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Research Article

Estimation of the Heritabilities for Body Shape and Body Weight in Yellow River Carp (*Cyprinus carpio haematopterus*) Based on a Molecular Pedigree

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Estimation of the heritability for a given phenotype would provide basic information for potential breeding programs. As one of the most precious common carp strains, Yellow River carp was subject to selection for fast growth and a slender body to meet market demands. In the present study, heritabilities for body shape (body length, BL and body height, BH) and body weight (BW) were estimated based on a molecular parentage assignment for 750 progenies from 58 half-sib and full-sib Yellow River carp families. Eight highly polymorphic microsatellites were used for the construction of the molecular pedigree, and the average observed heterozygosity (H_o), expected heterozygosity (H_e), and the polymorphism information content (PIC) were 0.841, 0.792, and 0.763, respectively. All 750 progenies were successfully assigned to single parental pairs with 100% accuracy. Using the linear mixed model, the heritabilities were estimated to be 0.268, 0.338, and 0.340 for BL, BH, and BW, respectively. High phenotypic (0.831–0.927) and genetic (0.952–0.987) correlations among these three traits suggested that selection for BW could also largely affect the body shape and vice versa. Moderate heritabilities and high genetic corrections revealed by this study strongly indicate substantial potentials for genetic improvement of both growth rate and body formation in Yellow River carp breeding programs.

1. Introduction

As one of the most important traditional breeding methods, selective breeding has been successfully applied to improve traits of economic interest in many aquatic animals [1, 2]. For example, in brown trout (*Salmo trutta fario*), selective breeding by an improved mass selection methodology yielded considerable weight gain (up to 25% per generation) [3]. To assess the utility of selective breeding for any economic traits, reliable estimates of genetic parameters are indispensable. Estimation of the heritability is recognized as an essential first step towards proceeding with a selective breeding program [4, 5]. For example, the growth, one of the most economically important traits determined by both genetic and environmental factors [6] with a large genetic variance, is very suitable for selection. Up to now, heritability estimates for growth-related traits have been performed in a number of aquaculture fish species, such as gilthead seabream (*Sparus aurata*) [7–9], rainbow trout (*Oncorhynchus mykiss*) [10, 11], grass carp (*Ctenopharyngodon idella*) [12], European sea bass (*Dicentrarchus labrax*) [13, 14], Nile tilapia (*Oreochromis niloticus*) [15, 16], Japanese flounder (*Paralichthys olivaceus*) [17–19], rohu carp (*Labeo rohita*) [20], and so on.

Parentage assignment is an essential tool for obtaining pedigree information in aquaculture species [21]. The estimation of genetic parameters based on pedigree information would contribute to eliminate environmental effects among different families and increase estimation accuracy of additive, maternal,

and dominance effects, thus achieving the goal of genetic improvement and hatchery management [1, 22]. Generally, reconstruction of pedigrees in an aquaculture species can be achieved by molecular parentage analysis based on DNA markers. Microsatellite markers, by virtue of their merits of multiallelic, PCR-based, and wide distribution in the vertebrate genomes [23], have been extensively applied to parentage assignment in aquatic animals [12, 24–27], which facilitate the estimation of heritabilities and family-based selection.

Common carp (*Cyprinus carpio*) has been one of the most important fish cultured world-wide [28], with an annual production recently over 4.4 million metric tons in the world [29]. Various genetic studies have been performed for this aquaculture species [30–34]. Heritability estimates for growth-related traits have been reported in mirror carp (*C. carpio carpio*), which presented a moderate-to-high heritability (0.2–0.7) [24, 35, 36]. However, few heritabilities were estimated for other common carp strains so far. As one of the precious common carp strains derived from Asian subspecies and historically formed by adapting to the natural environment of the Yellow River basin [37], Yellow River carp (*C. carpio haematopterus*) plays an important role in the fisheries market of north-central China. Since the past two decades, long-term artificial propagation and inappropriate management of brood stocks have resulted in the decline of economic traits in this strain. Therefore, Yellow River carp are subject to selection for fast growth and a slender body to meet the market demands. However, few reports were available on the quantitative genetic basis of growth-related traits in this carp strain up to now. It is urgently necessary to estimate the heritabilities of growth-related and/or other economic traits to guide and accelerate the selective breeding of Yellow River carp.

