



Child mortality and parental grief: An evolutionary analysis

Tania Reynolds^{a,*}, Brian Boutwell^{b,c}, Todd K. Shackelford^d, Viviana Weekes-Shackelford^e, Joseph Nedelec^f, Kevin Beaver^g, Mohaned G. Abed^h

^a Indiana University, Kinsey Institute & Department of Gender Studies, 420 Lindley Hall, 150 S. Woodlawn Ave, Bloomington, IN, 47405, USA

^b The University of Mississippi, Department of Legal Studies, H311 Hedleston Hall University, MS, 38677, USA

^c John D. Bower School of Population Health, University of Mississippi Medical Center, USA

^d Oakland University, Department of Psychology, 112 Pryale Hall, 654 Pioneer Dr., Rochester, MI, 48309, USA

^e Department of Sociology and Anthropology, 112 Pryale Hall, 654 Pioneer Dr., Rochester, MI, 48309, USA

^f University of Cincinnati, School of Criminal Justice: 660E Teachers College, Cincinnati, OH, 45221, USA

^g Florida State University, College of Criminology and Criminal Justice, 315C Eppes Hall, 112 S. Copeland St, Tallahassee, FL, 32306, USA

^h King Abdulaziz University, 315C Eppes Hall, 112 S. Copeland St, Tallahassee, FL, 32306, USA

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ABSTRACT

Across most of human history, infant and child mortality rates were very high, suggesting the death of a child was a challenge faced by many ancestral parents. Prolonged grief likely harmed grievers' fitness, yet grief is ubiquitous and often protracted, thereby presenting a puzzle for evolutionary arguments. We integrate existing theories of grief with patterns of parental bereavement to examine how human psychology has been shaped to respond to the death of a child. We contend that variation in life history strategy may explain the relative difficulty with which individuals recover from losing a child. We propose that the same physiological mechanisms underlying detachment and grief during dissolved romantic relationships may also underlie the intensity of parental attachment and bereavement. This theoretical review thus integrates evolutionary theory with extant grief research to provide a functional analysis of the immense suffering associated with the loss of a child.

Central to Darwin's (1859) theory of evolution by natural selection is differential reproductive success. Across human history, reproduction required that humans solved myriad adaptive problems, including attracting and retaining mates (Buss, 1988), conception, gestation, parturition, and raising offspring to reproductive age (Mace, 2000; Volk & Atkinson, 2013). Natural selection constructed human psychology over evolutionary history to solve these recurring adaptive obstacles through both biological predispositions and the erection of cultural tradition (Buss, 1995; Pinker, 1997; Tooby & Cosmides, 1992).

In the current article, we address one adaptive problem recurrently faced by ancestral humans: the death of a child. Previous work has addressed parental investment, with much research focused on attachment to offspring as a mechanism for enhancing children's survival (Bowlby, 1969/1982; Harris, 2011; Simpson & Belsky, 2008). However, less research has applied evolutionary theory to address how parents respond to a child's death. Nonetheless, estimates suggest infant and child mortality rates were very high over human history, indicating that ancestral parents may have evolved capacities to recover from the

emotional trauma of a child's death to pursue other fitness-relevant goals. Nonetheless, losing a child is perhaps one of the most painful experiences a human could endure, leading often to substantial dysfunction. The ubiquity and intensity of parental grief therefore present a paradox for evolutionary accounts of grief. With such detriments to grieving parents' fitness, how was such a costly emotional and behavioral response to a child's death maintained in the population? We evaluate the various evolutionary explanations of the human grief response for 1.) their ability to account theoretically for detriments to grievers' fitness as well as for their 2.) their coherence with the empirical literature on the trajectory and manifestations of the parental grief response. That is, we leverage both evolutionary logic and empirical data to adjudicate each hypothesis' power to account for the costliness of parental grief as well as the variation in dysfunction among bereaved parents.

Although the loss of a child is incredibly painful for most individuals, not all bereaved parents experience grief to the same extent. We therefore forward arguments based in inclusive fitness and life history theory

* Corresponding author. Kinsey Institute & Department of Gender Studies, Indiana University, Bloomington, USA.

E-mail addresses: tareyn@iu.edu (T. Reynolds), bboutwe@olemiss.edu (B. Boutwell), shackelf@oakland.edu (T.K. Shackelford), weekesh@oakland.edu (V. Weekes-Shackelford), joseph.nedelec@uc.edu (J. Nedelec), kbeaver@fsu.edu (K. Beaver), mabed@kau.edu.sa (M.G. Abed).

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to explain variation in both parental investment and bereavement. Life history theory contends that in response to the environmental conditions, individuals develop coordinated patterns of traits, which predict attachment to both mates and offspring. We therefore propose that the speed with which bereaved individuals recover from the loss of a child may rely on the same mental architecture associated with disinvestment from dissolved romantic relationships (Boutwell, Barnes, & Beaver, 2015). Specifically, we contend that the psychological and neurological mechanisms promoting romantic disinvestment also facilitate recovery following the death of a child.

1. Prevalence of infant and child death

Prior to the emergence of modern medicine, sanitation practices, and law enforcement, infancy and childhood presented an array of life-threatening perils (Stearns, 2006). Volk and Atkinson (2008, 2013) estimated that the average mortality rate was roughly 25% for infants and 40–50% for children across human evolution. That is, nearly half of our would-be ancestors did not survive to reproductive age. Among modern hunter-gatherers and forager-horticulturalists, 43% and 36% of children perished before reaching age 15 years, respectively (Gurven & Kaplan, 2007). Compared to other ape species, humans suffered higher childhood mortality rates, likely due to the extended period of childhood and, hence, protracted vulnerability (Volk & Atkinson, 2013). Although this extended childhood allows complex brain development, it left children vulnerable to peril before reproduction (Deaner, Barton, & Van Schaik, 2003). Disease, disability, infanticide, and abandonment were among the factors that most strongly compromised infant and child survivorship across human history (Rawson, 2003; Cunningham, 2005; Budnik & Liczbińska, 2006). Among extant hunter-gatherers and foragers-horticulturalists, illness (e.g., diarrhea, respiratory infections, malnutrition; 65%), violence (e.g., filicide, 17%), and accidents (8%) are the primary causes of infant and child mortality (Gurven & Kaplan, 2007). Altogether, these patterns suggest that parents throughout human history recurrently faced the challenges associated with not only promoting children's survival, but also responding adaptively when children died.

If early death presented a recurrent threat across human evolution, then natural selection may have favored psychological mechanisms among parents that minimized the likelihood of infant and child death, and if offspring perished, adaptively calibrated parents' responses. A wide body of research has explored the historical, environmental, societal, and behavioral predictors of child survival (Geary, 2000; Harris, 2011; Hrdy, 1999; Rutstein, 2005; Sear & Mace, 2008), along with how external contingencies shape parental investment in offspring (Quinlan, 2007). The current article explores the second of these two adaptive challenges. That is, we examine how parents navigate and optimize the trade-offs presented by the death of a child and how these strategies have been shaped by selection pressures. Toward that end, we first review genetically-informed explanations of parental investment. Next, we turn to a theoretical framework—life history theory—that may account for variation in the intensity of parental bereavement. Then, we review the existing evolutionary theories of human grief and integrate these with what is known about the pattern of parental bereavement. From these, we propose directions for future research to identify whether and how each theory accounts for the manifest pattern of parental grief following the death of a child. Last, we forward the possibility that the same neurological pathways implicated in recovery from dissolved romantic relationships also contribute to the intensity of parental grief.

