CHAPTER 13

ALLOPARENTAL CARE AND THE ONTOGENY OF GLUCOCORTICOID STRESS RESPONSE AMONG STEPCHILDREN

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Introduction

The human child has evolved to be highly dependent upon care provided by others over a long developmental period (Bogin, 1999; Lancaster and Lancaster, 1987; Leigh, 2004). The altricial (helpless) infant requires a protective environment provided by intense parental and alloparental care in the context of kin groups (Chisholm, 1999; Hewlett and Lamb, 2005; Hrdy, 2005). The extended family is of paramount importance in a child's world. Throughout human evolutionary history, parents and close relatives provided calories, protection, and information necessary for survival, growth, health, social success, and eventual reproduction. The human mind is therefore likely to have evolved special sensitivity to interactions with family caretakers, particularly during infancy and early childhood (Belsky, 2005; Geary and Flinn, 2001).

The family and other kin provide important cognitive "landmarks" for a child's understanding of its social environment. A child's family environment may be an especially important source and mediator of psychosocial stress with consequent effects on health. In this chapter we investigate the effects of alloparental relationships on the development of stress response and concomitant health status among stepchildren in 'Bwa Mawego,' a rural community on the eastern coast of the Caribbean island-nation of Dominica.

Stepparent-stepchild relationships

Providing scarce resources to an unrelated child appears to run counter to the logic of kin selection. Step relationships were likely to have been commonplace during human evolution, providing a basis for natural selection to have designed human neurobiology to respond appropriately to available proximate cues for kin recognition (Alexander, 1990; Flinn, 1992; Hurtado and Hill, 1996). We might expect, therefore, that stepchildren would be at high risk for neglect and abuse (Daly and Wilson, 1995).

Stepchildren, however, are not simply unrelated parasites; they are a special type of relative-by-marriage. Similar to other affines or "in-laws," step relationships hinge on the marital/mating relationship of a genetic relative and are embedded in the context of broader social networks. Traditional human societies have extensive networks of kin reciprocity, with favours often returned indirectly. Assessment of a potential mate by a woman involves what he has to offer her relatives, especially her children from previous relationships. The availability of alternative caregiving sources, such as grandparents who are able and motivated to provide alloparental investment, may be important considerations when evaluating new mating relationships. From the perspective of the child, there may be a wide range of relatives from whom to seek investment. For the stepchild, kin outside the immediate family may be of particular importance.

The initial establishment of a new mating relationship by a parent is a period of high risk for sub-optimal caretaking and, potentially, psychosocial stress, morbidity, and growth disruptions. The power dynamic between a child's parent and the new mate seems critical. Women with more to offer relative to their mates are in a position to demand more in the way of stepparental care. Emotional mediation (Aureli and Schaffner, 2001) in such relationships might be expected to result in greater feelings of tolerance or affection towards children of women with high perceived mate value. Conversely, women with less to offer may be less able to prevent neglect or abuse of their children. Indeed, if children from a previous relationship are a serious impediment to the establishment of new relationships, mothers may themselves be motivated to remove or minimize their own parental obligations. Here again, alloparents may be relied upon to take over caregiving responsibilities when parents seek to reduce investment in their offspring.

Social reputations are another important consideration. Humans observe and gossip about one another. Men and women who mistreat children may be stigmatized and considered less desirable as partners or social allies. In the case of potential stepfathers, it may be in a man's interests to convey the impression of a "good caretaker." Once having obtained the initial approval of a mother, however, negotiations concerning investment in her offspring are not finished. Stepchildren are active participants in the brokering of the new family deals, working hard to create the best situations for themselves. Because the presence of a stepfather may not be in their strategic interests, stepchildren may be upset by the new arrangements, and behave badly from the perspective of their stepfathers, who in turn may be frustrated by their mates' objections to steppaternal discipline. Stepchildren may be especially motivated to seek support from relatives outside the natal household, sometimes transferring residence if that is a viable option. And stepchildren are likely to leave the natal household at an earlier age to establish a new residence than are children co-resident with both genetic parents. For example, in the community of 'Grande Anse,' Trinidad (all specific places and names used in this chapter are pseudonyms) young women were more likely to emigrate from their natal households if a stepparent was co-resident (Flinn 1988b). Similarly, in the community of 'Bwa Mawego,' Dominica, the rate of emigration from maternal natal households (excluding school related residence changes) before age 17 is higher for stepchildren (15/21; 71.4%) than for non-stepchildren (5/23; 21.7%) during the 1990s.

