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Original Paper

Genotype by environment interaction for egg number and egg weight of five dual-purpose chicken breeds in different zones of Oromia region in Ethiopia

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The African Chicken Genetic Gain (ACGG) project (https://africacgg.net/) aims at backyard poultry optimization by commercial dual-purpose breeds introduction into Africa. To measure benefits, genotype by environment interaction (GxE) analysis provides guidance while predicting environmental effects on production traits of breeds. A survey among Ethiopian poultry smallholders showed egg sale being the most important purpose of keeping village chickens in Oromia. Data was available about laying of 894 ACGG chickens in Oromia. Hence current research questions were: 1) Does GxE take place? 2) Which breed performs best regarding laying and in which environment within Oromia? Traits investigated were egg number and egg weight of five breeds (S-RIR, Sasso, Horro, Kuroiler and Koekoek) located in three zones (East Hararge, East and West Shoa) and 5 districts (Adami Tulu, Bako Tibe, Dano, Dugda and Haromaya) in Oromia. Observations were taken as group measure performing weighted analyses. GxE was only present for egg number with magnitude strongest for zone. S-RIR performed best for both traits in both environments, except Kuroiler performing better in East Shoa for egg number and Koekoek for egg weight. This indicates success of crossbreed S-RIR. Sasso and Horro performed worst supported by previous research for Horro but not Sasso. Low precipitation in East Shoa caused bigger distance in egg number predictions, being higher for S-RIR and lower for Horro and Sasso compared to West Shoa. Apart from these final conclusions, social context of breeding and data collection difficulties should not be forgotten. Just like relevance of other performance trait analyses.

Keywords: Ethiopia, smallholder farming, poultry, laying, genetic gain

1 Introduction

Smallholder farming plays major socio-economic roles in developing countries with high percentage of African families reliant on it. Poultry farming, much present in Africa, shows positive contribution to these families (FAO, 2014, Vernooij et al., 2018). Livestock keeping generates 38.5% of income of Ethiopian poultry keeping households (Goromela et al., 2019). A challenge is the rising animal protein demand, with 70-80% expected increase from 2012 to 2050 and poultry expected to be the biggest component but having least environmental impact (Alexandratos et al., 2006, Oonincx and de Boer, 2012, Alexandratos and Bruinsma, 2012).
Multidisciplinary research supports local adaptation and tailoring of sustainable poultry production for Ethiopian smallholders being relevant for flexible implementation (Bettridge et al., 2018). For previously mentioned reasons, investigating optimization of African smallholder poultry production is relevant. The African Chicken Genetic Gain (ACGG) project (https://africacgg.net/), led by

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the International Livestock Research Institute (ILRI) in Addis Abeba, Ethiopia, aims at achieving optimization (ILRI, 2018). Strategy of ACGG was to introduce commercial dual-purpose breeds into Africa. To measure benefits, effects of new African environments breeds are placed in on production traits should be known. Analysis of genotype by environment interaction (GxE) can provide guidance here.

GxE is defined as change in phenotypic performance of two or more genotypes measured in different environments (Falconer, 1952, Falconer and Mackay, 1996). Genotype can be defined as single breed present in different environments of which performance is investigated (Lozano-Jaramillo, 2019). Environment is often categorical or continuous, examples being herd size, climate, management strategy, or location (Calus et al., 2004, Lozano-Jaramillo, 2019). GxE is commonly visualized by plotting genotype's performance against environment (if continuous) in linear random regression models (Hayes et al., 2016, Lozano-Jaramillo, 2019). If a genotype performs equally to another in both compared environments, the model plotted lines are parallel, meaning no GxE. If a genotype performs better in one environment compared to another, lines are not parallel, meaning that GxE is present. Genotype re-ranking occurs when lines intersect, meaning GxE magnitude being so big that choice on best genotype is determined by environment (Wakchaure et al., 2016, Hayes et al., 2016).

