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How prenatal cortisol levels relate to grandmother-mother relationships among a cohort of Latina women

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Abstract

Introduction: As part of the human reproductive strategy, mothers receive childcare assistance from others. For kin, allomothers are adaptively incentivized to provide assistance due to inclusive fitness benefits. Previous studies across a broad range of populations identify grandmothers as particularly consistent allomothers. Minimal attention has been paid to the possibility that allomothers may begin investing in offspring quality during the prenatal stage of life. Here, we innovate within the area of grandmother allocare research by examining the prenatal stage of life and biopsychosocial mechanisms by which prenatal grandmother effects may be enacted.

Methods: Data derive from the Mothers' Cultural Experiences study, a cohort of 107 pregnant Latina women in Southern California. At <16 weeks' gestation, we administered questionnaires, collected morning urine samples, and measured cortisol by enzyme-linked immunosorbent assay, correcting for specific gravity. We measured the soon-to-be maternal and paternal grandmothers' relationship quality, social support, frequency of seeing each other, communicating, and geographic proximity to pregnant mothers, that is, their daughters and daughters-in-law. These measures were self-reported by the pregnant mothers. We assessed how grandmother constructs related to the pregnant women's depression, stress, anxiety, and cortisol levels.

Results: We observed benefits conferred by maternal grandmothers for mothers' prenatal mental health and lower cortisol levels. Paternal grandmothers also conferred mental health benefits to pregnant daughters-in-law, but higher cortisol levels.

Conclusion: Our results suggest that grandmothers, especially maternal grandmothers, are able to improve their inclusive fitness by caring for pregnant daughters, and allomother support may positively impact prenatal health. This work extends the traditional cooperative breeding model by identifying a prenatal grandmother effect, and, by examining a maternal biomarker.

1 | INTRODUCTION

The human species exhibits many of the characteristics of a cooperative breeding system. Mothers rely on extensive help from kin and non-kin "allomothers," who assist the mother–child dyad (Hrdy, 2009; Kramer, 2010).

Allomother support has generally been studied as it relates to postnatal care, but, the prenatal stage of life also deserves consideration in this context (Figure 1). Fetal development represents a period of plasticity and vulnerability during which support and assistance directed towards the pregnant mother can have beneficial impact on offspring health and survivorship. Here, we contribute to the growing literature on human allomothering by expanding to a prenatal timeframe and examining a gestational stress related biomarker.

Although ecological diversity impacts which allomothers are most helpful (Hurtado et al., 1992; Kramer, 2010), grandmothers have been described as "an ace in the hole" (Hrdy, 2005). Grandmothers are especially reliable and effective allomothers due to their own experience as mothers, their knowledge gained from long lives, and, often, their lack of competing reproductive effort due to menopausal sterility (Chapman et al., 2018; Engelhardt et al., 2019; Gibson & Mace, 2005; Hrdy, 2005; Strassmann & Garrard, 2011). Although the reason for the postmenopausal extension of lifespan has been debated (Hawkes et al., 1998; Kaplan et al., 2000; Peccei, 2005), it is uncontroversial that grandmothering has adaptive benefits for the mother and child, associated with improved child survivorship (Sear et al., 2000; Sear & Mace, 2008) and shorter interbirth intervals (Chapman

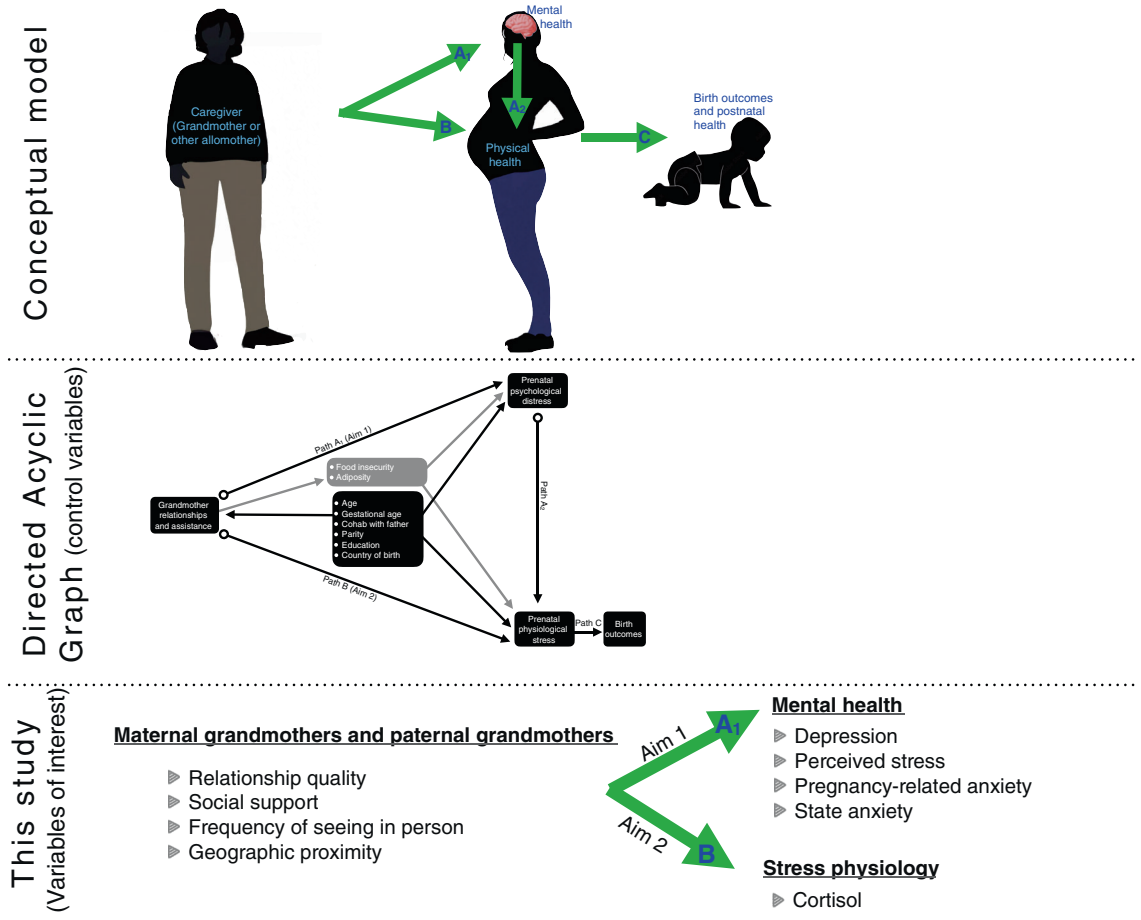

FIGURE 1 The top panel depicts the conceptual model on which this study is based. The middle panel depicts a directed acyclic graph (DAG) that shows our conceptually predicted relationships between variables. Even though our study design can only test correlation and not causality, arrows reflect our theoretically proposed directions of causality. Open circles reflect relationships that we suspect could be reciprocal, that is, bi-directional causality, but the DAG only includes the uni-directional arrows depicting the directionality of interest in this study. Black boxes contain the descriptions of variables in our models. The center black box shows the reason for including those as control variables, because they are suspected to, potentially, causally influence both predictors and outcomes of interest. The center gray box shows the reason for not including those as control variables, because they are suspected to be part of the causal pathway connecting predictors and outcomes of interest. The bot specifies the variables of interest in the subset of the model we empirically test here.

et al., 2021; Szabó et al., 2017). We previously argued that grandmothers and other kin may engage in allomothering effort directed towards a fetus before birth (Fox & Wiley, 2022; Knorr & Fox, 2022).

