Received: 1 November 2020 | Revised: 18 May 2021 | Accepted: 20 May 2021

DOI: 10.1002/dev.22148

RESEARCH ARTICLE

Developmental Psychobiology WILEY

Are fathers a good substitute for mothers? Paternal care and growth rates in Shodagor children

K. E. Starkweather[1,2,3] | M. H. Keith[4] | S. P. Prall[5] | N. Alam[6] | F. Zohora[6] | M. Emery Thompson[2]

[1] Department of Anthropology, University of Illinois Chicago, Chicago, Illinois

[2] Department of Anthropology, University of New Mexico, Albuquerque, New Mexico

[3] Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[4] Department of Anthropology, University of Washington, Seattle, Washington

[5] Department of Anthropology, University of Missouri, Columbia, Missouri

[6] Health Systems and Population Studies Division, ICDDR,B, Dhaka, Bangladesh

Correspondence
K. E. Starkweather, Department of Anthropology, University of Illinois Chicago, Chicago, IL 60607.
Email: kstark20@uic.edu

Abstract

Biparental care is a hallmark of human social organization, though paternal investment varies between and within societies. The facultative nature of paternal care in humans suggests males should invest when their care improves child survival and/or quality, though testing this prediction can be challenging because of the difficulties of empirically isolating paternal effects from those of other caregivers. Additionally, the broader context in which care is provided, vis-à-vis care from mothers and others, may lead to different child outcomes. Here, we examine the effects of paternal care on child growth among Shodagor fisher-traders, where fathers provide high levels of both additive and substitutive care, relative to mothers. We modeled seasonal *z*-scores and velocities for height, weight, and body mass index (BMI) outcomes using linear mixed models. Our evidence indicates that, as predicted, the context of paternal care is an important predictor of child outcomes. Results show that environmental seasonality and alloparental help contribute to a nuanced understanding of the impact of Shodagor paternal care on child physiology.

KEYWORDS
child growth, evolution, fathers, parental investment

1 | INTRODUCTION

Human fathers provide high levels of investment in their children, compared to most other mammalian fathers (Clutton-Brock, 1991; Kleiman & Malcolm, 1981; Lukas & Clutton-Brock, 2013). Parental investment theory predicts that this should benefit men's reproductive fitness (Clutton-Brock, 1991; Trivers, 1972), and yet, decades of research have produced mixed results on the effects of fathers on child outcomes across cultures (e.g., Blurton Hurtado & Hill, 1992; Jones et al., 1996; Leonetti et al., 2004; Sear & Mace, 2008; Sear et al., 2000; Winking et al., 2011). One reason for this may be the flexible nature of paternal care. Cross-cultural evidence shows that fathers titrate their investment based on proximate, socioecological circumstances (Harkness & Super, 1992; Helfrecht et al., 2020; Marlowe, 2000; Meehan, 2005; Prall & Scelza, 2020; Scelza, 2010; Winking et al., 2009), and that the amount and type (direct vs. indirect) of investment is variable across populations and between individuals (Gray & Anderson, 2010; Hewlett, 1992; Marlowe, 2000), all of which is likely to lead to variability in fitness outcomes. We also expect the conditions under which care is provided, vis-à-vis care provided by mothers and others, to influence how that care impacts children. That is, paternal care that is additive (that which does not reduce maternal investment) should impact a father's fitness differently than substitutive care (that which reduces maternal investment) (Hatchwell, 1999; Heinsohn, 2004; Kushnik, 2012). Here, we compare the effects of additive and substitutive direct paternal care (e.g., feeding, holding, bathing, watching) on child growth velocity, a sensitive measure of reproductive fitness, among Shodagor fisher-traders in Bangladesh. As Shodagor fathers regularly provide very high amounts of direct care, and small nuclear families limit the alternatives for intensive alloparental care, our data allow us to isolate the effects of fathers from those of mothers and others and contribute to an evolutionary understanding of the importance of fathers.

1.1 | Theory and background

Parental investment in offspring is, by definition, a costly behavior (Trivers, 1972), and parents should only pay the costs of investment when they are outweighed by the fitness benefits of doing so, such as when parental investment increases the likelihood of offspring survival and reproduction. In mammals, some investment by mothers is obligate for the survival of offspring. For fathers, the cost/benefit equation is more complicated; when their investment is not necessary for offspring survival, males can achieve greater fitness gains by investing in future mating opportunities (Clutton-Brock, 1991; Dunbar, 1976; Perrone & Zaret, 1979; Thornhill, 1976; Westneat & Sherman, 1993; but see Kerhoas et al., 2016; Ménard et al., 2001; Winking & Koster, 2015 for an argument that male care is one form of mating effort). Clutton-Brock (1991) suggests that is why most mammalian fathers do not invest in offspring following conception: in the vast majority of mammals, mothers can care for and provision young on their own and male contributions to care do not improve offspring survival enough to offset costs to a male's mating success (but see Lukas & Clutton-Brock, 2013). Critically, in those mammalian species in which fathers do regularly invest, investment is positively associated with offspring survival (Clutton-Brock, 1991; Krebs & Davies, 1993; Westneat & Sherman, 1993).

Biparental investment is a hallmark feature of human social organization, which is thought to be critical for raising large-brained, costly infants (Lancaster & Lancaster, 1983), and compared to most other mammals, human fathers' cooperation with mothers to care for young results in relatively high levels of investment (Bribiescas et al., 2012; Fernandez-Duque et al., 2009; Gettler et al., 2020; Kramer, 2010). Such widespread paternal investment is expected to correspond with clear fitness benefits for fathers, but decades of research have yielded mixed results (e.g., Blurton Jones et al., 1996; Hurtado & Hill, 1992; Leonetti et al., 2004; Sear et al., 2000; Sear & Mace, 2008; Winking et al., 2011; Winking & Koster, 2015), and the evolutionary origins of human fatherhood remain under debate.

Paternal effects may be difficult to demonstrate in part because fathers are often embedded within extensive networks of caregivers, where contributions from one individual are difficult to isolate (Helfrecht et al., 2020; Hrdy, 2009; Meehan, 2005; Page et al., 2021). Fathers should be attentive to the needs of mothers and young, and also to the type and amount of care being provided by other available helpers, and adjust their investment accordingly (Kramer, 2010). Such adjustments may account for the great deal of cross-cultural variability in expressions of paternal investment (Gray & Anderson, 2010; Hewlett, 1992; Marlowe, 2000). Additionally, care provided under different conditions, such as when fathers supplement or replace investment by mothers, may impact paternal fitness through different pathways.

1.1.1 | Additive care

One way for fathers to improve their own reproductive fitness through parental investment is by improving the likelihood of the survival and reproduction of their young. While this pathway has received the most attention in the literature, it is not always supported by the data (Sear & Mace, 2008; Winking, 2006). This may be at least partially attributable to the broad measures often used to operationalize paternal investment and child outcomes. Men's familial investments are often measured dichotomously (presence/absence) (Blurton Jones et al., 1996; Borgerhoff Mulder, 2005; Hurtado & Hill, 1992; Leonetti et al., 2004; Sear et al., 2000; Sear & Mace, 2008; Winking et al., 2011), and child survival and static measures of body size (height, weight) are the most commonly measured outcomes in the evolutionary literature (Blurton Jones et al., 1996; Borgerhoff Mulder, 2005; Hames et al., 2005; Hurtado & Hill, 1992; Leonetti et al., 2004; Sear et al., 2000; Sear & Mace, 2008; Winking et al., 2011). These studies have been informative of the fact that paternal care is not obligate in all human societies, but broad measures may be obfuscating more subtle, though still important, fitness effects of fathering. However, even when studies have examined more specific measures of investment, focusing on amount or quality of care provided, results are mixed across cultures (Alvergne et al., 2009; Boyette et al., 2018; Boyette et al., 2019a; Boyette et al., 2019b; Winking & Koster, 2015), and the mechanisms that should lead direct paternal care to enhance child well-being are not always clear.

One potential pathway for fathers' direct care to result in positive fitness outcomes is by providing additive care. When care is given in addition to mothers' and does not result in reduction of maternal care, any net effects of allomaternal care on young should be positive (Kushnik, 2012). This type of care has also been discussed as "constant breeder input" (Moehlman & Hofer, 1997), whereby a mother's allocation to direct care is insensitive to the presence of helpers, and young receive a total amount of care that is higher than they would receive from mother alone (Carranza et al., 2008). Such an effect has been shown in white-fronted bee-eaters, in which parents maintain the same provisioning effort regardless of the number of helpers, and total nestling provisioning rate is positively correlated with the number of helpers (Emlen & Were, 1991), and in silver-backed jackals, whereby a greater number of alloparental helpers was positively associated with number of surviving pups (Moehlman, 1979), as well as in other bird species (Emlen, 1991; Koenig & Mumme, 1990; Mumme, 1992).

In humans, additive direct care has been demonstrated in a number of contexts. For example, Karo Batak mothers increased the amount of time they spent holding their children (avg. 2.5 years) in the presence of matrilineal helpers (Kushnick, 2012), and in a contemporary Chinese cohort, the availability of maternal grandparents as helpers was not associated with differential levels of maternal caregiving (Chen et al., 2000). Across a number of societies, the presence of alloparents has a positive effect on child survival and other measures of fitness, including growth (Fox et al., 2010; Sorenson-Jamison et al., 2002; Sear et al., 2000; Sear & Mace, 2008; Voland & Beise, 2002).

The additive effects of direct paternal care have rarely been demonstrated in humans. For example, Page et al. (2021) show that contemporary Palanan Agta fathers' direct care increases the amount of time mothers spend caring for children up to 6 years old. Griffin and Griffin (1992) describe similar trends in paternal care among Cagayan Agta families, and there is no evidence that this care improves offspring survival or reproductive quality in either context. Perhaps the best example of fathers providing additive care comes from Hewlett's (1992) descriptions of Aka fathers' carrying of infants. Hewlett refers to this as "cooperative care" between mothers and fathers, in which both parents work together to care for children simultaneously. Alvergne et al. (2009) showed that increased reports of paternal investment were positively associated with child nutritional status for children between 2 and 7 years old, and similar results were found among Bondongo fisher-farmers in the Congo Basin for children up to 18 years of age (Boyette et al., 2018; Boyette et al., 2019a), though the contexts under which care was given, relative to care from others, were not specified in these studies.

Additive paternal care may also serve different functions from the mother. This can include complementing the mother's direct care with indirect care (e.g., providing resources), or providing resources that offer complementary macronutrients (Gurven et al., 2009). In Aché families, fathers provide very little direct care for children, but are responsible for the vast majority of daily calories a family consumes and play a critical role in protecting older children from dangerous situations (Hill & Hurtado, 1996). Through both types of investment, Aché father's presence increases the likelihood of child survival. Additive care can also include providing different forms of direct care, such as playing with a child or teaching knowledge or skills. For example, Yanomami fathers engage in more play and athletic activities with their children than do mothers (Eibl-Eibsfeldt, 1989). Although fathers in some Western settings play less with children than mothers do (Yeung et al., 2001), their specific style of play is different and has been linked to social outcomes for children in Canada (Flanders et al., 2010) and Germany (Grossmann et al., 2002). Similarly, fathers in some US families use more challenging language with children than mothers do (Leech et al., 2013), which may lead to improved academic and social outcomes (Varghese & Wachen, 2016). Regardless, when fathers do provide additive forms of direct care, this care should have effects that are similar to those demonstrated among other allomothers: children should experience a "net gain" and additive investments should lead to better fitness outcomes (Emmott & Page, 2019).

1.1.2 | Substitutive care

A second pathway for fathers' direct care to improve their fitness is by substituting for mothers' care. This kind of care, which is often called "load-lightening" (Brown et al., 1978; Heinsohn, 2004), is given in place of maternal care. It "frees up" mothers' time and energy that would have been spent on caring for a specific child, and allows them to invest that energy elsewhere. For example, among Agta families in the Philippines, Page et al. (2021) show that direct care from grandmothers reduces the amount of time mothers spend caring for the same child, and across three small-scale, sub-Saharan populations, more diverse networks of alloparents are consistently associated with decreases in frequency of maternal care (Helfrecht et al., 2020). In Maya and Pume families, every 10% increase in direct alloparental care was associated with a 25% decrease in the probability of maternal care (Kramer & Veile, 2018).

If substitutive care results in mothers re-investing "saved" energy into reproductive effort, reproductive success is improved via enhanced fertility. When rates of extra-pair paternity are low and paternity confidence is high (i.e., conditions that are predicted to lead to more paternal investment), fathers' fertility also benefits from mothers receiving substitutive care (Winking & Koster, 2015). While there are many cross-cultural examples of alloparental care improving maternal fertility (e.g., Kramer, 2005; Lee & Kramer, 2002; Page et al., 2017; Rotering & Bras, 2015; Sear et al., 2003; Turke, 1988), in one of the only studies of this effect for fathers, paternal care among Mayangna/Miskito horticulturalists of Nicaragua does not significantly increase couple fertility (Winking & Koster, 2015).

Mothers do not necessarily invest saved time and energy in fertility, though. In many contexts, when allomothers reduce mothers' childcare burden, mothers engage in economic activities that are not compatible with childcare. In many subsistence-based societies, infants accompany mothers while they work; however, even traditional subsistence activities like foraging, horticultural work, and subsistence agriculture are not always easily carried out while caring for toddlers and young children (e.g., Hames, 1988, 1992; Hill & Hurtado, 1996; Ivey, 2000; Levine, 1988; Meehan, 2009), and mothers need help in order to work efficiently. Fathers' care can also "lighten the load" for mothers and free them up to engage in subsistence activities. For example, Hiwi men frequently hold infants and carefully monitor older children while women work (Hurtado & Hill, 1992), and in one study, were coded as primary caretakers of children for 30% of women's foraging events (Hurtado et al., 1992). In Ifugao in the Philippines, fathers care for young children during the day while mothers work as traders (Milgram, 2011). Hadza fathers also provide substitutive care. Marlowe (2010) reported that men often watch toddlers who are left in camp while women are foraging, which "allows women to forage unencumbered by toddlers" (p. 206).

Unlike additive care, substitutive care is not necessarily expected to improve child outcomes, relative to mothers' care, because the total amount of care children receive remains the same (Kushnik, 2012). In the example above of Maya and Pume families, direct alloparental care was not associated with increased child weight measures (Kramer & Veile, 2018). In fact, if quality of care provided by a helper is lower than the quality provided by mother, receiving substitutive investments from fathers or others could lead to poorer child outcomes (e.g., Nelson, 2016). Several studies have shown no effect of paternal presence/absence on either the likelihood of child survival or child growth (Borgerhoff Mulder, 2005; Blurton Jones et al., 1996; Hames et al., 2005; Sear et al., 2000; Sear & Mace, 2008; Winking et al., 2011), and a more detailed study of direct paternal care among BaYaka forager families similarly showed no effect on child energetic condition (Boyette et al., 2019b). However, once again, the contexts under which care was provided are unclear, and thus, these noneffects cannot be confidently attributed to substitutive care. Evidence from Hiwi foraging families seems to suggest this relationship, though: despite Hiwi fathers being the primary caregiver of children 30% of the time while mothers worked, there was no effect of fathers' presence on child survival (Hurtado & Hill, 1992). In general, we expect that when fathers provide substitutive care, the care itself should not increase measures of child fitness (though additional resources provided by mothers might have this effect).

1.1.3 | Caregiver impacts on child growth

Quality of caregiving can act through a variety of different pathways to influence child health and well-being. Many of these inputs have the potential to influence growth, which is a sensitive, integrated marker of developmental stress. Large body size has adaptive advantages in many mammals (Brien, 1986; Brown et al., 1993), as does reaching maturity sooner (Johnson, 2003). While the relationship between human stature and fitness varies in complex ways across cultures, studies often find lower reproductive success for people with short stature; for men, stature influences wealth and mating prospects, while for women, it influences children's health and mortality (Courtiol et al., 2013; Pollet &Nettle, 2008; Sear et al., 2004; Sear, 2006; Sear, 2010; Stulp & Barrett, 2016). Beyond the direct effects of growth on fitness, impaired growth is also the most visible indicator of a myriad of other developmental compromises that can affect survival and fertility (Fernald & Grantham-McGregor, 2002; Lummaa & Clutton-Brock, 2002). For women, early onset of menarche can also have reproductive advantages in some environments (Apter & Vihko, 1983; Borgerhoff Mulder, 1989). Thus, investment in somatic growth is a key life history priority that must balance these benefits against resource constraints and competing priorities, such as investment in immune function. Accordingly, while growth has a strong genetic component, both adult stature and body weight covary reliably with indices of development and welfare (e.g., life expectancy) across populations and over time (Walker et al., 2006; Stulp & Barrett, 2016).