2. Inclusive fitness and parent-offspring conflict

In the following pages, we will forward an evolutionary analysis of parents' grief following a child's death. It is important to distinguish parents' psychological motivations, subjective emotional experiences,

and behaviors from the evolutionary explanations for those processes. Parents may cry, withdraw from social life, or create a memorial fund because they feel immense despair at the loss of their child. These feelings of despair are the *proximate* explanation, or immediate cause, for parents' grieving behaviors. However, one might also examine these behaviors from an *ultimate* perspective, contemplating how similar behaviors may have enhanced the inclusive fitness of ancestral parents. One might ask whether across human evolution, grieving parents were more likely to pass on their genes than those who expressed no grief at the loss of a child. Did experiencing profound grief offer ancestral parents any fitness advantages? These questions are examples of an *ultimate* analysis—or an investigation of how natural selection would have maintained the tendency to grieve in the population. It is worth noting that ultimate explanations do not imply conscious awareness of these forces. In the case of parental grief, for example, a bereaved parent may never hold any conscious awareness of the adaptive advantages of their grief. Rather, his or her conscious experiences (e.g., sorrow, yearning) are earnest and compel behaviors that enhanced ancestors' inclusive fitness on average, without necessitating any explicit awareness of those ultimate goals. The current article will examine parental grief from an evolutionary, or *ultimate* perspective. To do so, we first examine why parents invest so heavily in their children from an evolutionary perspective.

Although parental investment in children is present across all human populations, not all individuals invest equally in their offspring. This variation in parental care often follows predictable patterns, informed by genetic principles and evolutionary logic. In sexually reproducing chromosomally diploid species, such as humans, parents and offspring share approximately 50% of their genes by common descent. Offspring thus afford parents an opportunity to transmit half of their genetic material into subsequent generations. By investing in offspring, parents enhance the likelihood their offspring, who carry copies of their genes, survive long enough to reproduce (Dawkins, 1976; Hamilton, 1964). From a *proximate* perspective, parents care for children because they feel deep love for their children. From an evolutionary or *ultimate* perspective, however, parents invest in children because children carry copies of their own genes. Thus, parents propagate their own genetic material and enhance their inclusive fitness by protecting and caring for offspring.

Not only do children offer the possibility of enhancing parents' inclusive fitness through their high degree of genetic relatedness, children also hold high residual reproductive value when they have not yet passed their fertile years. Residual reproductive value is the potential number of future children an individual could sire, which generally peaks upon reaching sexual maturity (Fisher, 1930). Children have a greater potential to reproduce in the future than an elderly but similarly related individual, such as a parent, because they are younger and less likely to have passed their fertile years. Thus, investing in children offers higher inclusive fitness benefits than investing in an aging parent (Alexander, 1979; Fisher, 1930). In the tragic case of a child's death, parents' inclusive fitness, or their ability to transmit their genetic material through genetic relatives, is immensely harmed.

The sexes differ in their average genetic interest in children, however. Because gestation occurs in the female body, mothers, but not fathers, can be certain that their children are their genetic offspring. Men, in contrast, lack paternal certainty and risk investing in a child who is not their genetic descendant. For this reason, women's genetic interest in their children is certain, whereas men's genetic interest is contingent on their paternity status (Anderson, Kaplan, & Lancaster, 2007; Geary, 2000). Accordingly, men's likelihood of investing in children is more strongly predicted by their perceptions of the child's resemblance to themselves than is women's (Volk & Quinsey, 2002; 2007). Thus, women are always certain of their relatedness to children, whereas men's investment may track the likelihood children are their genetic descendants.

Beyond women's certain maternity status, their lifetime reproductive potential is constrained by menopause, few ova, and the length of

pregnancy. Women cannot produce as many children across their lifespan as can men, who are unbridled by the physiological constraints of pregnancy and lactation. Thus, even if men are relatively certain of their paternity status, fathers face greater opportunity costs when investing in any one child compared to mothers, on average, because some men have much greater future reproductive potential than do most women (Symons, 1979). Although human fathers are unique across the biological world for their often high levels of paternal investment (Clutton-Brock, 1989, 1991), men face higher opportunity costs when they divert resources and time towards children because effort allocated towards seeking new reproductive opportunities can offer higher fitness payoffs to men than women, on average (Buss & Schmitt, 1993; Trivers, 1972). In other words, because the female body is responsible for pregnancy, men could potentially sire many more children than women (on average) if they pursued additional opportunities to reproduce. In theory, however, a woman could produce as many children if she reproduced with one virile partner as if she pursued many sexual partners. Although we will review nuance to this pattern in the subsequent section on life history theory, ancestral men likely reaped higher genetic payoffs than did ancestral women on average from diverting more time, energy, and resources towards maximizing mating opportunities compared to investing in existing children. These sex differences suggest that mothers suffer greater decrements to their inclusive fitness than do fathers upon the death of a child. If the intensity of parental grief tracks inclusive fitness as some theorists contend (Littlefield & Rushton, 1986), this should lead to more prolonged suffering among bereaved mothers than bereaved fathers, a point we will return to below.

Parents also differ in their genetic relatedness to offspring as a function of their genetic similarity to their reproductive partner. Individuals often select mates with similar phenotypic traits, a phenomenon known as assortative mating (Buss, 1984). Individuals can enhance their inclusive fitness by preferentially helping and cooperating with those who share phenotypic traits, because those phenotypic similarities are often manifestations of similar underlying genes (Rushton, Russell, & Wells, 1984). This theory has been leveraged as a functional explanation of assortative mating. By selecting mates with similar phenotypic traits, individuals can increase their genetic similarity to their mates and, thus, enhance their genetic relatedness to any resulting offspring. Provided that genes of common descent do not produce this phenotypic similarity—in other words, so long as mates are not genetic relatives—this assortative pairing does not increase offspring mutation load as incest does. Thus, individuals who reproduce with more similar mates will tend to share more genes in common with their children than individuals who reproduce with less similar mates (Littlefield & Rushton, 1986). Consequently, parents who share more genes in common with one another will suffer greater inclusive fitness losses upon the death of a child than will those who reproduced with genetically dissimilar mates. To the extent that parent grief tracks inclusive fitness, it is possible that parents who are more assortatively matched will experience stronger grief than parents who are less phenotypically or genetically similar. This hypothesis, that parent similarity predicts the intensity of parental bereavement, has yet to be tested empirically, however.

Because parents and offspring do not share 100% of their genes in common, the genetic interests of parents and offspring are not perfectly aligned, resulting in parent-offspring conflict (Schlomer, Del Giudice, & Ellis, 2011; Trivers, 1974). From a parent's perspective, the optimal level of investment directed toward a child is lower than the optimal level of investment from the child's perspective. Any investment a parent makes in one child sacrifices time, energy or resources that could be directed towards other children or future potential children (e.g., by pursuing additional reproductive opportunities). A parent may therefore maximize his or her inclusive fitness by investing in children contingently, based on factors including the likely proportion of shared genes, the child's viability (i.e., health), the child's needs, parental resources, parental age, and environmental conditions (Anderson et al., 2007;

Clutton-Brock, 1991; Daly & Wilson, 1981, 1996; Geary, 2000; Sterns, 1992). That is, because parents face trade-offs in how they can allocate their time and resources, parents should invest less in children when that investment is less likely to produce payoffs and would be better directed towards other more profitable endeavors, such as when a child is severely ill (and thus unlikely to survive) or under extremely harsh environmental conditions (whereby parental investment is unlikely to reduce the child's risk of death). Likewise, the terminal investment hypothesis contends that parents will invest more heavily in current children (versus potential future children) when their future reproductive potential is low, such as when parents reach advanced age (Fisher, 1930; Williams, 1966). Indeed, mothers are more likely to invest in high-risk premature infants when they have more (compared to less) psychosocial resources or when mothers are older in age (Beaulieu & Bugental, 2008). These patterns suggest mothers make trade-offs between investment in current offspring and potential future offspring, such that they disinvest from offspring when resources are limited or future opportunities to reproduce may prove more favorable.