We endeavor to bridge the anthropological notion of allomothering with the concepts of social support and developmental origins of health and disease (DOHaD). Social support is the resources provided or perceived to be available from a known person; these resources can be financial, instrumental (e.g., child care), informational, or emotional support (Dunkel Schetter & Brooks, 2009). DOHaD is the idea that environments and exposures encountered during early-life, sensitive periods of development, especially prenatally, have lifelong consequences for disease-related phenotypes (Hoffman et al., 2017). Social support for pregnant women has been associated with fewer adverse pregnancy and birth outcomes (Elsenbruch et al., 2007; Feldman et al., 2000; Hetherington et al., 2015; Orr, 2004; Spry et al., 2021), as well as developmental benefits to the child such as higher Apgar scores at birth and less fearful temperament at 6–8 weeks of age (Collins et al., 1993; Stapleton et al., 2012). Applied behavioral science studies demonstrate that grandparent social support is beneficial for individuals from diverse ethnic/racial backgrounds and for families facing challenging life circumstances. For example, grandparents' nurturance of adolescent mothers resulted in higher empathic attitudes towards their children and greater parenting satisfaction (Lewin et al., 2011). An intervention study focused on multigenerational family support demonstrated that grandparent care of their incarcerated daughters' children led to prevention of early abuse and neglect and lower postnatal drug exposure (Engstrom, 2008). Others showed how maternal grandparents' support of their grandchildren with disabilities led to decreased maternal distress and higher quality affectional solidarity within the family (Crettenden et al., 2018).

We propose a novel evolutionary framework by which grandmothers may engage in prenatal allocare of grandchildren, thereby increasing their inclusive fitness. Based on the DOHaD approach, we are interested in how caregiving directed towards pregnant women may beneficially impact gestational physiology. Our framework highlights two pathways (A and B in Figure 1). The caregiver (e.g., grandmother) may provide emotional support that bolsters the pregnant woman's mental health, which in turn, beneficially modifies the maternal-placental-fetal physiological state, that is, pathway A in Figure 1. Our previous results demonstrate that social support from pregnant women's mothers (soon-to-be maternal grandmothers) and siblings (soon-to-be aunts and uncles) are associated with better prenatal mental health for pregnant mothers (Fox & Wiley, 2022; Knorr & Fox, 2023), justifying pathway A_1. Others also found that social support for pregnant mothers was associated with better mental health such as fewer symptoms of perinatal depression (Bedaso et al., 2021; Collins et al., 1993). Maternal psychological distress has been correlated with higher levels of cortisol, homocysteine, C-reactive protein, interleukin-6, and other pro-inflammatory markers and with lower levels of zinc, vitamin D and anti-inflammatory markers (Serati et al., 2016) Thus, prenatal psychological distress has a plausible biological signature that could influence the biochemistry of the intrauterine environment, that is, pathway A_2 in Figure 1.

Additionally, the caregiver (e.g., grandmother) may offer nutritional provisioning of the pregnant woman or relieve her of chores that diminish her physical labor, that is, pathway B in Figure 1. Provisioning pregnant women by others in the community has been documented in subsistence populations, although the academic focus has been on the benefits to the mother rather than the offspring (Kramer, 2018). Evidence already supports postnatal grandmother assistance in these domains that benefit mothers and children, for example, food procurement, housework, gardening, and childcare (Biesele, 1981; Hawkes et al., 1989; Hill & Hurtado, 1996; Jamison et al., 2002; Turke et al., 1988; Voland & Beise, 2002).

Women's prenatal mental and physical health problems have both been robustly linked with adverse offspring outcomes (pathway C in Figure 1) that suggest diminished fitness. For example, women's prenatal depression and anxiety symptoms have been associated with their children's negative affectivity (Davis et al., 2004), externalizing problems (Sandman et al., 2015), HPA axis dysregulation (Gutteling et al., 2005), and increased amygdala gray matter volume (Buss et al., 2012). In terms of physical health, infant cardiovascular abnormalities, immune suppression, and low-body weight have been shown to be linked with prenatal maternal stress (Beydoun & Saftlas, 2008). In addition, maternal obesity has been linked with infant metabolic and epigenetic dysregulation, factors linked with increased risk for later life psychiatric disorders and neurobiological dysfunction (Cirulli et al., 2020). Postnatal psychological distress has also been associated with lower completed fertility, a more direct measure of diminished fitness, via diminished likelihood of subsequent pregnancies (Myers et al., 2016). Therefore, support directed towards pregnant women that diminishes prenatal health problems would be adaptive for allomothers who can gain inclusive fitness benefits.

Of the myriad possible biomarkers to consider in pregnancy, we choose to look at cortisol. Cortisol is involved in both stress and normative homeostatic

processes. Cortisol plays an important role in maturation of fetal tissues during pregnancy and may play a role in the determination of gestational duration. Cortisol levels are also implicated in gestational health. High prenatal maternal cortisol levels have been associated with early pregnancy loss (Nepomnaschy et al., 2006), adverse effects on fetal development (Krontira et al., 2020) and growth (Duthie & Reynolds, 2013), and preterm birth (Giurgescu, 2009).

Previous observational and intervention studies suggest that, among pregnant women, social support is associated with lower maternal cortisol across various timepoints in early, mid, and late pregnancy (Field et al., 2013; Giesbrecht et al., 2013). Also, in nonpregnant populations, cortisol levels have been associated with relationship quality of romantic partnerships and psychological distress (Ditzen et al., 2011; Leach et al., 2013). Therefore, cortisol is a strong candidate biomarker to be correlated with grandmother allocare. Psychophysiological responses may be adapted to be responsive to certain social relationships if they had special importance for reproductive success across evolutionary history. Little is known about how support from specific individuals influence cortisol levels during pregnancy, so here we endeavor to elucidate this area.

Cortisol measured from maternal biosamples in pregnancy reflect dynamics of a biological axis involving maternal-placental-fetal components. In short, the maternal hypothalamus and placenta both secrete corticotropin-releasing hormone (CRH), which (via the pituitary's production of adrenal corticotropic hormone) stimulates the maternal adrenal medulla to produce cortisol. While the majority of circulating cortisol is bound to carrier proteins, the unbound and bioactive "free" cortisol may pass through the glomerulus of the kidneys and be excreted into urine (Beisel, Cos, et al., 1964; Beisel, Diraimondo, et al., 1964; Levine et al., 2007; Schedl et al., 1959). Thus, urinary cortisol represents a portion of free circulating cortisol.

In previous studies, the construct of grandmother assistance is often operationalized through proxies, often due to inherent constraints of data sources, for example, historical records (Beise & Voland, 2002; Kemkes-Grottenthaler, 2005; Madrigal & Meléndez-Obando, 2008; Voland & Beise, 2002). Most studies assessed the effects of grandmothers living versus deceased, co-residence, or geographic proximity on grandchild survivorship or daughter and daughter-in-law completed fertility (17 of the 19 studies reviewed in Sear & Mace, 2008). Here, we endeavor to improve upon past study designs by clarifying the ways in which grandmothers may exert influence on subsequent generations' health and development. We examine multiple domains of grandmothering care: relationship quality, social support, frequency of seeing in person, frequency of communication, and the more conventional measure, geographic proximity. By examining each domain separately, we can begin to discern in what ways prenatal grandmother effects may operate. Some of these domains are more reflective of emotional support and others instrumental support. We can also discern whether the mechanism by which grandmothers confer any observed benefits to pregnant women is contingent on geographic proximity or whether benefits can be conferred remotely. A few previous studies have made similar distinctions between domains of grandmother care (Emmott & Mace, 2015; Myers et al., 2021; Scelza & Hinde, 2019; Sheppard & Sear, 2016).