In addition to growth in stature, maintenance of body fat stores plays a critical role in child health as a buffer against nutritional instability and a larder for brain growth and immune defense (Kuzawa, 1998; Urlacher et al., 2018). While many populations face health risks from obesity, children in small-scale and developing populations often face greater risks from becoming underweight. Even mild to moderate malnutrition (60%–80% of the median weight-for-age) is associated with significantly increased risk of mortality in children (Pelletier et al., 1993; Pelletier et al., 1995; Schroeder & Brown, 1994).

The most obvious way that caregiving can impact growth is via nutrition. This includes the overall effects of energy intake on the budget available for increasing body mass, but also facets of nutritional quality. Deficiencies in nutrients such as zinc, iron, and calcium are linked to growth stunting, as well as collateral effects on cognition and immune function (Cole & Lifshitz, 2008; Ozmen et al., 2013). For example, compared to children raised by both parents, motherless (but not fatherless) Chinese children experienced growth faltering attributable to reduced intake of animal protein (Wang et al., 2016). Diets that are high energy but nutrient deficient, often the easiest to provide under caregiving constraints, can also yield a "dual burden" of nutrient-related chronic disease and obesity (Uauy et al., 2008).

Caregiving can also impact exposure to pathogens via hygiene practices, access to clean food and water, play environments, and access to medical treatments (Bliss et al., 2016; Bornstein et al., 2015; George et al., 2015; Langford et al., 2011; Nti & Lartey, 2008; Rah et al., 2015; Wodnik et al., 2018). Growth is highly sensitive to tradeoffs with the immune system (Garcia et al., 2020; Solomons et al., 1993; Weisz et al., 2011), with impairments detectable even during subclinical infection (Urlacher et al., 2018). Alternatives to maternal caregiving may specifically constrain access to breastmilk, increasing rates of diarrhea (Creek et al., 2010; Mølbak et al., 1997). Diarrhea not only contributes directly to growth faltering (Assis et al., 2005) but can trigger a cycle of infection, whereby the resulting malnutrition puts children at future risk of diarrhea and pneumonia (Moore et al., 2010; Schlaudecker et al., 2011; Victora et al., 1990).

Psychological stress associated with rearing environments is also a potent inhibitor of growth (Blizzard & Bulatovic, 1992). For example, impairments in attachment and caregiving related to maternal depression can affect growth and child feeding behavior (Rahman et al., 2004; Robertson et al., 2011; Stewart, 2007; Surkan et al., 2012), as can high rates of family conflict (Montgomery et al., 1997). Orphans often experience severe growth faltering while in institutional care (Dobrova-Krol et al., 2008; Johnson et al., 1992; Van IJzendoorn et al., 2007), but so do those cared for by relatives (Lindblade et al., 2003) and children in single-parent households (Bronte-Tinkew & DeJong, 2004; Cole & Cole, 1992). While the psychological effects of caregiving are difficult to disentangle from direct nutritional and health effects, inadequate caregiving may compound these effects (Pelto, 2000; Stansbury et al., 2000).

1.2 | Study population

Shodagor communities in Matlab, Bangladesh are traditionally semi-nomadic, boat-dwelling fishers and traders who are culturally distinct from the majority ethnicity in the country. Matlab, the mostly rural subdistrict where this research was conducted, is home to approximately 500 Shodagor families as well as 230,000 people who are majority Muslim, minority Hindu and primarily work as agriculturalists, wage laborers, and housewives, and who do not identify with the Shodagor ethnicity (ICDDRB, 2018). Branches of the Meghna River make up the northern and southern borders of the region, which is also bisected by a second large river, as well as its streams and canals. At the time of data collection in 2017, this river was home to around 150 Shodagor families who are the primary focus of this study. These families resided on small, wooden houseboats, clustered within five distinct groups along the rivers and canals, or had moved onto the land within the previous 10 years and lived in make-shift houses on the riverbanks.

Shodagor fisher-traders engage in a mixed subsistence and cash economy: people who catch fish sell their catch to middlemen in the markets in exchange for cash, and traders sell their goods for cash. However, 89% of Shodagor families also engaged in subsistence fishing. Most men (90%) work as fishermen for the majority of the year, and some also work as day-laborers (11%) or do other types of work (2%), with 18% of men reporting more than one occupation. More than half (52%) of Shodagor women work as traders, selling household goods (e.g., pots, pans, melamine products) door-to-door in villages during the dry season. The other half of women fish (45%) with their husbands for all or part of the year, and only a few women are primarily housewives who do not earn an income (3%). Households are primarily organized around the nuclear family, with most homes being too small to accommodate extended family members. The majority of childcare is done by members of the nuclear family, resources acquired by both men and women are pooled at the household level, and no systematic, community-wide norms of sharing daily-acquired resources exist within the society.

1.2.1 | Shodagor child growth

While child malnutrition and mortality in Bangladesh have fallen dramatically over the past 20 years, as of 2017 approximately 31% of children under 5 years of age were considered stunted, falling more than 2 standard deviations below the WHO standards for height-for-age, and 22% were wasted, falling more than 2 standard deviations below the standards for weight-for-age (National Institute of Population Research & Training, 2019). In Matlab, Bangladesh, where this study was conducted, children from the non-Shodagor, majority groups who are primarily engaged in agriculture and wage labor, show similar trends: between 2000 and 2012, 31% of children under 5 were stunted, and 26% were wasted, according to WHO standards (Das et al., 2015). For Shodagor children, data from 2014 report that 43% fell more than 2 standard deviations below the WHO standards in height-for-age, 23% in weight-for-age, and 21% in BMI-for-age (Starkweather & Keith, 2018). This could indicate that Shodagor children are particularly vulnerable to malnutrition. However, international growth standards, largely derived from urban populations and designed to reflect the growth of children under nonlimiting conditions, may not be appropriate for assessing growth in non-Western or subsistence-based societies (Blackwell et al., 2017; Guedes et al., 2010; Hasan et al., 2001; Hakeem et al., 2004; Mushtaq et al., 2012; Neyzi et al., 2006; Urlacher et al., 2016). Using growth standards specific to the Shodagor, only 4% of Shodagor children fell more than 2 standard deviations below the mean in height-for-age, 2% in weight-for-age, and 2% in BMI-for-age (Starkweather & Keith, 2018). Data from 2014 also show that environmental variation, which includes socioecological variables associated with the nuclear family, accounts for the majority of group-level variation in body size relative to genetic effects, so we expect caregivers to have an important impact on child growth.

1.2.2 | Shodagor paternal care

Male investment in children is an important aspect of Shodagor culture. While the majority of childcare is provided by members of the nuclear family, uncles provide direct and indirect care to nieces and nephews (Starkweather & Keith, 2019), grandfathers have close, affectionate relationships with their grandchildren, and older brothers regularly help care for younger siblings. The majority (99%) of marriages for Matlab Shodagor families are monogamous, rates of extra-pair paternity are expected to be low, and paternity confidence high (see Starkweather & Keith, 2019, p. 3 for a full explanation), all important predictors of paternal care (Lukas & Clutton-Brock, 2013; Møller & Birkhead, 1993; Queller, 1997; Trivers, 1972). It is not surprising, then, that Shodagor fathers report close, affectionate relationships with their children, as is common in other parts of Asia (Hewlett & MacFarlan, 2010), and provide resources for their families, investing indirectly in children throughout their lives. What makes Shodagor paternal investment unusual across cultures, though, is that most Shodagor fathers also provide very high levels of direct care and spend a great deal of time in close proximity with their young children. One likely reason for high levels of paternal care in this group is that ecological conditions that are somewhat unique to Shodagor families (i.e., living in households surrounded by water) present a high risk of drowning and necessitate vigilant caregiving for young children by responsible caregivers (discussed in more detail in Starkweather, 2017; Starkweather et al., 2020). For these reasons, we focus here on the importance of direct paternal care.

While type (direct vs. indirect) and amount of care vary throughout a father's life, depending on the ages of his children, the conditions under which care is provided relative to mothers' care (additive vs. substitutive) are closely related to household divisions of labor, which differ based on local ecological conditions, child age and breastfeeding status, and maternal occupation (Starkweather, 2017; Starkweather et al., 2020). We focus here on the two most common ways that Shodagor families divide labor and refer to them as *fishing families*, in which fathers provide *additive care*, and *trading families*, in which fathers provide *substitutive care* (Table 1). Demographic characteristics of families in fishing and trading households can be found in Table 2.

Additive paternal care in fishing families. In around half of Shodagor families in Matlab, men and women work together on their fishing boats during both seasons, accompanied by children of all ages. Most of these families live near the Meghna River—one of the three largest rivers in Bangladesh—where fishing is profitable year-round (Starkweather, 2017). On the fishing boat, both parents are engaged in roles that are critical for fishing success. Shodagor primarily fish using a hook-and-line method, which requires one adult on the boat to row and steer, while the other lays down the line across the river and later

TABLE 1 Shodagor household divisions of labor by season

	Rainy season	Dry season
Fishing families	Mother and father fish and care for children together	Mother and father fish and care for children together.
Trading families	Father fishes with other men Mother cares for children	Mother trades Father cares for children

TABLE 2 Household demographic information for households in which the primary caregiver is mother, father, or both, children are between the ages of 2–19, and for which there are no missing model data

	Fishing ($n = 29$)	Trading ($n = 29$)
No. of children	1.86 (1, 4)	1.69 (1, 4)
Children's age	7.24 (2.50, 16.00)	8.58 (2.50, 18.50)
Father's age	37.81 (20.50, 70.50)	38.99 (24.00, 64.50)
Mother's age	30.48 (17.50, 54.00)	31.24 (18.00, 54.50)
Household income (taka)	9551 (1200, 24583)	11964 (1911, 55500)
Father's education (years)	0 (0, 0)	0.23 (0, 5)
Mother's education (years)	0.15 (0, 2)	0.35 (0, 4)
Children's education (years)	0.12 (0, 6)	0.72 (0, 7)

pulls the lineup, removing fish from hooks as quickly and efficiently as possible. After pulling up the line, men and women are responsible for cleaning hooks and sorting the catch. Infants often lay on mothers' laps throughout this process, and can breastfeed while doing so. Fathers report holding and caring for infants during downtime on the boat. Once children are old enough to sit independently, they are often placed near the middle of the fishing boat, within reach of both parents, and parents report that whoever is closer to the child will attend to them as necessary. As children age, they continue to accompany parents on the fishing boat and are eventually given fishing tasks of their own. Children in fishing families are much less likely to attend school than their counterparts in trading households, and therefore, spend the majority of their days throughout childhood on the fishing boat in close proximity to both parents.

Given the near-constant, very close proximity to children, we do not expect mothers to reduce the amount of direct care they provide to children, and thus, paternal care in these families is additive. Additive care should have a significant, positive impact on child outcomes, so we predict that greater amounts of additive paternal care in fishing families will be positively associated with growth rates in children (Hypothesis 1).

Substitutive paternal care in trading families. In the other half of Shodagor families in the Matlab study population, parents change parenting and subsistence strategies seasonally: during the rainy season (April–September), men fish and women stay home to care for children; during the dry season (October–March), women work as traders and men stay home to care for young children (Table 1). These changes occur in response to seasonal, environmental changes (Starkweather, 2017; Starkweather et al., 2020). Most of these families live far from the Meghna River, which means that fishing is only a reliably profitable activity during the rainy season, when water levels rise. Monsoon rains and Himalayan snow melt result in regular flooding during the rainy season, covering large portions of land in Matlab with water, submerging auxiliary roads and walkways, making travel challenging for all who live in the area. During this time, men work with other men in the community, catching fish to eat and to sell for cash in a local marketplace. Trading families also live close to local markets, which opens up a niche for Shodagor women to work as traders (Starkweather et al., 2020). During the dry season, when water levels recede and travel is easier, women in these households resume their work as traders. Trading is an occupation that is totally incompatible with childcare; women leave home early in the morning, travel to remote villages in Matlab, carrying large baskets of trade goods on their heads, and often return after dark. In families with young children, fathers stay home during the dry season and care for children.

Shodagor fathers in these families provide substitutive direct care for their young children for around 6 months every year while mothers work as traders. During this time, fathers are the primary adult responsible for providing all types of direct care, including feeding, bathing, soothing, and play, and as children age, for supervising their safety and wellbeing. Fathers in all families are also responsible for teaching children to swim and fish. Fathers usually begin caring for children around age 2, after they are mostly weaned and mothers can return to work. Prior to this, fathers are usually the only person providing resources for the family and often work year-round. The most intensive period of caregiving by fathers occurs between the ages of 2 and 5, around when they are typically considered proficient swimmers (i.e., the risk of drowning has decreased significantly) and old enough to be left alone without a specified caregiver. Despite this, children are not expected to become primary caregivers (without an adult present) for younger siblings until at least age 10. So, depending on birth spacing, fathers will regularly be providing intensive care for a younger child, while an older sibling is also present. Fathers are not expected to watch children over 5 as closely and these children will frequently play with friends or engage in other activities outside of the view of home. However, fathers are still the adult primarily responsible for older children's safety and well-being, making sure they have food to eat during the day, and taking them to see a doctor when they are sick. Additionally, while some Shodagor children attend school, they usually only do so for a few hours per day. They start attending no sooner than age 5 and may only attend for a few years. Very few children in the Shodagor community attend school beyond age 10. Depending on an individual family's composition, including birth spacing and their decisions about sending older children to school, this can result in a minimum of 8 years in which the father is providing the majority of his children's care for half of the year, while mothers provide the majority of care during the other half.

Substitutive care provided by fathers is, itself, not expected to show a significant impact on child outcomes, relative to mothers' care. While lower quality substitutive care could have a negative impact, after children are weaned (as is the case with the sample used in this paper), there is no a priori reason to expect Shodagor fathers to provide low quality care. Therefore, we predict that child growth rates will not differ significantly between seasons when father is the primary caregiver and seasons when mother is the primary caregiver, controlling for household income (Hypothesis 2a) and that there should be no relationship between the amount of substitutive care a father provides and child growth (Hypothesis 2b). Additionally, given that we expect fathers' additive care to have a positive impact on child growth rates in fishing families, and fathers' substitutive care to show no effect on growth velocity in trading families, we also predict that children in fishing families will experience faster growth velocities (Hypothesis 3a) and have larger body sizes, overall, than children in trading families (based on static measures of height, weight, and BMI) (Hypothesis 3b).

2 | METHODS

2.1 | Data collection

Interview and anthropometric data were collected between 2014 and 2019 with all available members of Shodagor families in Matlab who live on boats or have recently moved onto the land. Demographic data (age, gender, household membership, mother's primary occupation) were collected and updated between 2014 and 2019. Longitudinal data on income, caretakers, and anthropometrics used in this manuscript were collected over 28 months between April 2017 and July 2019. Missing data are due to individuals being absent during a particular season, children being born after data collection began in 2017, an individual's death, or declining to participate. This study includes descriptive data from 209 children, between the ages of 0–18, from 119 households. In order to model the impacts of paternal care on growth velocity, models utilize data from a smaller sample of 103 children (47% female) between ages 2 and 18 years, from 58 households, for whom there were no missing data and at least two consecutive seasons of anthropometric measurements, and for whom primary caregiver (50% or more of care in a given season) was mother, father, or both parents together. Children under the age of 2 were excluded from models in order to help isolate the impact of fathers' care on children; most mothers in care-switching households do not work as traders during the first 2 years while breastfeeding children, and including data from these children would obfuscate any effect of fathers. All data were collected in accordance with procedures approved by the University of Missouri's Institutional Review Board, the International Centre for Diarrhoeal Disease Research, Bangladesh's (ICDDR,B) Research and Ethical Review Committees, and the Max Planck Institute for Evolutionary Anthropology's Department of Human Behavior, Ecology, and Culture.

2.1.1 | Anthropometrics

Anthropometric data were collected from all available children in the population (as well as adults, who are not included in this analysis) at the end of each rainy season (September and early October) and at the end of each dry season (March and early April) from 2017 to 2019, resulting in a possible maximum of 6 measurements for each individual. The 103 children included in the sample for this analysis had an average of 5.6 measurements each during this time span. Weights to the nearest 0.1 kg were collected using an electronic scale on a firm, flat surface. Heights to the nearest 0.1 cm were measured using a Seca stadiometer. All measurement procedures followed standard techniques (Lohman et al., 1988).