The rare cases of filicide (killing one's own children) also corroborate the contingent nature of parental investment. For example, parents are especially likely to kill their infants when the infants suffer poor health and therefore, are at increased risk of death or would require substantial investment and resources (Daly & Wilson, 1984; Hill & Ball, 1996; Hrды, 1999). Sex differences also emerge in the predictors of filicide. Compared to fathers, mothers are more likely to kill their infants when their infants suffer poor health, and this is especially true for younger women, who will likely have ample future opportunities to reproduce (Harris, Hilton, Rice, & Eke, 2007). Mothers are also more likely to commit infanticide when they lack sufficient resources or supportive partners (Dawson, 2015; Stone, Steinmeyer, Dreher, & Krischer, 2005). These patterns suggest that mothers disinvest in offspring when the costs of investment for their own fitness are higher or when future reproductive opportunities would offer better odds of child viability.

Fathers, on the other hand, are more likely to commit filicide when they experience marital discord with the child's mother or when they are the step-fathers, suggesting men's confidence in their paternity status shapes their disinvestment from offspring (Daly & Wilson, 1996; Harris et al., 2007; Weekes-Shackelford & Shackelford, 2004). Indeed, fathers (but not mothers) invest more heavily in offspring who resemble themselves (Alvergne, Faurie, & Raymond, 2009; DeBruine, 2004), which roughly indicates genetic relatedness (Fasolt, Holzleitner, Lee, O'Shea, & DeBruine, 2019). Taken together, these findings indicate that parental investment in offspring is neither uniform nor obligate, but instead follows predictable genetic patterns and contingently tracks cost-benefit tradeoffs for maximizing inclusive fitness.

From the perspective of inclusive fitness, the death of a child thus presents a conflict for parents. Because effort, resources, and time are limited, parents who devote resources to a deceased child are expending effort that might be directed toward other goals, such as promoting the survival of existing children or pursuing additional reproductive opportunities (Trivers, 1972; 1974). For example, a bereaved parent who expends household resources on an elaborate funeral or withdraws from caretaking responsibilities owing to severe psychological distress may compromise the survival and reproductive prospects of remaining offspring. The time, energy, and resources parents expend while grieving a child cannot be allocated to other fitness-relevant goals, such as rearing remaining children, garnering additional resources, or attracting mates. Any evolutionary explanation of the parental response to a child's death must therefore consider the fitness costs associated with grief, as outlined in the next section.

3. Human grief

In response to the death of a loved one, humans across cultures commonly display a suite of psychological and behavioral changes (Cowles, 2006; Murray, Fessler, Kerry, White, & Marin, 2017; White,

Marin, & Fessler, 2017). Although individuals vary in the manifestation, magnitude, and trajectory of these grief responses, most bereaved individuals experience a prolonged period of deep sorrow (Bonanno & Kaltman, 1999; Parkes, 1972). Grief typically proceeds in stages, beginning with disbelief, followed by yearning, anger, depression, and ending in acceptance (Maciejewski, Zhang, Block, & Prigerson, 2007). Grief can endure for years (Feigelman, Jordan, & Gorman, 2009; Meert et al., 2011), with depression typically peaking at six months post-loss (Maciejewski et al., 2007). Although grief-related symptoms typically improve after 6–12 months, roughly 10–20% of bereaved individuals experience complicated grief, whereby they experience intense and prolonged anhedonia, preoccupation with and yearning for the deceased, detachment from others, or denial of the death (Lobb et al., 2010; Shear et al., 2011). Indeed, individuals experiencing complicated grief may receive a clinical diagnosis of Prolonged Grief Disorder when they experience persistent (i.e., extending longer than six months) and intense longing for the deceased and emotional pain, leading to significant impairment in functioning (American Psychiatric Association, 2013).

Grief induced dysphoria can contribute to impairment in social functioning, including withdrawal from social life and disinterest in maintaining ongoing relationships or forming new ones (Archer, 1999; Averill, 1968; Schwab, 1992; Shear et al., 2011). Bereaved individuals, moreover, often suffer from sleep disturbances that can jeopardize their health and wellbeing (Hardison, Neimeyer, & Lichstein, 2005). Beyond this distress, impairment in functioning, and withdrawal from social support, grief can also increase susceptibility to illness and mortality (Hart, Hole, Lawlor, Smith, & Lever, 2007; Phillips, Carroll, Burns, Ring, Macleod, & Drayson, 2006). Moreover, suicidality is heightened among bereaved individuals (Shear et al., 2011; Zetumer et al., 2015). Such patterns suggest grief can be incredibly costly and thus, fitness-harming for bereaved individuals.

A wide body of evidence suggests the pattern of grief is particularly debilitating for parents who lose a child, compared to those who lose other valued social partners (Aoun et al., 2015; Kersting, Brähler, Glaesmer, & Wagner, 2011; Maccallum, Galatzer-Levy, & Bonnano, 2015; Middleton, Raphael, Burnett, & Martinek, 1998; Sanders, 1980; Zetumer et al., 2015). Bereaved parents experience heightened risk of hospitalization for psychiatric disorders and a diminished sense of purpose and psychological wellbeing (Li, Laursen, Precht, Olsen, & Mortensen, 2005; Rogers, Floyd, Seltzer, Greenberg, & Hong, 2008). Compared to parents who have not lost a child, grieving parents suffer impaired health and experience greater mortality risk (Li, Precht, Mortensen, & Olsen, 2003; Rostila, Saarela, & Kawachi, 2012; Song, Floyd, Seltzer, Greenberg, & Hong, 2010). Bereaved mothers are also at an increased risk of experiencing a stillbirth in subsequent pregnancies (László et al., 2013). Moreover, the marital and social relationships of bereaved parents often suffer following the death of a child (Buyutkcan-Tetik et al., 2017; Laasko & Paunonen-Ilmonen, 2002; Rogers et al., 2008). Thus, bereaved parents in modern contexts often suffer profusely, both in terms of health and social functioning.

Although these bereavement patterns are found among modern parents, living in Westernized contexts quite removed from those in which humans evolved, proto-Neolithic grave sites, including those from the Shanidar cave and Natufian people, contain buried infant and child skeletons along with offerings (Solecki, Solecki, & Agelarakis, 2004). The presence of these gravesites suggests funerary practices for deceased children extend at least 10,000 years back. Among late Neolithic tombs in Iberia, roughly 30% of all burials were non-adults (Waterman & Thomas, 2011). Because infant and child skeletons decay more readily than do adult skeletons, these numbers are likely underestimates of child funerary practices among ancestral humans (Lewis, 2007). Such archaeological findings suggest that parental bereavement is not a modern phenomenon, but instead stretches far back into human history, warranting evolutionary analyses.

Taken together, these patterns indicate that the loss of a child often

leads to substantial decrements in bereaved parents' physical health, psychological functioning, and social relationship quality. If ancestral parents similarly suffered, then how is it that the prodigious human grief response persisted in the population and evolved to be so protracted? The immense costs of grief present a puzzle for evolutionary explanations. The large decrements in grievers' wellbeing must be offset by fitness-relevant benefits (Winegard, Reynolds, Baumeister, Winegard, & Maner, 2014). If not, this protracted and deleterious suite of responses would have been winnowed out by natural selection. All else equal, parents who quickly overcame their child's death would have better competed for resources, status, social partners, and mates than those who allocated excessive energy and resources to their sorrow. From an evolutionary perspective, natural selection should have favored preemptive behavioral proclivities among parents that protected children from peril, if possible, over an elaborate period of dysfunction following a child's death. We now evaluate the degree to which child death was precludable across human history and the various protective strategies likely favored by natural selection.