In the present study, we first estimated the genetic parameters of body weight (BW), body length (BL), and body height (BH) for Yellow River carp by applying a mixed-family approach combined with a full-factorial design. Parentage assignment was performed retrospectively using highly polymorphic microsatellite markers. The main objective of this study is to understand the quantitative genetic bases (heritabilities) of the growth and body shape traits in Yellow River carp so as to facilitate and speed up selective breeding programs in this important carp strain.

2. Materials and Methods

2.1. Sampling and Morphometric Measurements. Based on the pedigree information and gonadal maturation of sixty candidate parents, eight dams and eight sires of Yellow River carp were selected to produce a mixed population by artificial reproduction in April 2019. All sixteen dams and sires of Yellow River carp were injected with exogenous hormones (pituitary gland and human chorionic gonadotropin, with the rejected dose of 5 mg and 1200 IU per kilogram of fish body, respectively) and put in a spawning tank with circulating water for natural fertilization, and then larval fish were raised in a muddy pond following standard culture conditions at the Henan Academy of Fishery Sciences (Zhengzhou, China). After eight months of cultivation, 750 progenies were randomly collected, and three parameters, including body weight (BW), body length (BL), and body height (BH), were recorded based on an electronic scale and a customized measuring plate. Fin clips of parental fish and progenies were sampled and ethanol-preserved, and genomic DNA was extracted following a traditional phenol-chloroform protocol [38]. The concentration of genomic DNA was determined using a NanoDrop 2000 UV-Vis Spectrophotometer (Thermo Scientific, USA).

2.2. Parentage Assignment. All available microsatellite markers in our lab were initially amplified and visualized by 10% PAG electrophoresis in parents for screening polymorphic loci, and finally eight markers with clear banding patterns and high polymorphisms were selected for parentage assignment (Table 1). Then forward primers of eight loci were labeled with fluorescent dyes and PCR products were sequenced by the 3730 DNA sequencer (ABI, USA). PCR was carried out in a total volume of 12.5 μL containing 1.25 μL 10 x reaction buffer, 0.4 μL dNTP (2.5 mM), 1 U Taq polymerase (TaKaRa, Dalian), 0.4 μL forward and reverse primer mixture (2.5 μM), 30–50 ng template DNA, and 9.4 μL sterile water. The thermo-profile was described as follows: 94°C denaturing for 4 min, followed by 30 cycles of 94°C for 35 s, optimal annealing temperature (Table 1) for 35 s and 72°C for 40 s, and a final extension at 72°C for 8 min.

The number of alleles (N), observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphic information content (PIC) were calculated by POPGENE ver. 3.4 software to assess genetic variability [39]. Parentage assignment was determined using the likelihood-based approach with CERVUS 3.0 software [40, 41].

2.3. Variance Components and Heritability Estimation. Genetic parameters were estimated using the ASReml software version 3.0 [42, 43]. In the matrix notation, the model is written as follows:

$$y = Xb + Zu + e, \tag{1}$$

where y is the phenotypic measure of the trait being analyzed, X and Z are incidence matrices related to the fixed and additive genetic effects, b is the vector of the fixed effects including overall mean and deformity status, u is the additive genetic effect of the individual animal, and e is the vector of residual effects.

Heritabilities for the traits were calculated based on the following univariate animal model:

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_e^2}, \tag{2}$$

where σ_A^2 is the additive genetic variance and σ_e^2 is the residual variance.

2.4. Statistical Analyses of the Phenotypic and Genetic Correlations. Phenotypic and genetic correlations were estimated from a series of bivariate and trivariate linear mixed models with the fixed and random effects as described above [42, 43]. ASReml allows you to specify different random

Table 1: Summary statistics of eight highly polymorphic microsatellite markers used in the molecular pedigree analysis of Yellow River carp.