2.1.2 | Income and father care variables

Income and caretaker data were collected via interview up to 4 times per month, every month between April 2017 and July 2019, for every individual in the population who was working at the time of data collection. Each person reported up to 3 days of income per interview, and indicated how they earned the income (fishing, trading, fixed salaried position, other), resulting in a potential maximum of 12 days of income per person, per month. Total profit per person was calculated by subtracting any money that was given to others (e.g., a middleman, a fishing partner) from the total amount earned that day. Average monthly income was calculated for each household for one month at the peak of each of three rainy seasons (2017–2019) and two dry seasons (2018–2019) by calculating an average daily income for each occupation, summing across all household members, and multiplying the household by 20 days, which is 5 days of work per week, and a relatively conservative estimate for most households. A dummy variable for *occupation* was created from these data. A family was coded as a *trading* household if a mother indicated her primary occupation was trading (this coding reflects the household pattern of care for most years, but variation in life course means that women don't work as traders every year, particularly for the 2 years after giving birth, thus our data includes some mothers in trading families who provide 100% of the childcare during some seasons). Families in which fishing was the primary occupation for mother and father were coded as *fishing* households.

After reporting on their earnings, every adult with at least one unmarried child who was under the age of 18 at the time of data collection was asked who cared for their children while they worked that day. If only one parent worked on a given day, he or she reported who cared for children, and answers were cross-checked with spouses when possible. Typically, when parents worked together, they were interviewed together, too. Due to this data collection method, all caregiving variables reflect parents' reports of who they charged with caring for their children and/or who they may have learned later helped with childcare. We think these data probably accurately reflect who provided the majority of care, especially for young children and in fishing families in which children were with their parents all day, but is likely to miss smaller amounts of care provided throughout the day. These data also only represent the care provided to children during the portion of the day while parents worked and neither reflects care given on days when neither parent worked, nor care given outside of working hours (i.e., in the mornings, evenings, and overnight). Respondents could name more than one person, could indicate that there was no specified caregiver for their children, or could indicate if they took their children with them to work.

From these data, three caregiving variables were created. For the first and second, a percent value was calculated for each category of caregiver (mother alone, father alone, both parents, grandmother, siblings, other caregivers, and none), dividing the number of times in each season that each caregiver was named by the total number of times any caregiver was named. This resulted in a variable for each season of data collection that reflects the amount of care that each category was responsible for, relative to others. Percentages of care given by each category of caregiver were used to create two different care variables. (1) *Primary caregiver* is defined as the individual(s) responsible for providing the majority of care for a child and maintaining his or her well-being during each season, and were coded as such (e.g., *father primary, mother primary, both primary*) if their care accounted for the majority of care given in each season, based on the calculated percentages. This variable reflects who children are receiving the majority of care from in a given season, and based on this, children from households in which mother, father, or both were the primary caregivers during a given season were retained in the sample. (2) The *care type* variable reflects whether the father was listed as sole caregiver for his children on at least 1 day during a given season and separates households in which father provided additive care from those in which father was the main provider of substitutive care.

These data were also used to create a third care variable, which we call *father care proportion*. This variable provides a probability estimate of the amount of care each father provided for his children during each season. In the data, the number of days of care reported varied widely by household and season. For example, some households had moved out of the study area for the majority of one season and, therefore, only a few days' worth of data were collected for that household during that season, while other households were contacted once per week and reported 3 days of income per week for 6 months. To account for this variation, predictions (and estimates of variance) for the proportion of care by household and season were generated using a Bernoulli model. This model included varying intercepts by season for each household to predict the probability of care by fathers on any given day. Using this model, we extracted posterior predictions, and estimates of variance, of father caregiving by household independently for each season. These predictions were then used in the Father Care Models described below. This method allowed us to better account for the variance in measurements by household and season and provide a more accurate estimate of the amount of care each father provided for his children.

2.2 | Analysis

We modeled seasonal *z*-scores and velocities for height, weight, and body mass index (BMI) outcomes using linear mixed models (LMMs). Our sample excludes data from breastfeeding infants and is limited to children between the ages of 2–18 years ($n = 103$). Given our aims to assess specific impacts of paternal care, this sample only includes data for children who received the majority of care from their mother, father, or both mother and father jointly in a given season, excluding data from children for whom other (e.g., grandmother, sibling) caregivers provided the majority of care, or who did not receive care from anyone (see Tables S1 and S2 for sample descriptions).

Height and weight data were cleaned using the sitar package in R v.4.0.0 to remove implausible outliers if velocity in a person's growth curve exceeded ±3 standard deviations from the median (Cole, 2020; R Core Team, 2020). We fit Lambda-Mu-Sigma (LMS) curves with the gamlss package to create population-specific *z*-scores for height, weight, and BMI across age (Rigby & Stasinopoulos, 2005). LMS curves were fit separately for males and females, and resulting *z*-scores account for both age and sex. We calculated velocities from height, weight, and BMI *z*-scores for these seasonal data by taking differences between consecutive measurements. For example, a velocity of 0.0 indicates that a child follows exactly the mean growth curve for their age and sex, while a velocity of 1.0 indicates an increase of one standard deviation relative to the standard since the previous season's measurement.

LMMs allowed us to control for repeated measures and common household environments while modeling specific predictors of growth velocity and *z*-score outcomes in these longitudinal data. All models included each *individual's ID* and *household ID* as random effects (Table 3). All models also included *household income* as a seasonal measure of household resources and a dummy variable for the type of *season* (1 = dry, 0 = rainy). Our first set of models evaluated the cumulative effects of household caregiving strategies on child height, weight, and BMI *z*-scores. In order to test Hypothesis 3b, these Cumulative Growth Models included the dummy variable for *occupation* as a predictor. This variable does not itself change each season, but indicates the household strategy for dividing labor and type of paternal care (corresponding to trading and fishing households; Table 1).

The subsequent three sets of models used three different measures of parental care to evaluate the season-specific relationship between growth velocity and caregiving. The Seasonal Growth Models included the same *occupation* dummy variable as the Cumulative Growth Model and an interaction term between *occupation* and *season* (rainy or dry) to predict height, weight, and BMI velocities and test Hypothesis 3a. The Father Care Models evaluated the impact of the father's relative contributions to care, alone or in addition to the mother, in order to test Hypothesis 1. The key predictors in this set of models were *father care proportion* and *care type*. Proportions of direct paternal care are estimates from the Bernoulli model predictions (see above), and we included the standard deviations around posterior mean care probabilities in these models to account for uncertainty. A father who provided 50% of care could have been equally coparenting with the mother on each day, or he could have been the sole caregiver on 50% of days. To distinguish these two possibilities, and the contrasting predictions we had about additive versus substitutive care, and test Hypothesis 2, we included an interaction between *father care proportion* and *care type*. To further examine this relationship, we constructed a set of Substitutive Care Models using a subset of the sample that excluded data when mothers and fathers provided joint primary care. This limited the downsample to children who received the majority of primary care (on work days) from either their mother alone or father alone in a given season ($n = 64$, 55% female). The Substitutive Care Models featured a

TABLE 3 Fixed effect predictors and random effects in each model set

Models	N	Outcomes	Fixed	Random
Null *z*-score	103	*z*-scores	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
Cumulative growth	103	*z*-scores	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
			Occupation (1 = trading, 0 = fishing)	
Null velocity	103	velocities	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
Seasonal growth	103	velocities	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
			Occupation (1 = trading, 0 = fishing)	
			Trading × Dry	
Father care	103	velocities	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
			Father care proportion	
			Care type (1 = substitutive, 0 = additive)	
			Substitutive × Father care proportion	
Null downsample	64	velocities	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
Substitutive care	64	velocities	Income (log)	ID
			Season (1 = dry, 0 = rainy)	Household
			Father primary (1 = yes, 0 = no)	

dummy variable indicating the type of *primary caregiver* for the season (1 = father, 0 = mother) (Table 3).

We used the brms package in *R* to fit models with Bayesian inference via Stan (Bürkner, 2017; Stan, 2021). We used weakly informative priors for all models which included a half Cauchy prior for random effects with a scale parameter of 1, a normal intercept prior with a mean of 0 and standard deviation of 0.5, and a normal prior for fixed effects with a mean of 0 and standard deviation of 1. We ran 4 chains for each model for 20,000 iterations with a warmup of 10,000, and all effective sample sizes exceeded 2000 parameter estimates from the posteriors. Visual trace plot inspections indicated sufficient chain mixing, and all Gelman–Rubin convergence statistics were approximately 1.00.

We also used each model's posterior predictive distribution to generate predicted height, weight, and BMI outcomes. We report marginal R^2 values that estimate the amount of variation in each outcome variable explained by only the fixed effect predictors in each model, as well as conditional R^2 values that indicate variation explained by the combined fixed and random effects of each model (Nakagawa & Schielzeth, 2013). We also report Watanabe–Akaike information criterion (WAIC) to compare penalized model fit with added parameters. Variance component ratios for individual IDs and household IDs indicate the amount of variation in outcomes explained by repeated measures and common household environments, respectively. Code and data for all models are available on GitHub (https://github.com/mhkeith/Shodagor-Paternal-Care.git).

3 | RESULTS

3.1 | Descriptive results

In this sample, limited to children for whom mother, father, or both were the primary caregivers (*N* = 103 children, 58 households), 80% of Shodagor children received direct paternal care during at least one season, and fathers were sole primary caregivers (i.e., without mothers, providing substitutive care) during at least one season for 31% of children. In trading households, fathers were named as caregivers on 45.2% of days during the dry season, with some fathers providing the majority of care on 98% of days. Mothers' care makes up 71.8% of the total care budget during the rainy season and 39.6% of care during the dry season; fathers' care shows the opposite pattern, trading-off seasonally with mothers'. Other caretakers account for 12.2% of care during the dry season and 8.6% of care during the rainy season, while parents report children have no specified caregiver for 3% and 7.4% of days during the dry and rainy seasons, respectively. Nonparental care conditions account for much more care in trading households than they do in fishing households. In fishing households, mothers provide the majority of childcare during both seasons and fathers provide care on an average 41.2% of days. Maternal and paternal values reflect the fact that, most of the time, mothers and fathers are providing care simultaneously, and occasionally, fathers opt to fish alone or with other men, especially during a short postpartum period for mothers. All other

TABLE 4 Proportion of time each category of caregiver was named during each season in trading and fishing households, for all Shodagor households in the sample used for this study ($N = 58$)

	Trading		Fishing	
Caregiver	**Dry**	**Rainy**	**Dry**	**Rainy**
Mothers	39.6%	71.8%	55.1%	57.5%
Fathers	45.2%	12.3%	41.8%	40.6%
Grandmothers	3.7%	1.2%	0.5%	0%
Siblings	8.5%	5.7%	2.4%	1.6%
None	3.0%	7.4%	0%	0.3%
Others	0%	1.7%	0%	0%

categories of caregivers account for 2.9% and 1.9% of care in the dry and rainy seasons, respectively, in fishing households (Table 4).

In the larger sample of households in the study ($N = 209$ children, 119 households), with at least one unmarried child between the ages of 0–18 years, and including all types of primary caregivers, seasonal patterns are similar (Figure S1, Table S5). Mothers in trading and fishing households account for the majority of care given to children, and fathers are the second most common type of caregiver in all cases except for trading families during the rainy season. In households that do not switch caregivers seasonally, parents provide 89.9% and 90.2% of the childcare during the dry and rainy seasons, respectively, and grandmothers are the third most common caregiver. Children in trading households receive much more care from alloparents, with siblings providing more care than grandmothers or others. In both samples, children in trading households are much more likely to have no specified caregiver than children in fishing households, but in the larger sample, children of traders have no caregiver 20.9% of the time during the rainy season and 20% of the time during the dry season. Only children over the age of 5 are ever left with no specified caregiver.

3.2 | Model results

3.2.1 | Cumulative Growth Models

Cumulative Growth Models include a dummy variable for household occupation that assesses variation in cumulative body size (*z*-scores) between children in trading and fishing households. Contrary to our prediction (H3b), this model set indicates that height, weight, and BMI *z*-scores are positively associated with trading, independent of income differences between households (Figure 1a, Table S3). Counterfactual plots of posterior predictions show that 90% intervals overlap substantially for predicted height, weight, and BMI between children in trading and fishing families, but weight and BMI are predicted to be more than 0.50 *z*-scores larger on average for children in trading families for whom care switches seasonally between parents (Figure 1b).

Height *z*-scores show a very small positive association with dry seasons, and income does not appear to have a consistent effect on these growth metrics (Figure 1a, Table S3). Variance components (Table S4) indicate that height and weight are more repeatable (0.83 and 0.75) within individual growth curves than BMI (0.57), and random-level household effects are greater for BMI (0.50) than for height and weight (0.38 and 0.39) (Table S4, rows 4–6).

Marginal R^2 estimates show that income, the type of season, and occupation explain approximately 9% of observed *z*-score variation for weight and BMI, and less than 3% for height (Table S4, column 4). Watanabe–Akaike information criterion (WAIC) indicate little improvement in model fit with the addition of the occupation variable in the Cumulative Growth Models (Table S4, column 3) compared to the null *z*-score models with only income and season fixed effects, but marginal R^2 values show that the variable has explanatory value (Table S4).

Across the remaining models with velocity outcomes, marginal R^2 values indicate that socioecological and care predictors explain between 1% and 8% of growth velocity variances (Table S4, row 4). Velocities are less repeatable across individual growth trajectories than the *z*-scores used to assess cumulative growth, and random-level household effects are estimated to explain between 3% and 7% of height, weight, and BMI variation across all velocity models (Table S4, columns 6–7).

3.2.2 | Seasonal Growth Models

Seasonal Growth Models include an interaction term between season (dry or rainy) and occupation (trading or fishing) variables to assess their effects on seasonal child growth velocities. For fishing households, which feature a consistent caregiving strategy across seasons and additive paternal care, coefficients from this model set show that height, weight, and BMI velocities are higher during dry seasons versus rainy seasons (Figure 2a, Table S3, row 14). Children in trading households show higher BMI velocities during rainy seasons when mothers were caring and fathers were fishing, and weight and BMI velocities show a negative association with trading during dry seasons, when fathers provided substitutive care (Figure 2, Table S3, row 16). This results in an inverse pattern of change in BMI velocity. While children in fishing households have BMI velocities an average of 0.24 *z*-scores higher during dry seasons than during rainy seasons (Figure 2b), children who experienced a seasonal switch of caregiver in trading households had BMI velocities an average of 0.21 *z*-scores higher during the rainy seasons than the dry seasons, although 90% predicted BMI intervals overlap to a large extent.

