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INTERGENERATIONAL EFFECTS OF EARLY-LIFE ADVANTAGE:
LESSONS FROM A PRIMATE STUDY

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ABSTRACT

This paper uses three decades of studies with Rhesus monkeys to investigate the intergenerational effects of early life advantage. Monkeys and their offspring were both randomly assigned to be reared together or apart from their mothers. We document significant intergenerational effects of maternal presence. We also estimate, for the first time, the intergenerational complementarity of early life advantage, where the intergenerational effects of maternal rearing are only present for offspring that were mother-reared. This finding suggests that parenting is the primary mechanism driving the intergenerational effects. Our paper demonstrates how studies of primates can inform human development.

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A data appendix is available at <http://www.nber.org/data-appendix/w27737>

1 Introduction

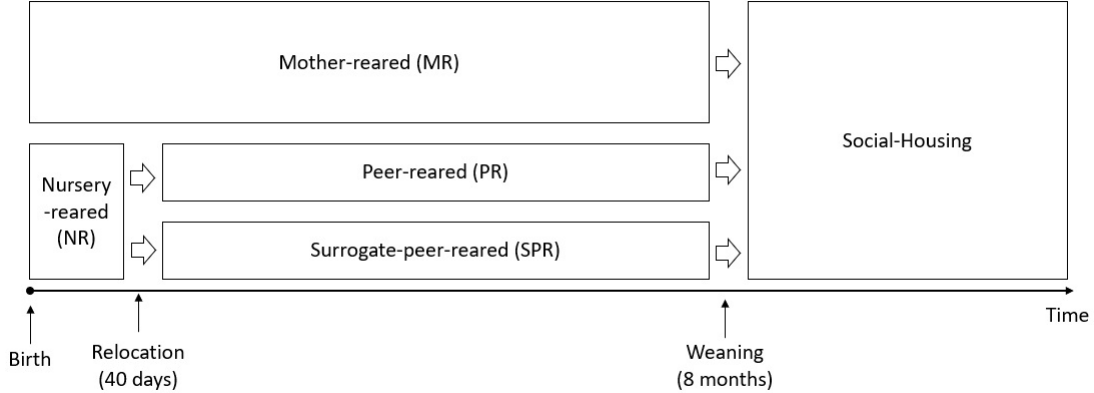
This paper presents experimental evidence on the intergenerational impact of early advantage on the health and social status of Rhesus monkeys. Rhesus monkeys have a close biological and behavioral resemblance to humans. Rhesus monkeys share 93% of the same DNA with humans (Gibbs et al., 2007), develop attachment behaviors at infancy and naturally form hierarchical social structures in the same way as humans (Dettmer and Suomi, 2014). Rhesus monkeys can be reared in highly controlled and experimentally manipulated environments in ways that are not possible with humans.

We use a decades-long study of Rhesus monkeys conducted at the Laboratory of Comparative Ethology (LCE) at the National Institutes of Health (NIH) to investigate the impacts on health and social status of multi-generational experimentally assigned adversity and non-adversity. Following the classic study of Harlow and Zimmermann (1959), generations of Rhesus monkeys are exposed at random to adverse or normal rearing conditions. Normally reared monkeys are reared by their mothers. Adversely reared monkeys are separated from mothers after birth and reared in a nursery by human caregivers during the first 40 days. At that point they are assigned to two rearing conditions that involve different amounts of peer contact. This is the primate analog of early life adversity.¹ The monkeys remain in these arrangements until weaning, which occurs when they are approximately 8 months old. After weaning they are moved to larger social groups where monkeys from all treatment groups live together. The study protocol is graphically depicted in Figure 1.

The multigenerational rearing experiment creates variation in family rearing sequences. This variation allows us to estimate a variety of new treatment effects, including the intergenerational complementarity (supermodularity) of early-life advantage, and to experimentally quantify the mechanisms of intergenerational transmission of early-life advantage. Consider two generations - what we analyze in this paper. Let $R = 0$ denote nursery-rearing (NR), or

¹Research by Rutter and O'Connor (2004) and Nelson, Fox, and Zeanah (2014) highlights the importance of child-caregiver interactions in the early years in fostering child development.

Figure 1: LCE Study Protocol



reared in adversity, while $R = 1$ denotes mother-rearing (MR), or reared in normal conditions. Let $s_{i,j}$ denote the rearing sequence of the monkey's family, where $i \in \{0, 1\}$ denotes the rearing of the monkey's mother (generation 1) and $j \in \{0, 1\}$ the monkey's own rearing (generation 2). The two-generation study creates four possible sequences depicted in Table 1.

Table 1: MULTIGENERATIONAL REARING ASSIGNMENT

| | | Gen. 2 | |
|--------|----------------------|---------------------|----------------------|
| | | Mother-reared (R=1) | Nursery-reared (R=0) |
| Gen. 1 | Mother-reared (R=1) | $s_{1,1}$ | $s_{1,0}$ |
| | Nursery-reared (R=0) | $s_{0,1}$ | $s_{0,0}$ |

The difference in the outcomes of monkeys assigned to the four rearing sequences reveals the many treatment effects of the intervention. Let $\Psi(s_{i,j})$ be the outcome of a monkey when the mother and the monkey are assigned to rearing sequence $s_{i,j}$, holding everything else constant. The difference, $\Psi(s_{0,1}) - \Psi(s_{0,0})$ reveals the benefit of MR rearing for offspring of disadvantaged (NR) mothers and tells us about whether it is possible to compensate for maternal disadvantage. Similarly, $\Psi(s_{1,1}) - \Psi(s_{1,0})$ reveals the benefit of sustained intervention across generations.

The difference in outcomes across rearing sequences also reveals the intergenerational effect of the intervention for offspring assigned to the two rearing conditions: $\Psi(s_{1,0}) - \Psi(s_{0,0})$ reveals the intergenerational effect of intervention on disadvantaged (NR) offspring and $\Psi(s_{1,1}) - \Psi(s_{0,1})$ the intergenerational benefit on non-disadvantaged (MR) offspring. The difference between the two intergenerational effects $[\Psi(s_{1,1}) - \Psi(s_{0,1})] - [\Psi(s_{1,0}) - \Psi(s_{0,0})]$ reveals the intergenerational complementarity (supermodularity) of rearing conditions. It describes how the effect of offspring rearing depends on parent rearing. Lastly, $\Psi(s_{1,0}) - \Psi(s_{0,1})$ tell us about the relative benefits of investing in the parental generation, in comparison to investing in the offspring generation.