4. Controllability of child mortality

Among modern hunter-gatherers and agriculturalists, who live in non-industrialized environments more closely paralleling ancestral ones, approximately 65% of child mortality is caused by upper respiratory and gastrointestinal disease, while 17% is attributable to violence and another 8% to accidents (Gurven & Kaplan, 2007; Hill, Hurtado, & Walker, 2007). Based on these patterns and other sources of evidence, researchers have contended that disease, infanticide, and abandonment most strongly contributed to infant and child mortality across human history (Budnik & Liczbińska, 2006; Cunningham, 2005; Gurven & Kaplan, 2007; Rawson, 2003).

To the extent that these mortality risk factors were controllable, natural selection should have favored traits or behavioral proclivities among parents that reduced children's exposure to such risks. The quality and amount of provisioning by an infant's mother is one of the best predictors of infant survival (Hrdy, 1999; Sear & Mace, 2008). For example, breastfeeding can reduce mortality among both infants and children by protecting against diarrhea and respiratory infections (Sankar et al., 2015; Victora et al., 2016). In harsh conditions, mothers' general intelligence predicts lower child mortality risk (Čvorović, Rushton, & Tenjević, 2008), suggesting that maternal traits facilitate offspring viability. Furthermore, firstborn children are more likely to die than are second-born children, suggesting a practice effect, such that parents develop skills or knowledge from rearing their first child, which reduce mortality risk for subsequent children (Mathews & MacDorman, 2007). Reproductive timing also shapes mortality risk, with longer intervals between births promoting infant and child survival (Rutstein, 2005). The quality of the relationship between a mother and father predicts child outcomes as well: infants are more likely to suffer injury and illness when their parents are not married, when their father is absent, or when their father is of low social status (Geary, 2000; Mathews & MacDorman, 2007). Outside of investment from fathers, the presence and caregiving of other relatives, such as grandparents and siblings, have been linked to enhanced infant and child survivorship (Sear & Mace, 2008; Strassmann & Garrard, 2011). Likewise, sanitation practices, such as avoiding defecation sites, can also promote infant survival (Geruso & Spears, 2018).

Taken together, these results reveal that child mortality risk was to some degree controllable, offering opportunities for natural selection to favor traits and behavioral proclivities among parents that precluded these tragedies, including sufficient resource provisioning, breastfeeding, intelligence, paternal investment, and sanitation concerns. However, human ancestors' immediate ecological contexts may have shaped the extent to which mortality risk was controllable. That is, environmental factors, such as pathogen prevalence, would have constrained the efficacy of such dispositional and behavioral adaptations

aimed at reducing child mortality (Quinlan, 2007).

5. Life history theory

Life history theory is a theoretical framework from biology that provides insight into human adaptations that reduced child mortality, and this framework also may offer applications for understanding variation among individuals in the intensity of their parental grief responses. Life history theory predicts and describes variation in how organisms (both within and across species) allocate effort towards competing fitness goals in response to environmental conditions (Charnov, 1993; Rushton, 1985). Because time and energy are limited, every organism faces trade-offs when allocating bioenergetic resources (Ellis, Figueredo, Brumbach, & Schlomer, 2009). Metabolic energy dedicated to growth (somatic effort) limits the energy that can be directed towards reproduction. Likewise, effort directed towards mating, such as searching for, appealing to, and guarding mates, limits the energy than can be directed towards protecting and raising offspring (parenting effort; Trivers, 1972). In response to these fitness tradeoffs, organisms develop coordinated patterns of traits and resource allocation—termed "strategies"—which vary along a continuum of "speed," from faster to slower (Del Giudice, Gangestad, & Kaplan, 2015; Figueredo et al., 2005). Strategy speed reflects the relative timing of the organism's maturation and reproduction. Conditions of the immediate environment can shift the viability of these strategy speeds.

Harsh environments, characterized by heightened risk of illness, injury, or death favor (in some cases) faster life history strategies (Del Giudice et al., 2015; Ellis et al., 2009). Likewise, when the mortality risk posed by environments is highly variable or unpredictable, this stochasticity will also favor the evolution of faster strategies because long-term investments (e.g., slow maturation) are less likely to reap anticipated payoffs (Belsky, Schlomer, & Ellis, 2012). When injury and death are less predictable and less controllable, organisms may adopt a faster life history strategy to orient towards maximizing short-term fitness. These organisms direct their energy and effort towards mating (acquiring sexual partners) over promoting the long-term survival of themselves (via somatic development) or their offspring (via parenting effort; Rushton, 1985). In other words, if tomorrow is uncertain or unlikely, reproducing today becomes the primary goal. Likewise, if mortality risk is less controllable, then there are diminishing returns to investing in offspring, who face the same external threats to survival (Harpending, Draper, & Pennington, 1990). Indeed, across non-industrialized societies, juvenile and adult mortality rates are highly correlated (Walker, Gurven, Hill, Migliano, Chagnon, De Souza et al., 2006), suggesting the overall mortality rate (versus the juvenile or adult specific rate) is a critical factor in predicting the adoption of faster life history strategies. When mortality risk reduces potential lifespan, an organism cannot afford to develop slowly, delay reproduction, or invest heavily in a few offspring.

More predictable and controllable environments, on the other hand, generally favor slower life history strategies, but especially under high population densities (Del Giudice et al., 2015; Ellis et al., 2009). Because death is not immediately looming, and can be, to some degree, precluded through behaviors and traits (i.e., mortality is controllable), slower life history strategists allocate more energy towards enhancing the long-term viability of themselves (via somatic development) and their offspring (via parenting effort). When mortality is more controllable or distal, an organism can reap greater inclusive fitness payoffs from developing slowly, delaying reproduction, and promoting the survival and competitiveness of offspring. That is, parents will invest more heavily in offspring when those behaviors or resource allocations effectively reduce offspring vulnerability to environmental threats. If, on the other hand, parents cannot preclude offspring injury or death through such investments, then this uncontrollable environmental harshness will favor a faster life history strategy, whereby parents produce a greater quantity of children to augment the probability at least

one survives. When the extrinsic threats to offspring survival can be precluded by parents' behaviors or investment and when the population is saturated (heightening competition for resources), parents who invest in offspring competitiveness will be favored over those who merely sire more offspring (Ellis et al., 2009). Thus, enhancing offspring competitiveness through parental investment is characteristic of a slower life history strategy, favored in relatively safe, predictable, or controllable environments.

These general strategy speeds (faster/slower) emerge as solutions to competing fitness tradeoffs and are comprised of coherent, coordinated patterns of traits (Figueredo et al., 2005). Across primate species, for example, longevity is associated with later age of reproduction and fewer offspring (Stearns, 1992; Walker, Burger, Wagner, & Von Rueden, 2006). Life history theory has been used not only to explain variation across species (e.g., Bielby et al., 2007), but also to explain variation within humans. Although humans are a relatively slow life history species, characterized by delayed maturation, few offspring, and high parental investment (Flinn & Ward, 2005; Hawkes, 2006), substantial variation exists among individuals in life history strategy (Ellis et al., 2009). In response to the controllability of the immediate environment's mortality risk, humans differentially allocate effort across competing fitness goals. Researchers have contended that a transition from a faster to slower life history strategy may have allowed human ancestors to reduce infant and child mortality to the controllable extrinsic threats (Ellis et al., 2009; Volk & Atkinson, 2013).