3.2.3 | Father Care Models

The Father Care Models feature an interaction term between the estimated proportion of care children received from their fathers and the type of fathers' care (substitutive or additive). Results show that height velocity increases with increasing proportion of direct father care, but only during seasons when fathers provided additive care to mothers (Figure 3a, Table S3, row 22). During seasons when fathers

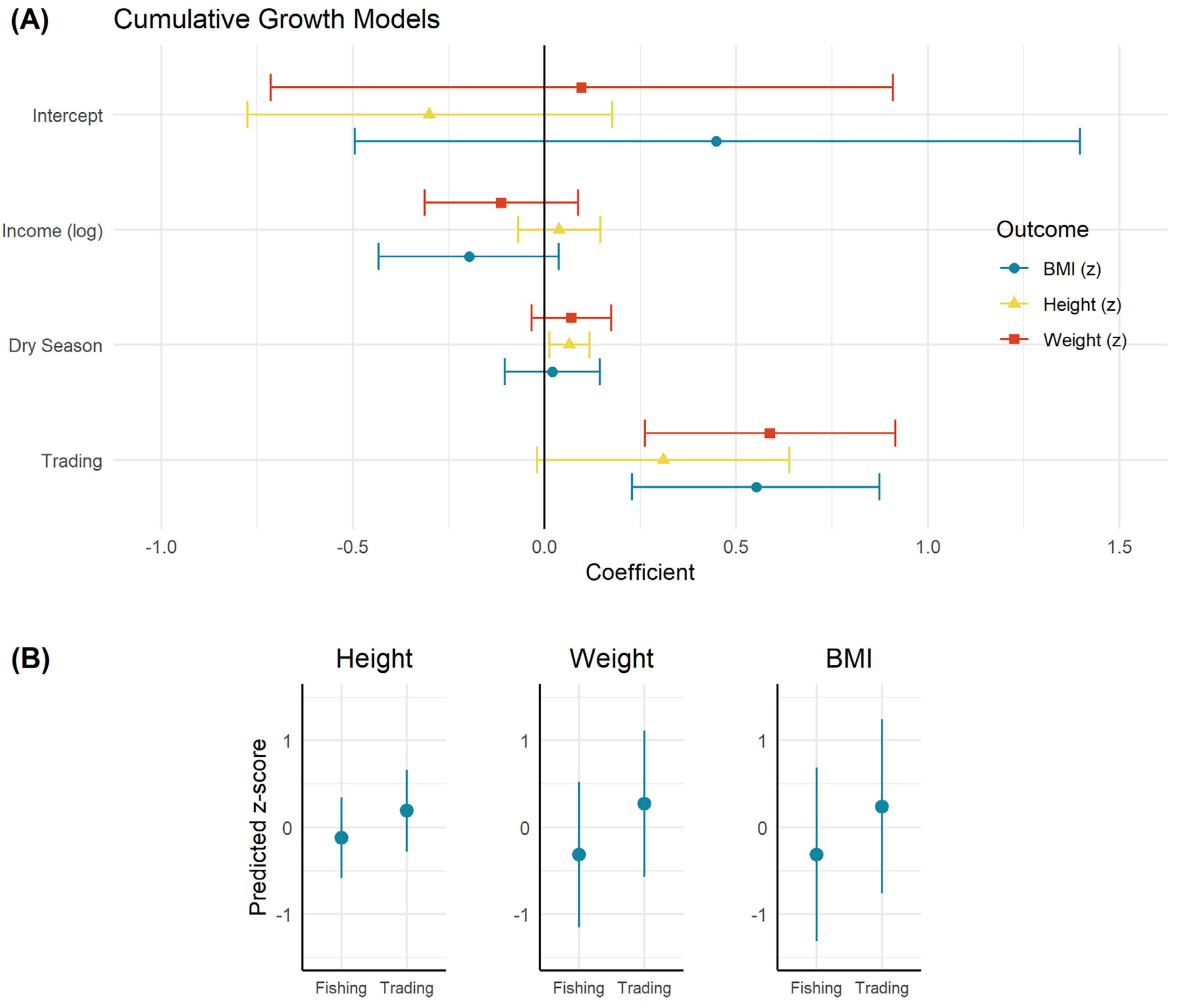

FIGURE 1 (a) Posterior means and 90% credible intervals for fixed effect coefficients in the Cumulative Growth Models ($n = 103$). (b) Posterior anthropometric means and 90% intervals predicted from the Cumulative Growth Models

provided substitutive care (when a higher percentage of paternal care indicates less care from mothers and alloparents), increasing proportion of father's care then shows negative associations with children's weight and BMI velocity, and height velocity shows a mostly negative trend (Figure 3). BMI and weight velocities are predicted to decrease by more than 0.75 *z*-scores for children as the proportion of father's substitutive care increases (Figure 3b). Height velocities are less affected relative to weight and BMI, but higher proportions of father's additive care show a small positive height trend.

3.2.4 | Substitutive Care Models

Given the frequency of coparenting, the above models largely tell us about the impact of having one caregiver versus two. In order to evaluate the impact of fathers as substitutes for mothers, we examined a downsample of children who received seasonal primary care from their mother or father, but not both ($n = 64$, 70% in trading households). The Substitutive Care Models show that posterior BMI velocities are, on average, 0.35 *z*-scores lower when fathers were the primary caregivers compared to when mothers were the primary caregivers, although 90% intervals are largely overlapping (Figure 4b). This difference in BMI resulted primarily from effects on child weight velocity, which was lower by an average of 0.23 *z*-scores when fathers were primary caregivers compared with mothers. While height velocity was not associated with caregiver identity, it was affected by income, which had a small positive effect (Figure 4a, Table S3, rows 27–29).

4 | DISCUSSION

Previously, Starkweather and colleagues (Starkweather, 2017; Starkweather et al., 2020) showed that local socioecological conditions influence whether Shodagor fathers provide complementary (in addition to

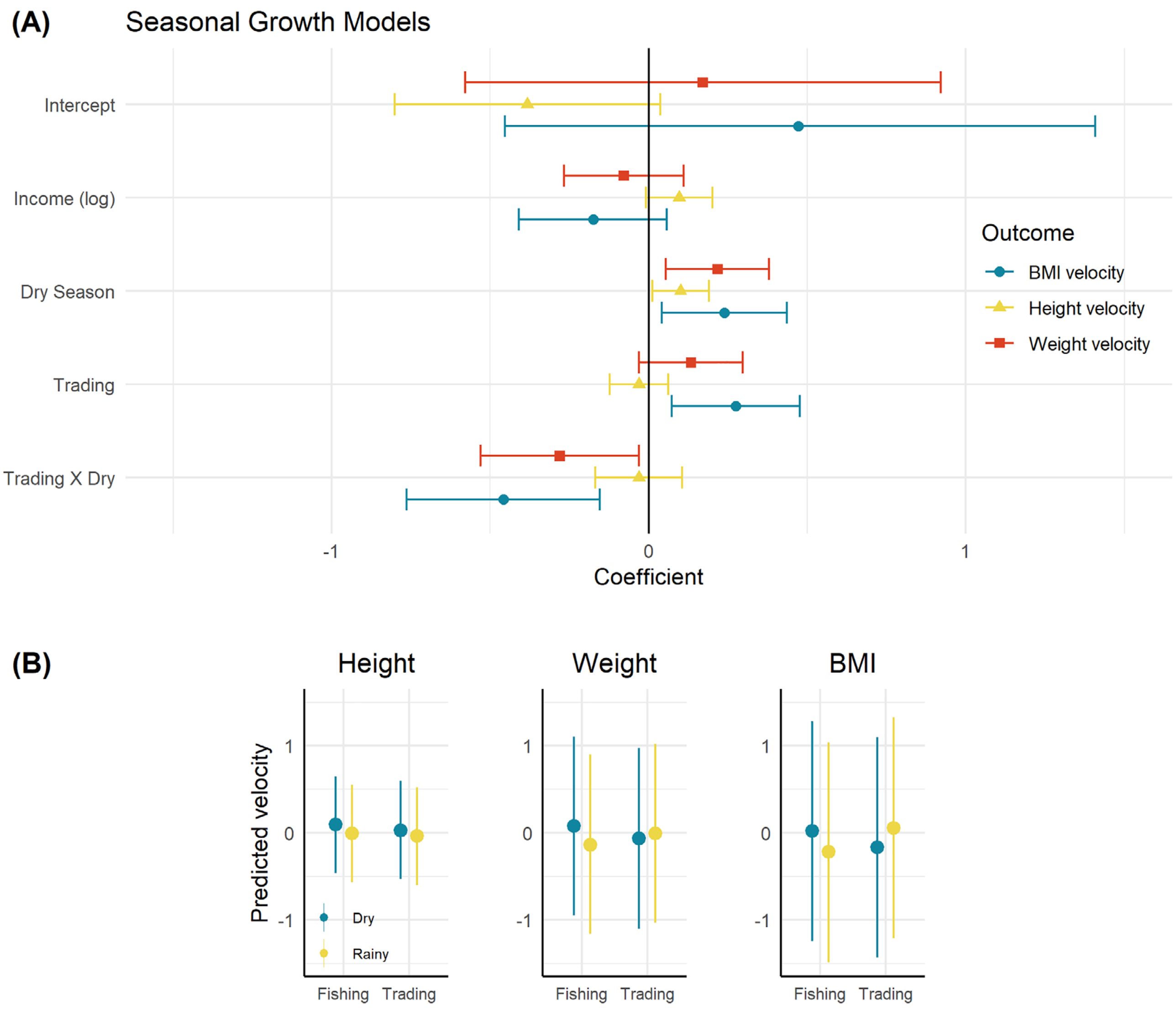

FIGURE 2 (a) Posterior means and 90% credible intervals for fixed effect coefficients in the Seasonal Growth Models ($n = 103$). (b) Posterior anthropometric means and 90% intervals predicted from the Seasonal Growth Models

mothers) or substitutive (in place of mothers) care for their children. Here, we demonstrate that fathers in most Shodagor households spend large amounts of time in close proximity with and provide high levels of direct care for young children. We then examine the effects of that care on child growth, a sensitive physiological marker and important fitness correlate, in order to test evolutionary models of human fatherhood. Results show that the effects of paternal care on growth were positive, but only when the father provided additive care during the dry season. This finding offers some support for the "additive care" hypothesis that care given in addition to mothers' benefits children's energetic condition and suggests that instead of merely dividing labor, some Shodagor men and women work together to produce greater parental investment. On the other hand, during seasons when fathers provided substitutive care because mothers were not available (i.e., in trading households), children grew less rapidly on average than when their mothers were the primary caregiver. Counterintuitively, children in these households were, on average, taller and heavier than children who received biparental care throughout the year, suggesting that positive effects of mothers' care may outweigh any detrimental effects of fathers' and that children fare better, overall, in households with substitutive care, compared to those with additive care. Although different measures of health may be differentially impacted by paternal care, results provided mixed support for the evolutionary prediction that paternal care has a positive impact on children's biological outcomes relevant to reproductive fitness, though potentially in complex ways. We discuss the evolutionary and cross-cultural implications of these results.

4.1 | Shodagor fathers provide very high levels of direct care (and sometimes more than mothers)

Our data also show that, compared to reported values in other populations, Shodagor fathers in both types of families provide a lot of direct

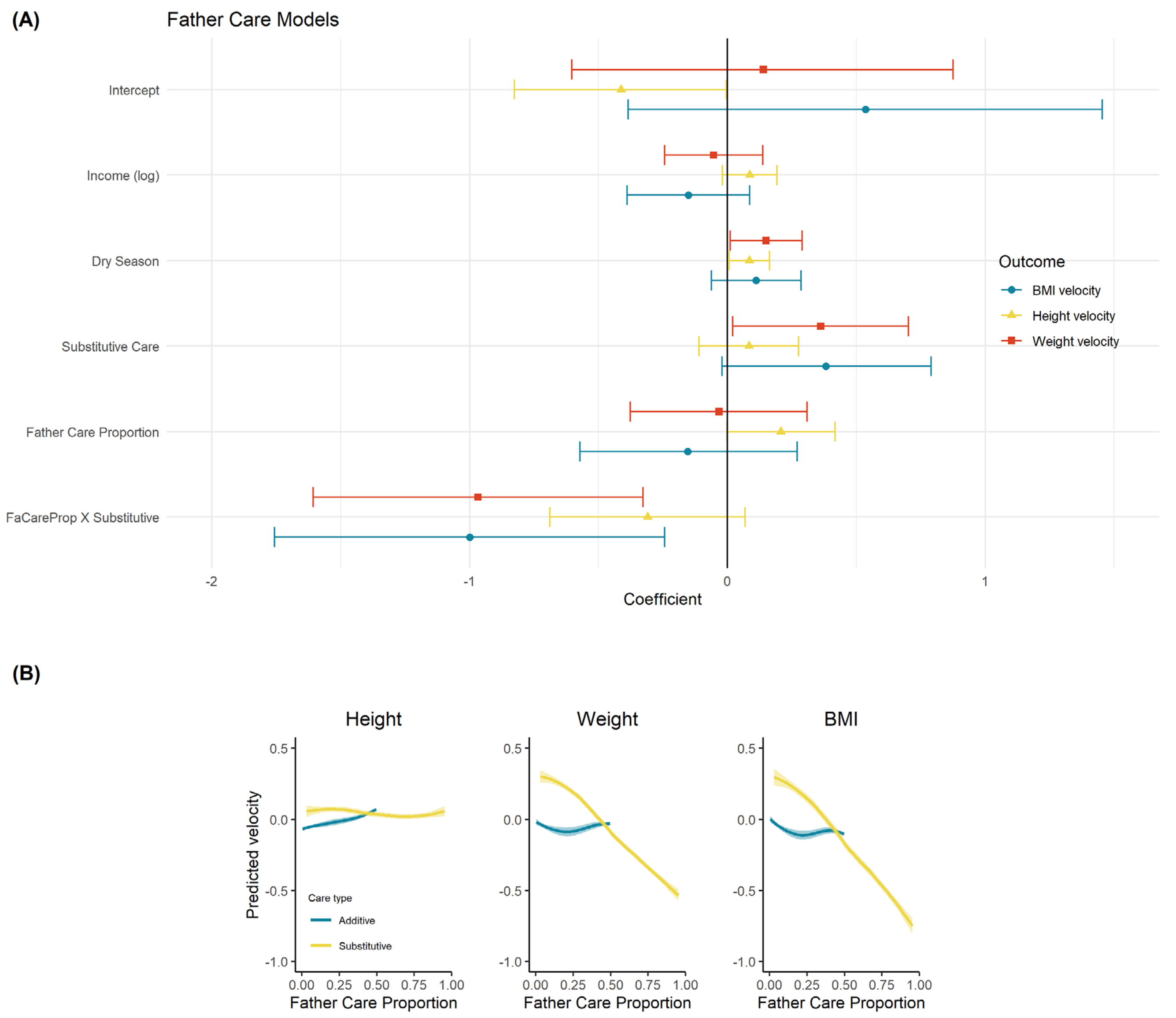

FIGURE 3 (a) Posterior means and 90% credible intervals for fixed effect coefficients in the Father Care Models ($n = 103$). (b) Loess curves and 90% confidence bands for anthropometric predictions from the Father Care Models

care. First, our data show that in trading families with children over the age of 2, during the dry season, Shodagor fathers are the primary caregiver on more days than mothers (Table 4, Figure 5). This pattern (fathers regularly providing more care than mothers) has never been documented before in subsistence-based societies (Gray & Anderson, 2010; Konner, 2005). Second, in previous cross-cultural comparisons, Aka fathers were reported to provide more than twice the amount of paternal care reported for other populations, as a proportion of all care received. Aka fathers held infants up to 4 months old 22% of the time (Hewlett, 1991) and were responsible for providing 15.8% of all types of direct care for children up to 18 months old (Hewlett, 1988). On average, across seasons, Shodagor fathers in both trading and fishing households were named as caregivers 26.3% of the time, with fathers in fishing households named as caregivers on 41.2% of days of the year, and fathers in trading households named on 45.2% of days for half of the year. However, the Aka and Shodagor data are not directly comparable for two reasons. First, Shodagor data were not generated through direct observation, as were many other reports of direct paternal care (e.g., Crittenden & Marlowe, 2008; Goodman et al., 1985; Hames, 1988; Hewlett, 1988; Kramer, 2005; Winking et al., 2009). They also do not reflect specific caregiving activities, like holding. Our data—specifically for fishing households—is, however, an excellent indicator of fathers' proximity to children, which is another commonly-used measure of paternal care (e.g., Hames, 1992; Hewlett, 1992). Fishing boats are approximately 14 feet long, from end to end, with around 6–8 feet of usable space in the middle, where all major activity takes place. Therefore, when a father spends the day on the fishing boat with his child, they are de facto in very close proximity the entire time. While proximity of fathers to children in trading households is unknown, when they are the primary caregiver of young children, they are responsible for the same care activities as mothers: feeding, bathing, watching, etc. For all fathers, we expect the 26.3% average to be a conservative estimate

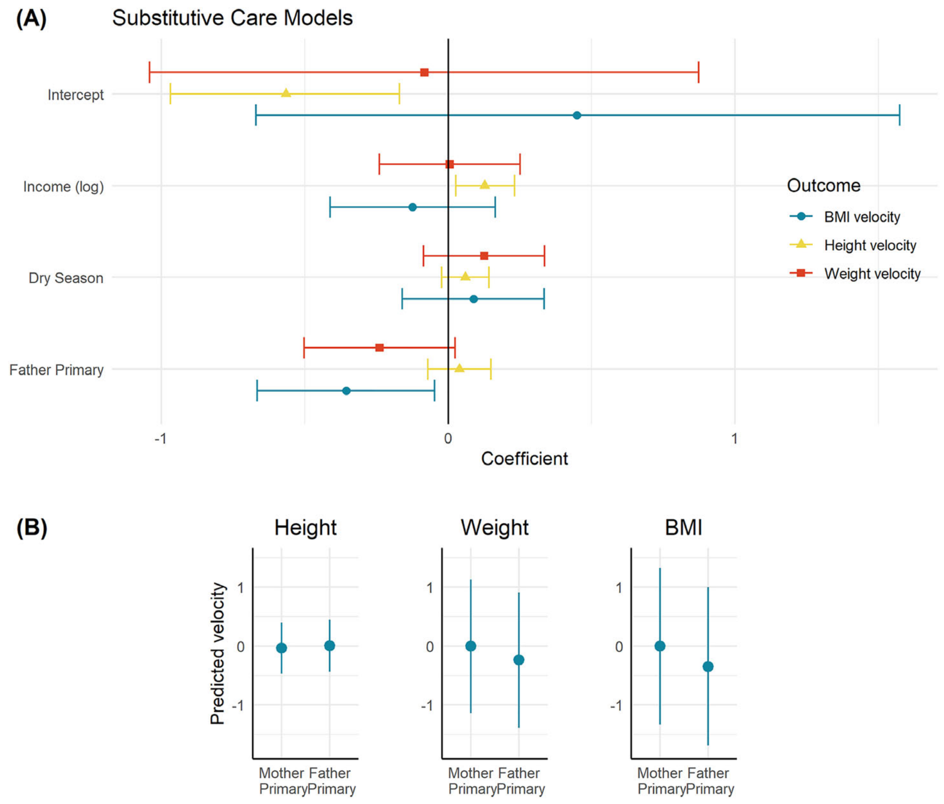

FIGURE 4 (a) Posterior means and 90% credible intervals for fixed effect coefficients in the Substitutive Care Models ($n = 64$). (b) Posterior anthropometric means and 90% intervals predicted from the Substitutive Care Models

of time spent with children. As our data reflect hours when parents are working during the day, they do not indicate who the caregivers are between the end of each workday and the beginning of the next workday. The small size of Shodagor boats and houses, and that all family members sleep together in the household, indicates that fathers are in close proximity to their children for a majority of the time that is not captured by our data.