Locus	GenBank accession no.	Repeat motif	Size range (bp)	Ta (°C)	Forward primer (5′–3′)	N_a	H_o	H_e	PIC
CA2225	JN687354	$(CTAT)_{22}$	220–380	53	F: TTTACTGGAAACAACACTGG R: TTCTATCTCTATGGGGACTG	10	0.913	0.860	0.845
CCE13	CF662230	$(TTCAA)_7$	170–210	60	F: CTGTGGGCAAGATCAAACCT R: CCTTGTATTGCCCCTAATGG	4	0.824	0.706	0.655
CCE23	CF662764	$(TATC)_{17}$	180–270	62	F: ATGGTTTGGACTTTGGAGCA R: CGTGAATCCACAGCGATCTA	9	0.946	0.853	0.836
CA1603	JN687261	$(AC)_{40}$	290–360	62	F: CGCTCGGTCCTCGTTCAG R: TGGTGTTCTTCCTCCTTCAG	8	0.862	0.799	0.772
HLJ1093	EU861305	$(TCTG)_{17}$	170–240	56	F: TCCAGCTGCATCAACTTCTTT R: TAGTGGTGGATTCCGTCCAT	9	0.750	0.721	0.687
CCE547	EX826168	$(TTA)_{10}$	200–280	60	F: AGCCTTGTGTTCTGCTCTGGA R: GCCTCTGGTGGCAATGATTAT	6	0.763	0.750	0.710
HLJ1140	EU861322	$(AGAT)_8$	190–250	52	F: TTTGCTGTATCCCAAAAATGC R: CATCAACATTGAATCGCAATC	8	0.913	0.824	0.800
HLJ3770	LN598345	$(ATCT)_{13}$	100–190	62	F: ATGACGAGAAACCCCCATTC R: AGGCTTGTGAAACTCTGTGC	7	0.753	0.825	0.800

Note. N_a, number of alleles; H_o, observed heterozygosity; H_e, expected heterozygosity; PIC, polymorphic information content.

effects for different traits in the model. Correlations were calculated as the covariance divided by the product of the standard deviations of traits:

$$r = \frac{\sigma_{12}}{\sqrt{\sigma_1}\sqrt{\sigma_2}}, \quad (3)$$

where σ_1 and σ_2 are the additive genetic or phenotypic variances of trait 1 and trait 2, respectively, and σ_{12} was the estimated additive genetic or phenotypic covariance between two traits.

3. Results

3.1. Microsatellites Polymorphism. The genetic parameters of eight microsatellite markers are listed in Table 1. A total of 61 alleles were detected, with an average of 7.63 alleles per locus. The number of alleles for all loci in offspring was in accordance with that in parents, which indicated that there was no allele missing in offspring. The average observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphism information content (PIC) were 0.841, 0.792, and 0.763, respectively, in the test population.

3.2. Family Pedigree and Trait Correlations. In a strict level of 95% confidence interval, the theoretical identification rate of eight microsatellite markers were 100% when the gender of all parents was known. All 750 progenies available for parentage assignment were 100% assigned to 58 out of the 64 possible families of Yellow River carp (Table 2). All parents had contributions to the next generation. The percentage of progenies from different female parents ranged from 3% to 31% with the highest number of 230 individuals of dam 8, and the percentage of progenies from different male parents ranged from 5% to 21% with the highest number of 189 individuals of sire 7. The sampled fish were not evenly distributed among different families. Among all 64 possible families, 6 families assigned no sampled fish, and other 58 families assigned the number of progenies per family ranging from 1 to 84. The combination of sire 7 and dam 8 contributes to the highest number of progenies.

The phenotypic values of body shape and body weight for 750 progenies are all in concordance with the normal distribution ($P > 0.05$). The coefficient variations of BL, BH, and BW for all progenies are 5.4%, 6.3%, and 16.5%, respectively, and the average values of three traits for each family are shown in Figure 1. The full-sib family produced by sire 8 and dam 4 has the heaviest average body weight of 396.5 g, and the family produced by sire 3 and dam 1 has the lightest average body weight of 264.0 g. As a whole, the average values of all three traits of the progenies produced by sire 8 were higher than those produced by other sires (Figure 1).