The ACGG project located five dual-purpose chicken breeds (S-RIR, Sasso, Horro, Kuroiler and Koekoek) across Oromia region, Ethiopia. Horro is an indigenous breed, originating from cool wet western highlands (altitude: 2,580-2,810 meter above sea level) of the Horro district in Oromia (Lozano-Jaramillo et al., 2019). Dana et al. (2011) revealed Horro's body weight having strong genetic correlation with egg number, revealing common genes for those selection traits and making their utilization promising. The other four breeds are exotic to Ethiopia, S-RIR (Sasso and Rhode Island Red) being a specific crossbreed for ACGG (Aman et al., 2017).
Oromia is the biggest Ethiopian province regarding human population and area. Its topography and climate are described as greatly physiographic diverse containing rich natural resource bases (FDRE, 2018). Performance data of ACGG breeds was obtained from various zones and districts of Oromia, making GxE analysis possible, considering breed as genotype and zone or district as environment. Hartman (1990) found GxE being more present for egg production of layers compared to weight traits of broilers in commercial poultry. A survey among Ethiopian smallholders showed egg sale being the most important poultry keeping purpose in Oromia (Esatu and EIAR, 2016). Another survey showed African smallholders desiring physically well appearing birds, high egg production and hatchability traits (Goromela et al., 2019). Hence, there is big interest for optimizing laying traits.

Previous research found egg production of ACGG breeds in Ethiopian smallholder farms being higher than that of an indigenous breed (Abegaz et al., 2019). S-RIR, followed by Kuroiler, Sasso, Koekoek and Horro had the highest average weekly egg production till 50 weeks of age. At the Ethiopian Debre Zeit research station, Horro scored lower for egg weight and hatchability than three breeds including Koekoek (Wondmeneh et al., 2011). More on-station research predicted Sasso followed by S-RIR having highest hen-housed egg production in three African countries, including Ethiopia (Bamidele et al., 2019a). In Oromia, no GxE analysis on laying of ACGG breeds has been conducted so far.

Hence, the aim of the current study was to perform GxE analysis using egg number and egg weight as performance traits, comparing ACGG breeds in zones and districts of Oromia. Two key research questions were:
1) Does GxE take place? i.e. Do different breeds react differently to zones and districts of Oromia?
2) Which breed performs best in terms of predicted egg number or egg weight and in which zone or district?

2 Material and methods

2.1 Data collection and cleaning

Five chicken breeds (S-RIR, Sasso, Horro, Kuroiler and Koekoek) were distributed over 222 households, 13 villages, 5 districts (Adami Tulu, Bako Tibe, Dano, Dugda and Haromaya), 3 zones (East Hararge, East and West Shoa), one cool sub humid agro-ecological zone in Oromia, Ethiopia. Table 1 provides district climate descriptions. In 2016, fertile eggs of the introduced breeds (S-RIR, Sasso, Kuroiler and Koekoek) were imported (Lozano-Jaramillo et al., 2019). In August 2016, distribution started placing ±25 six-week-old chicks of one breed per household. In January 2018, data collection ended. Household group measurements of 1,163 chickens were divided deriving average egg number per ACGG hen and egg weight per egg.

Table 1 Climate description of five Ethiopian districts (Adami Tulu, Bako Tibe, Dano, Dugda and Haromaya), of three zones (East Hararge, East and West Shoa) in Oromia. Mean annual values or ranges of temperature, rainfall and altitudes are given

Zone	East Harage	East Shoa		West Shoa	
District	Haromaya	Adami Tulu	Dugda	Bako Tibe	Dano
Climate	*Tropical rainy and Tropical dry*	*Fluctuating bimodal rain pattern*	*Sub-tropical, bimodal rain pattern*	*June–September receive 70-80% rain*	-
Temp. (˚C)	*16.34 (10-26)*	*14-27*	*19-23*	*15-28*	*15-30*
Rain (mm)	*819.2*	*748*	*500-900*	*1,244-1,260*	*900-1,400*
Altitude (m)	*High + low land areas*	*1,500-2,300*	*1,500-2,300*	*1586*	*80%: 1,500-2,200*
Sources	*(Mohammed* et al., *2017, Oromia BOFED, 2009)*	*(Shiferaw, 2008, de Putter et al., 2012)*	*(Oromia BOFED, 2009)*	*(Oranu et al., 2018)*	*(Kassie et al., 2007)*

For reliability, data cleaning was conducted. Data of households containing eggs of hens before ACGG breed introduction was deleted to prevent miscounting. Restrictions per hen were set to minimum 1 and maximum 30 eggs per month (30 days) for egg number and minimum 20 and maximum 80 grams of egg weight. After editing, 894 observations were left for both traits. Normality was checked through Q-Q plots, plotting egg number or egg weight against zone or district.