Social cooperation, for example, is facilitated by adaptations that allowed humans to conquer environments characterized by predictable or controllable threats (Alexander, 1990). By relying on social partners, humans could exchange valuable information and more effectively extract resources to combat the hostile (but precludable) forces of nature, such as inclement weather, predators, or inconsistent food supply (Figueredo et al., 2005). However, cooperation is a time-dependent strategy, with higher payoffs over longer periods of time and over repeated interactions. If extrinsic mortality risk is heightened, on the other hand, individuals cannot afford to wait to reap the delayed benefits of cooperation, such as those gained through reciprocal altruism. Furthermore, some ecological conditions, such as high parasite load, are relatively uncontrollable and cannot be reduced through cooperation. Cooperation is therefore more characteristic of a slower than faster life history strategy (Figueredo et al., 2005). Faster life history individuals instead tend to seek short-term gains from social partners, resulting in fleeting, opportunistic, and antagonistic social relationships (Figueredo et al., 2018; Figueredo & Jacobs, 2010). Slower life history strategy individuals, on the other hand, espouse a cooperative social schema, viewing others as possessing well-meaning intentions, thereby maintaining enduring and cooperative social relationships. Such cooperation may have facilitated infant and child survival by reducing intragroup violence and increasing access to food through sharing (Volk & Atkinson, 2013).

Beyond cooperation, another manifestation of a slower life history strategy is heightened effort directed towards parenting. When extrinsic sources of mortality are low or controllable, humans (as with other organisms) can enhance the viability and success of children through investing in their children's health, development, and social competitiveness (Quinlan, 2007). Among human populations, slower life history strategies correspond to producing fewer children, greater investment in each, higher quality parent-child relationships, and more altruism directed towards family members (Figueredo, Vasquez, Brumbach & Schneider, 2007). Perhaps most importantly, smaller family size has been associated with lower child mortality rates (Knodel & Hermalin, 1984), suggesting these behavioral adaptations enhanced child survival.

When extrinsic mortality risk is high and less controllable, on the other hand, parents can less easily enhance child survival through provisioning and protection. These less predictable and less controllable environments instead favor reproductive bet-hedging, whereby producing many children with different sexual partners—to increase

genetic diversity among children—better increases the likelihood of child survival (Bogin, 1996; Fox & Rauter, 2003; Simons, 2007). That is, by siring many offspring with divergent traits (e.g., immune responses) and abilities, parents can enhance the likelihood that at least one or a few offspring survive the harsh conditions. Indeed, compared to their slower life history counterparts, individuals with faster life history strategies display a preference for short-term romantic relationships and demonstrate greater desire for casual sex and more sexual partners (Gladden, Sisco, & Figueredo, 2008). In contexts without effective contraception, this heightened desire for sex with different partners would often result in genetically diversified children.

Life history theory may prove to be an illuminative framework for understanding parental grief. In environments characterized by controllable extrinsic threats to survival, parents should produce fewer offspring and invest more heavily in each, congruent with a slower life history strategy (Simons, 2007). Although reducing the number of children produced was a behavioral strategy that enhanced offspring survival because it permitted greater parental investment in each (Rutstein, 2005), this reduction simultaneously increased the fitness costs of losing a child. If parental grief is proportional to the fitness payoffs of offspring, as Archer's (1999) by-product theory would contend, parent grief should be more pronounced among slower life history individuals, who invest extensively in fewer offspring and develop strong attachments to each. Prolonged parental grief may be a manifestation of the greater parental investment characteristic of slower life history strategies (see Table 1).

Although this hypothesized link between life history strategy and the intensity of parental grief has yet to be tested directly, extant evidence is tentatively supportive. In environments characterized by high levels of infant mortality, such as among the Mehinaku Indians or the Alto people of Timbaúba, Brazil, parents show relatively low levels of distress following the death of their infants (Gregor, 1988; Scheper-Hughes, 2017). These patterns suggest that grief is diminished in environments with heightened extrinsic mortality, which typically favor faster life history strategies. Moreover, parental grief is heightened among parents who have none or fewer remaining children (Stroebe et al., 2013; Wijngaards-de Meij et al., 2005). If slower life history individuals tend to produce fewer offspring and invest heavily in each, then this pattern supports that prolonged parental grief corresponds to fewer offspring (and perhaps greater parental investment), indicative of a slower life history strategy. Furthermore, parents who have more responsive care-giving styles (indicating higher parenting effort) show more complicated grief responses than those with less responsive caregiving styles (presumably indicative of lower parenting effort, characteristic of faster life history strategies; Meert et al., 2011). Bereaved parents who feel more concern for their spouses also experience intensified grief (Stroebe et al., 2013), which is consistent with slow life strategists' greater investment in both mates and children. Likewise, some evidence suggests parental grief is heightened among older parents (Buyutk-can-Tetik et al., 2017). If slow life history strategists tend to delay reproduction, then it is possible that these older parents grieve more intensely due to their slower life history strategy, rather than their age *per se*. These findings provide some tentative indirect support for the predicted association between life history strategy and parental grief intensity.

However, other findings in the literature do not align with the contention that slower life history individuals exhibit intensified grief responses. For example, there is a well-documented link between perceptions of greater social support and lessened grief (Bonanno et al., 2002; Burke, Neimeyer, & McDevitt-Murphy, 2010; Vanderwerker & Prigerson, 2004). If cooperation is more characteristic of a slower life history strategy (Figueredo et al., 2018; Figueredo & Jacobs, 2010), then this pattern casts doubt on the link between a slower life history strategy and prolonged grief. Similarly, individuals who felt more satisfied with their marriages also reported less intense grief (Engler & Lasker, 2000). A slower life history strategy is associated with greater investment

toward both mates and children and thus, this indirect evidence also casts doubt on the link between a slower life history strategy and intensified grief. Moreover, some studies find that those who reported abuse, the loss of a parent, or separation anxiety during childhood were at an intensified risk for experiencing chronic grief (Silverman, Johnson, & Prigerson, 2001; Vanderwerker, Jacobs, Murray-Parkes, & Prigerson, 2006). If individuals' life history strategies are predicted by their early life experiences or heritable traits (e.g., Figueredo, Vasquez, Brumbach, & Schneider, 2004), then these patterns suggest those who experienced harsher parenting or early stressors, which are linked to developing faster life history strategies, exhibit more intense grief. Because none of these studies measured grievers' life history strategies directly, more research is needed before conclusions can be drawn about the association between an individual's life history strategy and their parental bereavement.

However, as outlined above, extensive grief carries high opportunity costs for bereaved parents. Although slower life history parents may receive increased fitness payoffs from investing heavily in few offspring, bereaved parents, regardless of their life history strategy, forfeit resources and time when grieving that could be directed towards advancing other fitness-relevant goals. Even if a slower life history strategy corresponds to protracted grief responses, bereaved parents must still reap fitness benefits to outweigh the costs imposed by grief. We now turn to the various proffered evolutionary theories of grief, assessing their alignment with extant data on variation in grief intensity as well as their ability to account for the immense costs of a prolonged grief response (see Table 1).