This multi-generational randomization allows us to learn more than the benefit of the intervention in a given generation. It also allows us to learn about the importance of sustained interventions and the importance of investing early in the parental generation versus compensating the environments of offspring.

The specific design of the intervention in the form of maternal separation allows us to experimentally quantify the relative importance of pre and post-birth mechanisms in the intergenerational transmission of early-life advantage. Nursery-reared monkeys do not interact with their mothers (and fathers) after birth, so any and all transmission of early-life advantage on NR monkeys operate via pre-birth factors, such as in-utero investments and transgenerational epigenetic effects. For mother-reared monkeys, early-life advantage can be transmitted via mother-offspring interactions after birth (parenting) in addition to the pre-birth factors. The difference in the intergenerational effects of the intervention across MR and NR offspring reveals the relative importance of the parenting mechanisms from in-utero or transgenerational epigenetic mechanisms, which are two alternative pathways driving intergenerational treatment effects that do not involve parent-offspring interaction after birth.²

²See Gluckman and Hanson (2005), Almond and Currie (2011) and Almond and Mazumder (2013) for three detailed reviews of the fetal-origins hypothesis. Also, see Jablonka and Raz (2009) and Heijmans et al. (2008) for a detailed discussion of the transgenerational epigenetic mechanism.

This paper makes three main contributions to the literature. First, using the data collected over four decades at LCE, we document significant intergenerational effects of early life advantage on offspring outcomes. We show the intergenerational effects start at birth and persist until adulthood. Second, we present the first evidence of intergenerational complementarities of early life advantage. We show that the benefits of the intervention (mother-rearing) are only positive for the offspring of mothers that also received the positive intervention. This highlights the value of sustained intervention across generations. Third, we present evidence that parenting is the primary channel of intergenerational transmission of early-life advantage.

The rest of the paper is organized as follows: Section 2 provides background on research using non-human primates and describes the study conducted at the LCE along with its main lessons for human development. Section 3 describes the data and outcomes used in this paper in more detail. Empirical findings are presented in Section 4. Section 5 concludes.

2 Non-Human Primate Research

Non-human primates (NHPs), particularly macaques, have been utilized for decades as models for the study of child development. Harlow’s early experiments in the 1950s and 1960s demonstrated that infant monkeys develop attachments to contact comfort figures and depend on attachments to thrive (Harlow, 1958, 1959; Harlow and Zimmermann, 1959; Harlow and Harlow, 1962, 1965). These studies transformed child-rearing practices in the U.S., which previously emphasized little physical contact in order to provide clean, sterile environments for infants. Since Harlow’s initial studies, decades of research has repeatedly demonstrated the value of NHPs for child development research. NHPs, and macaques, in particular, are biologically similar to humans (we share approximately 93% of the same DNA Gibbs et al., 2007), they possess neurological, anatomical, and physiological systems that are present in humans but are lacking in other animal models (Phillips et al., 2014), and they engage in highly complex social interactions with a period of infancy in which the young

are highly dependent on their mothers and other caregivers (Suomi, 2005). Moreover, NHPs satisfy criteria for attachment (see Dettmer and Suomi, 2014 for a review), with infants exhibiting predictable behavioral and physiological stress responses when separated from their caregivers that subside when reunited.

Besides demonstrating attachment behaviors, and myriad other social behaviors, that are similar to those of humans, NHPs exhibit similar neurological development to human infants. They are capable of learning complex cognitive tasks that assess brain functions in ways similar to human children. For instance, the Primate Neonatal Assessment (PNNA; Schneider and Suomi, 1992; Schneider, Champoux, and Moore, 2006) was developed on the basis of the Brazelton Neonatal Assessment Scale for human infants (Brazelton, 1973), and considerable experience using this instrument has demonstrated similar reflex, motor skill, and sensorimotor development across humans and NHPs (Schneider, Roughton, and Lubach, 1997; Schneider et al., 1999, 2001, 2007; Schneider and Moore, 2000). In addition, cognitive tasks for human children developed by Jean Piaget (Piaget, 1954) have been modified for the study of cognitive development in NHPs (Dettmer et al., 2009; Diamond and Goldman-Rakic, 1989; Filion, Washburn, and Gullledge, 1996; Sackett et al., 1981), as have other complex cognitive tasks that measure learning, cognitive flexibility, and impulsivity (Clarren et al., 1992; Dettmer et al., 2007; Dettmer, Murphy, and Suomi, 2015; Sackett et al., 2006)

Rhesus monkeys naturally form rigid dominance hierarchies, and social rank is transmitted via the maternal line, with mothers, siblings, and aunts caring for and reinforcing a young monkey's place in the hierarchy. From infancy, both human and macaque infants are able to understand asymmetric relationships in social dominance, with fully-developed dominance relationships among peers present at toddlerhood (see Wooddell et al., 2017a for a review). Similar to humans, high-ranking monkeys have greater access to resources – namely, preferred social partners, high-value food items, and mating opportunities. Low-ranking monkeys exhibit detrimental alterations in stress reactivity pathways, disease resistance, and other key biological pathways (see Boyce and Hertzman, 2018 for a review; Hoffman et al., 2010;

Snyder-Mackler et al., 2016; Zumpe and Michael, 1987). Such social stratification manifests as socioeconomic status (SES) in humans (Boyce and Hertzman, 2018), thereby making the study of macaque social rank yet another strength of this model species.

Several advantages to the NHP model of child development make them ideal for the scientific study of development. First, as previously noted, NHPs develop about four times faster than humans, making long-term follow-up and intergenerational analyses easier than in humans. Second, NHPs can be reared in highly controlled environments, allowing for experimental control over specific variables such as the amount of adult social interaction individuals receive early in development. Third, NHPs can be randomly assigned to differential rearing conditions from birth. The randomizations can be repeated across generations. Finally, repeated and long-term collection of biological samples and behavioral data is much more feasible in NHPs, allowing for detailed analyses of developmental processes. All of these features enhance our understanding of primate and human development. In this paper, we rely on the repeated randomization of early rearing conditions across generations to estimate intergenerational complementarities of early-life advantage for the first time.

