to this result, scholars (Ghafouri-Kesbi & Gholizadeh, 2017; Kesbi & Tari, 2015) reported the effect of sex and birth year of animals on PRGR of sheep.

4.2 | Genetic parameter estimates

Co(variance) components and heritability of Fogera calves estimated using five animal models for BWT, WWT, PADG, PKR, PGE and PRGR are presented in Table 4. Based on the log-likelihood ratio tests (Meyer, 1992), Model 2 was the best model selected to estimate the heritability of BWT. The direct heritability of BWT for Fogera cattle obtained in this study was 0.21 ± 0.07. This result is in line with other findings (Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b; Tesfa & Garikipati, 2014). However, the value is lower than the report by Schoeman and Jordaan (1999) for multi-breed beef cattle in South Africa, and larger than the value previously reported for the same breed (Bekele et al., 2016; Zeleke et al., 2016) and Horro cattle by Demeke et al. (2003). The heritability estimates for the BWT of Fogera cattle recorded in this study confirmed some scope of selection

TABLE 6 Phenotypic and genetic parameter estimates of growth traits of local cattle breeds in Ethiopia

	Phenotypic performances						Heritability						
Breed	BWT (kg)	WWT (kg)	PADG (g)	PKR	PGE	PRGR	BWT	WWT	PADG	PKR	PGE	PRGR	Source
Fogera	21.3 ± 0.05	98.0 ± 0.67	320 ± 2.79	10.1 ± 0.04	3.51 ± 0.35	1.95 ± 0.00	0.21 ± 0.07	0.27 ± 0.01	0.55 ± 0.19	0.53 ± 0.18	0.33 ± 0.00	0.50 ± 0.00	Current study
Fogera	21.0 ± 0.03	88.6 ± 0.33	280 ± 0.00	–	–	–	0.06 ± 0.02	0.08 ± 0.03	0.06 ± 0.03	–	–	–	(Bekele et al., 2016)
Fogera	20.7 ± 0.11	88.6 ± 1.30	297 ± 3.63	–	–	–	–	–	–	–	–	–	(Menale et al., 2011)
Fogera	21.3 ± 0.09	102 ± 0.77	–	–	–	–	0.24 ± 0.09	0.18 ± 0.05	–	–	–	–	(Tesfa & Garikipati, 2014)
Horro	22.9 ± 0.3	95.2 ± 1.3	401.4 ± 7.1	–	–	–	0.14 ± 0.03	0.08 ± 0.03	0.07 ± 0.02	–	–	–	(Demeke et al., 2003)
Boran	22.9 ± 0.30	95.2 ± 1.30	–	–	–	–	–	–	–	–	–	–	(Demeke et al., 2003)
Boran	23.3 ± 0.36	–	–	–	–	–	0.25 ± 0.05	0.43 ± 0.04	–	–	–	–	(Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b)
Barka	22.6 ± 0.50	92.0 ± 1.90	–	–	–	–	–	–	–	–	–	–	(Demeke et al., 2003)
Ogaden	21.5 ± 0.29	91.6 ± 1.67		–	–	–	–	–	–	–	–	–	(Mekuriaw et al., 2009)

Abbreviations: BWT, birthweight; HF, Holstein Friesian; PADG, pre-weaning average daily weight gain; PGE, pre-weaning growth efficiency; PKR, pre-weaning Kleiber ratio; PRGR, pre-weaning relative growth rate; WWT, weaning weight.

responses for BWT, and it also indicated the presence of modest variation within the study population.

Model 3, which included direct and maternal additive genetic effects with non-zero covariance between direct and maternal effects, was selected to estimate the heritability (0.27 ± 0.01) of WWT. The direct heritability estimates were higher than the corresponding direct maternal heritabilities. The lower direct maternal heritability compared to direct additive heritability for WWT could be explained by high environmental pressures and low level of management existed at WWT. The direct maternal genetic correlation was high (0.77 ± 0.18) which indicates the possibility of selection based on direct genetic effect in addition to improving the management. Similar heritability value of WWT was reported for Fogera*Holstein Friesian crosses (0.24 ± 0.07) by Zeleke et al. (2016). However, larger (Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b; Schoeman & Jordaan, 1999) and smaller (Abera et al., 2012; Bekele et al., 2016; Demeke et al., 2003) direct heritability estimates of WWT were reported in the literature.

Models 5 and 3 were appropriate to estimate the heritability of PADG (0.55 ± 0.19) and PKR (0.53 ± 0.18), respectively. Unlike the current study, smaller heritability estimates of PADG (Bekele et al., 2016; Demeke et al., 2003) and PKR (Köster et al., 1994; Steyn et al., 2014) were reported. A similar larger PKR heritability value was reported by Schoeman and Jordaan (1999) for a multi-breed beef cattle herd in South Africa. The larger direct heritability estimates of PADG and PKR indicate that these traits could be used as a guide during selection programmes for GE.