3.3. Heritability and Correlations between Body Shape and Body Weight. All 750 progenies of Yellow River carp were successfully assigned to the single parent of the expected families, and then they were used for heritability estimates. The means (±SD) of BL, BH, and BW were 23.2 ± 1.26 cm, 7.69 ± 0.48 cm, and 0.33 ± 0.05 kg, respectively. As expected, correlations between body shape and body weight were close to each other ($P < 0.01$ for all, Table 3), and both of these two types of economic traits had high values for phenotypic correlations (0.831–0.927) and genetic correlations (0.952–0.987). On average, the genetic correlations were higher than the phenotypic correlations in Yellow River carp.

Table 3 also presents the heritability estimates for three traits obtained with the animal model. All heritabilities are significantly different from zero and fall in the range of moderate heritabilities (0.2–0.4). BH and BW have slightly higher heritabilities (0.338 and 0.340, respectively) than BL (0.268).

Table 2: Distribution of the progenies among Yellow River carp families as revealed by a molecular pedigree.

Cross	Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Male 8	Total
Female 1	3	5	2	3	2	3	2	5	25
Female 2	8	61	11	14	8	0	47	23	172
Female 3	1	7	4	2	0	27	4	7	52
Female 4	3	7	0	1	13	4	4	4	36
Female 5	8	7	2	4	13	7	4	9	54
Female 6	3	0	3	4	6	1	12	6	35
Female 7	28	35	7	15	21	0	32	8	146
Female 8	44	38	6	10	7	0	84	41	230
Total	98	160	35	53	70	42	189	103	750