6. Theoretical explanations of grief

6.1. By-product theory of grief

Because children offer parents a means by which to transmit copies of their genes, parents typically develop deep attachments to and devote substantial investment in their offspring. The love parents feel towards their children functions as a proximate psychological mechanism which compels behaviors that facilitate offspring survival, such as protection, provisioning of resources, and instruction (Bowlby, 1969/1982). Archer (1999) contended that the grief response is an ineluctable consequence, or by-product, of this human attachment system. He argued that the distress individuals experience at a loved one's absence is functional—if the individual has gone missing—by prompting behaviors that locate the loved one, preserve the relationship, or promote the survival of the absent partner. Upon separation, for example, a distressed individual might search for an absent social partner and when located, provision for the individual or rekindle the relationship. This separation response should therefore track the extent to which the missing partner enhanced the individual's inclusive fitness.

Grief, according to the by-product account, is a misapplication of this evolved separation response. When a loved one dies, the bereaved individual engages in the same searching behaviors associated with absence, but these efforts are in vain. If the costs of *not* searching for a valuable social partner who was alive outweigh the costs of searching for a partner who is in fact deceased, then this search response may have been preserved by natural selection (Barrett & Behne, 2005). From an error management perspective (Haselton & Buss, 2000), it may have been costlier for humans to incorrectly assume an absent individual was dead when they were truly alive and relatively less costly to search misguidedly when an individual was dead. Indeed, some evidence suggests non-human primates engage in behaviors that may function to verify a conspecific is deceased. For example, chimpanzees will occasionally inspect, probe, or carry the carcass of a deceased chimpanzee for a day or two post-loss (Cronin, Van Leewen, Mulenga, & Bodamer, 2011; Stewart, Piel & O'Malley, 2012). These patterns support that natural selection can favor behaviors similar to a search response, whereby the organism ensures the lost partner is in fact dead before

Table 1
Evolutionary explanations of grief, degree of support, and directions for future research.

Evolutionary Explanation	Argument	Theoretical and Empirical Support	Theoretical and Empirical Counter-evidence	Research Needed
By-product (Archer, 1999)	Grief is the maladaptive misfiring of a separation response, which was advantageous for promoting searching behaviors when a loved one was absent, but alive. Because absence is more common than death, and because certain bonds are fitness enhancing, it is less costly to assume the absent individual is missing, but alive compared to dead.	Congruent with error management theory (Haselton & Buss, 2000) Vigilance behaviors are found in non-human primates following a conspecific's death (Cronin et al., 2011; Stewart, Piel, & O'Malley, 2012). Dreaming of deceased and ruminating about deceased during sleep corresponds to complicated grief (Hardison et al., 2005). Suddenness of death is a predictor of more severe grief (Wijngaards-de Meij et al., 2005). Intensity of parental grief corresponds to parents' presumed genetic relatedness and child's residual reproductive value (Crawford et al., 1989; Littlefield & Rushton, 1986; Wijngaards-de Meije et al., 2005; Youngblut et al., 2017).	Cannot explain grief's protracted time-course or severity. In the case of death, costly and maladaptive misfirings of the separation response should have been weeded out by natural selection. Children across cultures reliably develop a cognitive understanding of death (Astuti & Harris, 2008; Barrett & Behne, 2005). Funerary practices extend far back into history, suggesting an ancestral awareness of death (Solecki et al., 2004; Waterman & Thomas, 2011). Exposure to the body (a reliable cue of death) may not reduce grief (Feigelman et al., 2009).	Do individuals experience vigilance related grief symptoms during loved ones' absences? Do bereaved individuals experience a desire to search for the deceased (e.g., restlessness, dreams of searching)? What degree of separation is required to trigger activation of this separation response? Does exposure to cues of death (e.g., viewing or touching the corpse) diminish grief severity? Is mothers' grief severity more strongly linked to age than fathers'?
Bargaining Model (Hagen, 2003; Watson & Andrews, 2002)	Grief signals the griever's relative need to social partners to induce support or resource provisioning.	Lower perceptions of social support correspond to intensified grief (Schultz et al., 2006; Vanderwerker & Prigerson, 2004). Financial problems contribute to risk for complicated grief (Melhem et al., 2004). Crying and desiring social support are heightened during social loss compared to other causes of depression (Keller & Nesse, 2006).	Grief should be highest when individuals lose someone they depended on (rather than cared for). Yet, grief is particularly intense among bereaved parents who lose children (Maccallum et al., 2015). Bereaved caregivers who reported higher pre-loss burden show intensified grief responses (Schulz et al., 2006)	Does grief intensity correspond to the amount of foregone support and resources previously provided by the deceased? Does the support provided by social partners correspond to the griever's degree of dysfunction?
Prevention (Keller & Nesse, 2006; Nesse, 2005)	The pain associated with grief instills lessons within the griever to prevent similar losses in the future.	Parental grief is intensified following deaths due to violence or accidents (Scholtes & Browne, 2015; Wijngaards-de Meije et al., 2008). Guilt and self-blame are common features of grief (Stroebe et al., 2014; Zetumer et al., 2015). Feeling as though one could have prevented the death corresponds to protracted grief symptoms (Melhem et al., 2004). Bereaved parents (who are responsible for their children's welfare) experience heightened grief compared to those who lose other social partners (Aoun et al., 2015; Kersting et al., 2011; Maccallum et al., 2015; Zetumer et al., 2015).	Cannot account for grief's protracted time-course. Protracted dysfunction is a very costly and inefficient mechanism for learning lessons about preventable deaths. Parental grief is heightened among parents who have no remaining children (Dyregrov et al., 2003) and presumably have less to gain by learning such lessons.	Do parents show grief related symptoms following children's preventable injuries or illnesses? Does the number of remaining children or young kin (e.g., nieces/nephews) contribute to grief severity? Does the preventability of death predict grief intensity? Does the intensity of parents' grief predict a lower likelihood of future children's perishing? Do social partners extract lessons about the prevention of child death, contingent upon parents' grief responses?
Social Signaling (Reynolds et al., 2015; Winegard et al., 2014)	Prolonged grief reliably signals the griever's latent ability to form committed and enduring bonds. Individuals who experienced more intense grief were preferentially selected as social partners, thereby prolongating the grief response.	Accounts for grief's protracted time course and severity. Individuals assume the intensity of others' grief response is diagnostic of grievers' trustworthiness and make social decisions accordingly (Reynolds et al., 2015). 20% of grievers endorse belief that grieving less would indicate being uncaring, heartless or cold (Skritskaya et al., 2017). Relationships to deceased that are closer, supportive or dependent are associated with intensified grief (Lobb et al., 2010). Bereaved parents who felt more concern for their spouse also experience intensified grief (Stroebe et al., 2013), suggesting those who form stronger attachments in general experience more intense grief.	The intensity of parents' grief corresponds to lower, rather than higher relationship satisfaction (Buyutkan-Tetik et al., 2017).	Are more (versus less) intensely grieving parents preferred as social partners or mates? Does the intensity of parents' grief track their capacity to form committed bonds generally?
Life History (current article)	Slow life history strategy individuals will exhibit more pronounced grief	Life history strategy predicts individuals' investment in both mates	Childhood stressors and abuse (correlates of faster life history	Does environmental harshness or predictability

(continued on next page)

Table 1 (continued)

Evolutionary Explanation	Argument	Theoretical and Empirical Support	Theoretical and Empirical Counter-evidence	Research Needed
	than faster life history strategists due to their increased parental effort and inclination towards cooperation.	and children (Figueredo et al., 2005). Parents who have more responsive care-giving styles (indicating higher parenting effort) show more complicated grief responses (Meert et al., 2011). Bereaved parents who felt more concern for their spouse also experience intensified grief (Stroebe et al., 2013), which is consistent with slow life history strategists' greater investment in both mates and children. In environments characterized by high levels of infant mortality, parents show relatively low levels of distress following the death of their infants (Gregor, 1988; Scheper-Hughes, 2017).	strategies) are risk factors for developing complicated grief later in life (Silverman et al., 2001; Vanderwerker et al., 2006). Augmented social support is associated with lessened grief (Bonanno et al., 2002; Burke et al., 2010; Vanderwerker & Prigerson, 2004).	predict grief intensity? Do slower life history parents grieve more intensely upon the death of their child than faster life history parents? Does ease of recovery from dissolved relationships correspond to parental grief severity? Do physiological correlates of distress following relationship dissolution also underlie grief intensity? Do slower (vs faster) life history strategists prefer parents who grieve more intensively as mates or social partners?

abandoning it.