A second reason why the Aka and Shodagor data are not directly comparable is that they do not compare care for children of similar ages. Our data show that Shodagor fathers' primary caregiving peaks when children are between the ages of 2.5 and 5 years old (Figure 6). This is not surprising, given that mothers' care is not easily substituted until children are weaned (Bove et al., 2002), and that most Shodagor women wean their children around the age of 2 (Starkweather et al., 2020). Additionally, Shodagor children tend to be watched very closely until around the age of 5, at which point they are often considered proficient swimmers and no longer at risk of drowning, should they fall off of the boat. It is clear that Aka and Shodagor fathers' caregiving are serving different purposes, which is consistent with the facultative nature of human fatherhood, as well as the fact that fathers' contributions to their children vary a great deal across cultures, based on child age (e.g., Crittenden & Marlowe, 2008; Harkness & Super, 1992; Scelza, 2010; Shenk & Scelza, 2012; Shenk et al., 2013; Prall & Scelza, 2020; Winking et al., 2009).

Despite limitations with our data, it is clear that Shodagor fathers provide very high levels of direct care for their young children during the dry season, and that fathers in trading households are the primary caregivers of their children more often than mothers, which is a pattern of care that has never before been documented in a subsistence-based society. Given these unusually high levels of care, we expect Shodagor fathers' care to have a significant impact on their children's growth.

4.2 | When fathers' additive care increases, children exhibit slightly faster growth velocities

Trivers (1972) suggests that increasing amounts of parental care should not necessarily correspond to increasing likelihood of offspring survival or reproduction. And while the facultative nature of paternal care in humans implies that as paternal care becomes more necessary, fathers who provide more care should experience positive returns to that care, in the form of increased likelihood of child survival, good health, and other measures of well-being, the context in which that care is provided, in relationship to care from others, should also play a role. Specifically, additive care, which does not decrease investment from mothers and, thus, increases the total amount of care one child receives, should be associated with gains in growth and other outcomes, while substitutive care, which takes the place of mothers' and results in children receiving the same amount of care, should not lead to noticeable differences. Our results show that contribution of paternal care does not have a predictable impact on child growth on its own,

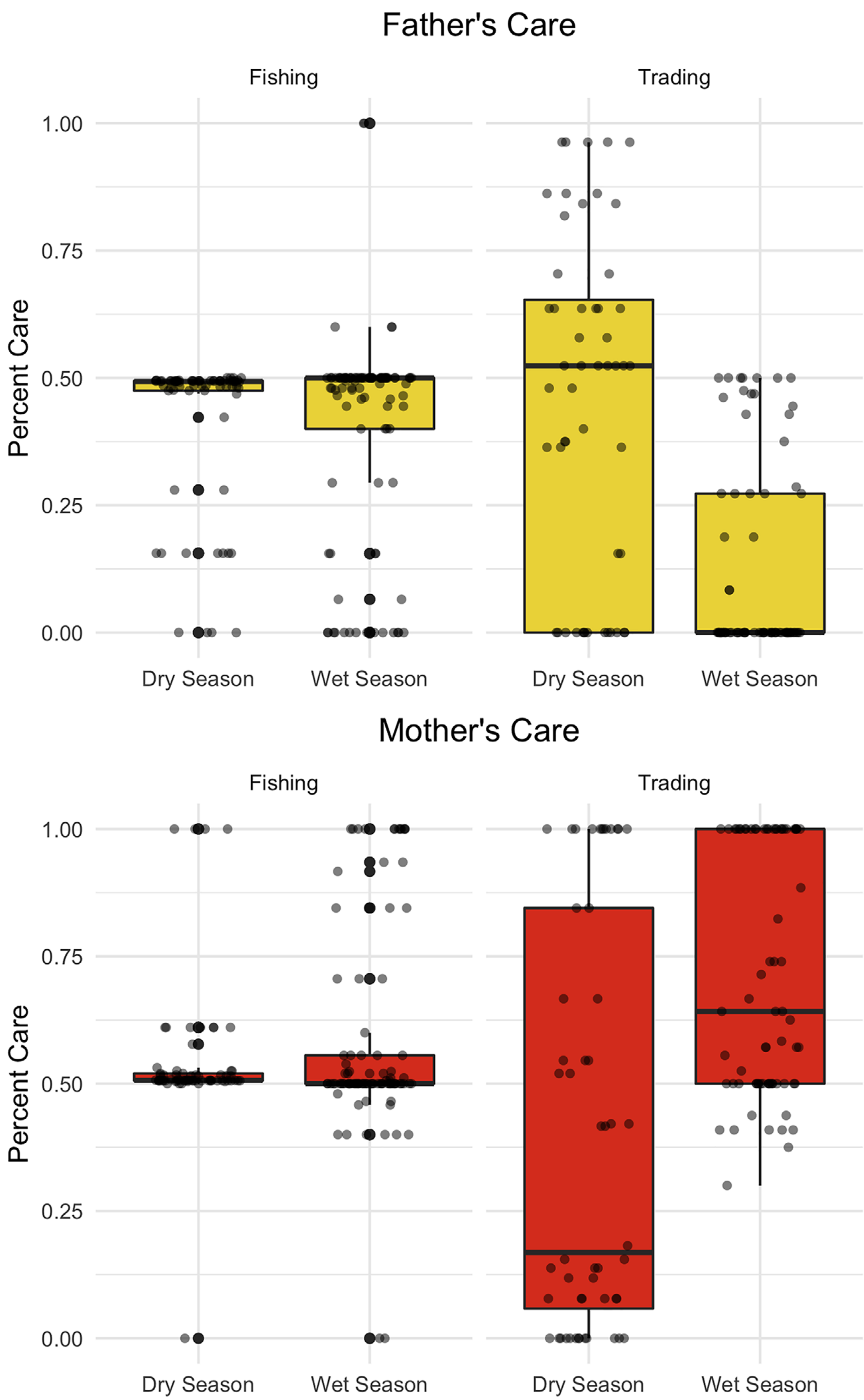

FIGURE 5 Average percentages of fathers' and mothers' direct care, for trading and fishing households, by season

but that, as predicted, when paternal care is additive, it shows a weakly positive association with faster height velocity (Figure 3a).

Positive effects of additive care have been demonstrated in other species, increasing reproductive success (Bales et al., 2002; Emlen & Wrege, 1991; Hatchwell, 2004; Komdeur, 1994; Russell et al., 2007; Tanaka et al., 2018) through accelerated offspring growth (Bell et al., 2014; Dickinson et al., 1996; Hodge, 2005) and reduced offspring starvation (Dickinson et al., 1996; Hatchwell, 1999, 2004; Heinsohn, 1995; Kingma et al., 2010). Examples of additive paternal care can be found among humans, in addition to the Shodagor case. When full-time

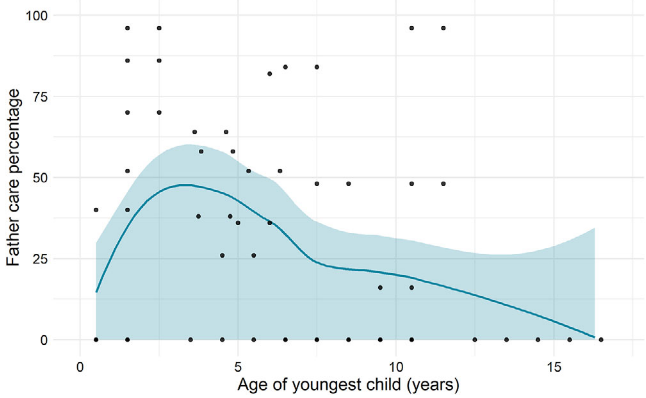

FIGURE 6 Percentage of direct childcare provided by fathers during dry seasons in trading families ($n = 34$ households). Loess curve and 90% confidence band of care percentage by the youngest child's age in each household

employed Australian fathers engage in childcare, an average of 74% of the time they spend with children is also spent in the company of their spouse (Craig, 2002). Aka mothers provide the majority of direct care for children (Meehan, 2005), but while net hunting, mothers and fathers are accompanied by their children and both parents are responsible for care (Hewlett, 1991). In Agta families, fathers' direct care primarily takes the form of low-investment activities, such as proximity or "watching," and their presence in camp does not reduce maternal childcare workload (Page et al., 2021). However, in these cases, the impact of fathers' additive care on child outcomes is unknown.

Our results provide weak support for the hypothesis (H2) that additive direct care should improve growth outcomes for human children, and show no support for the hypothesis that growth velocities are higher for children in fishing families. In addition to the Father Care Model results, which show that as the proportion of fathers' additive care increases, children gain height at a slightly faster rate, results from the Seasonal Growth Models indicate that Shodagor fathers' additive care doesn't have a consistent, predictable effect on child growth. These results show that children in fishing households gain height, weight, and body mass at a faster rate than children in trading households, but only during the dry season, and the effect is reversed during the rainy season (Figure 2a). If additive paternal care impacted children consistently, we would be unlikely to see major seasonal differences in growth velocities, but would, as predicted, see larger average growth velocities than children in trading households year-round. Possibly, ecological circumstances are exerting far greater influence on child growth, as we discuss below, and drowning out most of the impact of caregiving.

4.3 | Is fathers' care a good substitute for mothers'? Only when fathers receive help from alloparents

One of the most important functions of alloparents is that their direct care can reduce overall care burden on mothers. This allows mothers to invest energy in other activities, such as production, leisure, or caring for other children (Flinn, 1989; Kramer, 2005; Sear et al., 2002; Turke, 1988). Across cultures, fathers provide substitutive direct care for relatively short periods of time (e.g., Craig, 2002; Eibl-Eibesfeldt, 1989), but can also provide more substantial amounts of care. Hiwi fathers were their children's primary caregivers during 30% of mothers' foraging outings (Hurtado et al., 1992), and Ifugao fathers in the Philippines also care for children during the day while mothers work (Milgram, 2011). Shodagor fathers in trading households serve as a robust example of such substitutive paternal care in which fathers in this sample are primary caregivers an average of 45.2% of days during the dry season, exceeding mothers' 39.6%, and patterns of care clearly demonstrate a seasonal inverse relationship between paternal and maternal care (Figure 5). Previous studies of Shodagor women's trading conclude that paternal care is a critical socioecological component that allows women with young children to work as traders (Starkweather, 2017; Starkweather et al., 2020).

Such substitutive care, in which mothers invest in economic activities, is not expected to produce "net positive" fitness effects for children, as they are—theoretically—receiving the same amount of direct and indirect investment, just from different investors (Brown et al., 1978; Heinsohn, 2004). Therefore, we predicted there would be no significant difference in children's growth between seasons when mother was primary and father was primary (H2a), and that increasing amounts of substitutive paternal care would not have a significant impact on child growth (H2b). Contrary to these predictions, our results consistently show that children from trading families grow at a slower rate when fathers substitute for mothers as primary caregivers. Seasonal Growth Models show that during the dry season, in trading households, children gain weight and body mass at a slower rate than they do during the rainy season when mother is primary, or than children from fishing households do during the dry season (Figure 2). Similarly, the Substitutive Care Models show that during seasons when fathers are the primary caregivers, children gain body mass (and possibly also weight) at slightly slower rates, on average, than seasons when mothers are primary (Figure 4). And finally, the Father Care Models show that as the proportion of fathers' substitutive care increases, the velocity at which children gain weight and body mass decreases (Figure 3).

Our results indicate that there are qualitative differences in care provided by mothers and fathers that lead to differences in children's energetic status. These may include differences in care that directly impact energy intake, such as providing enough, high-quality food for children, or ensuring that they eat regularly. Feeding of very young children is a time-intensive activity, and some caregivers may have more success than others. For example, care from older siblings is often associated with poorer nutritional outcomes for young children (e.g., Popkin, 1980), especially when sibling caregivers are also young (Shah, 1978), owing to caregivers' inattention to child feeding practices. Results may also reflect maternal diligence for children consuming safer food and water, encouraging children to engage in behaviors that prevent illness (Bliss et al., 2016;Bornstein et al., 2015; George et al., 2015; Langford et al., 2011; Nti & Lartey, 2008; Rah et al., 2015;

Wodnik et al., 2018), like hand washing, or for treating illnesses more quickly or aggressively (Case & Paxon, 2001), preventing energetic stress associated with increased immune activation. It is also possible that, rather than substantive seasonal changes in quality of care, children experience higher levels of stress due to change in caregivers; however, if stress were related to switching, and not caregiver, we would expect similarly slow growth regardless of caregiver.

Our results also indicate that substitutive paternal care may have the most negative impact on child growth when it is provided on its own—in other words, without help from others. While the Father Care Models suggest that more substitutive care by fathers results in slower growth, they also emphasize the importance of alloparental help, showing that when fathers are responsible for smaller proportions of total care given to children, other caregivers make up the difference, and children gain weight and body mass at a higher velocity. One interpretation of this result is that paternal care alone is detrimental to child growth, but help from alloparents can buffer this effect. This is consistent with findings from Starkweather et al. (2020), which show that care from both fathers and alloparents predict mothers' trading, indicating that both play an important role in trading households with young children. These results suggest that the combination of paternal and alloparental care, which allows mothers to engage in work that is incompatible with childcare and provide critical resources to their households, also improves children's energetic condition, which has important fitness implications.

4.4 | Seasonal changes in growth velocity differ by household division of labor

In addition to the influence of caregivers on growth, our results show that children in trading and fishing families experience seasonal changes in growth rates, a trend that has been documented across multiple populations around the world (Huss-Ashmore, 1988; Ulijaszek & Strickland, 1993). However, results also indicate that the "growing" seasons for children in these families are different (Figure 2b), with children in trading families growing at faster rates, on average, during the rainy season than the dry, and children in fishing families growing at faster rates, on average, during the dry season than the rainy. Though seasonal changes in caregivers—switching between mother and father as the primary caregiver—appears to explain some of the variance in seasonal differences in trading families, it can neither explain seasonal differences in fishing families (as caregiving does not change seasonally), nor why children in these two family types experience opposite "growing" seasons.