2.1 The LCE Study

Randomization of early rearing conditions in NHPs has most often been achieved by comparing infants reared with their mothers, either in mother-infant dyads or in social groups (i.e., mother-rearing or MR), to those hand-reared in a nursery by human caregivers with differing amounts of peer-contact (i.e., nursery-rearing or NR). The LCE conducted such comparative studies for over 30 years as part of the National Institute of Child Health and Human Development (NICHD) Intramural Research Program. In these studies, infant macaques were randomly assigned to be either MR or NR beginning within the first days of life through about 6-8 months of age. The rearing assignment only depended on the mother's primiparous status, where first-born monkeys were more likely to be assigned to the MR condition. Thereafter MR and NR infants were "weaned," whereby they were removed from

their mothers or the nursery and then housed in similar conditions. Thus, behavioral or biological differences observed after the first 6-8 months can be attributed to the differential early social experiences infants received prior to that time.

In the NR paradigm, infants were randomly assigned to be reared in one of two conditions. The first is peer-rearing (PR), where, after the first 40 days of life being hand-reared by human caregivers, groups of four or five infants were housed together permanently for the duration of their NR (i.e., 8-10 months). The second is surrogate-peer-rearing (SPR), in which, after the first 40 days of life being hand-reared by human caregivers, infants were reared in single cages with mobile cloth-covered surrogates and also given daily two-hour play sessions with three other SPR peers.³ These play groups remained constant throughout the duration of their nursery rearing. The two groups of nursery-reared infants (SPR and PR) never physically socialized with each other, although they did live in the same housing room where they could see, hear, and smell each other.

Importantly, every study with animals must undergo a rigorous review process prior to the approval of the study and the collection of any data. This review is conducted by the institutional animal care and use committee (IACUC), which is comprised of experts in the field, non-expert scientists, veterinarians, and members of the general public. Unlike any other use of animals (i.e., food, clothing, entertainment, etc.), the research must be ethically justified in the application process and approved prior to the onset of any study. In each study, scientists make meticulous considerations of the potential benefits of the research versus the potential harms to the animals. These considerations are based on many factors and are also evaluated in the study application and approval processes (Tardif et al., 2013).

³It has been shown that infant rhesus monkeys form attachments to the surrogate mothers Harlow and Zimmermann (1959). However, research also demonstrates that they develop stronger attachments to biological mothers than to inanimate surrogate ones Meyer et al. (1975)

3 Data

The LCE studied close to fifteen-hundred Rhesus monkeys over three decades. Many of the monkeys in the study were offspring of mothers that also participated in the study, allowing us to study the intergenerational effects of the rearing intervention.

In this paper, we consider all offspring-mother pairs that participated at any point in time in the LCE study. In total, we follow 728 pregnancies from about 371 females that were part of the rearing experiment. Of the 728 pregnancies, 656 monkeys grew up to be part of the rearing experiment. Some of the pregnancies ended up in stillbirths, some offspring died after birth, and some were assigned to alternative rearing conditions.⁴ Importantly the rearing assignment was randomized in both generations. As a result, the rearing assignment of offspring monkeys (generation 2) did not depend on the rearing assignment of their mothers (generation 1). We describe the rearing allocation for the 656 offspring-mother pairs in Table 2.

Table 2: MULTIGENERATIONAL REARING ASSIGNMENT

| | | Gen. 2 | | Total |
|--------|----------------------|------------------------|-------------------------|-----------------|
| | | Mother-reared (R=1) | Nursery-reared (R=0) | |
| Gen. 1 | Mother-reared (R=1) | 158 [24.09%] | 152 [23.17%] | 310 [47.26%] |
| | Nursery-reared (R=0) | 189 [28.81%] | 157 [23.93%] | 346 [52.74%] |
| Total | | 347 [52.90%] | 309 [47.10%] | 656 [100%] |

We analyze a series of different outcomes to understand the intergenerational impacts of the rearing intervention. In order to understand the initial intergenerational impacts of the intervention on the second generation, we study pregnancy outcomes obtained from birth records. In order to study the long-lasting intergenerational effects of the intervention, we consider health outcomes measured after the end of the intervention, in adolescence,

⁴Among the small number of live births that we exclude, the majority were reared by a different mother, in a cross-fostering experiment.

and measures of social status measured during adulthood. Table 3 provides the summary statistics for the outcomes of interest (Elo ranking is a measure of social status discussed further below).

We consider three pregnancy outcomes: whether the pregnancy resulted in a birth, whether the offspring survived the first month of life, and the offspring’s birth-weight. Out of the 728 pregnancies, 700 (96.2%) resulted in a live birth. Also, out of the 700 births, 674 (96.3%) offspring survived the first month of life. Out of the 700 births, we only have birth-weight information on 474 births since birth-weight only started being collected in 2004.

Table 3: GENERATION 2 OUTCOMES

| | # Obs | Mean | Std. Dev. | Min | Max |
|---------------------|---------|---------|-----------|-------|-----|
| Live birth | 700/728 | 0.962 | 0.192 | 0 | 1 |
| Survived 1st month | 674/700 | 0.963 | 0.189 | 0 | 1 |
| Birthweight (g) | 474 | 491.902 | 78.230 | 278 | 820 |
| % in Good Health | 109 | 0.904 | 0.127 | 0.375 | 1 |
| Elo Percentile rank | 106 | 0.540 | 0.291 | 0.053 | 1 |

Notes: This table provides summary statistics for the generation 2 monkeys. Live birth and Survived 1st month were coded as 0 (no) and 1 (yes). We define these outcomes in detail in the text. Elo Percentile rank is a measure of social status capturing a macaque’s position in the social hierarchy.

We have access to health records from veterinary exams between 2003 and 2009. Veterinary exams occurred on a quarterly basis. We are interested in health outcomes after the end of the rearing experiment, at ten months, and before monkeys joined larger social groups, at age 3. This period corresponds to the period from late early childhood through early adolescence for humans. For that reason, in the analysis, we include all monkeys born between 2002 and 2006, for which we have complete health records for ages ten months to 3 years. Also, we restrict the analysis to monkeys where the monkey and its mother were mother-reared or nursery-reared. In total, we have health information on 121 monkeys.