Pregnancy and birth of a child fathered by the new mate complicates the situation. Now stepchildren are competing directly with their stepfather's genetic offspring for parental care. Mothers may be less able to defend the interests of their children from previous relationships because mothers are more dependent upon their new mates to provide for the new babies and, burdened with new babies, they are less attractive to other males (e.g., Flinn, 1988a). The utility of stepchildren as alloparental caregivers (e.g., "baby-sitters") or as links to useful social connections for their maternal half-siblings may provide a rationale for continued tolerance by stepfathers.

Some of the challenges faced by stepchildren change with age. Social and economic support of a father can be critical for young adult males to acquire the resources and social status necessary to attract mates in many societies. Sexual pressure from stepfathers and the need to obtain support from adult males may influence adolescent girls to establish mating relationships that facilitate leaving the stepfamily environment. These aspects of family environment may influence life history traits such as age at menarche (Ellis et al., 2003; Quinlan, 2006).

In summary, the absence of a genetic relation between stepchildren and stepparents may affect the quality and quantity of care — including specific behaviors that affect nutrition, sleep routines, hygiene, medical attention, work loads, breastfeeding, instruction, comforting, protection, and so forth — with consequent effects on psychosocial stress and child well being (Daly and Wilson, 1988a, 1988b; Dunn, 2004; Flinn, 1988a; Flinn, et al., 1999; Hetherington, 2003a, 2003b). Stepchildren, therefore, may be in special need of care from relatives outside their natal households, such as nearby grandparents, aunts and uncles, older siblings, and even great-grandparents.

Stress response mechanisms

Current psychosocial stress research suggests that the stress hormone cortisol is stimulated by uncertainty that is perceived as significant and for which behavioral responses will have unknown effects (Dickerson and Kemeny, 2004; Kirschbaum and Hellhammer, 1994). Cortisol release is associated with unpredictable, uncontrollable events that require full alert readiness and mental anticipation. In appropriate circumstances, temporary moderate increases in stress hormones (and associated neurotransmitters such as dopamine) may enhance mental activity for short periods in localized areas and prime memory storage, hence improving cognitive processes for responding to social challenges (Beylin and Shors, 2003; Boyce and Ellis, 2005; Hui et al., 2004; LeDoux, 2003; McGaugh, 2004; de Quervain et al., 2000). Mental processes unnecessary for appropriate response may be inhibited, perhaps to reduce external and internal "noise" (Servan-Schreiber et al., 1990; cf. Kirschbaum et al., 1996; Lupien et al., 2002; Newcomer, et al., 1994).

Stress response involves an optimal allocation problem (Sapolsky, 1994). Energy resources are diverted to muscular and immediate immune functions and other short-term (stress emergency) functions, at cost to long-term functions of growth, development, and building immunity. Under normal conditions of temporary stress, there would be little effect on health. Indeed, there may be brief enhancement and directed trafficking of immune (Dhabbar and McEwen, 2001) and cognitive function. Persistent stress and associated hyper- or hypo-cortisolemia, however, is posited to result in pathological immunosuppression, depletion of energy reserves, and damage to or inhibition of neurogenesis in parts of the hippocampus (e.g., Santarelli et al, 2003; Sheline, Gado, and Kraemer, 2003). This perspective highlights the problems with a stress response system that evolved to cope with short-term emergencies. The chronic stress produced by modern human – or other primates with complex relationships – social environments may present novel challenges that the system is not designed to handle, hence potentially resulting in maladaptive pathology (Sapolsky, 1994).