As applied to parent-child relationships, Archer's (1999) by-product theory suggests that parents who experienced distress at the absence of their child would, on average, engage in behaviors designed to locate their missing child. When a child went missing, these seeking behaviors would promote reunion and, ultimately, continued provisioning for the child, thereby enhancing parents' inclusive fitness. In the case of a child's death, parents may engage in these same search behaviors without the associated benefits. Thus, according to Archer, parental grief is a by-product of strong parent-child attachments, which was preserved by the fitness advantages accrued by parents who successfully located their absent but living children. From this perspective, parental grief offers no fitness advantages when the missing child is deceased, but was maintained in the population because abandoning an absent—but living—child was very costly to inclusive fitness.

Research on the manifestations of grief provides some support for the by-product theory of grief (see Table 1). For example, parental grief is intensified when the child's death was sudden or unexpected (Lobb et al., 2010; Stroebe et al., 2013; Wijngaards-de Meije et al., 2005). Likewise, yearning for reunion is one of the core symptoms of grief, which decreases over time as acceptance increases (Maciejewski et al., 2007). If this yearning prompted ancestral parents' seeking behaviors, then grief may have promoted reunion with lost children. Indeed, one symptom associated with complicated grief is searching for the deceased (Lobb et al., 2010). Bereaved individuals also report dreaming of the deceased and nightly rumination (Hardison et al., 2005), suggesting psychological experiences may facilitate search behaviors or a lowered cognitive threshold for detecting cues to the lost loved one. fMRI studies of bereaved pet owners demonstrate that grief corresponds to an attentional bias to stimuli associated with the deceased pet (Freed, Yanagihara, Hirsch, & Mann, 2009). Likewise, attachment to a deceased pet predicts false recognitions of the pet postmortem, which also diminish with time (White & Fessler, 2013). These patterns suggest that individuals experiencing grief display heightened vigilance for cues linked to the deceased. In the case of living but missing individuals, such vigilance might facilitate locating those absent social partners. These patterns may explain why most cultures exhibit mortuary practices involving some contact with the corpse, and often rather intimate contact (Murray et al., 2017; White et al., 2017). That is, perhaps exposure to tangible and immediate cues of death diminishes some of the searching or vigilance symptoms of grief (White, Fessler, & Gomez, 2016).

However, some findings in the bereavement literature cast doubt on the by-product account of grief. For example, bereaved parents who encountered the body of their deceased child (either at the time of death or prior to the funeral) showed more intense grief than parents who did

not view their child's body (Feigelman et al., 2009). If grief is a misapplied search response, then parents should forego their "searching" when they encounter reliable cues of their child's death. To be sure, however, observing a body in a modern funerary setting may be a poor indicator of death because bodies are often prepared to appear alive (e.g., through the application of makeup; White & Fessler, 2018). Likewise, cues suggesting the deceased may still be alive, such as photographs of the lost loved one, may prolong some of the vigilance symptoms of grief, perhaps because such cues provide justification to continue seeking out the deceased (White & Fessler, 2013). Yet, some findings suggest individuals who witnessed the scene of death show impaired functioning post-loss compared to those who did not (Melhem et al., 2004). This result suggests that encountering strong and immediate cues of death does not diminish the grief response. If grief represents a misfiring of a search strategy, presumably it would diminish when the griever recognizes reliable cues of death, as contended by proponents of the cognitive vigilance account of grief, a variant of the by-product account of grief (White et al., 2016). On the other hand, some self-reports from griever's (of various types of loss) suggest viewing a corpse can assist with death acceptance (Chapple & Ziebland, 2010). Thus, additional empirical research is needed before conclusions can be drawn about whether exposure to a body or other reliable cues of death diminish grief responses, but perhaps especially the cognitive vigilance symptoms.

Other patterns in the bereavement literature support the by-product account. To the degree that grief is a by-product of the attachment system, the severity of grief should parallel the strength of the griever's attachment, which presumably tracks the inclusive fitness benefits offered by the missing (or deceased) individual. Littlefield and Rushton (1986) tested this prediction by investigating the severity of bereaved parents' grief responses. Mothers grieved more intensely than fathers, which is consistent with women's maternal certainty and greater fitness interest in each child (due to their limited reproductive careers, relative to men). Although this pattern of more severe maternal than paternal grief is replicated in other studies (Rostila et al., 2012; Stroebe et al., 2013; Wijngaards-de Meij et al., 2008; Youngblut, Brooten, Glaze, Promise, & Yoo, 2017), women's stronger grief response is not limited to parental grief, but is found across many lost social relationships (e.g., Chen et al., 1999; Dyregrov, Nordanger, & Dyregrov, 2003). It is unclear, then, whether to classify the stronger maternal than paternal grief response as a by-product of genetically-informed attachment processes or the consequence of other sex differences, such as in personality traits.

Other evidence also supports that grief intensity tracks the griever's inclusive fitness with the deceased. For example, parents grieve more intensely for children they perceive to more closely resemble their side of the family (Littlefield & Rushton, 1986), suggesting parental bereavement corresponds to shared genetic interests with the lost

individual. Moreover, parents grieve longer for healthy children than for unhealthy children, suggesting an attunement to the child's viability and residual reproductive value (Littlefield & Rushton, 1986). Indeed, using hypothetical scenarios, parents' expectations of their grief intensity corresponded to the residual reproductive value of the lost child (Crawford, Salter, & Jang, 1989). Likewise, in one sample of bereaved parents, grief was highest among those who lost a child at age 17, further suggesting parental grief tracks a child's residual reproductive value and is thus heightened at periods of sexual maturity (Wijngaards-de Meije et al., 2005). Among bereaved mothers, grief was highest among those who lost an adolescent compared to those who lost younger aged children (Youngblut et al., 2017). Taken together, these findings suggest that the intensity of parental grief parallels the level of attachment to the deceased child, as would be predicted by the parent's shared genetic interests with the child as well as the child's residual reproductive value.

Likewise, limited evidence suggests grief is heightened among older than younger bereaved parents (Buyutkcan-Tetik et al., 2017). This pattern is consistent with the terminal investment hypothesis (Fisher, 1930; Williams, 1966) whereby older parents are hypothesized to invest more heavily in children than younger parents because older individuals have fewer future reproductive opportunities. However, because women's reproductive potential is more constrained by advanced age than men's, this pattern age-dependent grief should be most pronounced among women. Future evidence is needed to assess whether bereaved mothers exhibit a stronger link between advanced age and grief intensity than do bereaved fathers (see Table 1).