Our outcome of interest is the proportion of veterinary exams in which the monkey was

in good health and did not exhibit a health problem. The most common health problems included diarrhea (not uncommon in captive primate colonies) and having a wound requiring treatment and monitoring (typically resulting from fights with other animals). Other, infrequent health issues included skin rash or dermatitis, periodic surgeries such as cesarean section or ovariectomy, spontaneous abortions, and vaginal or rectal prolapses. During the two-year period, monkeys experienced an average of 8.4 health visits from a veterinarian, ranging from 6 to 9. On average, the monkeys exhibited no health problems in 90% of the visits. Moreover, 54% of the monkeys did not exhibit a health problem in any of the visits in the two-year window.

Social status in Rhesus monkeys is often measured by position in the dominance hierarchy. Rhesus monkeys exhibit a rigid linear dominance hierarchy, in which the top-ranking monkey outranks the next-ranking monkeys, and so on down the line. In general, once formed, the dominance hierarchy remains stable. Methods for assessing dominance rank typically rely on observations of dyadic interactions in which wins and losses are recorded. For example, if monkey A successfully displaces, threatens, chases, or physically attacks another monkey without “losing” the interaction (i.e., showing submissive behaviors such as moving out of the way, fear-grimacing, screaming, or being wounded) every time against monkey B, then monkey A will outrank monkey B. Monkey B will only “lose” to monkey A, but not to monkey C, and so on.

Social status is often measured via Elo-ratings. These ratings were first developed to rank chess players in 1978 (Elo, 1978), and have since been adapted for use in animal hierarchies (Albers and Vries, 2001; Neumann et al., 2011; Wooddell et al., 2016, 2017b). Elo-ratings are calculated based on the expectation of winning an interaction. Points are given to the winner and loser after each interaction. More points are attributed to the interactions where the outcome was unexpected. For example a low-rating animal winning an interaction against a high-rating animal receives more points than a high-rating animal winning against a low-rating animal. This numerical system tracks rank changes over time by constantly updating

values according to wins and losses. We rely on Elo-ratings computed for adult female monkeys from >4,000 dominance interactions in 30-min observation sessions between 2013 and 2016, following previously established methods (Wooddell et al., 2016, 2017a; Wooddell, Kaburu, and Dettmer, 2019).

Our measure of interest is the within-cohort Elo-rating percentile rank. Dominance was measured seven times between 2013 and 2016. The age at measurement varied significantly from 21 months to 15 years of age. Elo-rating ranges from negative 100 (low ranked) to 2400 (high ranked). Our preferred measure is the within-cohort Elo-rating percentile rank, which ranges from 0.05 (lowest-ranked) to 1 (highest-ranked), and adjusts for differences in size between the different rearing groups (Dettmer et al., 2017; Wooddell et al., 2017a, 2019).

4 Empirical Results

We now examine the intergenerational effects of early life advantage, and complementarities between maternal and offspring rearing assignment. The experimental rearing assignment, including independence in treatment assignment across generations, makes identification of treatment effects straightforward. We report augmented-inverse probability weighting (AIPW) estimates of the various treatment effect parameters in the main body of the paper. The AIPW estimator is “doubly-robust.” It is consistent for the average treatment effect (ATE) if either the propensity score model or the outcome regression is properly specified (Robins, Rotnitzky, and Zhao, 1994; Lunceford and Davidian, 2004; Kang and Schafer, 2007; Cattaneo, 2010). We perform a variety of robustness exercises in Appendix A.

4.1 Effects of Maternal Rearing on Maternal Fertility

We first explore the effects of rearing assignment on fertility for generation 1 (mothers).⁵ Understanding the impact of maternal rearing on fertility is important, as selection into fertility may lead to selection bias into the outcomes of the second generation. We consider four outcomes constructed from birth and pregnancy records: whether the female monkey had ever been pregnant, the total number of pregnancies, the total number for those with at least one pregnancy, and the age at first birth. Table 4 reports the average treatment effect of the intervention on the fertility outcomes of generation 1.

Table 4: FERTILITY EFFECTS ON GENERATION 1 FEMALES

| Generation 1 Outcome: | Any Offspring? | Age at 1st Birth | # Pregnancies | # Preg. (> 0) |
|---------------------------------|------------------|---------------------|------------------|-------------------|
| $\Psi(s_{*,1}) - \Psi(s_{*,0})$ | 0.025 (0.052) | -0.332** (0.135) | 0.008 (0.300) | -0.209 (0.436) |
| Mean: | 0.469 | 5.530 | 1.984 | 4.229 |
| Obs. | 371 | 174 | 371 | 174 |

Notes: This table provides AIPW estimates for average treatment effects of generation 1 mother-rearing on fertility outcomes of generation 1 monkeys. The inference is under the null that the parameter of interest is zero. The notation is such that $\Psi(s_{*,j})$ describes the outcome under the j th rearing assignment of females in generation 1 irrespective of their mothers' rearing assignment. $j = 1$ if the monkey was assigned to the MR condition and zero otherwise. Standard errors are reported in parentheses. The * correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

We find no significant impacts of maternal rearing on the probability of ever being pregnant. Females assigned to the MR and NR conditions both have about a 50% probability of ever being pregnant. We also do not find any differences across the two rearing groups on the number of pregnancies, with females in both groups having, on average, two offspring. However, we do find significant differences in the age of the generation 1 female at first birth.

⁵Our data are not rich enough to allow us to analyze the impact of a father's rearing status. First, for a few offspring we don't know anything about the identity of the father. Second, for some offspring we know of two potential fathers, without knowing for sure which one it was. Third, for the fathers that we can identify, some did not participate in the experiment (they were brought in for mating but were not born in the colony). Finally, among the fathers that we identify and were part of the experiment, a few alpha macaques are often responsible for fathering many of the animals in our offspring generation. There was no explicit sorting strategy. Exploring the impact of assortative mating on child outcomes is a topic left for future research.

We find that MR females have the first offspring 0.332 years (or 4 months) earlier than NR females. The difference in fertility timing could be problematic when estimating the intergenerational effects. For this reason, we re-estimate our main parameters under different specifications in Appendix A. We find that our results are robust to different specifications, including when controlling for sample selection.