2.2 Statistical analysis

Genotype by environment interaction effects on egg number per hen and egg weight were estimated implementing a weighted fixed effects linear model using PROC GLM of SAS software version 9.4 (SAS Institute Inc., 2020). Average egg number and egg weight were based on observation per household which was added as weight statement. Model and weight statement are:

$$y_{ijk} = \mu + Breed_i + Environment_j + BxE_{ij} + e_{ijk}$$

$$\sum w_{ijk} \left(y_{ijk} - \hat{y_{ijk}}\right)^2$$

where y_{ijk} is the observed egg number per hen per month or egg weight; $\hat{y}_{ijk}$ is the predicted egg number per hen per month or egg weight; μ is the overall mean; $Breed_i$ is the fixed breed effect (n = 5); $Environment_j$ is the fixed environment effect, run for either zone (n = 3) or district (n = 5); BxE_{ij} is the fixed breed by environment interaction effect, so GxE; e_{ijk} is the random residual effect, assumed to be $\sim N(0, I\sigma^2{}_e)$, with I being an identity matrix of appropriate order and $\sigma^2{}_e$ being the residual variance. The w_{ijk} are ACGG hen number and weighted egg number variables used as weight statements for egg number and egg weight, respectively. Graphs for GxE were made plotting breed's predicted egg number or egg weight against environment (zone or district).

3 Results and discussion

All effects included in the model for egg number significantly affected the trait (P <0.01; Table 2). Figure 1 shows boxplots derived from GxE model predicting egg number, the environment being the zone. Exact least squares means (LSM) and standard errors (SE) of GxE model for egg number, with environment being the zone, are given in Table 3. The effect of district nested within zone was not significant, hence results of district as environment are not reported.

Key results were S-RIR predicted having highest egg number in East Hararge, followed by Kuroiler in East Shoa. S-RIR was the only breed present in East Hararge zone and had highest predicted egg number in every zone for every breed, except for Kuroiler. East Hararge zone showed therefore the highest predicted egg number. Kuroiler as a breed was only present in East Shoa zone, just like Koekoek was only present in West Shoa. Horro and Sasso had similarly low predicted egg number. Predicted egg number of all breeds in West Shoa was closer to each other, or less spread, than in

East Shoa. This means smaller distance between predicted egg number in West Shoa, being lower for S-RIR and higher for Horro and Sasso compared to East Shoa.