While it is generally agreed that maternal grandmothers (MGM) are adaptively incentivized to assist daughters in childrearing, controversy exists regarding paternal grandmothers (PGM). Henceforth, we sometimes refer to the PGM as "mother-in-law" as shorthand to refer to the baby's father's mother, regardless of marital or relationship status. PGMs have less reliable genetic relatedness to grandchildren due to paternity uncertainty, although the impact of this on grandmother behavior has been argued to be minimal outside of societies with exceptionally high rates of extra-pair paternity (Anderson, 2006; Fox et al., 2010, 2011; Pashos, 2017). Accordingly, MGMs have generally (but not always Hill & Hurtado, 2009; Strassmann & Kurapati, 2010) been observed to confer benefits to grandchildren, while PGMs have been observed to be harmful, neutral, and beneficial towards grandchild survivorship (Chapman et al., 2021; Nenko et al., 2021; Sear & Mace, 2008). Additionally, the lifelong relationship between a woman and her own mother, compared to her mother-in-law, suggests a stronger connection between MGM-mother than PGM-mother (Knorr & Fox, 2022). Therefore, because PGMs have both a weaker adaptive incentive to invest in grandchildren and a shorter relationship duration with mothers, we expect to observe a weaker or less consistent effect for PGMs. Our previous results showed that MGM but not PGM social support and communication was related to mental health in another cohort of Latina pregnant women (Knorr & Fox, 2022), underscoring the likelihood our predictions are more likely to be endorsed for MGMs than for PGMs.

We implement our research questions in a cohort study of 107 Latina women in Southern California for three reasons. Firstly, many of the diverse cultures included in the Latino category are characterized by prominent familism values (Smith-Morris et al., 2013). Familism is a value system in which family is prioritized and central to individuals' identities, decisions, and relationships (Sabogal et al., 1987). There are important anthropological critiques of simplifying cultural behavior, especially of a diverse ethnic group. However, this

ideology is often described qualitatively by study participants, even without the same terminology (Smith-Morris et al., 2013). The frequency with which this ideology occurs among Latinos allows us to more easily detect allocare effects of family members even when the cohort is embedded in a sociopolitical context in which other forms of perinatal care exist (e.g., medical, state-sponsored, etc). Secondly, Latinos have the highest rates of three-generation homes of any ethnic group in the U.S. (Cohn & Passel, 2018; PEW Research Center, 2010), and yet, Latinos frequently have family geographically separated living in other countries due to their status as the largest migrating group (PEW Research Center, 2020). The combination of frequent cohabitation and frequent separation of grandmothers-mothers-grandchildren affords us the unique opportunity to have wide variability in our constructs of interest, even with a modest sample size. Geographic proximity has been an especially problematic proxy for grandmother effects in previous studies situated in post-industrial settings because economic deprivation confounds the effects of interest as it is broadly associated with both poor health and development as well as co-residence with grandparents. However, in the Latino community in which co-residence or close geographic proximity to grandparents is often a social preference rather than economic necessity, the confounding effect is less (Carrillo et al., 2004; Hughes et al., 2007). Thirdly, Latina women have high rates of perinatal mood disorders (Lara-Cinisomo et al., 2016) and adverse birth outcomes (Borrell et al., 2016). Thus, understanding if and how various elements of social support can mitigate perinatal risk in Latina women has public health value.

Our over-arching research question is: do grandmother relationship quality, social support, frequency of seeing in person, communication frequency, and geographic proximity exert beneficial effects on pregnant daughters/daughters-in-law, before the birth of their grandchildren? We pursue this question with two specific aims: (1) test the hypothesis that grandmother allocare is positively associated with maternal prenatal mental health, in order to recapitulate our previous cohort study results, and (2) test the hypothesis that grandmother allocare is positively associated with maternal prenatal urinary cortisol levels (Figure 1). We hypothesize stronger effects for MGMs than PGMs.

2 | METHODS

2.1 | Cohort

The study cohort come from Wave 2 of the Mothers' Cultural Experiences (MCE) study, an investigation of how socio-cultural, environmental, and political stressors influence maternal psychology and biology during pregnancy and postpartum and infant development. MCE methods have been previously described (Fox, 2021, 2022; Fox & Wiley, 2022). In short, Wave 1 was a cross-sectional cohort of pregnant and postpartum women and Wave 2 is a new, longitudinal cohort of 107 women followed beginning in early pregnancy. MCE Wave 2 involves questionnaires and biosample collections. To be eligible to enroll, women were aged at least 18-years old, English or Spanish speaking, ≤16 weeks pregnant, and self-identified as Latina, Hispanic, Chicana, Mexicana, and/or Latin American. Data for this paper come from the first timepoint only for MCE Wave 2, and thus our analyses are cross-sectional. First timepoint data collection occurred 2018-Dec-11 to 2020-March-03. This study was approved by the Institutional Review Boards of all participating institutions with appropriate reliances. The study adheres to the tenets of the Declaration of Helsinki.

2.2 | Protocol

Women were recruited in the waiting rooms of three prenatal clinics in the Los Angeles metropolitan area: Olive View-UCLA Medical Center, located in Sylmar, CA; Venice Family Clinic Simms/Mann Health and Wellness Center, located in Santa Monica, CA; West Medical-UCLA Medical Center, located in Los Angeles, CA. Written, informed consent was obtained after full study procedures were described. Study sessions occurred at two prenatal and two postpartum timepoints. Data for the present study derive from timepoint one, which occurred at ≤16 weeks' gestation, during mornings. Two re-scheduled participants had timepoint one assessments after outside this window (17 w and 19 w) but were still included.

2.3 | Measuring cortisol

Cortisol can be measured from various matrices. Urine is held in the bladder for several hours before being voided, therefore, urinary cortisol levels reflect an integrative measurement across the multi-hour period between voids. This summary information is less vulnerable to the noise of cortisol's pulsatility compared to other matrices such as saliva and plasma (Sarkar et al., 2013). Also, cortisol has a diurnally variable production schedule, so, by limiting our sample collection to mornings, we capture a similar phase of the diurnal pattern. Benefits of urinary cortisol sampling are the minimally-invasive and self-administered nature of sample collection (Urlacher et al., 2022).

Cortisol was measured from clean-catch urine samples. Urine was kept at refrigerator temperature until the session was over. It was then transported in a hard-sided refrigerator-temperature cooler to the UCLA Biological Anthropology of Motherhood Lab. The specimen was vortexed, aliquoted, and frozen at −80°C. Upon the completion of all participant biosample collections, cortisol was quantified using enzyme-linked immunosorbent assay (ELISA) method according to kit manufacturer instructions (Cortisol ELISA Kit, Arbor Assays, Ann Arbor, MI). Specific gravity was measured for each individual urine sample using a refractometer (USG-Chek Digital Handheld Refractometer, Reichert, Inc., Depew, NY). Cortisol concentrations were corrected for specific gravity (SG) following established methods (raw concentration*[mean of SG-1]/[SG-1]) (Miller et al., 2004). The mean intra-assay coefficient of variability was 11.1%. The mean inter-assay coefficient of variability was 12.0%.

2.4 | Measuring grandmother allocare

Grandmother allocare was measured in five domains, each for the MGM and PGM. Because most of the continuous variables were highly skewed, data were dichotomized to improve interpretability. MGM questions were prefaced with the instruction "These questions are about the mother who raised you." PGM questions were prefaced with the instructions "These next questions are about the mother of your baby's father. This might be your mother-in-law, your boyfriend's mother, or someone else."

Social support was assessed using the Multidimensional Scale of Perceived Social Support (MPSS) (Zimet et al., 1988), an instrument designed to measure perceived adequacy of social support from family, friends, and a significant other that has been validated in Latino (Edwards, 2004) and other diverse populations (Canty-Mitchell & Zimet, 2000). We modified the original MPSS family sub-scale questions to be specifically about the MGM or PGM. For example, the item "I get the emotional help and support I need from my family" was modified to "I get the emotional help and support I need from my mother" in reference to the MGM. For the PGM, the set of MPSS questions were prefaced with the instructions "How true is each statement about the mother of your baby's biological father?" followed by each item, for example, "I get the emotional help and support I need from her." Thus, each of our variables reflecting social support is constructed from 4 questions each with 3 response choices 1 = Not true, 2 = Somewhat true, 3 = Very true. Mean scores were calculated. We dichotomized this variable using a cutoff of the median value of the combined MGM and PGM scores, thus, scores above 2.5 were coded as 1 and equal or below coded as 0.