4.2 Intergenerational Effects of a Mother’s Rearing Assignment on Offspring’s Pre-Treatment Outcomes

Next, we estimate the intergenerational effects of the mother’s rearing condition on the offspring’s birth outcomes. This intergenerational effect could operate through the effect of the mother’s rearing assignment on the pre-birth (in-utero) investments received by the offspring (see Almond and Currie, 2011; Gluckman and Hanson, 2005), and the impact of these investments on offspring early outcomes. Alternatively, it could operate through some form of intergenerational epigenetic transmission (see Jablonka and Raz, 2009). We report the estimated intergenerational effects in Table 5.

Table 5: BIRTH OUTCOMES OF GENERATION 2 MONKEYS

| Generation 2 Outcome: | Live birth | Survived 1st month | Birthweight (g) |
|---------------------------------|------------------|--------------------|---------------------|
| $\Psi(s_{1,*}) - \Psi(s_{0,*})$ | 0.005 (0.015) | 0.029** (0.015) | -15.352 (10.850) |
| Outcome mean: | 0.962 | 0.963 | 491.902 |
| Generation 2 obs. | 728 | 700 | 474 |
| Generation 1 obs. | 174 | 171 | 140 |

Notes: This table provides AIPW estimates for average treatment effects of generation 1 mother-rearing on birth outcomes of generation 2 monkeys. The inference is under the null that the parameter of interest is zero. The notation is such that $\Psi(s_{i,*})$ describes the outcome of generation 2 monkeys with mothers assigned to the i th rearing condition irrespective of their own eventual assignment. $i = 1$ if the monkey’s mother was assigned to the MR condition and zero otherwise. Standard errors clustered at the mother level are reported in parenthesis. The stars correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

We find no intergenerational effects on the probability that a pregnancy ends in a live birth. Pregnancies of both MR and NR females have about a 3.8% chance of resulting in a

stillbirth. However, we find significant intergenerational effects of a mother’s MR assignment on the probability of offspring survival in the first month of life. The first-month survival for the offspring of MR mothers is 2.9 percentage points higher than that for the offspring of NR mothers. These findings are consistent with Zipple et al. (2019), which shows that maternal early life adversity is associated with offspring’s early mortality in wild baboons.⁶ At the same time, we find that offspring with MR mothers are born with about 15g lower birth-weight than offspring of NR mothers. Even though this effect is not statistically significant, the negative impact on birth-weight is interesting and could signal a mechanism for possible intergenerational transmission of resilience to adversity.

4.3 Intergenerational Effects of a Mother’s Rearing Assignment on Offspring’s Post-Treatment Outcomes

We explore the intergenerational effects of rearing conditions assigned to generation 1 mothers on outcomes for generation 2 offspring. The offspring outcomes studied here are measured *after* the offspring’s own treatment with alternative rearing conditions has concluded. Therefore, unlike the outcomes examined in the previous subsection, these offspring outcomes can be affected not only by the mother’s rearing condition but also by the offspring’s own rearing condition. The outcomes we analyze are health and social rank.

Health: We first discuss our estimates of the intergenerational effects of alternative rearing conditions in generation 1 mothers on the frequency with which the offspring is found to be in good health between 1 and 3 years of age. We report the estimated intergenerational effects in Table 6. We present intergenerational effects separately for offspring assigned to the nursery-reared $\Psi(s_{1,0}) - \Psi(s_{0,0})$ and mother-reared $\Psi(s_{1,1}) - \Psi(s_{0,1})$ conditions in rows 3 and 4 respectively. Note that $\Psi(s_{1,1}) - \Psi(s_{0,1})$ reveals the benefit of a sustained intervention

⁶The intergenerational effect on early mortality could potentially lead to selection bias in the other offspring outcomes. In the accompanying appendix (Appendix A), we estimate a version of the IPW estimator that accounts for sample selection to estimate the ATE among survivors. We find that controlling for sample selection bias does not substantially change our findings.

across generations whereas $\Psi(s_{1,0}) - \Psi(s_{0,0})$ reveals the intergenerational effect of intervention on disadvantaged (NR) offspring.

Table 6: LONG-TERM OUTCOMES OF GENERATION 2 MONKEYS

| Generation 2 Outcome: | % in Good Health (1-3y) | Elo Percentile Rank (2-15y) |
|---------------------------------|-------------------------|-----------------------------|
| $\Psi(s_{0,1}) - \Psi(s_{0,0})$ | -0.019 (0.034) | -0.109 (0.071) |
| $\Psi(s_{1,1}) - \Psi(s_{1,0})$ | 0.078** (0.033) | 0.134** (0.066) |
| $\Psi(s_{1,0}) - \Psi(s_{0,0})$ | -0.030 (0.031) | -0.075 (0.068) |
| $\Psi(s_{1,1}) - \Psi(s_{0,1})$ | 0.067** (0.034) | 0.168** (0.079) |
| $\Psi(s_{1,0}) - \Psi(s_{0,1})$ | -0.011 (0.040) | 0.034 (0.076) |
| Outcome mean: | 0.904 | 0.540 |
| Generation 2 obs. | 109 | 106 |
| Generation 1 obs. | 59 | 68 |

Notes: This table reports AIPW estimates of the different treatment effects of maternal vs. nursery rearing on long-term outcomes of Generation 2 monkeys. The inference is under the null that the parameter of interest is zero. The notation is such that $\Psi(s_{i,j})$ describes the outcome of generation 2 monkeys when assigned to the j th rearing condition and with mothers assigned to the i th rearing condition. $i = 1$ ($j = 1$) if the monkey (monkey's mother) was assigned to the MR condition and zero otherwise. Standard errors clustered at the mother level are reported in parenthesis. The stars correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

We find a positive and statistically significant intergenerational effect on the frequency of time in good health. However, this significant intergenerational effect is only present for offspring that were assigned to be reared with their mother (row 4). Indeed, for MR offspring, having a mother who was MR instead of NR increases the frequency of time in good health between ages 1 and 3 years by 6.7 percentage points.

In addition to intergenerational effects, we also explore the effects of alternative con-

figurations of mother-offspring multi-generational assignment. In particular, we estimate the effects of the offspring’s rearing condition on the offspring’s own health, while keeping constant the mother’s rearing condition. We do this separately for offspring with NR $\Psi(s_{0,1}) - \Psi(s_{0,0})$ and MR $\Psi(s_{1,1}) - \Psi(s_{1,0})$ mothers. The estimates are presented in rows 1 and 2. We find strong, statistically significant positive effects of offspring’s assignment to maternal rearing on own health outcomes, but only for those whose mothers were also maternally-reared (row 2).