The strict version of the novelty hypothesis, however, is difficult to reconcile with the long evolutionary histories of complex sociality in primates, and especially humans, accompanied by dramatic changes in the brain. Why, given all the extensive modifications of the human brain, would selection not have weeded out this apparent big mistake? Modern human environments have many novelties that elicit stress response, but social challenges in general seem to have a much more ancient evolutionary depth, and may be a key selective pressure for the large human brain (Alexander, 1989; Flinn, 2006). One possibility is that the demands of preparing for potential dangers are an unavoidable costly insurance, akin to expensive febrile response to pathogens that are usually benign – the "smoke-detector" principle (Nesse and Young, 2000). The idea is that, although physiological stress response to social challenges is costly, and most often wasteful, it may have helped our ancestors cope with rare and unpredictable serious conflicts often enough to be maintained by selection. The benefit/cost ratio could be improved by fine-tuning stress mechanisms in response to environmental conditions during ontogeny. A complementary approach to the mismatch hypothesis suggests that the neuroendocrine stress response may guide adaptive neural reorganization, such as enhancing predator detection and avoidance mechanisms (Buwalda et al., 2005; Dal Zatto et al., 2003; Le Doux, 2000; Manzanares et al., 2005; Meaney, 2001; Wiedenmayer, 2004). The neurological effects of the stress response may underlie adaptation to both short-term contingencies and guide long-term ontogenetic adjustments of behavioural strategies (Flinn, 2006b).

If physiological stress response promotes adaptive modification of neural circuits in the limbic and higher associative centers that function to solve psychosocial problems (Huether et al, 1999), then the paradox of psychosocial stress would be partly resolved. Temporary elevations of cortisol in response to social challenges could have advantageous developmental effects involving synaptogenesis and neural reorganization (Buchanan and Lovallo, 2001; Huether, 1996, 1998) if such changes are useful and necessary for coping with the demands of an unpredictable and dynamic social environment. Elevating stress hormones in response to social challenges makes evolutionary sense if it enhances specific acute mental functions and helps guide cortical remodeling of 'developmental exuberance' (Innocenti and Price, 2005; Sur and Rubenstein, 2005). Alloparental care, particularly comfort and advice, may be important for this developmental process.

Ontogeny of stress response to psychosocial stimuli: The Dominica study

Assessment of relationships among psychosocial stressors, hormonal stress response, and health is complex, requiring (a) longitudinal monitoring of social environment, emotional states, hormone levels, immune measures, and health, (b) control of extraneous effects from physical activity, circadian rhythms, and food consumption, (c) knowledge of individual differences in temperament, experience, and perception, and (d) awareness of specific social and cultural contexts. Multi-disciplinary research that integrates human biology, psychology, and ethnography is particularly well suited to these demands (Bogin, 1999; Panter-Brick, 1998; Werner, 1985). Physiological and medical assessment in concert with ethnography and coresidence with children and their families in anthropological study populations can provide intimate, prospective, longitudinal, naturalistic information that is not feasible to collect in clinical studies. For the past eighteen years (1988 – present) I have conducted such research with the help of many colleagues and students and the extraordinary cooperation of a wonderful study population.

The study village

"Bwa Mawego" is a rural community located on the east coast of Dominica. About 500 residents live in 160 structures/households that are loosely clumped into five "hamlets" or neighbourhoods. The population is of mixed African, Carib, and European descent. The community is isolated because it sits at the dead-end of a rough road. Part-time residence is common, with many individuals emigrating for temporary work to other parts of Dominica, other Caribbean islands, the United States, the United Kingdom, or Canada. Most residents cultivate bananas and/or bay leaves as cash crops, and plantains, dasheen, and a variety of fruits and vegetables as subsistence crops. Fish are caught by free diving with spear guns and using lines and nets from small boats (hand built wooden "canoes" of Carib design). Land is communally "owned" by kin groups, but parceled for long-term individual use.

Most village houses are strung closely together along roads and tracks. Older homes are constructed of wooden planks and shingles hewn by hand from local forest trees; concrete block and galvanized roofing are more popular today. Most houses have one or two sleeping rooms, with the kitchen and toilet as outbuildings. Children usually sleep together on foam or rag mats. Wealthier households typically have "parlours" with sitting furniture. Electricity became available in 1988; during the summer of 1995 about 70% of homes had "current," 41% had telephones, 11% had refrigerators, and 7% had televisions. Water is obtained from streams, spring catchments, and run-off from roofs; public piped water became available in June 1999, but few households are connected.