Relationship quality was assessed with the question "What is your relationship with her like?" with response choices on a Likert scale 1 = Very good, 2 = Good, 3 = Okay, 4 = Bad, and 5 = Very bad. We dichotomized this variable using a cutoff of the median value of the combined MGM and PGM responses, thus, responses of 1 were coded as 1 and 2–5 were coded as 0. This median value based dichotomization was necessary to aid in the interpretation of this highly skewed variable, for example, of nondeceased MGMs, only 17% selected option choices 3–5. Therefore, because the data already only empowered us to distinguish between option choices 1 and 2+, our analyses reflect this.

Frequency of seeing each other in person and communicating were each assessed from a single item with response choices on a Likert scale of 1 = Every day, 2 = More than once a week, 3 = More than once a month, 4 = Once a month or less, 5 = Never. We dichotomized these variables using a cutoff of the median value of the combined MGM and PGM responses, thus, responses of 1 were coded as 1 and 2–5 were coded as 0. As above, this median value based dichotomization was necessary to aid in the interpretation of these highly skewed variables, for example, of nondeceased MGMs, only 5% selected option choices 3–5. Therefore, because the data already only empowered us to distinguish between option choices 1 and 2+, our analyses reflect this.

Geographic proximity was assessed from a question asking how nearby the MGM or PGM lives, with response choices on a Likert scale of 1 = In my home, 2 = In my neighborhood, 3 = Outside my neighborhood but close enough to visit during the day, 4 = Too far to visit during the day. We dichotomized this variable using a cutoff of the median value of the combined MGM and PGM responses, thus, responses of 3 or lower were coded as 1 and 4 was coded as 0. We felt this median value reflected a face-valid distinction between grandmothers close enough to visit during the day and those further.

When MGM was deceased ($n = 14$), frequency of seeing each other in person, communication frequency, and geographic proximity measures were coded as 0, and relationship quality and social support were coded as missing. When PGM was deceased ($n = 7$) or if the baby's biological father had been unknown and there was no other indicated main father figure or mother-in-law ($n = 1$), those three PGM allocare measures were coded as 0, and relationship quality and social support were coded as missing.

In order to ensure that our results were not the spurious consequence of the way we coded missingness, post-

hoc, we repeated models 3–5 using an alternative coding for the frequency of seeing each other in person, communication frequency, and geographic proximity measures in which deceased or unknown individuals were coded as missing (Table S30). The results are qualitatively the same, with no differences in which predictors of interest were statistically significant or the valence of the statistically significant beta values.

2.5 | Measuring mental health

All mental health measures were analyzed as continuous variables. Perinatal depressive symptoms were assessed via the Edinburgh Postnatal Depression Scale (EPDS); (Cox et al., 1987, 1996; Matthey et al., 2006), 9-item version that excluded the question about self-harm due to ethical concerns, as is common practice and has been shown to correlate 0.998 with the original 10-item scale (Qiu et al., 2022). EPDS possible scores ranged 0–27, with a sum score of 10 or more indicating possible clinical depression (Garcia-Esteve et al., 2003), which we used only for descriptive purposes (Table 1). Our cohort had Cronbach's $\alpha = 0.86$. Perceptions of stress was measured with a shortened 4-item Perceived Stress Scale (PSS); (Cohen et al., 1983; Lee, 2012). PSS possible scores ranged 0–16, with higher summed scores indicating greater levels of experienced stress. Our cohort had $\alpha = 0.42$. Anxiety related symptoms were assessed with the state form of the Spielberger State–Trait Anxiety Inventory-Short Form scale (STAI-SF); (Tluczek et al., 2009). STAI-SF possible scores ranged 0–24, with higher sum scores indicating greater state anxiety in the past few days. Our cohort had $\alpha = 0.69$. We also employed the Pregnancy Related Anxiety Scale (PRA); (Rini et al., 1999), with possible scores ranging 0–4 based on an average of item responses, with higher scores indicating greater levels of concern for their personal health, the baby's health, labor and delivery, or childcare. Our cohort had $\alpha = 0.83$.

2.6 | Potential confounders

We adjusted our statistical models for the effects of variables that we suspected could confound our relationships of interest. Our choices of these control variables were determined by a directed acyclic graph (DAG) approach (Figure 1), which itself was informed by evidence from previous studies. We selected control variables that, we suspected, may causally influence our predictors and outcomes of interest. We purposefully did not control for variables we suspected could be on the causal pathway linking our predictors and outcomes of interest. (a) We were concerned that the mother's relationship with the PGM could act as a proxy for her relationship to the baby's father. Therefore, we controlled for whether the mother was cohabitating with the baby's biological father. Although our definition of PGM did not specify "biological" father ("the mother of your baby's father"), cohabitation with the biological father was the best item for our purposes because the alternative option, relationship status, was asked at a later timepoint not concurrent with the cortisol measurement, and had more missingness ($n = 34$). The analytic cohort included four women who were in a relationship with someone other than the baby's biological father, but one of them still thought of the baby's biological father as the baby's father figure. Ultimately, we decided cohabitation with the baby's father had the highest chance of confounding our relationships of interest because of the allocare potential of a cohabitating partner, so we used this as our control variable. (b) We posited that the mother's age would potentially influence the availability of the MGM and PGM as well as psychological state and cortisol levels. Younger mothers would likely have younger MGMs and PGMs who may still be raising dependent children of their own and therefore have competing interests (Cant & Johnstone, 2008), and older mothers would likely have older MGMs and PGMs who may be less capable of providing care (Chapman et al., 2019). Baseline cortisol levels have been shown to vary by age (Roelfsema et al., 2017). Prenatal psychological risk has been shown to vary by maternal age (Nidey et al., 2020). (c) Cortisol levels have been shown to change across the course of pregnancy (Jung et al., 2011), and psychological states can also change across pregnancy (Ahmed et al., 2019; Lee et al., 2021). Because of evidence that romantic relationship quality and satisfaction change across the course of pregnancy (Sagiv-Reiss et al., 2012), it is plausible that other close family relationships may follow a similar pattern, necessitating that our models control for gestational age. (d) Parity could potentially influence allomaternal assistance because there may be changes in relationship quality or availability to help depending on how many other children the mother has; previous studies have found multiparous women receive less social support than primiparous women (Salari et al., 2014). Prenatal psychological distress and stress physiology have been shown to vary by parity (Gillespie et al., 2018; Sockol & Battle, 2015). (e) Evidence suggests that educational attainment can influence relationship quality (Woszidlo & Segrin, 2013) and occupational stress which can be both psychological and physiological (Assari & Bazargan, 2019) as well as perinatal depression risk (Pooler et al., 2013). (f) Country of birth could influence allomother availability due to distance and cross-border