We also report estimates of the effects of changing the dynastic timing of advantage and disadvantage, $\Psi(s_{1,0}) - \Psi(s_{0,1})$. We do this by comparing offspring outcomes in families assigned to mother advantage followed by offspring disadvantage $\Psi(s_{1,0})$ with offspring outcomes in families that, conversely, were assigned to mother disadvantage followed by offspring advantage $\Psi(s_{0,1})$. Note that $\Psi(s_{1,0}) - \Psi(s_{0,1}) = \Psi(s_{1,0}) - \Psi(s_{0,0}) - [\Psi(s_{0,1}) - \Psi(s_{0,0})]$ informs us about the relative benefits of investing in the parent of a disadvantage child compared to investing in the child itself.⁷ There is no statistically significant difference (see row 5).

Social Status: We find similar patterns when we explore the intergenerational effects of mother’s early-life advantage on offspring social dominance. We report the estimated effects in the second column of Table 6 for the within-cohort Elo percentile rank. We find a positive and significant intergenerational effect on the percentile rank measure for MR offspring. Among MR offspring, having a mother who was MR, instead of NR, increases the offspring’s percentile rank measure of social status by 0.168 points (row 4)

Similarly to our findings for health outcomes, we find strong, significant effects of offspring’s own rearing condition on offspring’s social status only for offspring whose mothers were also maternally-reared (row 2). Our estimates in row 5 indicate no statistically significant effects from permutating advantaged/disadvantaged rearing conditions within mother-offspring pairs.

⁷Note that this parameter is equivalent to the difference in the parameters estimated in rows 3 and 1. This is not equivalent to the concept of intergenerational complementarity which we discuss in the section, and that involves a comparison between the parameters estimated in rows 3 and 4.

It has recently become feasible to document intergenerational effects like $\Psi(s_{1,*}) - \Psi(s_{0,*})$, measuring the impact of parental treatment in early childhood on offspring life outcomes. The advantage of our research design stems from its ability to estimate, in addition, the intergenerational complementarity $\Psi(s_{1,1}) - \Psi(s_{0,1}) - [\Psi(s_{1,0}) - \Psi(s_{0,0})]$ and to unpack the different mechanisms of intergenerational influence. We turn to this next.

4.4 Intergenerational Complementarity

The difference in intergenerational effects provides an estimate of the intergenerational complementarity of early life advantage (maternal rearing). Therefore, rejecting the null of zero differences would indicate a statistically significant intergenerational complementarity. Recall that $\Psi(s_{1,0}) - \Psi(s_{0,0})$ denotes the intergenerational effect of mother’s rearing assignment on NR offspring whereas $\Psi(s_{1,1}) - \Psi(s_{0,1})$ denotes the intergenerational effect of mother’s rearing assignment on MR offspring. The difference between these two intergenerational effects $[\Psi(s_{1,1}) - \Psi(s_{0,1})] - [\Psi(s_{1,0}) - \Psi(s_{0,0})]$ identifies the intergenerational complementarity (supermodularity) of the treatment. It describes how the effectiveness of the offspring intervention depends on parental exposure to the intervention.

Table 7 reports point estimates and statistical inference for the intergenerational complementarity in our two post-treatment outcomes. We document a strong and significant intergenerational complementarity of early life advantage for both health and social rank outcomes. This represents the first evidence of intergenerational complementarities of early life advantage. The estimates imply that the effect of maternal *advantage* is more beneficial for offspring who themselves experienced early life *advantage*.

In Table 7, we report that the intergenerational complementarity effect on the frequency in good health is 0.097. That means that the difference in the intergenerational effect of the mother’s MR assignment on MR vs. NR offspring outcomes is $0.067 - (-0.030) = 0.097$. Similarly, we find that the intergenerational complementarity for the percentile rank is 0.244, meaning that the mother’s MR assignment increases the relative social rank for MR offspring

Table 7: INTERGENERATIONAL COMPLEMENTARITY

| Generation 2 Outcome: | % in Good Health (1-3y) | Elo Percentile Rank (2-15y) |
|---|-------------------------|-----------------------------|
| $[\Psi(s_{1,1}) - \Psi(s_{0,1})] - [\Psi(s_{1,0}) - \Psi(s_{0,0})]$ | 0.097** (0.047) | 0.244** (0.103) |
| Generation 2 obs. | 109 | 106 |
| Generation 1 obs. | 59 | 68 |

Notes: This table reports AIPW estimates of the intergenerational complementarity of maternal vs. nursery rearing on long-term outcomes of Generation 2 monkeys. The inference is under the null that the difference in the intergenerational effects is zero. The notation is such that $\Psi(s_{i,j})$ describes the outcome of generation 2 monkeys when assigned to the j th rearing condition and with mothers assigned to the i th rearing condition. $i = 1$ ($j = 1$) if the monkey (monkey’s mother) were to be assigned to the MR condition and zero otherwise. Standard errors clustered at the mother level are reported in parenthesis. The stars correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

by 0.244 points more than for the NR offspring (0.168 vs. -0.075).

4.5 Mechanisms of Intergenerational Transmission

The positive intergenerational effects of a mother’s advantageous rearing condition on her offspring outcomes may arise through two possible mechanisms. One mechanism operates through the effect of the mother’s rearing assignment on offspring pre-treatment outcomes (e.g., via in-utero effects) coupled with the effect of these induced changes in early outcomes on later outcomes through the self-productivity of early skills. A second mechanism operates via parenting, whereby the mother’s rearing assignment influences maternal parenting skills, which in turn impact the offspring outcomes via improved parental investments after birth.

As it turns out, the *difference* in intergenerational effects across NR and MR offspring groups can also inform about the relative importance of alternative mechanisms of intergenerational transmission. Our findings in Section 4.3 suggest that parenting is the primary mechanism of intergenerational transmission, as the intergenerational effects we find are only significant for MR offspring. However, to formally assess whether parenting is the key intergenerational pathway, we must test whether the difference in these two intergenerational effects is statistically significant. This is precisely what the tests in Section 4.4 accomplish.

Given that the complementarities are positive and significant, we interpret the intergenerational effects as driven mainly by MR mothers having superior skills and the fact that these skills can be more easily transmitted to their offspring via maternal-offspring interactions after birth, which are only possible for MR monkeys. This interpretation is in line with results in Sproul Bassett et al. (2020), which shows that nursery-reared mothers exhibit higher rates of premature infant rejection than maternal-reared mothers.