Two of the most commonly reported mechanisms driving seasonal differences in child growth are resource access and pathogen exposure and the subsequent illness associated with it. In countries like the Gambia, the "growth rate is very clearly related to climatic factors associated with the timing of the rainy season or seasons, through their influence on food availability, parasite load, and infection" (Cole, 1993, p. 89). In rural Nepal, changes in child growth rates were attributed to seasonal changes in diet and recurrent illnesses (Panter-Brick,

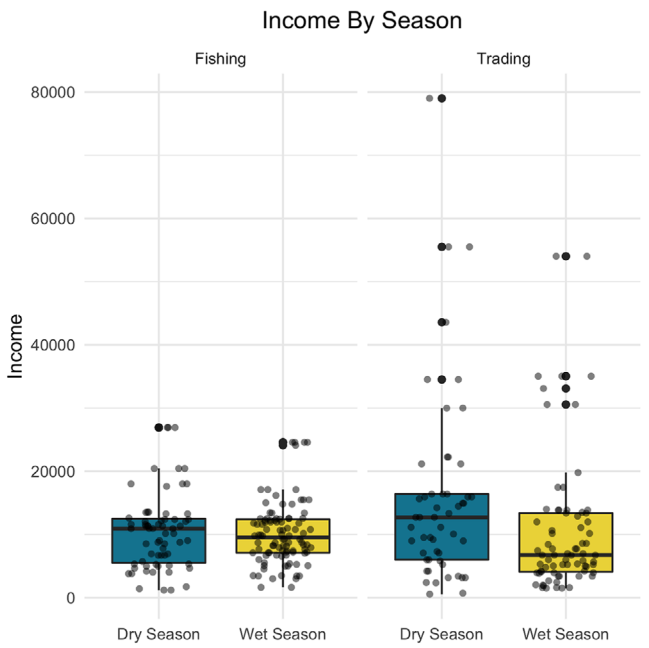

FIGURE 7 Average monthly income for trading and fishing households by season

1997), and among children in rural Timor-Leste, seasonal resource scarcity accounted for changes to body mass (Spencer et al., 2017). In Bangladesh, studies have repeatedly demonstrated that nutritional deficit (Brown et al., 1982; 1985; Hillbruner & Egan, 2008) and slowed growth in children (Brown et al., 1982; Chen et al., 1979) are most likely to occur during the rainy season, with some studies showing that resource shortages are greatest toward the end of the season (between August through October) (Chaudhury, 1981; Chen et al., 1979).

In our models of Shodagor child growth, we use household income during peak months of the rainy (July) and dry (January) seasons as a proxy measure for access to resources like food and medical care. Only in the Substitutive Care Models did income have a predictable relationship with growth. These results indicate that in trading families, more household income during a given season predicts that children gain height at a faster rate (Figure 4, Table S3), and bivariate results show that, in these households, average household income is higher during the dry season than during the rainy season (Figure 7). Taken together, these results suggest that children in trading families should be growing at a faster rate during the dry season, but this is not the case. Additionally, there is no indication that income is an important predictor of child growth, nor that income differs significantly by season in fishing families.

While income is of critical importance for multiple aspects of Shodagor life and a key predictor of energetic condition in many cultural contexts (e.g., Huda et al., 2018; Kennedy & Peters, 1992; Popkin, 1978), it is not the only way that Shodagor families can access food. As is the case for many societies whose economies represent a mixture of cash and subsistence-based resources (e.g., foraging, hunting, gardening resources that are used to directly feed one's family), Shodagor families use cash earned from trading and fishing to purchase a variety of foods for their households, such as rice, lentils, chicken, and beef, but also regularly engage in subsistence fishing, eating (rather than selling) the fish that they catch. Adults report that they are most likely to do this when their catch is small and they do not anticipate earning much money if they were to sell it in the market. Therefore, fish may provide a buffer against shortfalls in income and prevent growth faltering for Shodagor children. Given that adults in trading families primarily fish during the rainy season (i.e., the season when children are experiencing faster growth rates), this explanation could help explain seasonal differences in child growth for trading families, but it is not clear that this explains why children in trading families grow at a faster rate than children in fishing families during the rainy season, nor why children in fishing families grow at a faster rate during the dry than the rainy season. Data from 2014 suggest that neither fishing nor income alone predicted body size among Shodagor parents and children, but that both together may have some explanatory power (Starkweather & Keith, 2018). In future studies, the relationship between subsistence fishing and income will be investigated in greater detail, as will their collective impact on child growth and adult nutritional status.

Seasonality of pathogen exposure and illness are also common throughout the world (Fisman, 2007) and have been linked to patterns in child growth (Cole, 1993; Panter-Brick, 1997; Paynter et al., 2013). Given the high prevalence of diarrheal (Sarker et al., 2016) and respiratory (Imran et al., 2019) diseases in Bangladesh, we certainly expect pathogen loads among Shodagor individuals to be high. We have some evidence to suggest that children in trading households experience a higher frequency of illness (Starkweather & Keith, 2019), but these data do not show seasonal differences in child illness for either trading or fishing families. Therefore, we have no reason to expect that pathogen exposure is a primary driver of seasonal differences in these households, though this is an area that requires further study.

4.5 | Despite seasonal deficits, children in trading households are taller, weigh more, and have higher BMIs than children in fishing households

This seemingly counterintuitive finding suggests two potential explanations. First, children in trading households—who experience slower growth during the dry seasons when fathers are primary caregivers—may be experiencing more catch-up growth in the rainy seasons than children in fishing households are during the dry season. Second, the growth rates of children in fishing households may slow down more during the rainy season than do the rates of children in trading households during the dry season. One or both of these processes in which the magnitudes of growth velocities differ between trading and fishing families could be responsible for children in trading families having bigger body sizes, though the Seasonal Growth counterfactual plot (Figure 2b) suggests more support for the second explanation with slightly larger seasonal differentials in predicted weight and BMI for children in fishing households than children in trading households.

Harkening back to a question posed by Winking (2006), "Are men really that bad as fathers?" our results suggest that, no, fathers are not *bad* caregivers, per se. Taken together, model results indicate that in a cultural and ecological setting where biparental care and high-investing fathers are common, paternal care accounts for a small, but predictable amount of variance in child growth velocities and plays two important roles in shaping child growth. First, care given in addition to mothers' care is associated with slightly faster rates of increase in child height, compared to substitutive paternal care. Second, substitutive care, which allows mothers to work and provide resources for their families, is associated with slower gains in weight and body mass, especially when fathers have less help from alloparents. However, the magnitude of change in these measures between paternal and maternal care conditions is small, especially compared to the sluggish growth experienced by children in fishing families during the rainy season, and children in trading households have larger overall body sizes. This indicates that the slower growth rates they experience when fathers provide substitutive care is not a major hindrance to their overall energetic condition, relative to other children in the Shodagor community. In other words, though fathers' care is not interchangeable with mothers' in trading households, it is not such a poor substitute that it prevents children from attaining relatively better energetic condition, overall.

Our results illustrate a point made by many others: variables often used to measure paternal investment (i.e., father presence) and child outcomes (i.e., survival, adult body size), which are effective measures in other species (Clutton-Brock, 1991), do not adequately capture the effects of paternal care in humans. In Shodagor families, cumulative measures of child body size do not necessarily reflect the process by which they were achieved, indicating that attainment of height, weight, and BMI is the result of a detailed process that is sensitive to fluctuations in caregiving, a finding that would have been otherwise obfuscated by studying only cumulative measures of body size.

5 | CONCLUSIONS

Though fathers played an important role in human evolution and in contemporary societies, decades of study have not yet determined how paternal care impacts child physiology. Our results show that in a socioecological context in which fathers provide very high levels of direct care, it has a predictable impact on child growth velocity. However, the impact is only positive when fathers are not the sole care providers: when they give care alongside mothers or when they receive help from alloparents. These findings echo other studies showing that where direct paternal care is important, it has a positive impact on child health and growth (Boyette et al., 2018; Winking & Koster, 2015). They also emphasize the evolutionary importance of both biparental and alloparental care, suggesting that even when mothers and fathers account for the vast majority of care children receive, alloparents play a critical role in improving children's energetic condition and, thus, supporting parents' reproductive fitness. Similar to other contexts (Helfrecht et al., 2020), Shodagor fathers give care within a larger network of caregivers, which includes mothers and alloparents. In other populations, maternal care remains consistent, while fathers modify their care in response to the presence of other alloparents (e.g., Helfrecht et al., 2020; Meehan, 2005; Winking et al., 2009). In all Shodagor families, fathers appear to modify care in response to mothers', and in trading families, provide care at a critical juncture when children are weaned but not yet able to fend for themselves so that mothers can work (Starkweather et al., 2020). The facultative nature of human paternal care suggests that fathers should provide care under conditions when it is most needed and can have the greatest positive impact on child survival and well-being. Results from this study indicate this is the case for Shodagor fathers and document the importance of both additive and substitutive paternal care for improving one measure of reproductive fitness: child growth.

ACKNOWLEDGMENTS

The authors would like to thank the Shodagor communities in Matlab, Bangladesh for their participation in this project, as well as their generosity, kindness, and friendship. We would also like to thank Siddiqudzaman, Laila Parveen, and Ummahani Akter for their assistance with data collection and various other tasks in the field, as well as Taslim Ali, and the HDSS staff at ICDDRB in both Matlab and Dhaka for providing logistical support. Finally, we thank Richard McElreath and the Max Planck Institute for Evolutionary Anthropology's Department of Human Behavior, Ecology, and Culture for providing funding and support for this project.

AUTHOR CONTRIBUTIONS

KS was responsible for securing project funding and collecting data, with assistance from NA and FtZ. KS designed this study in consultation with MK, SP, and MET, and KS, MK, and MET wrote the article with input from all coauthors. MK conducted all statistical analyses, in consultation with SP, and MK and SP created graphical representations of the data and results.

DATA AVAILABILITY STATEMENT

Code and anonymized data for all models are available on GitHub at https://github.com/mhkeith/Shodagor-Paternal-Care.git.

ORCID

K. E. Starkweather https://orcid.org/0000-0002-1554-4567

REFERENCES

Alvergne, A., Faurie, C., & Raymond, M. (2009). Father-offspring resemblance predicts paternal investment in humans. *Animal Behavior*, *78*, 61–69.

Apter, D., & Vihko, R. (1983). Early menarche, a risk factor for breast cancer, indicates early onset of ovulatory cycles. *Journal of Clinical Endocrinology and Metabolism*, *57*, 82–86.

Assis, A. M. O., Barreto, M. L., Santos, L. M. P., Fiaccone, R., & da Silva Gomes, G. S. (2005). Growth faltering in childhood related to diarrhea: A longitudinal community based study. *European Journal of Clinical Nutrition*, *59*, 1317–1323.

Bales, K., French, J. A., & Dietz, J. M. (2002). Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behavior*, *63*, 453–461.

Bell, M., Cant, M., Borgeaud, C., Thavarajah, N., Samson, J., & Clutton-Brock, T. (2014). Suppressing subordinate reproduction provides benefits to dominants in cooperative societies of meerkats. *Nature Communications*, *5*, 4499.

Blackwell, A. D., Urlacher, S. S., Beheim, B., von Rueden, C., Jaeggi, A., Stieglitz, J., Trumble, B. C., Gurven, M., Kaplan, H. (2017). Growth references for Tsimane forager-horticulturalists of the Bolivian Amazon. *American Journal of Physical Anthropology*, *162*(3), 441–461.

Bliss, J. R., Njenga, M., Stoltzfus, R. J., & Pelletier, D. L. (2016). Stigma as a barrier to treatment for child acute malnutrition in Marsabit County. *Kenya. Maternal and Child Health*, *12*, 125–138.

Blizzard, R. M., & Bulatovic, A. (1992). 12 Psychosocial short stature: A syndrome with many variables. *Baillière's Clinical Endocrinology and Metabolism*, *6*, 687–712.

Blurton Jones, N. G., Hawkes, K., & O'Connell, J. F. (1996). The global process and local ecology: How should we explain differences between the Hadza and the !Kung? In S. Kent (Ed.), *Cultural diversity among twentieth-century foragers: An African perspective* (pp. 159–187). Cambridge, U.K: Cambridge University Press.

Borgerhoff Mulder, M. (1989). Early maturing Kipsigis women have higher reproductive success than late maturing women and cost more to marry. *Behavioral Ecology and Sociobiology*, *24*, 145–153.

Borgerhoff Mulder, M. (2005). Cooperative breeding in humans: Which kin help and why? *Paper presented at the XXV IUSSP International Population Conference*, *2005*, Tours, France

Bornstein, M. H., Putnick, D. L., Bradley, R. H., Lansford, J. E., & Deater-Deckard, K. (2015). Pathways among caregiver education, household resources, and infant growth in 39 low- and middle-income countries. *Infancy*, *20*, 353–376.

Bove, R., Valeggia, C., & Ellison, P. (2002). Girl helpers and time allocation of nursing women among the Toba of Argentina. *Human Nature*, *13*, 457–472.

Boyette, A. H., Lew-Levy, S., & Gettler, L. T. (2018). Dimensions of fatherhood in a Congo Basin village: A multimethod analysis of intracultural variation in men's parenting and its relevance for child health. *Current Anthropology*, *59*(6), 839–847.

Boyette, A. H., Lew-Levy, S., Sarma, M. S., & Gettler, L. T. (2019a). Testosterone, fathers as providers and caregivers, and child health: Evidence from fisher-farmers in the Republic of the Congo. *Hormones and Behavior*, *107*, 35–45.

Boyette, A. H., Lew-Levy, S., Sarma, M. S., Valchy, M., & Gettler, L. T. (2019b). Fatherhood, egalitarianism, and child health in two small-scale societies in the Republic of the Congo. *American Journal of Human Biology*, *32*(4), e23342.

Bribiescas, R. G., Ellison, P. T., & Gray, P. B. (2012). Male life history, reproductive effort, and the evolution of the genus *Homo*: New directions and perspectives. *Current Anthropology*, *53*, S424–S435.

Brien, F. (1986). Review of the genetic and physiological relationships between growth and reproduction in mammals. *Animal Breeding Abstracts*, *54*, 975–997.

Bronte-Tinkew, J., & DeJong, G. (2004). Children's nutrition in Jamaica: Do household structure and household economic resources matter? *Social Science & Medicine*, *58*, 499–514.

Brown, K. H., Black, R. E., & Becker, S. (1982). Seasonal changes in nutritional status and the prevalence oof malnutrition in a longitudinal study of young children in rural Bangladesh. *American Journal of Clinical Nutrition*, *36*, 303–313.

Brown, K. H., Black, R. E., Robertson, A. D., & Becker, S. (1985). Effects of season and illness on the dietary intake of weanlings during longitudinal studies in rural Bangladesh. *The American Journal of Clinical Nutrition*, *41*, 343–355.

Brown, J. H., Marquet, P. A., & Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *The American Naturalist*, *142*, 573–584.

Brown, J. L., Dow, D. D., Brown, E. R., & Brown, S. D. (1978). Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behavioral Ecology and Sociobiology*, *4*, 43–59.

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28.

Carranza, J., Polo, V., Valencia, J., Mateos, C., de la Cruz, C. (2008). How should breeders react when aided by helpers? *Animal Behavior*, *75*, 1535–1542.

Case, A., & Paxson, C. (2001). Mothers and others: Who invests in children's health? *Journal of Health Economics*, *20*(3), 301–328.

Chaudhury, R. H. (1981). The seasonality of prices and wages in Bangladesh. In R. Chambers, R. Longhurst, & A. Pacey (Eds.), *Seasonal dimensions to rural poverty* (pp. 87–92). London: Frances Pinter.

Chen, L. C., Chowdhury, A. K. M. A., Huffman, S. L. (1979). Seasonal dimensions of energy protein malnutrition in rural Bangladesh: The role of agriculture, dietary practices, and infection. *Ecology of Food and Nutrition*, *8*, 175–187.

Chen, F., Short, S., & Entwise, B. (2000). The impact of grandparental proximity on maternal childcare in China. *Population Research and Policy Review*, *19*, 571–590.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Cole, C.R., & Lifshitz, F. (2008). Zinc nutrition and growth retardation. *Pediatric Endocrinology Reviews*, *5*, 889–896.

Cole, T. (2020). Sitar: Super imposition by translation and rotation growth curve analysis. R package version 1.1.2. https://CRAN.R-project.org/package=sitar

Cole, T. J. (1993). Seasonal effects on physical growth and development. In S. J. Ulijaszek & S. Strickland (Eds.), *Seasonality and human ecology* (pp. 89–106). Cambridge: Cambridge University Press.

Cole, T.J., & Cole, A.J. (1992). Bone age, social deprivation, and single parent families. *Archives of Disease in Childhood*, *67*, 1281–1285.

Cook, J. T., Frank, D. A., Berkowitz, C., Black, M. M., Casey, P. H., Cutts, D. B., Meyers, A. F., Zaldivar, N., Skalicky, A., Levenson, S., Heeren, T., Nord, M. (2004). Food insecurity is associated with adverse health outcomes among human infants and toddlers. *The Journal of Nutrition*, *134*(6), 1432–1438.

Courtiol, A., Rickard, I. J., Lummaa, V., Prentice, A. M., Fulford, A. J., & Stearns, S. C. (2013). The demographic transition influences variance in fitness and selection on height and BMI in rural Gambia. *Current Biology*, *23*, 884–889.