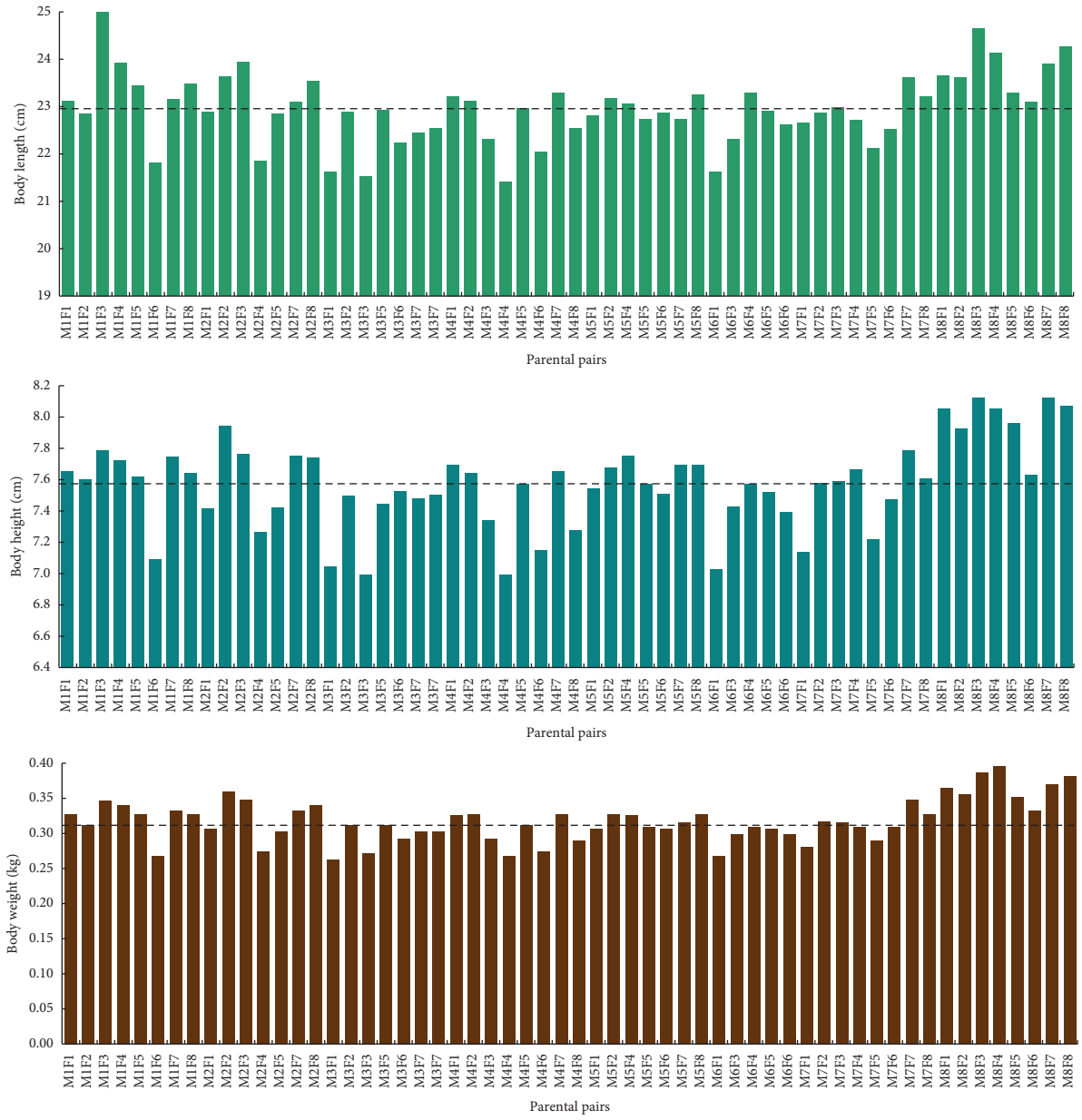

Figure 1: Average values of body length, body height, and body weight for the 58 families of Yellow River carp after molecular parentage assignment. The dotted lines on each trait indicate the average value for 58 families.

Table 3: Phenotypic correlations ± standard error (above the diagonal), genetic correlations ± standard error (below the diagonal), and heritability ± standard error (diagonal) of body weight and body shape estimated from 750 Yellow River carp at 8 months posthatching.

Traits	Body length	Body height	Body weight
Body length	**0.268 ± 0.107**	0.831 ± 0.015	0.927 ± 0.007
Body height	0.952 ± 0.004	**0.338 ± 0.124**	0.913 ± 0.009
Body weight	0.980 ± 0.015	0.987 ± 0.011	**0.340 ± 0.124**

The bold value in table 3 represent the heritability of different growth traits, and there is no statistical analysis of heritabilities. Therefore, we had not labeled the significance.

4. Discussion

4.1. Microsatellite Polymorphism and Population Diversity. Parentage assignment is conducive to eliminating the environmental effects and decreasing the cost of fish rearing separately. Microsatellite DNA, as one of the highly polymorphic and co-dominant markers, has been widely used for genetic analyses of plants and animals. Microsatellite-based parentage assignment has also been performed in many aquatic species and proved to be an effective traceability method for acquiring pedigree information [24, 26, 27, 44–46].

The amount and the polymorphism of microsatellite directly affect the efficiency of the parentage assignment [44], and our results confirm the power of a limited number of highly polymorphic microsatellite markers in a molecular pedigree analysis. All eight microsatellite markers used in this study presented high polymorphisms with an average observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphism information content (PIC) of 0.841, 0.792, and 0.763, respectively. These results were similar to our previous parentage assignment in another cultured population of Yellow River carp [44], in which eleven microsatellite markers produced an average H_o, H_e, and PIC of 0.792, 0.792, and 0.76, respectively. Compared with other wild and domestic populations of common carp, the average H_o and H_e obtained in this study were slightly lower than other wild populations (around 0.82) and significantly higher than domestic populations (around 0.68) [47]. These results indicate the high polymorphism of our microsatellite markers and also reveal the genetic diversity of the population we constructed for Yellow River carp, which laid a foundation for parentage assignment and heritability estimation.