Model 3 also provided the best fit for the estimation of the heritability (0.33 ± 0.00) for PGE. In contrast to this study, smaller PGE heritability values were reported (Ghafouri-Kesbi & Gholizadeh, 2017).

The direct heritability value of PRGR (0.50 ± 0.00) as estimated by Model 2 was larger than the corresponding maternal heritability estimate. This could indicate that PRGR depends more on individual animal performance than on maternal ability of their dams. The model included the direct additive and maternal genetic effect as a random factor. Similar larger heritability values of PRGR have been reported in the literature (Schoeman & Jordaan, 1999).

4.3 | Phenotypic and genetic correlations

Phenotypic and genetic correlations measure the strength of the relationship between two performance traits. Phenotypic correlations provide an observable measure of the relationship between two traits (Bourdon, 2000; Schoeman & Jordaan, 1999; Singh et al., 2016).

The genotypic correlations estimated from a bivariate animal model ranged from small and negative (−0.20 ± 0.04) to large and positive (0.99 ± 0.00). The genetic correlations between BWT-ADG, WWT-PADG, PGE-PADG and PRGR-PADG were moderate and positive, indicating that selection for one trait would improve the other (Bourdon, 2000).

Similar to genetic correlations, small and negative (−0.03 ± 0.20) to a large and positive (0.99 ± 0.00) phenotypic correlations were found

in this study. The phenotypic correlations among BWT-WWT, BWT-PADG, WWT-PADG and PADG-PGE traits were moderate and positive.

The negative and moderate phenotypic and genetic correlations between BWT-PKRA imply that selection of Fogera cattle based on BWT will not improve the PKR and vice versa. On the other hand, larger phenotypic correlations between traits indicate the possibility of correlated selection responses. The genetic correlation between BWT and WWT was higher than the phenotypic correlation. This result was higher than the previous findings (Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b; Zeleke et al., 2016). Previously, scholars reported smaller (Haile, Ayalew, et al., 2011a; Haile, Joshi, et al., 2011b; Tesfa & Garikipati, 2014), even negative (Singh et al., 2010) values of genetic correlations between BWT-WWT. Similar (del Carmen Chin-Colli et al., 2016; Pires et al., 2016) and higher (Schoeman & Jordaan 1999; Zeleke et al., 2016) genetic correlations have been previously reported for Fogera cattle and elsewhere in the world. The result implies that selection based on individual performance at BWT will be effective to increase PGE and PRGR traits. In contrast to the current study, Schoeman and Jordaan (1999) reported a smaller and negative genetic correlation between BWT-PRGR and no association between BWT-PKR. A higher correlation between PKR and feeding efficiency has been reported on lambs (Eskandarinasab et al., 2010; Talebi 2012).

5 | CONCLUSIONS

The BWT and WWT performances of Fogera cattle in this study are comparable with other indigenous cattle breeds in Ethiopia. The effects of sex of calf, birth season and year of birth were significant for all the traits studied except for PRGR that was not affected by season of birth.

The moderate additive genetic variation in growth traits and large additive genetic variation in GE-related traits indicate an opportunity for genetic improvement for these traits through selective breeding. Moreover, significant maternal effects on pre-weaning growth and efficiency-related traits indicated the importance of including maternal effects in genetic evaluation of traits measured early in life.

The large phenotypic and genetic correlations between most of the traits indicate the potential use of these traits to improve the growth rate of Fogera cattle. The negative phenotypic and genetic correlation between BWT-PKRA implies that the selection of Fogera calves based on either of the traits could have an adverse effect on the other. Therefore, caution should be taken when designing the selection criteria for growth improvement.

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AUTHOR CONTRIBUTIONS

DK: Conceptualisation (lead); writing—original draft (lead); formal analysis (lead); writing—review and editing (equal); MT: Conceptualisation (lead); writing—original draft (lead); formal analysis (lead); writing—review and editing (equal); DK: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); writing—review and editing (equal); MT: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (equal); AT: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); AB: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); AK: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); writing—review and editing (supporting); MM: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); EL: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); TB: Conceptualisation (supporting); writing—original draft (supporting); formal analysis (supporting); AH: Writing—original draft (supporting); formal analysis (supporting); writing—review and editing (equal).

CONFLICT OF INTEREST

Authors clarify that there is no conflict of interest with any financial, personal or other relationships with other people or organisations related to the material discussed in the manuscript.

DATA AVAILABILITY STATEMENT

The data used for analysis during study are available from the corresponding author on reasonable request.

PEER REVIEW

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