Since NR monkeys do not interact with their mothers after birth, any intergenerational effect on their outcomes has to operate only via pre-birth factors. Similarly, any evidence of positive intergenerational effects that is present for MR monkeys but not for NR monkeys has to be attributed to parenting effects, since parenting effects are only possible for MR monkeys, and in-utero effects should be present for both. Therefore, we conclude that improved parenting is the principal channel through which early life advantage in the parent's generation is transmitted to the next generation.

5 Discussion and Conclusion

This paper uses three decades of studies with Rhesus monkeys conducted at the Laboratory of Comparative Ethology (LCE) at NIH to investigate the magnitude and mechanisms of the intergenerational effects of early life advantage in the form of maternal rearing relative to a more disadvantaged rearing condition.

Using the data collected at LCE, we document positive intergenerational effects of a mother's early life advantage on her offspring outcomes. We find the positive intergenerational effects start very early on and persist until adulthood. Moreover, early life maternal presence (or separation) influences different dimensions of offspring development, including health and social outcomes. In short, we find that the offspring of females that experienced early life advantage via maternal presence are more likely to survive in the first month of life than offspring of females reared apart from their mothers. Moreover, the offspring of females

that experience early life advantage are less likely to suffer from health problems between ages 1 and 3 years and more likely to achieve a high social rank in adulthood.

Our findings are in line with results from a social experiment on humans. Heckman and Karapakula (2019) document the intergenerational effects of the Perry Preschool Project, which was a randomized social experiment in the 1960s that provided high-quality preschool experiences to socially disadvantaged children. They find that the positive effects of the preschool program were transmitted into the next generation. The offspring of the treated participants were more likely to have better health, achieve higher education, and were more likely to be employed than the offspring of the non-treated participants. In the same way that early-life advantage via maternal presence for rhesus-monkeys led to improved health and higher social rank for their offspring, early-life advantage via high-quality preschool in humans led to better health and social outcomes for their children.

The particular feature of the LCE study also allows us to cleanly identify the mechanisms through which early-life conditions are transmitted across generations by controlling for each generation's environments and treatment status. We find strong evidence that parenting is the main channel of intergenerational transmission. This follows from the finding that the positive effects of maternal early-life advantage are only present for MR offspring. The insignificant intergenerational effect on NR offspring is evidence that in-utero investments cannot explain the intergenerational effects. This finding, combined with the large intergenerational effects for the MR offspring, is indicative that parenting is the main channel of intergenerational transmission of advantage. These results are also in line with the Perry study. Heckman and Karapakula (2019) provide evidence that the intergenerational effects of the preschool program were mainly driven by an improvement in the family environment experienced by the children of the Perry participants. This evidence is also in line with studies of extreme deprivation in humans, such as the study on Romanian orphans after the fall of the Ceaucescu regime.⁸ The studies of the Romanian orphans demonstrate the

⁸It is important to mention that while the findings are related, the treatment in the LCE study is not

importance of early life interactions and social attachment for the development of cognitive and social skills and a variety of health outcomes (see Rutter, 1998; O'Connor et al., 2000; Cunha et al., 2006).⁹

The repeated randomization of early rearing conditions across generations in the LCE study allows us – for the first time – to experimentally estimate the intergenerational complementarity of an intervention. We document strong and statistically significant intergenerational complementarities of early life advantage on health and social status. The estimated complementarities highlight the importance of sustained intervention for monkeys' health and social status. Future work should explore, perhaps using more feasible non-experimental approaches, whether the complementarities we document in Rhesus monkeys are also present in similar interventions in humans.

NHPs have been utilized for decades to understand child development within a generation. This paper demonstrates that they can also be used to study the intergenerational effects of early life advantage. Monkeys and humans share many common features: they share with us approximately 93% of the same DNA, demonstrate attachment behaviors, and have hierarchical social structures. Monkeys are similar enough in biology and social structure to be informative about human development. Studies with NHPs present several advantages that make them essential complements to human studies. We have shown that NHP studies provide a way to cleanly identify mechanisms in a way that is not possible in human studies and to identify parameters never previously estimated.

equivalent or comparable to what happened with the Romanian orphans. NR monkeys were not extremely deprived and had constant contact with human caregivers in their first month of life, and daily contact with peers during the rest of their developmental period.

⁹In the future, as the Romanian children complete their fertility, it will also be possible to study the intergenerational effects of extreme deprivation in humans. However, even then it will not be possible to estimate intergenerational complementarities because the children of the Romanian orphans are unlikely to be exposed to extreme deprivations like those of their parents.

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Online Appendix

“New Title”

Amanda M. Dettmer, James J. Heckman, Juan Pantano, Victor Ronda, and Stephen J. Suomi.

Appendix A Additional Specifications

In the main text, we report intergenerational treatment effects estimated by augmented inverse probability weighting (AIPW) estimates. In this section, we test for the robustness of our results under different assumptions. We focus on two main issues. One concern is selection into treatment. This shouldn't be a significant issue in our study since the researchers at the lab had complete control over the treatment assignment. Differently than human studies, the monkeys could not select out of the assignment treatment. However, we know that researchers were more likely to assign first-born monkeys to the maternal-rearing condition. It is also possible for the treatment assignment to change over the years. A second concern is that of sample selection. We do not observe the outcomes of every monkey in the study. For example, we only observe the health outcomes for 109 out of the 656 offspring in our sample. Often, the reason for the missing outcomes is that the outcome was only collected for a subset of the cohorts or during a restricted period. For example, we only have access to veterinarian health records from 2002 to 2009, limiting the sample with observable health outcomes. While this is not a cause for concern, it is also possible for the treatment assignment to influence the sample selection. For example, we find that the offspring of maternal-reared females were more likely to survive the first month of life than offspring of nursery-reared females.