Craig, L. (2002). *Caring differently: A time-use analysis of the type and social context of child care performed by fathers and by mothers*. Discussion Paper No. 116. Sydney: Social Policy Research Centre, University of New South Wales.

Creek, T. L., Kim, A., Lu, L., Bowen, A., Masunge, J., Arvelo, W., Smit, M., Mach, O., Legwaila, K., & Motswere, C. (2010). Hospitalization and mortality among primarily nonbreastfed children during a large outbreak of diarrhea and malnutrition in Botswana, 2006. *Journal of Acquired Immune Deficiency Syndromes*, *53*, 14–19.

Crittenden, A. N., & Marlowe, F. W. (2008). Allomaternal care among the Hadza of Tanzania. *Human Nature*, *19*(3), 249.

Das, S. K., Chisti, M. J., Malek, M. A., Das, J., Salam, M. A., Ahmed, T., Al Mamun, A., & Golam Faruque, A. S. (2015). Changing childhood malnutrition in Bangladesh: Trends over the last two decades in urban-rural differentials (1993-2012). *Public Health Nutrition*, *18*, 1718–1727.

Devi, M. R., Kumari, J. R., & Srikumari, C. (1985). Fertility and mortality differences in relation to maternal body size. *Annals of Human Biology*, *12*, 479–484.

Dickinson, J. L., Koenig, W. D., & Pitelka, F. A. (1996). Fitness consequences of helping behavior in the western bluebird. *Behavioral Ecology*, *7*, 168–177.

Dobrova-Krol, N. A., van Ijzendoorn, M. H., Bakermans-Kranenburg, M. J., Cyr, C., & Juffer, F. (2008). Physical growth delays and stress dysregulation in stunted and non-stunted Ukrainian institution-reared children. *Infant Behavior and Development*, *31*, 539–553.

Dunbar, R. I. M. (1976). Some aspects of research design and their implications in the observational study of behaviour. *Behaviour*, *58*, 78–98.

Eibl-Eibesfeldt, I. (1989). *Human ethology*. New York: Aldine.

Emlen, S. T. (1991). Evolution of cooperative breeding in birds and mammals. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (4th edn., pp. 301–337). Oxford: Blackwell.

Emlen, S. T., & Wrege, P. H. (1991). Breeding biology of white-fronted bee-eaters at Nakuru: The influence of helpers on breeder fitness. *Journal of Animal Ecology*, *60*, 309–326.

Emmott, E. H. & Page, A. E. (2019). Alloparenting. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science* (pp. 1–14). Cham: Springer International Publishing. https://doi.org/10.31219/osf.io/mcpv2

Fernald, L.C. & Grantham-McGregor, S.M. (2002). Growth retardation Is associated with changes in the stress response system and behavior in school-aged Jamaican children. *Journal of Nutrition*, *132*, 3674–3679.

Fernandez-Duque, E., Valeggia, C. R., & Mendoza, S. P. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology*, *38*, 115–130.

Fisman, D. N. (2007). Seasonality of infectious diseases. *Annual Review of Public Health*, *28*, 127–143.

Flanders, J. L., Simard, M., Paquette, D., Parent, S., Vitaro, F., et al. (2010). Rough-and-tumble play and the development of physical aggression and emotion regulation: A five-year follow-up study. *Journal of Family Violence*, *25*, 357–367.

Flinn, M. V. (1989). Household composition and female reproductive strategies in a Trinidadian village. In A.E. Rasa, C. Vogel, & E. Voland (Eds.), *The sociobiology of sexual and reproductive strategies* (pp. 206–233). London: Chapman and Hall.

Fox, M., Sear, R., Beise, J., Ragsdale, G., Voland, E., & Knapp, L. A. (2010). Grandma plays favourites: X-chromosome relatedness and sex-specific childhood mortality. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 567–573.

Garcia, A. R., Blackwell, A. D., Trumble, B. C., Stieglitz, J., Kaplan, H., & Gurven, M. D. (2020). Evidence for height and immune function trade-offs among preadolescents in a high pathogen population. *Evolution, Medicine, & Public Health*, *2020*(1), 86–99. https://doi.org/10.1093/emph/eoaa017

George, C. M., Oldja, L., Biswas, S. K., Perin, J., Lee, G. O., Ahmed, S., Haque, R., Sack, R. B., Parvin, T., & Azmi, I. J. (2015). Fecal markers of environmental enteropathy are associated with animal exposure and caregiver hygiene in Bangladesh. *American Journal of Tropical Medicine and Hygiene*, *93*, 269–275.

Gettler, L. T., Boyette, A. H., & Rosenbaum, S. (2020). Broadening perspectives on the evolution of human paternal care and fathers' effects on children. *Annual Review of Anthropology*, *49*, 141–160.

Godoy, R., Tanner, S., Reyes-Garcia, V., Leonard, W. R., McDade, T. W., Vento, M., Broesch, J., Fitzpatrick, I. C., Giovannini, P., Huanca, T., Jha, N., & Bolivian TAPS Study Team (2008). The effect of rainfall during gestation and early childhood on adult height in a foraging and horticultural society of the Bolivian Amazon. *American Journal of Human Biology*, *20*, 23–34.

Goodman M, Griffin P, Estioko-Griffin A, Grove J. (1985). The comparability of hunting and mothering among the Agta hunter-gatherers of the Philippines. *Sex Roles*, *12*, 1199–1209

Gray, P. B. & Anderson, K. G. (2010). *Fatherhood: Evolution and human paternal behavior*. Cambridge: Harvard University Press.

Griffin, P. B., & Griffin, M. B. (1992). Fathers and childcare among the Cagayan Agta. In B. S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 297–320). New Brunswick: Transaction Publishers.

Grossmann, K., Grossmann, K. E., Fremmer Bombik, E., Kindler, H., Scheuerer-Englisch, H., & Zimmerman, A. P. (2002). The uniqueness of the child-father attachment relationship: Fathers' sensitive and challenging play as a pivotal variable in a 16 year longitudinal study. *Social Development*, *11*, 301–337.

Guedes, D. P., De Matos, J. A. B., Lopes, V. P., Ferreirinha, J. E., & Silva, A. J. (2010). Physical growth of schoolchildren from the Jequitinhonha Valley, Minas Gerais, Brazil: Comparison with the CDC-2000 reference using the LMS method. *Annals of Human Biology*, *37*, 574–584.

Gurven, M., Winking, J., Kaplan, H. S., von Rueden, C., & McAllister, L. (2009). A bioeconomic approach to marriage and the sexual division of labor. *Human Nature*, *20*(2), 151–183.

Hakeem, R., Shaikh, A. H., & Asar, F. (2004). Assessment of linear growth of affluent urban Pakistani adolescents according to CDC 2000 references. *Annals of Human Biology*, *31*, 282–291.

Hames, R. B. (1988). The allocation of parental care among the Ye'kwana. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behavior* (pp. 237–252). Cambridge: Cambridge University Press.

Hames, R. B. (1992). Variation in paternal care among the Yanomamö. In B. S. Hewlett (ed.), *Father-child relations* (pp. 85–110). New York: Aldine.

Hames, R., Oliver, W. J., Chagnon, N. A. (2005). *Growth, development, and health of Yanomamo orphans in relation too parental loss and kinship*. Paper presented at the 17th Annual Meeting of the Human Behavior and Evolution Society, Austin, TX.

Harkness, S. & Super, C. M. (1992). The cultural foundations of fathers' roles: Evidence from Kenya and the United States. In B. S. Hewlett (Ed.), *Father-child relations* (pp. 191–211). New York: Aldine.

Hasan, M. A., Batieha, A., Jadou, H., Khawaldeh, A. K., & Ajlouni, K. (2001). Growth status of Jordanian schoolchildren in military-funded schools. *European Journal of Clinical Nutrition*, *55*, 380–386.

Hatchwell, B. J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *The American Naturalist*, *154*, 205–219.

Hatchwell, B. J. (2004). Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*, *15*, 1–10.

Heinsohn, R. G. (1995). Hatching asynchrony and brood reduction in cooperatively breeding white-winged choughs *Corcorax melanorhamphos*. *Eme*, *95*, 252–258.

Heinsohn, R. G. (2004). Parental care, load-lightening and costs. In W. D. Koenig & J. L. Dickinson (Eds.), *Ecology and evolution of cooperative breeding in birds* (pp. 67–80). Cambridge: Cambridge University Press.

Helfrecht, C., Roulette, J. W., Lane, A., Sintayehu, B., & Meehan, C. L. (2020). Life history and socioecology of infancy. *American Journal of Physical Anthropology*, *173*, 619–629, doi: 10.1002/ajpa.24145

Hewlett, B. S. (1988). Sexual selection and paternal investment among Aka pygmies. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behaviour: A Darwinian perspective*. Cambridge: Cambridge University Press.

Hewlett, B. S. (1991). Demography and childcare in preindustrial societies. *Journal of Anthropological Research*, *47*(1), 1–37.

Hewlett, B. S. (1992). Husband-wife reciprocity and the father-infant relationship among Aka Pygmies. In B. S. Hewlett (ed.), *Father-child relations* (pp. 153–176). New York: Aldine.

Hewlett, B. S., & MacFarlan, S. J. (2010). Fathers' roles in hunter-gatherer and other small-scale cultures. In M. E. Lamb (Ed.), *The role of the father in child development* (pp. 413–434. Hoboken, NJ: Wiley.

Hill, K., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. New York: Aldine.

Hillbruner, C. & Egan, R. (2008). Seasonality, household food security, and nutritional status in Dinajpur. *Bangladesh. Food and Nutrition Bulletin*, *29*, 221–231.

Hodge, S. J. (2005). Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*, 2479–2484.

Hrdy, S. (2009). *Mothers and Others: The evolutionary origins of mutual understanding*. Harvard: Harvard University Press.

Huda, T. M., Hayes, A., El Arifeen, S., & Dibley, M. J. (2018). Social determinants of inequalities in child undernutrition in Bangladesh: A decomposition analysis. *Maternal & Child Nutrition*, *14*, e12440.

Hurtado, A. M. & Hill, K. (1992). Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: Implications for modeling pair bond stability. In B. S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 31–55). New York: Aldine de Gruyter.

Hurtado, A. M., Hill, K., Kaplan, H., & Hurtado, I. (1992). Trade-offs between female food acquisition and child care among Hiwi and Ache foragers. *Human Nature*, *3*, 185–216.

Huss-Ashmore, R. (1988). Introduction: Why study seasons? In R. Huss-Ashmore, J. J. Curry, & R. K. Hitchcock (Eds.), *Coping with Seasonal Constraints* (pp. 5–8, vol. *5*). Research Papers in Science and Archaeology. University of Philadelphia: The Museum Applied Science Center for Archaeology; MASCA.

ICDDRB (2018). *Health and demographic surveillance system—MATLAB: Annual Report (Scientific Report No. 140). Mohakhali*. Dhaka: ICDDRB.

Imran, M. I. K., Inshafi, M. U. A., Sheikh, R., Chowdhury, M. A. B., Uddin, M. J. (2019). Risk factors for acute respiratory infection in children younger than five years in Bangladesh. *Public Health*, *173*, 112–119.

Ivey, P. (2000). Cooperative reproduction in the Ituri Forest hunter-gatherers: Who cares for Efe infants? *Current Anthropology*, *41*, 856–866.

Johnson, D. E., Miller, L. C., Iverson, S., Thomas, W., Franchino, B., Dole, K., Kiernan, M. T., Georgieff, M. K., & Hostetter, M. K. (1992). The health of children adopted from Romania. *JAMA*, *268*, 3446–3451.

Kennedy, E., & Peters, P. (1992). Household food security and child nutrition: The interaction of income and gender of household head. *World Development*, *20*, 1077–1085.

Johnson, S. E. (2003). Life history and the competitive environment: Trajectories of growth, maturation, and reproductive output among chacma baboons. *American Journal of Physical Anthropology*, *120*, 83–98.

Kennedy, E., & Peters, P. (1992). Household food security and child nutrition: The interaction of income and gender of household head. *World Development*, *20*, 1077–1085.

Kerhoas, D., Kulik, L., Perwitasari-Farajallah, D., Agil, M., Engelhardt, A., & Widdig, A. (2016). Mother-male bond, but not paternity, influences male-infant affiliation in wild crested macaques. *Behavioral Ecology and Sociobiology*, *70*, 1117–1130.

Kingma, S. A., Hall, M. L., Arriero, E. & Peters, A. (2010). Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: A consequence of fidelity? *Journal of Animal Ecology*, *79*, 757–768.

Kleiman, D. G. & Malcom, J. R. (1981). The evolution of male parental investment in primates. In D. J. Gubernick & P. H. Klopfer (Eds.) *Parental care in mammals* (pp. 347–387). New York: Plenum.

Koenig, W. D., & Mumme, R. L. (1990). Levels of analysis and the functional significance of helping behavior. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and explanation in the study of animal behavior* (pp. 269–303). Boulder, CO: Westview.

Komdeur, J. (1994). Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology*, *34*, 175–186.

Konner, M. (2005). Hunter-gatherer infancy and childhood: The !Kung and others. In B. Hewlett & M. Lamb (Eds.), *Hunter-gatherer childhoods* (pp. 19–64). New Brunswick, NJ: Aldine.

Kramer, K. L. (2005). Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology*, *14*, 224–237.

Kramer, K. L. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, *39*, 417–436.

Kramer, K. L., & Veile, A. (2018). Infant allocare in traditional societies. *Physiology of Behavior*, *193*, 117–126.

Krebs, J. R. & Davies, N. B. (1993). *An introduction to behavioural ecology* (3rd edn.). Oxford: Blackwell.

Kushnick, G. (2012). Helper effects on breeder allocations to direct care. *American Journal of Human Biology*, *24*, 545–550.

Kuzawa, C.W. (1998). Adipose tissue in human infancy and childhood: An evolutionary perspective. *American Journal of Physical Anthropology*, *107*, 177–209.

Lancaster, J. B. & Lancaster, C. S. (1983). Parental investment: The hominin adaptation. In D. Ortner (Ed.), *How humans adapt: A biocultural Odyssey* (pp. 33–65). Washington D.C: Smithsonian Press.

Langford, R., Lunn, P., Brick, C.P. (2011). Hand-washing, subclinical infections, and growth: A longitudinal evaluation of an intervention in Nepali slums. *American Journal of Human Biology*, *23*, 621–629.

Lee, R. D., & Kramer, K. L. (2002). Children's economic roles in the Maya family life cycle: Cain, Caldwell, and Chayanov revisited. *Population and Development Review*, *28*, 475–499.

Leech, K. A., Salo, V. C., Rowe, M. L., Cabrera, N. J. (2013). Father input and child vocabulary development: The importance of wh questions and clarification requests. *Seminars in Speech and Language*, *34*, 249–259.

Leonetti, D. L., Nath, D. C., Hemam, N. S., & Neill, D. B. (2004). Do women really need marital partners for support of their reproductive success? The case of the matrilineal Khasi of N.E. India. *Research in Economic Anthropology*, *23*, 151–174.

Levine, N. (1988). Women's work and infant feeding: A case from rural Nepal. *Ethnology*, *27*, 231–251.

Lindblade, K. A., Odhiambo, F., Rosen, D. H., DeCock, K. M. (2003). Health and nutritional status of orphans< 6 years old cared for by relatives in western Kenya. *Tropical Medicine & International Health*, *8*, 67–72.

Lohman, T. G., Roche, A. F., Martorell, R. (1988). *Anthropometric standardization reference manual*. Champaign, IL: Human Kinetics Publishers, Inc.

Lukas, D. & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, *341*, 526–530.

Lummaa, V., Clutton-Brock, T. (2002). Early development, survival and reproduction in humans. *Trends in Ecology & Evolution*, *17*, 141–147.

Marlowe, F. W. (2000). Paternal investment and the human mating system. *Behavioral Processes*, *51*, 45–61.

Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Berkeley: University of California Press.

Meehan, C. L. (2005). The effects of residential locality on parental and alloparental investment among the Aka foragers of the Central African Republic. *Human Nature*, *16*, 58–80.

Meehan, C. L. (2009). Maternal time allocation in two cooperative childrearing societies. *Human Nature*, *20*, 375–393.