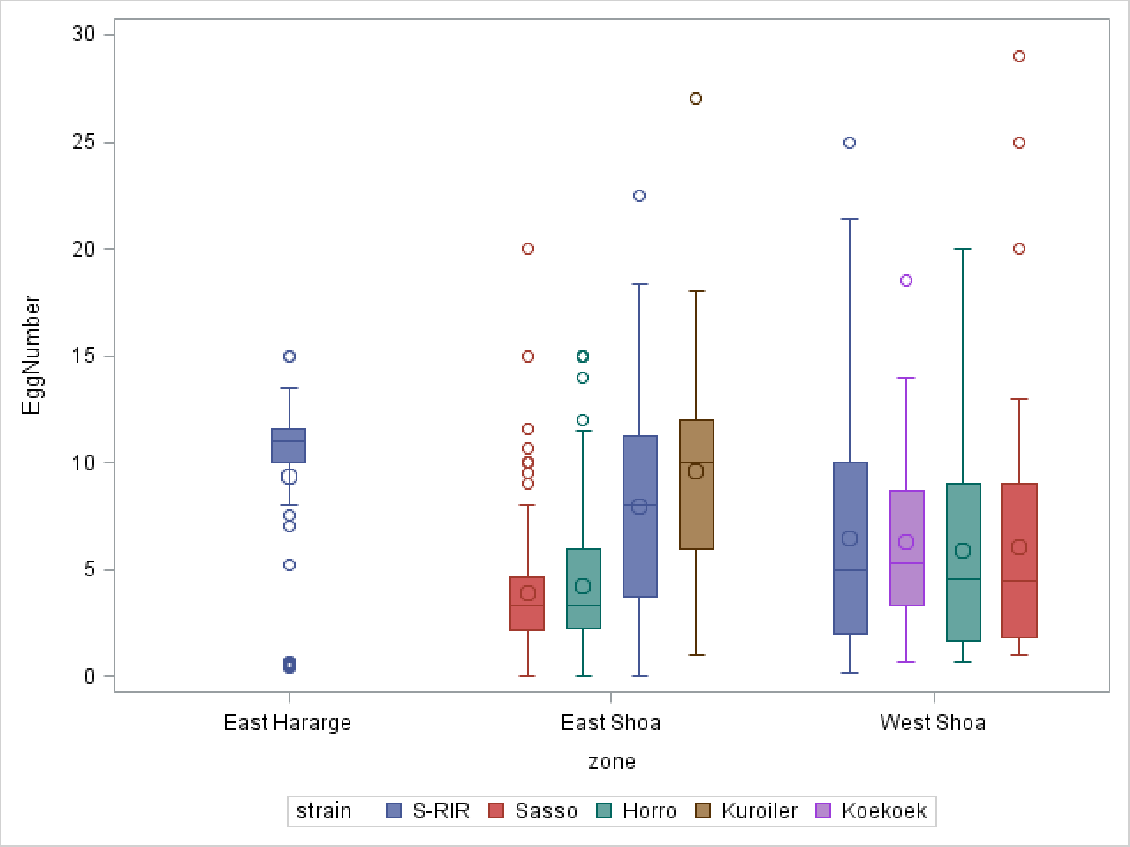

Figure 1 GxE boxplots made using breed by zone interaction model for egg number. Horizontal lines in the box represent breeds median, length box represents interquartile range and big circle in or close to box represents breeds mean

Table 2 P-values of GxE model predicting egg number. GxE is Breed by Environment effect (BxE), displayed in bold. Two environments analysed: zone and district

Effect:	Breed	Environment	BxE
Zone	*<0.0001*	*<0.0001*	***0.0002***
District	*0.0003*	*<0.0001*	***0.0057***

Table 3 Least squares means (LSM) and standard errors (SE) of egg number from GxE model. GxE was Breed (S-RIR, Sasso, Horro, Kuroiler and Koekoek) by Zone (East Hararge, East and West Shoa)

	East Hararge	East Shoa	West Shoa
	LSM (SE)	LSM (SE)	LSM (SE)
S-RIR	*8.94 (0.37)*	*7.64 (0.35)*	*6.69 (0.42)*
Sasso	-	*3.96 (0.49)*	*5.61 (0.67)*
Horro	-	*3.50 (0.32)*	*5.76 (0.52)*
Kuroiler	-	*8.91 (0.49)*	-
Koekoek	-	-	*6.00 (0.63)*

Table 4 shows the significance of main and GxE effects for egg weight. No GxE effects for this trait were detected. Considering the zone effect, both breed and environment were significant (*P* <0.05 and *P* <0.0001, respectively), whereas considering the district effect, only environment was significant (*P* <0.0001).

Table 4 P-values of GxE model predicting egg weight. GxE is Breed by Environment effect (BxE), displayed in bold. Two environments analysed: zone and district

Effect:	Breed	Environment	BxE
Zone	*0.0392*	*<0.0001*	***0.8137***
District	*0.2248*	*<0.0001*	***0.1973***

Because of lacking of GxE significance, only LSM and SE of breed and zone as main effects are given in Table 5. District effect is not displayed as the effect of district nested within zone was not significant.

Table 5 Least squares means (LSM) and standard errors (SE) of egg weight for the main effects of breed and zone

		LSM (SE)
Breed	S-RIR	*49.62 (0.64)*
	Sasso	*46.20 (1.19)*
	Horro	*47.56 (0.98)*
	Kuroiler	*48.65 (1.20)*
	Koekoek	*51.39 (1.81)*
Zone	East Hararge	*53.05 (1.50)*
	East Shoa	*35.30 (0.64)*
	West Shoa	*57.70 (0.77)*

Results showed Koekoek followed by S-RIR breed and West Shoa zone having the highest predicted egg weight. Koekoek has high SE as it is based on 35 animals. Sasso followed by Horro had low predicted egg weight.