TABLE 1 Descriptive statistics for the study cohort

n	75
Age (mean [SD])	29.87 (5.36)
Country of birth (%)	
U.S.	35 (46.7)
Mexico	28 (37.3)
El Salvador	4 (5.3)
Guatemala	5 (6.7)
Other Latin America	2 (2.7)
NA	1 (1.3)
Education (%)	
Less than high school	15 (20.0)
High school or equivalent	48 (64.0)
Any college or beyond	12 (16.0)
Work or school status (%)	
Job	23 (30.7)
No job	30 (40.0)
School	4 (5.3)
Job and school	6 (8.0)
Maternity leave	9 (12.0)
NA	3 (4.0)
Food insecurity = Food insecure (%)	15 (20.0)
Gestational age at assessment (mean [SD])	12.27 (3.05)
Number of children (mean [SD])	1.39 (1.45)
Number of pregnancies (mean [SD])	3.27 (2.65)
Marital status (%)	
Never married	34 (45.3)
Married	32 (42.7)
Separated	2 (2.7)
Divorced	2 (2.7)
Widowed	1 (1.3)
NA	4 (5.3)
Cohabitating with the baby's biological father = Yes (%	59 (78.7)
Relationship quality with MGM = High (%)	41 (54.7)
Social support from MGM = High (%)	51 (68.0)
Frequency of seeing MGM = Every day (%)	27 (36.0)
Communication frequency with MGM = Every day (%)	44 (58.7)
Geographic proximity to MGM = Close enough to visit during the day (%)	44 (58.7)
Relationship quality with PGM (%) = High (%)	26 (34.7)
Social support from PGM (%) = High (%)	14 (18.7)
Frequency of seeing PGM = Every day (%)	4 (5.3)
Communication frequency with PGM = Every day (%)	8 (10.7)
Geographic proximity to PGM = Close enough to visit during the day (%)	30 (40.0)
Clinical depression likely (EPDS ≥9) = Yes (%)	19 (25.3)
Perinatal depression (EPDS, 0–27) (mean [SD])	5.25 (4.54)

TABLE 1 (Continued)

Perceived stress (PSS, 0–16) (mean [SD])	4.87 (2.89)
State anxiety (STAI, 0–24) (mean [SD])	13.69 (1.91)
Pregnancy-related anxiety (1–4) (mean [SD])	1.70 (0.52)
Cortisol (urinary) pg/ml (mean [SD])	185434.79 (177810.21)
Cortisol corrected for specific gravity (mean [SD])	210547.06 (133826.38)
Cortisol corrected for specific gravity, natural log transformed (mean [SD])	12.05 (0.69)
Specific gravity of urine samples (mean [SD])	1.02 (0.01)

Abbreviations: EPDS, Edinburgh postnatal depression scale; MGM, maternal grandmother; PGM, paternal grandmother; PSS, perceived stress scale; SD, standard deviation; STAI; state–trait anxiety scale.

families. Country of birth could influence psychological distress in myriad ways, for example, stress related to immigration, acculturation, and discrimination. Country of birth could influence physiology via diet and environmental exposures.

Post-hoc, we considered including food insecurity and prepregnancy body mass index (ppBMI) as control variables, but decided against them because we deemed them likely to be on the causal pathway of interest (Figure 1). Allomother support may diminish food insecurity which could, consequently, lead to lower stress-related psychology and physiology. Allomother support may improve nutrition which could lead to lower adiposity and therefore lower ppBMI, which could, consequently, lead to lower psychological distress and cortisol levels. These causal pathways seem more likely than the opposite direction that would be worthy of inclusion as control variables (i.e., food insecurity or ppBMI influencing allomother support).

We are interested in the potential confounding effect of MGM and PGM ages, but unfortunately we lack data on PGM age. Our inclusion of maternal age in the models may, at least partially, control for MGM and PGM ages. Post-hoc testing revealed that MGM age was not correlated with any of our outcome variables (Table S1). For this combination of reasons, it was not added to models.

In the spirit of open science, we report correlations between all potential control variables that were and were not selected based on the DAG and literature review, even though we did not use the bivariate correlation criteria to design our models (Tables S1, S2, S3). We note that no un-selected variables were significantly correlated with any outcome variables.

2.7 | Statistical methods

Cortisol values were natural log transformed to improve the symmetry of distribution.

A series of five multivariate multiple regression (MMR) models measured the relationships between grandmother allocare and outcomes of interest. MMR modeling was chosen because it facilitates more than one outcome variable to be regressed onto the same set of predictors (Breiman & Friedman, 1997). MMR balances goodness of fit with interpretability because it provides coefficients that reflect the contribution of each term in the model (Gordon et al., 2018). Each MMR model assessed how a domain of grandmother allocare was correlated with Aim 1 outcomes (the 4 domains of mental health) and the Aim 2 outcome, cortisol. The five models reflect the five domains of grandmother allocare. MGM and PGM variables were both in each model in order to distinguish the effects of one after accounting for the other. Model *p*-values are corrected for multiple testing using Bonferroni correction. A benefit of MMR modeling is that it takes into account the covariance between coefficients from the five internal models. We consult the Pillai trace statistic produced by MANOVA as a further level of analysis to decide if the predictor variable is meaningfully contributing to both internal models.

Each model controlled for whether the participant was co-residing with the baby's biological father; her age; gestational age at the timepoint 1 assessment; parity; her educational attainment operationalized as 1 = less than high school, 2 = high school or equivalent, 3 = any college or beyond; and a binary variable reflecting whether she was U.S. born or foreign born.

We chose to model each domain of grandmother care separately to aid in interpretability of results. For example, it would be difficult to interpret the effect of frequency of seeing each other in person adjusting for geographic proximity and frequency of communication. Because of the partial conceptual overlap (and some collinearity, Figures S1, S2, S3) between these domains, we were more interested in modeling their contributions to the response variables separately rather than examining marginal effects of each after adjusted for the other four.

Homoskedasticity was assessed with Breusch-Pagan tests. When significant, robust standard errors were calculated, which only occurred for one model (Allison, 1999) (Tables S4, S5). Multicollinearity was assessed with variance-inflation factors (VIF) and tolerance (Table S4). Our thresholds for multicollinearity were VIF >2.5 (Craney & Surles, 2002; Johnston et al., 2018) and tolerance < 0.2 (Weisburd & Britt, 2013). We use Benjamini-Hochberg procedure with 10% false discovery rate to correct for multiple comparisons. We report partial f^2 Cohen's effect sizes for each coefficient in each model (Tables S5–S29).

Analyses were conducted in the R statistical programming language and environment, version 4.2.1.

3 | RESULTS

3.1 | Descriptives and data exploration

From an original cohort of $n = 107$ pregnant women, our final analytic cohort was $n = 75$ because we omitted women who were missing data on grandmothers ($n = 20$), missing urine sample ($n = 5$), and had outlier cortisol values (+2 SD, $n = 6$). All of the control variables were either complete or missing at most $n = 1$ in which case we replaced with median value (Table 1).

The analytic cohort was 47% U.S.-born, 84% educated to high school or less, 39% working at a job, 13% in school (some overlap), 12% on maternity leave, 43% married, and 20% food insecure (Table 1). Participants were, on average, 29.9 years old (range 20.1–41.40), 12 weeks pregnant, and had, on average, 1.5 children and 2.7 prior pregnancies. Seventy nine percent of participants were cohabitating with the baby's biological father. Seventeen percent of participants were classified as likely having clinical depression, consistent with the relatively high levels of perinatal depression exhibited by Latina women compared to other ethnic groups (Lara-Cinisomo et al., 2018).

All of the mental health measures were significantly correlated with each other with the exception of pregnancy-specific anxiety and perceived stress, which were not significantly correlated (Figure S1). Cortisol levels were not significantly correlated with any of the mental health measures, consistent with some but not all previous studies of pregnancy (Orta et al., 2018).

Our data suggest that geographic proximity and frequency of seeing each other in person are not reflective of relationship quality or social support, indicating that these variables capture unique aspects of relationships, potentially instrumental support. Specifically, geographic proximity was not significantly correlated with relationship quality or social support for either MGM or PGM (Figures S2, S3). Frequency of seeing each other in person was not significantly correlated with relationship quality for either MGM or PGM, or social support for PGM (Figures S2, S3). While relationship quality and social support were highly correlated, their different relationships with frequency of seeing each other in person for MGMs suggest the possibility that they capture slightly different aspects of the allocare relationship, that is, relationship quality may reflect emotional support regardless of instrumental support, whereas, our measure of social support may capture some element of instrumental support that must be delivered in person in addition to the larger contribution of emotional support to this construct. Frequency of communication and seeing each other were the highest correlated allocare constructs, but again, were differentially correlated with other constructs, evidence that they are not completely interchangeable (Figures S2, S3).