The community of Bwa Mawego is appropriate for the study of relations between a child's social environment and physiological stress response for the following reasons: (1) there is substantial variability among individuals in the factors under study (family environments, social challenges, and stress response), (2) the village and housing are relatively open, hence behaviour is easily observable, (3) kin tend to reside locally, (4) the number of economic variables is reduced relative to urban areas, (5) the language and culture are familiar to the investigator, (6) there are useful medical records, and (7) local residents welcome the research and are most helpful.

The study involves 282 children and their caregivers residing in 84 households. This is a nearly complete sample (> 98%) of all children living in four of the five village hamlets during the period of fieldwork. Of these, 48 children in 18 families were co-resident with a stepfather during some period of the research.

Methods and field techniques

In this study, sequential longitudinal monitoring was used to identify associations among psycho-social stress, health, and alloparental care among stepchildren. Data analyses examined both long term (ten years) and short term (day-to-day, hour-by-hour) associations among cortisol levels, family composition, socioeconomic conditions, behavioural activities, events, temperament, growth, medical history, immune measures, and illness. Saliva is collected from children by members of the research team at least twice a day, wherever the children happen to be (usually at their household). This direct collection and observation procedure avoids errors that occur with at-home self- or parent-collection and report protocols. Access to pharmaceuticals is rare, so extraneous effects of medications (such as aspirin on cortisol levels) are very limited. The large sample size of cortisol measures for each child (>100 samples for most children) in a variety of naturalistic contexts provides a much more extensive and reliable picture of hypothalamic-pituitary-adrenal (HPA) stress response than small sample designs.

Data analyses examine both long term (10+ years) and short term (day-to-day, hour-by-hour) associations among cortisol levels, family composition, socioeconomic conditions, behavioural activities, events, temperament, growth, medical history, immune measures, and illness. *Physiological stress response* is assessed by radioimmunoassay (RIA) of cortisol levels in saliva. Analyses include mean values, variation, and day-to-day and hour-by-hour profiles of standardized (circadian time controlled z-scores by 5-minute intervals from wake-up time) cortisol data (Flinn, 1999; Flinn and Quinlan, in prep.). *Family composition* is assessed by age, sex, genealogical relationship, and number of individuals in the household. *Caregiving* is assessed by (a) observed frequencies and types of behavioral interaction, (b) informant ratings of caregiving that children received, and (c) informant interviews. Here we use a dichotomous (above median, below median) composite measure of alloparental caregiving. *Immune response* is assessed by turbidimetric immunoassay of secretory-immunoglobulin A from saliva; however, relatively few samples have been assayed (N=212), and interpretation is uncertain, so inferences are preliminary. *Health* is assessed by (a) observed type, frequency, and severity of medical problems (diarrhea, influenza, common cold, asthma, abrasions, rashes, etc.; most of the morbidity data analyzed here are from the period 1989-94), (b) informant (parents, teachers, neighbors) ratings, (c) medical records, (d) growth (standard anthropometric measures, including height, weight, and skinfolds) and fluctuating asymmetry patterns (Flinn et al., 1999) and (e) physical examination by a medical doctor. The primary measure of health used here is *percentage of days ill,* the proportion of days that a child was observed (directly by researchers) with common benign temporary infectious disease (89% were common-cold upper respiratory tract infections with nasal discharge, cough, or myalgia — e.g., rhinovirus, adenovirus, parainfluenza, and influenza; 6% were diarrhoeal; 5% were miscellaneous indeterminate — e.g., febrile without other symptoms). *Daily activities* and *emotional states* are assessed from (a) caretaker and child self-report questionnaires, and (b) systematic behavioural observation (focal follow and instantaneous scan sampling). Multiple sources of information are crosschecked to assess reliability (Bernard et al., 1984).

In the following section I briefly review some of the results from this study that may provide useful insights into the ontogeny of stress response to psycho-social challenges.