To answer the first research question (does GxE take place considering various zones and districts in Oromia?), results indicated that it does for egg number (Table 2) but not for egg weight (Table 4). These findings are supported by Hartman (1990) stating more serious consequences of GxE present for egg production traits, particularly large effects expected for laying rate. We note that conclusions of

Hartman (1990) were based on commercial poultry, not backyard poultry. Statement remains relevant anyway as Hartman (1990) remarked GxE present between experimental stations and commercial farms while breeding for improved backyard farm poultry also takes place on research stations, causing GxE in a similar manner. Environment (zone or district) always had highly significant effects on both traits while breed had a high significant effect on egg number or on egg weight with zone as environment (Table 2 and Table 4), indicating environment plays an important role for both traits.

Answering the second research question (which breed performs best in terms of predicted egg number or weight and in which zone or district?), needs to be reviewed elaborately. This is needed due to relevance of the review, containing most viable information for local smallholders.

Generally, S-RIR performed best for both traits in most environments. Exceptions are S-RIR being outperformed by Kuroiler for egg number and by Koekoek for egg weight based on limited observations (*n* = 35) (Figure 1, Table 3 and Table 5). This supports previous research. Abegaz et al. (2019) predicted average weekly egg production highest for S-RIR followed by Kuroiler at smallholder farms across Ethiopia. At research stations in three African countries, including Ethiopia, Bamidele et al. (2019a) predicted S-RIR having highest hen-housed egg production. Wondmeneh et al. (2011) predicted Koekoek having highest average egg weight compared to three other breeds, including Horro, at the Debre Zeit station.

Results indicate that crossbreeding Sasso with Rhode Island Red, i.e. producing S-RIR, gave successful layers under Ethiopian smallholder conditions. Kuroiler having high predicted egg number is beneficial as it performs well on meat traits in Africa, making Kuroiler dual-purpose suitable and scavenging adaptive (Sharma et al., 2015, Bamidele et al., 2019b). Koekoek having high predicted egg weight is beneficial as it has higher disease resistance than specialized layers kept under low management conditions in Oromia (Esatu et al., 2011). Moreover, the colour pattern of Koekoek is sex-linked, alleviating selection by smallholders while breeding for eggs (Getachew et al., 2016).

Generally, Sasso and Horro performed worst for both traits in most environments. For Horro, this is supported by previous research, while previous results for Sasso were partly contradictory to current results. Horro kept on Ethiopian smallholder farms had lowest weekly egg production and the production of the Sasso breed was intermediate to those of other ACGG breeds (Abegaz et al., 2019). Horro performed worst for laying in two districts in Oromia (Ada and Horro) and for egg weight at the Debre Zeit station (Wondmeneh et al., 2016, Wondmeneh et al., 2011). Bamidele et al. (2019a) predicted Sasso having even highest hen-housed egg production on-station in Tanzania. Bamidele et al. (2019b) and Ajayi et al. (2020) show consistent low Sasso egg numbers.

Low performance of Horro can be explained by its young breeding program, implemented in 2008 only (Wondmeneh et al., 2014a). Yet, after seven breeding generations improved Horro had significantly better laying, weight gain and survival than its ancestral population (Wondmeneh et al., 2016). Improvement in Wondmeneh et al. (2016), measured as LSM differences of improved versus indigenous Horro were 57.8, 30.0, 26.0 and 25.4% hen housed egg production at 3, 6, 9 and 12 months, respectively, 204.8, 260.8, 264.9 and 279.4 grams body weight at 8, 12, 16 and 20 weeks, respectively, and 10.0% survival rate at week 20. Breeding success and Ethiopian smallholders preferring an indigenous based dual-purpose breed, favour Horro as village poultry (Dana et al., 2010). Moreover, farmers having livestock as main income adopt exotic chickens less likely although adoption rate increases when other income sources are present (Wondmeneh et al., 2014b). According to Wondmeneh et al. (2015) productivity of improved Horro can be raised leading to higher income of farmers in Oromia. Although, the interventions needed to be able to achieve this come with additional costs which unfortunately do not seem to be outweighed by this higher farmer income. In literature, Sasso performed high to average on laying and well on weight gain traits while comparing breeds. Sasso was predicted heavier than other ACGG breeds on Ethiopian smallholder farms and on farms in three African countries including Ethiopia (Lozano-Jaramillo et al., 2019, Abegaz et al., 2019). This indicates Sasso can deal with low-input conditions, making it interesting for further on-farm testing in Ethiopia (Lozano-Jaramillo et al., 2019). Sasso performed well for meat production on Nigerian research stations (Bamidele et al., 2019b). Despite current low laying results, Sasso remains promising for dual-purpose breeding, especially for body weight.