4.2. Microsatellite-Based Parentage Assignment. Many factors may affect the efficiency of parentage assignments. Previous studies had proved that the probability of exclusion is proportional to the number and the polymorphism of microsatellite markers [27, 40, 44, 48]. Other factors, such as the number of parents, the genetic relationships among parents, and the frequency of null alleles, could also affect the efficiency of parentage analysis [7, 40, 49]. The unambiguous parentage assignment for the 750 progenies of Yellow River carp should be largely attributed to those eight highly polymorphic microsatellites used in the present study and a moderate number of parents or families.

Compared with previous studies on parentage assignment in common carp [24, 35, 36, 44], we obtained the highest assignment efficiency (100% vs. 75–95%). An accurate pedigree is essential for genetic parameter estimates [50], especially in mass-spawning species where the contribution of breeders is unknown. Therefore, the pedigree information of Yellow River carp in our study is well suited for the estimation of genetic parameters including body shape and body weight, and the calculated values for heritabilities are reliable.

4.3. High Correlations between Body Shape and Body Weight. In the present study, high genetic and phenotypic correlations (0.987 and 0.927, respectively, $P < 0.01$) were detected between body shape and body weight in Yellow River carp. A similar phenomenon was also detected in other cultured fishes, including mirror carp [24, 35, 36], silver carp [26], European sea bass [13], grass carp [12], and so on. Falconer and Mackay [51] pointed out that the magnitude of genetic correlations between traits reflects the extent to which the same genes are involved in the expression of the traits. Therefore, selective breeding programs for either growth-related or body shape traits (including BL, BH, and BW) of Yellow River carp would result in considerably increased fish size at harvest. And for body weight, which is much easier to measure on a large number of fish samples in field trips, may be considered as the most desirable trait for selective breeding in Yellow River carp.

4.4. Estimates of Heritability. Moderate heritabilities (0.268–0.340) were estimated for body shape and body weight in this study, which is within the usual ranges of heritabilities for growth-related traits in commercial aquaculture species [52]. And these results also agree with other published data on heritabilities in common carp [24, 36, 53], except for the one published by Kocour et al. [35], in which an extremely high heritability (0.7) was calculated for BW of mirror carp. Meanwhile, moderate heritabilities of growth-related traits in the majority of aquatic animals were relatively higher than those recorded in other special aquatic species, such as giant freshwater prawn (*Macrobrachium rosenbergii*) [54] and tiger prawn (*Penaeus monodon*) [55].

The different levels of heritabilities between aquatic species mentioned above may be affected by several factors [51]. First, mixed rearing could minimize the environmental components of phenotypic variations among families, which has become a widely used aquaculture model, especially in genetic parameter estimates and selective breeding programs [13, 17, 26, 27, 35]. Second, the statistical models might also affect heritability estimates. Based on two algorithms, Fu et al. [12] obtained two different values of heritabilities for BW of grass carp at 10 months of age. In addition,

heritabilities could be also attributed to some other factors, such as the population structure, target traits, and ages of the fish [17].

Moderate heritabilities estimated by this study suggest that the Yellow River carp has considerable genetic effects on the performance of body shape and body weight, and a substantial fraction of selection differentials would be expected to gain through selective breeding program [45]. BW is the most important growth-related trait in majority of aquatic animals including Yellow River carp, and selection for fast growth has been the main theme of selective breeding programs in this species. Interestingly, as one of the four Chinese historically well-known fish, Yellow River carp is famous for its golden-color and spindle-shaped body, therefore, the selection of body shape is also important for this aquaculture species. Heritability estimation showed that body weight possessed a slightly higher heritability than body shape, coupled with a high correlation between them. Consequently, we thought that the selection for Yellow River carp should be mainly based on body weight, and if allowed, body shape auxiliary.

In conclusion, reconstruction of the pedigree of Yellow River carp is feasible using microsatellite-based parentage assignment. High phenotypic and genetic correlations suggested that selection for BW could also largely affect the body shape and vice versa. Moderate heritabilities were estimated for body shape and body weight and resulted from genetic parameters that suggest substantial potentials for genetic improvement of growth and body formation traits in Yellow River carp. Therefore, this study would accelerate practical selective breeding and marker-assisted selection programs for this important common carp strain.

Data Availability

The data supporting the findings of this study are available within the article.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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