Cortisol response to naturally occurring social challenges

Our analyses of naturally occurring stressors in children's lives in Bwa Mawego indicate that social challenges are important stressors, with the emphasis upon the family environment as both a primary source and mediator of stressful stimuli (Flinn and England, 1995, 1997, 2003; Turner et al., 1995). Temporary moderate increases in cortisol are associated with common activities such as eating meals, active play (e.g., cricket), and hard work (e.g., carrying loads of wood to bay oil stills) among healthy children. These moderate stressors – "arousers" might be a more appropriate term – usually have rapid attenuation, with cortisol levels diminished to normal within an hour or two (some stressors have characteristic temporal "signatures" of cortisol level and duration).

High-stress events (cortisol increases from 100% to 2000%), however, most commonly involved trauma from family conflict or change (Flinn and England, 2003; Flinn et al., 1996). Punishment, quarreling, and residence change substantially increased cortisol levels, whereas calm, affectionate contact was associated with diminished (-10% to -50%) cortisol levels. Of all the cortisol values that were more than two standard deviations above mean levels (i.e., indicative of substantial stress), 19% were temporally associated with traumatic family events (residence change of child or parent/caretaker, punishment, "shame," serious quarreling, and/or fighting) within a 24-hour period – for comparison, 12% were associated with minor family conflicts, 9% with peer conflicts or school problems, 8% with illness, and 6% with physical exertion, the next highest categories; 43% had no recorded abnormal event. In addition, 42% of traumatic family events were temporally associated with substantially elevated cortisol (i.e., at least one of the saliva samples collected within 24 hours was > 2 SD above mean levels) – other consistent predictors of elevated cortisol included illness with fever and high profile competitive sports events. Chronic elevations of cortisol levels may also occur, but are more difficult to assess quantitatively.

There was considerable variability among children in cortisol response to family disturbances. Not all individuals had detectable changes in cortisol levels associated with family trauma. Some children had significantly elevated cortisol levels during some episodes of family trauma but not during others. Cortisol response is not a simple or uniform phenomenon. Numerous factors, including preceding events, habituation, specific individual histories, context, and temperament, might affect how children respond to particular situations.

Nonetheless, traumatic family events and social self-conscious emotions such as guilt and shame (Flinn, in press a) were associated with elevated cortisol levels for all ages of children more than any other factor that we examined. These results suggest that family interactions were a critical psychosocial stressor in most children's lives, although the fact that the sample was biased towards collection during periods of relatively intense family interaction (early morning and late afternoon) may have exaggerated this association.

Children residing in bi-parental, single mother with kin, and grandparental households have moderate cortisol levels (Figure 1), with a higher proportion of elevations occurring in the context of positive affect situations such as competitive play, physical work, and excitement regarding novel situations. Comparison of mean cortisol levels of stepchildren with those of their half-siblings living in the same household (their mutual mother's co-resident spouse is their stepfather and genetic father, respectively) indicates a similar pattern of elevated cortisol for stepchildren (Figure 2).

Figure 1 about here
Figure 2 about here.

Although elevated cortisol levels are associated with traumatic events such as family conflict, long-term stress may result in diminished cortisol response. In some cases, chronically stressed children had blunted response to physical activities that normally evoked cortisol elevation. Comparison of cortisol levels during "nonstressful" periods (no reported or observed crying, punishment, anxiety, residence change, family conflict, or health problem during 24-hour period before saliva collection) indicates a striking reduction and, in many cases, reversal of the family environment-stress association (Flinn and England, 2003). Chronically stressed children sometimes had subnormal cortisol levels when they were not in stressful situations. For example, cortisol levels immediately after school (walking home from school) and during noncompetitive play were lower among some chronically stressed children (cf. Long, Ungpakorn, and Harrison, 1993). Some chronically stressed children appeared socially "tough" or withdrawn and exhibited little or no arousal to the novelty of the first few days of the saliva collection procedure. These sub-normal profiles may be similar in some respects to those of individuals with post traumatic stress disorder (e.g., Yehuda et al., 2005).

Although elevated cortisol levels in children are usually associated with negative affect, events that involve excitement and positive affect also stimulate the stress response (Flinn, in press a). For example, cortisol levels on the day before Christmas were more than one standard deviation above normal, with some of the children from two-parent households and those having the most positive expectations exhibiting the highest cortisol (Flinn, in press b). Cortisol response appears sensitive to social challenges with different affective states. Other studies further suggest that the cognitive effects of cortisol may vary with affective states, such as perceived social support (Ahnert et al., 2004; Quas et al., 2004).