3.2 | Aim 1: Mental health

Aim 1 was broadly endorsed by the data. Three domains of both grandmothers' allocare were statistically significantly associated with better mental health (Table 2).

A pregnant woman's relationship quality with the MGM and social support from the MGM were both negatively associated with her depression. Specifically, having a better relationship with the MGM was associated with an average 3.8 points lower on the EPDS scale (95% CI [−5.9, −1.5], possible scores range 0–27), compared to women who had worse relationships with the MGM ($p < .01$) (Table S5). Receiving more social support from the MGM was associated with an average 3.3 points lower EPDS (CI [−5.9, −0.6]), compared with women who received less social support from the MGM ($p = .04$) (Table S6).

A pregnant woman's relationship quality with the PGM was negatively associated with perceived stress and pregnancy-related anxiety. Specifically, having a better relationship with the PGM was associated with an average 2.6 points lower on the PSS ((CI [−3.9, −1.3]) possible scores range 0–16, $p < .01$) and 0.4 points lower on the PRA scale ((CI [−0.6, −0.15]) possible scores range 0–4, $p < .01$), compared to women who had worse relationships with the PGM (Tables S10, S20). In the context of PGM results, we re-iterate that all models adjusted for co-residence with the baby's father.

Geographic proximity to the PGM was associated with less depression and lower pregnancy-related anxiety. Specifically, living close to the PGM was associated with, on average, 3.0 points lower on the EPDS scale (CI [5.1,

−1.0], $p = .01$) and 0.3 points lower on the PRA scale (CI [−0.5, 0.1], $p = .03$) (Tables S9, S24).

No significant effects were observed for state anxiety related to any grandmother construct. No significant effects were observed for the relationships of any mental health variable with how frequently the pregnant woman saw the MGM or PGM in person or communicated with her (Table 2).

3.3 | Aim 2: Cortisol

Aim 2 was statistically significantly endorsed by the data for MGM but not PGM (Table 2), as expected based on previous findings from our lab and others.

A pregnant woman's relationship quality, social support, and frequency of seeing the MGM were negatively associated her cortisol levels. Specifically, having a one-standard-deviation better relationship with the MGM was associated with an average 17.72% lower cortisol-adjusted-for-specific-gravity (95% CI [4.13, 29.42], $p = .04$, Table S25). Receiving one-standard-deviation higher social support from the MGM was associated with an average 17.53% lower cortisol-adjusted-for-specific-gravity (CI [3.5, 29.54], $p = .04$). Seeing the MGM one-standard-deviation more frequently was associated with an average 19.74% lower cortisol-adjusted-for-specific-gravity (CI [5.96, 31.49], $p = .02$).

We anticipated weaker or absent effects of PGM allocare on maternal prenatal cortisol, and indeed, no statistically significant effects were observed for three of the four predictors. Better relationship quality with the PGM was, unexpectedly, positively associated with higher cortisol levels compared to women with lower relationship quality, with a large effect magnitude. Specifically, having a one-standard-deviation better relationship quality with the PGM was associated with an average 35.97% higher cortisol-adjusted-for-specific-gravity (CI [16.18, 59.13], $p < .01$).

3.4 | Model comparison

Because our models have the same set of predictors for multiple outcomes, we used the Pillai trace statistics produced by MANOVA of MMR models to assess whether each predictor is worthy of inclusion for all outcomes in that model. Pillai's traces suggested that relationship quality with both MGM and PGM as well as social support from MGM (borderline) should be included as predictors for all dependent variables (mental health measures and cortisol) even after accounting for their covariances (Tables S31, S32). MANOVA rejected inclusion of the other grandmother allocare variables in all models, which is accordant with their inconsistent significance across dependent variables (Tables S33–S35).

4 | DISCUSSION

We innovate within the area of grandmother allocare research by examining the prenatal stage of life and a biopsychosocial mechanism by which prenatal grandmother effects may be enacted. Our results suggest that grandmother allocare is associated with better mental health (Aim 1) for pregnant daughters and daughters-in-law, and lower cortisol levels (Aim 2) for pregnant daughters. These effects were observed more consistently for MGM than PGM, for whom better relationship quality was associated with greater levels of cortisol after adjusting for the other variables in the model. All our other observations were in the expected direction.

Our results from Aim 1 find that both MGM and PGM can be beneficial to maternal psychology, perhaps in unique ways, but more MGM relationship characteristics were significant than PGM relationship characteristics. Specifically, we found that MGM social support was negatively related to maternal depression. These results fit within a broad array of findings that describe a positive relationship between social support and prenatal mental health (Bedaso et al., 2021; Collins et al., 1993; Giurgescu et al., 2006; Xie et al., 2009). Much of this previous work has focused on general measures of social support such as total perceived levels of support in various domains rather than support from specific individuals. By focusing on grandmothers, we consider how one specific type of relative can impact the psychology of a pregnant woman. Previous studies have shown MGM support to be helpful towards parenting satisfaction and minimizing distress (Crettenden et al., 2018; Lewin et al., 2011). Additionally, one published study and one preprint study indicate that higher *quality* support - from mostly maternal grandparents - was associated with lower perinatal depressive symptoms (Borcherding et al., 2005; Riem, Bakermans-Kranenburg, Cima, & van IJzendoorn, 2021). Our's is the first paper, to our knowledge, connecting the important role grandmothers can play to the biological processes that make up the developmental origins of disease risk. While we focus on grandmothers as often particularly helpful individuals, this role can be played by other individuals within a network. Future work can explore involvement of other allomothers including and beyond romantic partners, fathers, and grandmothers.

We also find that MGM relationship quality was negatively associated with maternal depression, while PGM

TABLE 2 This table shows the results from a series of five models

	Depression		Perceived stress		State anxiety		Pregnancy-related anxiety		Cortisol[a] (natural-log)	
	MGM	PGM	MGM	PGM	MGM	PGM	MGM	PGM	MGM	PGM
Mod1: Relationship quality	−3.748 [−5.949, −1.546][d]	−1.746 [−3.997, 0.505]	−1.348 [−2.599, −0.096][b]	−2.632 [−3.912, −1.352][d]	−2.122 [−3.574, −0.67][c]	−1.89 [−3.375, −0.405][c]	−0.084 [−0.304, 0.136]	−0.38 [−0.605, −0.155][d]	−0.398 [−0.711, −0.086][c]	0.627 [0.306, 0.948][d]
Mod2: Social support	−3.272 [−5.939, −0.605][c]	−2.156 [−4.936, 0.625]	−0.582 [−2.208, 1.045]	−1.751 [−3.447, −0.055][b]	−2.157 [−3.929, −0.385][c]	−1.544 [−3.391, 0.303]	0.025 [−0.244, 0.293]	−0.312 [−0.591, −0.032][b]	−0.47 [−0.854, −0.087][c]	0.433 [0.033, 0.834][b]
Mod3: Frequency of seeing in person	−1.222 [−3.471, 1.028]	1.983 [−2.243, 6.21]	−0.004 [−1.385, 1.377]	2.713 [0.119, 5.308][b]	−0.071 [−1.678, 1.535]	1.357 [−1.661, 4.375]	−0.177 [−0.418, 0.065]	0.262 [−0.191, 0.716]	−0.458 [−0.788, −0.128][c]	0.206 [−0.414, 0.826]
Mod4: Communication frequency	−1.022 [−3.069, 1.025]	−0.123 [−3.408, 3.163]	−0.783 [−2.025, 0.46]	1.586 [−0.409, 3.581]	0.185 [−1.27, 1.641]	0.632 [−1.704, 2.969]	−0.135 [−0.356, 0.086]	−0.025 [−0.38, 0.329]	−0.157 [−0.466, 0.153]	0.088 [−0.408, 0.585]
Mod5: Geographic proximity	1.346 [−0.763, 3.454]	−3.055 [−5.074, −1.036][c]	−0.244 [−1.611, 1.123]	−0.414 [−1.723, 0.896]	0.346 [−1.208, 1.9]	−0.923 [−2.411, 0.565]	0.078 [−0.153, 0.309]	−0.291 [−0.512, −0.07][c]	−0.241 [−0.57, 0.089]	−0.113 [−0.428, 0.203]