Ménard, N., von Segesser, F., Scheffrahn, W., Pastorini, J., Vallet, D., Gaci, B., Martin, R. D., & Gautier-Hion, A. (2001). Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? Les relations males-enfants chez le magot (*Macaca sylvanus*): investissement paternal et/ou tactique d'accouplements? *Comptes Rendus de l'Académie des Sciences*, *324*, 601–610.

Milgram, B. L. (2011). Situating handicraft market women in Ifugao, Upland Philippines: A case for multiplicity. In L. J. Seligmann (Ed.), *Women traders in cross-cultural perspective: Mediating identities, marketing wares*. Stanford, CA: Stanford University Press.

Moehlman, P. D. (1979). Jackal helpers and pup survival. *Nature*, *277*, 382–383.

Moehlman, P., & Hofer, H. (1997). Cooperative breeding, reproductive suppression, and body mass in canids. In Solomon, N. & French, J. (Eds.), *Cooperative breeding in mammals* (pp. 76–128). Cambridge: Cambridge University Press.

Mølbak, K., Jensen, H., Ingholt, L., Aaby, P. (1997). Risk factors for diarrheal disease incidence in early childhood: A community cohort study from Guinea-Bissau. *American Journal of Epidemiology*, *146*, 273–282.

Møller, A. P., & Birkhead, T. R. (1993). Certainty of paternity covaries with paternal care in birds. *Behavioral Ecology and Sociobiology*, *33*, 261–268.

Montgomery, S. M., Bartley, M. J., Wilkinson, R. G. (1997). Family conflict and slow growth. *Archives of Disease in Childhood*, *77*, 326–330.

Moore, S. R., Lima, N. L., Soares, A. M., Oriá, R. B., Pinkerton, R. C., Barrett, L. J., Guerrant, R. L., & Lima, A. A. M. (2010). Prolonged episodes of acute diarrhea reduce growth and increase risk of persistent diarrhea in children. *Gastroenterology*, *139*, 1156–1164.

Mumme, R. L. (1992). Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology*, *31*, 319–328.

Mushtaq, M. U., Gull, S., Mushtaq, K., Abdullah, H. M., Khurshid, U., Shahid, U., Shad, M. A., Akram, J. (2012). Height, weight and BMI percentiles and nutritional status relative to the international growth references among Pakistani school-aged children. *BMC Pediatrics*, *12*, 31.

Nakagawa, S., & Scheilzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

National Institute of Population Research and Training, ICF (2019). *Bangladesh Demographic and Health Survey 2017–18: Key Indicators*. Dhaka, Bangladesh and Rockville, MD: NIPORT and ICF.

Nelson, R. G. (2016). Residential context, institutional alloparental care, and child growth in Jamaica. *American Journal of Human Biology*, *28*, 493–502.

Neyzi, O., Furman, A., Bundak, R., Gunoz, H., Darendeliler, F., & Bas, F. (2006). Growth references for Turkish children aged 6 to 18 years. *Acta Paediatrica*, *95*, 1635–1641.

Nti, C. A., Lartey, A. (2008). Influence of care practices on nutritional status of Ghanaian children. *Nutrition Research and Practice*, *2*, 93–99.

Ozmen, H., Akarsu, S., Polat, F., Cukurovali, A. (2013). The levels of calcium and magnesium, and of selected trace elements, in whole blood and scalp hair of children with growth retardation. *Iranian Journal of Pediatrics*, *23*, 125.

Page, A. E., Chaudhary, N., Viguier, S., Dyble, M., Smith, D., Salali, G., Mace, R., Migliano, A. B. (2017). Hunter-gatherer social networks and reproductive success. *Scientific Reports*, *7*, 1153.

Page A. E., Emmott E. H., Dyble M., Smith D., Chaudhary N., Viguier S., Migliano A. B. (2021). Children are important too: juvenile playgroups and maternal childcare in a foraging population, the Agta. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1827), https://doi.org/10.1098/rstb.2020.0026.

Panter-Brick, C. (1997). Seasonal growth patterns in rural Nepali children. *Annals of Human Biology*, *24*, 1–18.

Paynter, S., Ware, R. S., Lucero, M. G., Tallo, V., Nohynek, H., Simões, E. A. F., Weinstein, P., Sly, P. D., Williams, G., the ARIVAC Consortium (2013). Poor growth and pneumonia seasonality in infants in the Philippines: Cohort and time series studies. *PLOS ONE*, *8*, e67528.

Pelletier, D. L., E A Frongillo, J., Habicht, J. P. (1993). Epidemiologic evidence for a potentiating effect of malnutrition on child mortality. *American Journal of Public Health*, *83*, 1130–1133.

Pelletier, D. L., Frongillo, E. A., Jr, Schroeder, D. G., Habicht, J.-P. (1995). The effects of malnutrition on child mortality in developing countries. *Bulletin of the World Health Organization*, *73*, 443.

Pelto, G.H. (2000). Improving complementary feeding practices and responsive parenting as a primary component of interventions to prevent malnutrition in infancy and early childhood. *Pediatrics*, *106*, 1300–1300.

Perrone, M., & Zaret, T. M. (1979). Parental care patterns of fishes. *The American Naturalist*, *113*, 351–361. https://doi.org/10.1086/283394

Pollet, T.V., Nettle, D. (2008). Taller women do better in a stressed environment: Height and reproductive success in rural Guatemalan women. *American Journal of Human Biology*, *20*, 264–269.

Popkin, B. M. (1978). Economic determinants of breast-feeding behavior: The case of rural households in Laguna, Philippines. In W. H. Mosley (Ed.), *Nutrition and human Reproduction*. New York: Plenum Press.

Popkin, B. M. (1980). Time allocation of the mother and child nutrition. *Ecology of Food and Nutrition*, *9*, 1–13.

Prall, S. P. & Scelza, B. A. (2020). Why men invest in non-biological offspring: Paternal care and paternity confidence among Himba pastoralists. *Proceedings of the Royal Society, B: Biological Sciences*, *287*, 20192890.

Queller, D. C. (1997). Why do females care more than males? *Proceedings of the Royal Society B: Biological Sciences*, *264*, 1555–1557.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation.

Rah, J. H., Cronin, A. A., Badgaiyan, B., Aguayo, V. M., Coates, S., Ahmed, S. (2015). Household sanitation and personal hygiene practices are associated with child stunting in rural India: A cross-sectional analysis of surveys. *BMJ Open*, e005180-e005180, *5*.

Rahman, A., Iqbal, Z., Bunn, J., Lovel, H., Harrington, R. (2004). Impact of maternal depression on infant nutritional status and illness: A cohort study. *Archives of General Psychiatry*, *61*, 946–952.

Rigby, R. A., and Stasinopoulos, D. M. (2005). Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, *54*(3), 507–554.

Robertson, J., Puckering, C., Parkinson, K., Corlett, L., Wright, C. (2011). Mother–child feeding interactions in children with and without weight faltering; nested case control study. *Appetite*, *56*, 753–759.

Rotering, P. P. P., & Bras, H. (2015). With the help of kin? Household composition and reproduction in The Netherlands, 1842–1920. *Human Nature*, *26*, 102–121.

Russell, A., Young, A., Spong, G., Jordan, N., & Clutton-Brock, T. (2007). Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*, 513–520.

Sarker, A. R., Sultana, M., Mahumud, R. A., Sheikh, N., Van Der Meer, R., and Morton, A. (2016). Prevalence and health care-seeking behavior for childhood diarrheal disease in Bangladesh. *Global Pediatric Health*, *3*, 1–12.

Scelza, B. A. (2010). Fathers' presence speeds the social and reproductive careers of sons. *Current Anthropology*, *51*, 295–303.

Schlaudecker, E. P., Steinhoff, M. C., Moore, S. R. (2011). Interactions of diarrhea, pneumonia, and malnutrition in childhood: Recent evidence from developing countries. *Current Opinion in Infectious Diseases*, *24*, 496.

Schroeder, D.G., Brown, K.H. (1994). Nutritional status as a predictor of child survival: Summarizing the association and quantifying its global impact. *Bulletin of the World Health Organization*, *72*, 569.

Sear, R. (2006). Height and reproductive success. *Human Nature*, *17*, 405–418.

Sear, R. (2010). Height and reproductive success: Is bigger always better?. In U. J. Frey C. Störmer & K. P. Willführ (Eds.), *Homo novus—A human without illusions* (pp. 127–143). Berlin: Springer.

Sear, R., Mace, R., & McGregor, I. A. (2000). Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society, B: Biological Sciences*, *267*, 1641–1647.

Sear, R., Steele, F., McGregor, I. A., & Mace, R. (2002). The effects of kin on child mortality in rural Gambia. *Demography*, *39*(1), 43–63.

Sear, R. Mace, R., & McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, *24*, 25–42.

Sear, R., Allal, N., & Mace, R. (2004). Height, marriage and reproductive success in Gambian women. *Research in economic anthropology*, *23*, 203–224.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, *29*, 1–18.

Shah, P. (1978). *Main nutrition problems during the weaning period and their solution*. International Conference of Nutrition, Rio de Janeiro, Brazil.

Shenk, M. K., & Scelza, B. (2012). Paternal investment and status-related child outcomes: Timing of father's death affects offspring success. *Journal of Biosocial Science*, *44*, 549–569.

Shenk, M. K., Starkweather, K. E., Kress, H. C., & Alam, N. (2013). Does absence matter? A comparison of three types of father absence in rural Bangladesh. *Human Nature*, *24*, 76–110.

Solomons, N. W., Mazariegos, M., Brown, K. H., & Klasing, K. (1993). The underprivileged, developing country child: Environmental contamination and growth failure revisited. *Nutrition Reviews*, *51*, 327–332.

Sorenson Jamison, C., Cornell, L. L., Jamison, P. L., & Nakazato, H. (2002). Are all grandmothers equal? A review and a preliminary test of the "grandmother hypothesis" in Tokugawa Japan. *American Journal of Physical Anthropology*, *119*, 67–76.

Spencer, P. R., Sanders, K. A., Amaral, P. C., & Judge, D. S. (2017). Household resources and seasonal patterns of child growth in rural Timor-Leste. *American Journal of Human Biology*, *29*, 1–17.

Stan Development Team. (2021). Stan Modeling Language Users Guide and Reference Manual, Version 2.26. https://mc-stan.org

Stansbury, J. P., Leonard, W. R., & Dewalt, K. M. (2000). Caretakers, child care practices, and growth failure in highland Ecuador. *Medical Anthropology Quarterly*, *14*, 224–241.

Starkweather, K. E. (2017). Shodagor Family Strategies: Balancing work and family on the water. *Human Nature*, *28*(2), 138–166.

Starkweather, K. E., & Keith, M. H. (2018). Estimating impacts of the nuclear family and heritability of nutritional outcomes in a boat-dwelling community. *American Journal of Human Biology*, *30*(3), 1–17.

Starkweather, K. E., & Keith, M. H. (2019). Mother's work and child illness: Disease ecology of Shodagor women's work. Presented for the Evolutionary Anthropology Society at the 118th Annual Meeting. Vancouver, BC: American Anthropological Association.

Starkweather, K. E., Shenk, M. K., McElreath, R. (2020). Biological constraints and socioecological influences on women's pursuit of risk and the sexual division of labor. *Evolutionary Human Sciences*, *2*, e59.

Stewart, R. C. (2007). Maternal depression and infant growth—a review of recent evidence. *Maternal & Child Nutrition*, *3*, 94–107.

Stulp, G., Barrett, L. (2016). Evolutionary perspectives on human height variation. *Biological Reviews*, *91*, 206–234.

Surkan, P. J., Ettinger, A. K., Ahmed, S., Minkovitz, C. S., Strobino, D. (2012). Impact of maternal depressive symptoms on growth of preschool- and school-aged children. *Pediatrics*, *130*, e847–e855.

Tanaka, H., Kohda, M., & Frommen, J. G. (2018). Helpers increase the reproductive success of breeders in the cooperatively breeding cichlid *Neolamprologus obscurus*. *Behavioral Ecology and Sociobiology*, *72*, 152.

Thornhill, R. (1976). Sexual selection and paternal investment in insects. *The American Naturalist*, *110*, 153–163. https://doi.org/10.1086/283055

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man 1871–1971* (pp. 136–179). Chicago: Aldine de Gruyter.

Turke, P. (1988). Helpers at the nest: Childcare networks on Ifaluk. In L. Betzig, M. Borgerhoff Mulder, and P. Turke (eds.), *Human reproductive behavior: A Darwinian perspective* (pp. 173–188). Cambridge: Cambridge University Press.

Uauy, R., Kain, J., Mericq, V., Rojas, J., Corvalán, C. (2008). Nutrition, child growth, and chronic disease prevention. *Annals of Medicine*, *40*, 11–20.

Ulijaszek, S. J. & Strickland, S. S. (1993). *Seasonality and human ecology*. Cambridge: Cambridge University Press.

Urlacher, S. S., Blackwell, A. D., Liebert, M. A., Madimenos, F. C., Cepon Robins, T. J., Gildner, T. E., Snodgrass, J. J., Sugiyama, L. S., Sugiyama, L. S. (2016). Physical growth of the Shuar: Height, weight, and BMI references for an indigenous Amazonian population. *American Journal of Human Biology*, *28*, 16–30.

Urlacher, S. S., Ellison, P. T., Sugiyama, L. S., Pontzer, H., Eick, G., Liebert, M. A., Cepon-Robins, T. J., Gildner, T. E., Snodgrass, J. J. (2018). Trade-offs between immune function and childhood growth among Amazonian forager-horticulturalists. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, E3914-E3921.

Van IJzendoorn, M. H., Bakermans-Kranenburg, M. J., Juffer, F. (2007). Plasticity of growth in height, weight, and head circumference: Meta-analytic evidence of massive catch-up after international adoption. *Journal of Developmental & Behavioral Pediatrics*, *28*, 334–343.

Varghese, C. & Wachen, J. (2016). The determinants of father involvement and connections to children's literacy and language outcomes: Review of the literature. *Marriage and Family Review*, *52*, 331–359.

Victora, C. G., Barros, F. C., Kirkwood, B. R., Vaughan, J. P. (1990). Pneumonia, diarrhea, and growth in the first 4 y of life: A longitudinal study of 5914 urban Brazilian children. *The American Journal of Clinical Nutrition*, *52*, 391–396.

Voland, E. & Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioural Ecology and Sociobiology*, *52*, 435–443.

Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., Djurovic, G., Hames, R., Hurtado, A.M., Kaplan, H. (2006). Growth rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology*, *18*, 295–311.

Wang, H., Tian, X., Wu, S., Hu, Z. (2016). Growth disparity of motherless children might be attributed to a deficient intake of high-quality nutrients. *Nutrition Research*, *36*, 1370–1378.

Weisz, A., Meuli, G., Thakwalakwa, C., Trehan, I., Maleta, K., Manary, M. (2011). The duration of diarrhea and fever is associated with growth faltering in rural Malawian children aged 6–18 months. *Nutrition Journal*, *10*, 25.

Westneat, D. F., and Sherman, P. W. (1993). Parentage and the evolution of parental behavior. *Behavioral Ecology*, *4*, 66–77. https://doi.org/10.1093/beheco/4.1.66

Winking, J. & Koster, J. (2015). The fitness effects of men's family investments: A test of three pathways in a single population. *Human Nature*, *26*, 292–312.

Winking, J. (2006). Are men really that bad as fathers? The role of men's investments. *Social Biology*, *53*, 110–115.

Winking, J., Gurven, M., Kaplan, H., & Stieglitz, J. (2009). The goals of direct parental care among a South Amerindian population. *American Journal of Physical Anthropology*, *139*, 295–304.

Winking, J., Gurven, M., & Kaplan, H. (2011). Father death and adult success among the Tsimane: Implications for marriage and divorce. *Evolution and Human Behavior*, *32*, 79–89.

Wodnik, B. K., Freeman, M. C., Ellis, A. S., Awino Ogutu, E., Webb Girard, A., Caruso, B. A. (2018). Development and application of novel caregiver hygiene behavior measures relating to food preparation, handwashing, and play environments in Rural Kenya. *International Journal of Environmental Research and Public Health*, *15*, 1994.

Yeung, W., Sandberg, J., Davis-Kean, P., Hofferth, S. (2001). Children's time with fathers in intact families. *Journal of Marriage and Family*, *63*, 136–154.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Starkweather, K. E., Keith, M. H., Prall, S. P., Alam, N., Zohora, F., & Emery Thompson, M. (2021). Are fathers a good substitute for mothers? Paternal care and growth rates in Shodagor children. *Dev Psychobiol*, 1–24. https://doi.org/10.1002/dev.22148