There are some age and sex differences in cortisol profiles, but it is difficult to assess the extent to which this is a consequence of neurological differences (e.g., Butler et al., 2005), physical maturation processes, or the different social environments experienced, for example, during adolescence as compared with early childhood (Flinn et al, 1996; Flinn and Quinlan, in preparation; Geary and Flinn, 2002). For instance, young adult women have a higher incidence of depression and associated abnormal cortisol profiles than children or young men in this community.

The emerging picture of HPA stress response in naturalistic context from the Dominica study is one of sensitivity to social challenges (Flinn, in press b), consistent with clinical and experimental studies. The results further suggest that family environments are an especially important source and mediator of stressful social challenges for children. Children from difficult family environments usually have higher average cortisol levels because they have a higher frequency of stressful events, and they may ruminate trying to solve their difficult social problems. This focus of stress response on family issues unfortunately may leave fewer resources available for coping with other stressors such as school and peer relationships. In brief, elevating cortisol is not so much the problem as is what cortisol is elevated for. In the next section data on the longitudinal effects of early traumatic experiences are examined to assess the domain-specificity of changes in stress response.

Ontogeny: the early trauma → HPA dysfunction hypothesis

Early experiences can have profound and permanent effects on stress response. Exposure to pre-natal maternal stress, or prolonged separation from mothers in rodents and non-human primates, can result in life-long changes in HPA stress response (Maccari, et al., 2003; Meaney 2001; Suomi, 1997, 2005; cf. Levine, 2005). Research on the developmental pathways has targeted the homeostatic mechanisms of the HPA system, which appear sensitive to exposure to high levels of glucocorticoids during ontogeny. Glucocorticoid receptors in the hippocampus that are part of the negative feedback loop regulating release of corticotropin-releasing hormone (CRH) and adrenocorticotropic hormone (ACTH) can be damaged by the neurotoxic levels of cortisol associated with traumatic events (Sapolsky, 1992b, 2003, 2005). Hence early trauma is posited to result in permanent HPA dysregulation and hypercortisolemia, with consequent deleterious effects on the hippocampus, thymus, and other key neural, metabolic, and immune system components (Mirescu et al., 2004; Zhang et al., 2005). These effects have additional consequences resulting from high density of glucocorticoid receptors in the pre-frontal cortex in primates (DeKloet et al., 1999; Patel et al., 2000; Sanchez et al., 2000).

Children in the Bwa Mawego study who were exposed to the stress of hurricanes and political upheavals during infancy or *in utero* do not have any apparent differences in cortisol profiles in comparison with children who were not exposed to such stressors. Children exposed to the stress of parental divorce, death, or abuse (hereafter "early family trauma" or EFT), however, have significantly higher cortisol (Figure 3a) and higher morbidity (Figure 3b) levels at age ten than other children. Based on analogy with the non-human research, two key factors could be involved: (1) diminished hippocampal glucocorticoid receptor functioning, resulting in less effective negative feedback regulation of cortisol levels; and (2) enhanced sensitivity to perceived social threats. Children usually elevate cortisol in response to strenuous physical activity, but rapidly return to normal levels (see example in Figure 4). If EFT has affected the negative feedback loop, then recovery to normal cortisol levels would be slower. Contrary to this damaged feedback loop hypothesis, resumption of normal cortisol levels after physical stressors is similar regardless of early experience of family trauma (Flinn, 2006b). Cortisol profiles following social stressors, however, indicate that EFT children sustain elevated cortisol levels longer than non-EFT children (Flinn 2006b).

Figure 3a about here
Figure 3b about here
Figure 4 about here

The enhanced HPA stress response of children in this community that were exposed to EFT appears primarily focused on social challenges, suggesting that the ontogenetic effects of early trauma on stress response may be domain-specific and even context-specific. These results are consistent with studies of the effects of social defeat with non-human models (e.g., Kaiser and Sachser, 2005). In the following section we examine the potentially mediating effects of close alloparental relationships on the stress response of stepchildren, most of whom experienced EFT.