Note: Each row represents one multivariate multiple regression (MMR) model. Each MMR model has five outcomes (columns) that reflect Aim 1 (depression; perceived stress; state anxiety; pregnancy-related anxiety) and Aim 2 (cortisol). Cortisol levels are morning urinary ng/ml natural log transformed. Each cell shows the grandmother-related predictor of interest's beta coefficient [95% confidence interval] with super indicating *p*-value. Each model controls for cohabitation with the baby's father; age; gestational age; parity; education; country of birth. All variable beta coefficients, standard errors, *p*-values, and 95% confidence intervals as well as model fitting statistics are detailed in the supplementary materials. Model *p*-values are corrected for multiple testing using Bonferroni correction.

[a]Cortisol was corrected for specific gravity and natural log transformed.

[b]$p < .10$.

[c]$p < .05$.

[d]$p < .01$.

relationship quality was negatively associated with maternal stress and pregnancy-related anxiety. Our findings suggest that relationship quality may play a large role in mental health, greater than other aspects of allomaternal involvement such as geographic proximity and frequency of communication and seeing in person. This corresponds to previous research that has shown that greater communication or proximity in a relationship is not always positive (Barnett et al., 2012; Scelza, 2011). Indeed, support or contact can be unwanted and further exacerbate stressful situations. Thus, relationship quality is an important measure to disentangle when help is offered, given, and when it is appreciated.

Little research has shown a link between PGM social support and positive maternal mental health outcomes. The preprint study mentioned above suggests that paternal grandparent involvement may, instead, lead to worse mental health risk (Riem et al., 2021). Overall, our results suggest that positive relationship quality with PGMs (rather than involvement) seems to be the most critical factor in their impact on maternal mental health.

For our second aim, our study found small to medium effect sizes of the relation between grandmother allocare and maternal urinary cortisol (Tables S5–S29). While we observed no such correlations in our cohort (Figure S1), previous studies of prenatal urinary cortisol found medium to large effect sizes for correlations with maternal depression ($r = 0.37$ and $r = 0.52$) as well as gestational age at birth ($r = -0.59$ and $r = 0.42$) and fetal growth rate ($r = -0.39$), although the authors did not provide units of cortisol measurement so direct comparison is difficult (Diego et al., 2009; Field et al., 2004). Others found no significant correlations between prenatal urinary cortisol and their constructs of interest (Luiza et al., 2015; Rouse & Goodman, 2014a). Similar to our results, most studies of prenatal cortisol found no relation to mental health when measured in blood (reviewed in [Orta et al., 2018]). Hoffman and colleagues found medium effect sizes for correlations of second trimester cortisol measured from hair with gestational age at delivery and perceived stress (Hoffman et al., 2016).

We unexpectedly observed a positive correlation between PGM relationship quality and maternal cortisol levels. We are hesitant to over-interpret this finding because results were null for the other four PGM constructs. We acknowledge many possible evolutionary interpretations, for example, perhaps better relationship quality with PGM indicates that the PGM is fulfilling a role typically played by other important, missing figures such as friends or medical providers, which could act as an adaptive signal to accelerate fetal development. Any interpretation would be very speculative at this stage, so future studies are needed.

4.1 | Fetal exposure to maternal cortisol

Cortisol in maternal circulation may influence the fetal compartment through at least two biological pathways. Firstly, cortisol diffuses from the maternal compartment through the placenta into the fetal compartment, with only partial inactivation by the enzyme 11β-hydroxysteroid dehydrogenase type 2 (11β-HSD2; Benediktsson et al., 1997). Moreover, maternal psychological distress has been associated with lower placental 11β-HSD2 levels, permitting more maternal cortisol to pass directly to the fetal compartment (O'Donnell et al., 2012). Secondly, maternal cortisol stimulates placental production of CRH, which activates the fetus' hypothalamic–pituitary–adrenal (HPA) axis function (Sandman et al., 2006). Maternal and fetal levels of cortisol have been shown to be correlated, further underscoring how measuring maternal cortisol levels reflects not only maternal but also fetal exposure to this hormone (Gitau et al., 2004; Smith et al., 2011).

4.2 | Life history scheduling and fetal programming

Our results are consistent with the possibility that a better relationship between a pregnant woman and her fetus' future grandmother could improve the pregnant woman's mental health and manifest in lower cortisol levels. These results imply that better prenatal grandmother allocare may prolong the duration of the pregnancy. Higher cortisol levels between 7 to 24 and 27 to 37 weeks' gestation have been associated with greater risk of preterm birth (Giurgescu, 2009). Higher levels of placental CRH have also been associated with earlier gestational age at birth and greater risk of preterm birth and fetal growth restriction (Hobel et al., 1999; Wadhwa et al., 2004). Thus, lower maternal prenatal cortisol levels could suggest an adaptive strategy such that those women who benefit from more prenatal MGM allocare have the luxury to invest extra time and energy into a pregnancy to ensure the highest possible quality offspring. Conversely, those women with low prenatal MGM allocare may accelerate the timing of birth in order to reduce the somatic cost of a temporally and energetically expensive pregnancy when they lack the necessary support from their mothers.

This work expands upon the integration of DOHaD and cooperative breeding theory by suggesting that grandmothers may offset maternal prenatal stress in ways that benefit their grandchildren before birth. Grandmother allocare may cause pregnant women to have better mental health, which, in turn, may cause lower

cortisol levels, but with our small cohort size we are underpowered to explore statistical mediation. This idea reflects the broader stress buffering hypothesis proposed by Cohen and colleagues, which suggests that social support attenuates responsivity to stressors (Cohen & Wills, 1985). Others have observed similar effects among pregnant women not with grandmothers but with romantic partners (Giesbrecht et al., 2013) and the baby's father (Kofman et al., 2019). The possibility that grandmother allocare could causally improve maternal mental health which could, in turn, lower cortisol secretion in pregnancy is a pattern that could indicate a slow (or, conversely, fast) life-history strategy for the mother and fetus. However, links to other life history traits would be necessary to establish a broad strategy beyond the one particular trait of gestational length (Sear, 2020).

The adaptive strategy could also be driven by fetal interests. A fetal programming perspective would suggest that the fetus detects cues from the intrauterine environment that signal information about extrinsic conditions. Various theories have suggested that the fetus "interprets" these cues as indicative of past, current, or forecasted future conditions (Lea et al., 2017; Lea & Rosebaum, 2020). The adaptive interpretation of prenatal cues is an active area of research. Our study here does not attempt to distinguish between these competing theories. Rather, we reveal the observation that the fetus has access to a proxy cue of allocare by monitoring cortisol levels.