Egg number predictions were closer to each other in the West Shoa zone, including the Bako Tibe and Dano districts, compared to East Shoa. Dano generally has higher precipitation (900-1,400 mm) and bigger annual temperature fluctuations (15-30˚C) than other districts (Table 1). Predictions of Bako Tibe were based on four observations only, making this district less relevant. Dano was based on 264 observations. East Shoa contained 78 observations in Dugda and 468 observations in Adami Tulu, making it the most relevant district. Dugda has constant mean annual temperature fluctuations (19-23˚C) and low precipitation (500-900 mm), and Adami Tulu has the lowest mean annual rainfall of 748 mm (Table 1). This indicates that especially wet environment, but also large temperature fluctuations decrease differences of laying performances between breeds. Dryer conditions with smaller temperature fluctuations show greater differences between predicted egg numbers, highest for S-RIR and lowest for Horro and Sasso.

Interestingly, Lozano-Jaramillo et al. (2019) previously stated that the Horro breed survives better during dry season and therefore potentially also in dryer areas. This assumption was partly made based on Bettridge et al. (2018) identifying the Horro district as being known for higher hatchability of eggs during dry season due to lower disease risk. The Horro breed originates from a wet environment containing two rainy and one dry season, and purebred Sasso originates from warm and dry areas in Southern France (Lozano-Jaramillo et al., 2019, Getachew et al., 2016).

A survey showed egg sale being most important purpose of keeping village chickens among smallholders in Oromia (Esatu and EIAR, 2016). Yet, many other traits and breeding practices were preferred by local farmers (Abegaz et al., 2019, Dana et al., 2010). Despite improved Horro performing low in current and other analyses, it is a locally sourced breed and is therefore likely preferred by Ethiopian smallholders (Dana et al., 2010, Wondmeneh et al., 2014b, Wondmeneh et al., 2016, Bamidele et al., 2019a, Abegaz et al., 2019). Local adaptation and tailoring of sustainable poultry production are important for flexible implementation among smallholders (Sölkner et al., 1998, Mueller et al., 2015, Bettridge et al., 2018). This indicates preferences of local Ethiopian farmers should not be ignored while breeding for them. Laying, although preferred in Oromia, is not the only performance measurement option. Growth, survival, feed and fertility traits are interesting for future on-farm research in the region (Lozano-Jaramillo, 2019, Wondmeneh et al., 2014a, Wondmeneh et al., 2016, Bamidele et al., 2019a, Ibrahim et al., 2019).

Large population, pedigree, performance recording and small environmental variation conditions are often lacking with on-farm data collection and caused problems related to breeding in developing countries (Lozano-Jaramillo, 2019, Besbes, 2009, Dana et al., 2010). Moreover, lacking motivation of farmers and chicken mortality cause Ethiopian smallholders dropping out of research (Wondmeneh et al., 2016). Those lacking on-farm breeding conditions can be solved by on-station data collection, which often causes new GxE of on-station African chickens significantly outperforming on-farm (Bekele et al., 2009, Ali et al., 2000, Lwelamira, 2012). Getachew et al. (2019) aim for investment in proper data collection in Ethiopia as they are convinced it is essential for faster genetic gains.

4 Conclusions

Finding which breed performs best in which region of Ethiopia provides very valuable information to smallholder farmers, if GxE exists. Our results indicate the existence of GxE for egg number, but not for egg weight. Generally, S-RIR performed better for both traits compared to other breeds, indicating success of crossbreeding strategy. Exceptions were S-RIR being outperformed by Kuroiler in East Shoa for egg number and by Koekoek for egg weight. Sasso and Horro performed worst for both traits. Previous research supports current findings of Horro while current findings of Sasso are only partly supported. Smaller temperature fluctuations, but especially dry environment give greater distances between predicted egg numbers, i.e. higher for S-RIR and lower for Horro and Sasso in East compared to West Shoa.

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