Alloparental care and stepchild stress and health

Comparative analysis of the patterns of stress response for stepchildren in the previous two sections indicate that early family trauma is associated with higher cortisol levels among children in this community, particularly in response to unpredictable social challenges (see also Flinn, 2006b, 2006d). The different cortisol response patterns to social and physical stressors suggest that domain-specific mechanisms have been affected by EFT. In this section we examine whether close relationships with alloparents during early childhood are associated with individual differences among stepchildren in several outcome measures. The general hypothesis is that alloparental care reduces psychosocial stress for stepchildren. The potential negative effects of the stepfamily environment on child development are predicted to be moderated by alloparental care, as measured by cortisol levels, growth, and morbidity. This is a risky hypothesis for several reasons. Perhaps, most importantly, children who have endured the most difficult family home environments may be most likely to seek outside care. Here we do not evaluate or control for such differences among stepchildren.

Analyses of data indicate that stepchildren who have close relationships with alloparents (high alloparental care) have lower cortisol (Figure 5a), lower morbidity (Figure 5b), and higher growth percentiles (Figure 5c) than stepchildren with low alloparental care. Stepchildren that have high alloparental care do not have lower average fluctuating asymmetry (Figure 5d) or lower gastrointestinal parasite loads (Figure 5e) than stepchildren with low alloparental care.

Figure 5a about here
Figure 5b about here
Figure 5c about here
Figure 5d about here
Figure 5e about here

These results are generally consistent with the hypothesis that alloparents make important material (e.g., providing meals) and psychological contributions to stepchild well-being in this population. From these analyses it is not possible to determine the extent to which alloparents help stepchildren develop social competencies, nor the relations between social competencies and health outcome measures. It is our general impression, however, from watching interactions between children and their grandparents, aunts and uncles, siblings, and other relatives over nearly two decades that such relationships are of great importance for the development of emotional regulation, social skills, and self-confidence, especially for children in difficult family environments.

Conclusions

Alloparental care appears to be a significant mediator of HPA stress response and associated morbidity among stepchildren in the study community. Maternal grandmothers are especially important alloparents, although a variety of other kin (e.g., aunts, siblings, grandfathers) may also contribute, and in special cases, may be primary caregivers. These results are likely to be specific to the context of the kin networks of this community, and are likely to be contingent upon the specific patterns of kinship, although maternal grandparent-grandchild relationships appear to be broadly important cross-culturally (Lahdenperå et al, 2004; Sear et al, 2000; Voland and Biese, 2002). These results are consistent with the hypotheses that the importance of alloparents in human evolution may involve their role as providers of social information (e.g., emotional comfort, social competencies, traditions – see Coe, 2003) in addition to providing calories and protection (Alexander, 1974; Hawkes, 2003; Hrdy, 2005).

Returning to the paradox of why natural selection favoured sensitivity of stress response to social stimuli in the human child, several points emerge. Human childhood is a life history stage that appears necessary and useful for acquiring the information and practice to build and refine mental algorithms critical for negotiating the social coalitions that are key to success in our species. Mastering the social environment presents special challenges for the human child. Results from the Dominica study indicate that family environment is a primary source and mediator of stressful events in a child's world. The sensitivity of stress physiology to the social environment may facilitate adaptive responses to this most salient and dynamic puzzle.

Coping with social challenges, however, can have significant health consequences, ranging from dysregulation of emotional control and increased risk of psychopathology (Gilbert, 2001, 2005; Nesse, 1999) to broader health issues associated with social and economic disparities (Adler et al., 1994; Barker, 1998; Dressler et al, 2005; Marmot, 2004; Marmot and Wilkinson, 1999). The potential for intergenerational cycles that perpetuate social relationships promoting stress and poor health are of particular concern (Belsky, 2005; Belsky et al., 2005; Fleming et al., 2002; Francis et al., 1999; Maestripieri et al., 2005) .

We are still far from identifying the specific connections from family environment, to stress response, to the ontogenetic plasticity of components of the limbic system and pre-frontal cortex that are involved with the acquisition of social competencies. An evolutionary developmental perspective can be useful for understanding this critical aspect of a child's world by integrating knowledge of physiological causes with the logic of adaptive design by natural selection. It reminds us that our biology and psychology have been profoundly affected by our evolutionary history as fundamentally social creatures.

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