4.3 | Grandmother intergenerational effects

While previous studies have shown that grandmother survivorship, cohabitation, and proximity are sometimes positively associated with daughter/daughter-in-law completed fertility and grandchild survivorship and growth (Chapman et al., 2021; Sear et al., 2000), the mechanism by which grandmothers confer these benefits remains ambiguous. Here, we looked beyond the simple operationalizations of grandmother survival or geographic proximity to include relationship quality, social support, communication, and frequency of seeing each other in person to begin to discern how grandmother effects are conferred. Scholars have debated whether grandmothering inclusive fitness benefits and longevity evolution are driven by maternal, paternal or both lineages of grandmothers (Euler & Weitzel, 1996; Jamison et al., 2002; Kemkes-Grottenthaler, 2005; Sheppard & Sear, 2016; Voland & Beise, 2002). Under a DOHaD framework, both grandmothers' adaptive interests should be aligned to invest in the developing offspring. However, we generally find that positive relationships with MGMs and PGMs—and not other allocare indicators—are most critical to improving mental health outcomes (Aim 1). Additionally, we observe more consistent benefits associated with maternal than paternal grandmothers, especially in regards to cortisol levels (Aim 2); likely due to a closer social and biological relationship between mother-daughter dyads than mother-in-law-daughter-in-law dyads. This is consistent with the broader literature that compares postnatal MGM and PGMs and finds MGMs to be more consistently positive for reducing infant mortality (Coall & Hertwig, 2010; Sear & Mace, 2008; Strassmann & Garrard, 2011).

We observed that PGM relationship quality was positively correlated with cortisol levels, and it is interesting to note the consistency of these findings with postnatal studies. Sheppard and Sear found, in a Guatemalan cohort, that frequency of seeing the PGM in person during the first 12-months postpartum was associated with shorter-length infants, whereas frequency of seeing the MGM was associated with longer-length infants (Sheppard & Sear, 2016). We posit that, if similar patterns of contact existed prenatally, it is plausible that their observed effect could have been attributed, in part, to differential cortisol exposures adjusting fetal growth patterns (their models did not adjust for birth length). Voland and Beise found PGM geographic proximity was associated with higher infant mortality in the first month of life among a historical German population (Voland & Beise, 2002). We posit that their results could also be attributed to prenatal effects, as higher cortisol levels could be associated with shorter gestation length, which would be a strong risk factor for neonatal mortality. Leonetti et al. found that, among a patrilineal cultural group in India, PGM presence was associated with greater completed fertility for daughters-in-law (Leonetti et al., 2005). We posit this pattern could be related to our observation of higher cortisol such that shorter length of gestation would lead to shorter inter-birth intervals and ultimately greater fertility, although the effect of gestation length on completed fertility is probably very small. Future studies are needed to assess whether gestation duration could play a mediating role between PGM-daughter-in-law relationships and grandoffspring growth and survivorship as well as mothers' completed fertility.

Our study suggests that certain benefits of grandmother allomaternal care may be transmitted intergenerationally through relationship quality, social support, and seeing each other in person. It is also possible that our study's metrics act as proxies for some other, unmeasured construct, and future studies are needed to clarify precisely how grandmothers influence mothers' prenatal psychobiology. Nonetheless, the suggestion that grandmothering

may offer benefits to grandchildren even before birth extends the benefits of allomothering into the prenatal period.

Future studies should take the next step by including an even wider range of mechanisms by which grandmother effects can be enacted, such as instrumental, material, pedagogical, and financial support (Emmott & Mace, 2015; Myers et al., 2021; Scelza & Hinde, 2019; Sheppard & Sear, 2016).

4.4 | Socio-cultural context

Our observation that better, closer relationships with grandmothers is associated with better prenatal mental health among Latina women has implications for developing interventions to benefit this vulnerable population. Previous studies point to social and structural problems that contribute to psychological distress among perinatal Latinas, such as everyday discrimination and political victimization (Fox, 2021, 2022). Our results imply that relationships between pregnant women and their mothers and mothers-in-law could, potentially, improve mental health in ways that offset the negative impacts of socio-political stressors.

In cultural contexts in which grandmother (or mother and mother-in-law) support is crucial for family well-being, it may be the case that in the absence of grandmothers (or mothers and mothers-in-law), other kin or non-kin classes provide support that does not fully compensate for the loss, leaving a detectable biopsychological signature. In more structurally flexible cultural contexts, even if grandmother (or mother and mother-in-law) support is expected, its absence may not leave a discernible signature if other individuals can sufficiently compensate with their support. More cross-cultural research is needed to further explore this variation.

4.5 | Limitations

Our observational study design does not allow us to test causality. Thus, it is equally possible that the direction of causality is opposite to what we proposed here, that is, having worse mental health or lower cortisol may cause pregnant women to perceive their relationships with their mothers and mothers-in-law negatively. Additionally, self-reported data can be biased or erroneous (Van de Mortel, 2008). The short forms of STAI and PSS lack the accuracy of the full-length versions (Marteau & Bekker, 1992; Spielberger et al., 1983; Tluczek et al., 2009). Our results utilizing the PSS scale should be interpreted with caution because of low Cronbach's alpha. The most integrated measure of cortisol available for this study was urinary, which summarizes across several hours (Sarkar et al., 2013), and future studies should consider measuring cortisol from other matrices with longer-term integration, for example, hair (Urlacher et al., 2022). Our morning urine collection was not strictly first morning void (FMV), which could potentially integrate across more hours; however, women in early pregnancy void much more often throughout the night than nonpregnant peers (Brown, 1978), so the benefits of FMV are attenuated. Previous studies of prenatal maternal urinary cortisol similarly use mid-morning prenatal clinical visit samples (Diego et al., 2009; Field et al., 2004; Field et al., 2006; Field et al., 2009; Luiza et al., 2015; Rouse & Goodman, 2014). Our study is limited by lack of information on the timing of participants' previous void, which would help interpret how many hours of cortisol production the samples reflect. Our analyses would be strengthened by utilizing more information about the grandmothers, such as their age, relationship status, other children, other grandchildren, employment, and health, but our data lacked these details. Our study is limited exclusively to self-identified Latinas who were mostly of Mexican origin or heritage. The U.S. Latino community is comprised of a wide variety of geographical and cultural origins and heritage throughout Latin America, and it is plausible that variation in cultural value systems contributes to variation in the degree to which family influence mental health, for instance, if other individuals in a pregnant woman's community are more primary sources of support. Further research is needed among other diverse cohorts of Latinas and for other ethnic and cultural groups. Finally, research conducted among post-industrial populations has only limited ability to test hypotheses about the evolution of biopsychosocial traits in humans, and further research should be conducted among small-scale societies in order to determine the impact of family relationships in the absence of state-sponsored sources of support, medical obstetric practice, and mothers' and grandmothers' employment in large institutions. The roles of grandmothers may adjust in different settings depending on the other resources available to and other demands on mothers and grandmothers.

5 | CONCLUSIONS

This study found that relationship quality and social support from a pregnant woman's mother or the mother of her baby's father was related to better maternal prenatal mental health and, for her mother only, lower cortisol levels in early pregnancy. Geographic proximity to the

baby's father's mother was also associated with better prenatal mental health. These observations have relevance for understanding fetal programming of life history traits because cortisol is a cue of the mother's family relationships that could potentially transmit information to the fetus and participate in regulation of gestational age at birth. These observations also have evolutionary relevance because of the implication that grandmothers may be able to enhance their inclusive fitness by improving the mental and physical health of pregnant daughters or daughters-in-law.

AUTHOR CONTRIBUTIONS

Molly M. Fox conceptualized and designed the project, conducted statistical analyses, and led writing the manuscript. Delaney A. Knorr contributed to data collection (e.g., recruitment; informed consent; sample collection), manuscript writing, and citations. Dayoon Kwon and Michael H. Parrish conducted data cleaning, variable construction, and codebook creation, as well as contributing citations. DK also created supplementary figures and tables. Kyle S. Wiley conducted assays and contributed to manuscript writing and citations. All co-authors contributed to manuscript editing.

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CONFLICT OF INTEREST STATEMENT

The author declares there is no potential conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are not publicly available because participants did not consent to sharing individual-level data publicly.

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