For these reasons, we check for the validity of the results presented in Section 4. We re-estimate the parameters in Table 6 under four alternative specifications. We present these in Tables A1-A2. In column (1), we present unconditional mean estimates by comparing the outcomes between monkeys assigned to two different rearing sequences. This approach exploits the random assignment to the rearing sequences to compute the treatment effects of interest but does not account for selection into treatment or sample selection. In column (2), we present conditional mean estimates, where we control for sex, birth order, and cohort effects in the outcome regression. In column (3), we present inverse probability weighting (IPW) estimates, where we control for sex, birth order, and cohort effects in the propensity score model. In column (4), we present augmented inverse probability weighting (AIPW) estimates, where we control for sex, birth order, and cohort effects in the outcome regression and the propensity score model. The AIPW combines the advantages of the IPW and

conditional mean estimates. The AIPW estimator had the advantage of being ‘doubly-robust,’ and it is consistent for the ATE if either the propensity score model or the outcome regression is properly specified. We report the AIPW estimates in the main paper. These latter three methods account for the presence of selection into treatment. To account for the possibility of sample selection, in column (5), we estimate a modified version of the IPW estimator proposed by Huber (2014). The approach weights the observations by the inverse of a nested propensity score that characterizes both the selection probability into the treatment and the observable sample. This approach accounts for both the fertility selection and mortality selection discussed in Sections 4.1 and 4.2.

We do not find any systematic differences in the estimates across the five models. Parameter estimates across the five models are not statistically different from each other. These results are reassuring. The results provide evidence that the estimates presented in Section 4 are not driven by either selection into treatment or sample selection.

Table A1: ALTERNATIVE SPECIFICATIONS: % IN GOOD HEALTH

| Generation 2 Outcome: Specification | % in Good Health | | | | |
|--|---------------------|--------------------|---------------------|--------------------|--------------------|
| | (1) | (2) | (3) | (4) | (5) |
| $\Psi(s_{0,1}) - \Psi(s_{0,0})$ | -0.019 (0.033) | 0.007 (0.034) | -0.009 (0.031) | -0.019 (0.034) | -0.009 (0.029) |
| $\Psi(s_{1,1}) - \Psi(s_{1,0})$ | 0.122*** (0.039) | 0.102** (0.040) | 0.100*** (0.037) | 0.078** (0.033) | 0.099** (0.039) |
| $\Psi(s_{1,0}) - \Psi(s_{0,0})$ | -0.088** (0.041) | -0.034 (0.037) | -0.054 (0.040) | -0.030 (0.031) | -0.053 (0.042) |
| $\Psi(s_{1,1}) - \Psi(s_{0,1})$ | 0.053* (0.029) | 0.061* (0.034) | 0.055* (0.029) | 0.067** (0.034) | 0.054* (0.028) |
| $\Psi(s_{1,0}) - \Psi(s_{0,1})$ | -0.068 (0.044) | -0.041 (0.043) | -0.045 (0.042) | -0.011 (0.040) | -0.044 (0.043) |
| Outcome mean: | 0.904 | 0.904 | 0.904 | 0.904 | 0.904 |
| Generation 2 obs. | 109 | 109 | 109 | 109 | 109 |
| Generation 1 obs. | 59 | 59 | 59 | 59 | 59 |

Notes: This table compares the treatment effects estimates for the probability of being in good health under different specifications. Column (1) presents unconditional mean estimates. Column (2) presents conditional mean estimates, where we control for the offspring's sex, primiparous status and birth cohort, and maternal primiparous status and birth cohort. Column (3) presents IPW estimates, where we allow the offspring sex and maternal or offspring year of birth trends and primiparous status to influence the propensity score for intergenerational and intragenerational models, respectively. Column (4) AIPW estimates, where we control for the offspring's sex, primiparous status, and birth cohort in the regression model in addition to the propensity score controls. Model (5) presents IPW estimates that control for sample selection. We report the AIPW estimates in the main paper. In model (5), we allow for the probability of having the outcome observed to influence the propensity score, in addition to the other controls. The inference is under the null that the parameter of interest is zero. Standard errors clustered at the mother level are reported in parenthesis. The stars correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.

Table A2: ALTERNATIVE SPECIFICATIONS: ELO PERCENTILE RANK

| Generation 2 Outcome: Specification | Elo Percentile Rank | | | | |
|--|---------------------|-------------------|--------------------|--------------------|---------------------|
| | (1) | (2) | (3) | (4) | (5) |
| $\Psi(s_{0,1}) - \Psi(s_{0,0})$ | 0.008 (0.093) | -0.101 (0.074) | -0.127* (0.070) | -0.109 (0.071) | -0.155** (0.066) |
| $\Psi(s_{1,1}) - \Psi(s_{1,0})$ | 0.216*** (0.076) | 0.142* (0.077) | 0.135* (0.074) | 0.134** (0.066) | 0.142* (0.079) |
| $\Psi(s_{1,0}) - \Psi(s_{0,0})$ | -0.062 (0.074) | -0.077 (0.071) | -0.067 (0.069) | -0.075 (0.068) | -0.075 (0.066) |
| $\Psi(s_{1,1}) - \Psi(s_{0,1})$ | 0.147 (0.090) | 0.167* (0.087) | 0.196** (0.078) | 0.168** (0.079) | 0.222*** (0.077) |
| $\Psi(s_{1,0}) - \Psi(s_{0,1})$ | -0.069 (0.083) | 0.025 (0.080) | 0.060 (0.079) | 0.034 (0.076) | 0.080 (0.075) |
| Outcome mean: | 0.540 | 0.540 | 0.540 | 0.540 | 0.540 |
| Generation 2 obs. | 106 | 106 | 106 | 106 | 106 |
| Generation 1 obs. | 68 | 68 | 68 | 68 | 68 |

Notes: This table compares the treatment effects estimates for the within-cohort percentile social-rank under different specifications. Column (1) presents unconditional mean estimates. Column (2) presents conditional mean estimates, where we control for the offspring's sex, primiparous status and birth cohort, and maternal primiparous status and birth cohort. Column (3) presents IPW estimates, where we allow the offspring sex and maternal or offspring year of birth trends and primiparous status to influence the propensity score for intergenerational and intragenerational models, respectively. Column (4) AIPW estimates, where we control for the offspring's sex, primiparous status, and birth cohort in the regression model in addition to the propensity score controls. Model (5) presents IPW estimates that control for sample selection. We report the AIPW estimates in the main paper. In model (5), we allow for the probability of having the outcome observed to influence the propensity score, in addition to the other controls. The inference is under the null that the parameter of interest is zero. Standard errors clustered at the mother level are reported in parenthesis. The stars correspond to the following p-value levels: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$.