Although some evidence is supportive of Archer's (1999) by-product theory of grief, the prolonged and intense nature of grief can be devastating to griever's psychological, physiological, and social functioning, and likely would have substantially harmed the fitness of ancestral grievers. The by-product theory of grief presumes that natural selection could not have disentangled functional separation distress (in the case of a living but missing loved one) from nonfunctional distress (in the case of death). However, by ages 4–7, children across diverse cultures develop an understanding that death is distinguishable from sleep, whereby mental and bodily faculties cease (Astuti & Harris, 2008; Barrett & Behne, 2005). This developmental trajectory suggests humans achieve a cognitive awareness of death by a young age, which may have been favored by natural selection to differentially attune behavioral responses towards living versus dead organisms. Likewise, as outlined by Winegard et al. (2014), many features of grief reveal an explicit awareness that the deceased are somehow distinct from living individuals, such as elaborate funerary rituals. If funerary practices extended relatively far back into human history (e.g., Solecki et al., 2004; Waterman & Thomas, 2011), then ancestral humans may have possessed an ability to distinguish cognitively the cause of their beloved's absence.

Moreover, emotions are often specified to contextual factors, suggesting that cognitive appraisals guide emotional reactions to promote fitness-enhancing behavioral responses (Nesse, 1990). Although cognition and emotions are not synonymous, they often inform one another. For example, negative emotional responses (e.g., depression) manifest differently when an individual suffers a social loss compared to a personal failure (Keller & Nesse, 2006). This distinction suggests cognitive appraisals of negative situations guide resultant emotional trajectories. It is possible that cognitive representations of a loved one's absence could similarly guide emotional responses. If, for example, one's romantic partner was away on military duty, one might experience sadness and desire for reunion. However, should that individual learn their romantic partner was, in fact, living in another city engaged in an alternative romantic relationship, the individual's emotional response would quickly shift to jealousy, hurt, or anger. This hypothetical scenario suggests human cognition can appreciate the cause of the absence, offering a mechanism by which natural selection could fine-tune the resultant distress response and possibly eliminate the costly misfiring of the attachment system in the case of death.

However, it is also possible that the vigilance response exhibited during grief is a low-level feature of human psychology, outside the conscious control of cognition. For example, individuals exhibit many physiological responses characteristic of fear when donning virtual reality goggles (Diemer, Mühlberger, Pauli, & Zwanzger, 2014). This fear response suggests that conscious awareness of the virtual nature of the stimuli is insufficient to extinguish the body's response to cues that approximate ancestrally relevant threats. If a loved one's absence is also processed in a low-level fashion, outside of conscious control, then it is possible some of the vigilance features of grief would persist irrespective of an explicit awareness of death. If these grief symptoms are relatively unaltered by cognition, then they should also manifest in many other contexts when loved ones are absent (e.g., vacation, military leave, long distance relationships). It remains unclear what degree or duration of absence is required to activate this hypothesized separation response (see Table 1).

If it is possible for humans to cognitively recognize causes of absence (e.g., vacation versus death) and emotionally calibrate accordingly, it is perplexing that the human grief response, particularly in the case of a deceased child, is so prodigious. Although shared genetic interests with children and their residual reproductive potential offer palatable explanations for the heightened grief response to deceased children compared to other relatives (Crawford et al., 1989), the immense costs of enduring grief still should have severely harmed bereaved parents' fitness. That is, to explain parental bereavement in terms of children's lost residual reproductive value commits the sunk cost fallacy because a parent's investments have already been allocated (Arkes & Blumer, 1985). The amount of time or effort parents already invested in children does not compensate the lost time, resources, health, and social relationships expended towards grief. Given the ubiquity and extent of the human grief response (Cowles, 2006), ancestral grievers must have reaped adaptive benefits that outweighed the fitness costs associated with grief. If not, then individuals who experienced distress at a loved one's absence—but not death—should have outcompeted those who suffered distress at both absence and death. That is, if it were possible for human cognition to discern the causes of loved ones' absences and calibrate emotional responses accordingly, then ancestral parents who experienced adaptive distress when their children were missing, but not maladaptive distress when their children were deceased, would have enjoyed greater fitness compared to those who maladaptively wallowed in suffering following their children's death. The high costs of grief should have strongly favored this cognitive discernment and linkage to emotion if it were possible. Such a linkage would have allowed natural selection a mechanism to disentangle functional from dysfunctional separation responses.

6.2. Bargaining model of grief

Other theorists have contended that the grief response is not a by-product, but instead reflects the designed output of adaptation. Hagen (2003) proposed a functional account of depression that can be leveraged to understand the evolution of human grief. He forwarded the bargaining model of depression, arguing that depression functions similarly to a labor strike. That is, individuals experience apathy and lethargy when treated unfairly by social partners as a mechanism to renegotiate the contracts of their social relationships. By reducing their own productivity, depressed individuals inflict costs on their social partners, which serve as a bargaining strategy to evoke greater investment or effort from their partners (Watson & Andrews, 2002). Indeed, in the case of postpartum depression, a spouse's depression-induced decrement in childcare corresponds to their partner's increased childcare efforts (Hagen, 2002). These patterns suggest that social partners, or at minimum, committed romantic partners, provide augmented support when a loved one exhibits symptoms of depression. From the bargaining perspective, withdrawal from a relationship and from social obligations is relatively uncostly for the depressed individual because he

or she is already underserved in the social arrangement and, thus, loses less from the strike than does his or her social partners. This withdrawal strategy may have been especially valuable for those who did not possess other means to influence their social partners, such as women, who often possessed less physical strength or social status than their male romantic partners across history.

Experiencing the death of a loved one is one of the most predictive risk factors for developing depression (Cole & Dendukuri, 2003). Indeed, many of the symptoms of grief are often closely linked to depression (Barry, Kasi, & Prigerson, 2002; Onrust & Cuijpers, 2006; Zisook & Kendler, 2007), and both follow similar trajectories following the death of a loved one (Wijngaards-de Meij et al., 2008). Thus, grief may be understood through the lens of the bargaining model. In the case of grief, bereaved individuals may signal credibly their need for additional support from their social partners. Moreover, the particular symptoms of grief may be designed to recruit this support. For example, a griever's desire for social closeness may foster new or existing social bonds, whereas crying may evoke sympathy and resources (Keller & Nesse, 2006).

Indeed, bereaved individuals report increased levels of social support following the loss of a loved one (Stroebe, Zech, Stroebe, & Abakoumkin, 2005). Furthermore, perceptions of support and satisfaction with support during bereavement generally predict decrements in grief symptomatology and depression (Aoun et al., 2015; Bonanno et al., 2002; Burke et al., 2010; Vanderwerker & Prigerson, 2004; but see Stroebe et al., 2005). Among bereaved parents, those who experience greater (versus lesser) social support from their social partners, romantic partners, and medical staff recover more quickly from their grief (Kreicbergs, Lannen, Onelov, & Wolfe, 2007). Likewise, bereaved parents who felt more compared to less satisfied with the support they received tended to show less intense grief symptoms (Meert et al., 2010). Not only do perceptions of social support correspond to lessened grief, bereaved mothers who felt more satisfied with their marriages also reported less severe grief responses (Engler & Lasker, 2000). These patterns suggest grief is heightened under conditions of low social support, but if support is provided, grief subsides, thereby granting some support to the bargaining model of grief.

However, the bargaining model of grief might suggest grief should be amplified when an individual loses a social partner upon whom he or she heavily depended. That is, if grief functions similar to a labor strike and serves the purpose of renegotiating social contracts and eliciting support, then grief responses should track, to some degree, the extent to which the bereaved depended on the deceased for resources and support. If, for example, an individual lost a social partner who was not provisioning many resources, then the bereaved should less strongly need to renegotiate social arrangements or recruit compensatory aid. Some findings support these assertions. For example, widows and widowers who more strongly depended upon their spouses show intensified grief responses compared to those who were less dependent on their lost partners (Bonanno et al., 2002). Likewise, individuals experiencing concurrent stressors during the loss, such as financial problems, are at a heightened risk for developing prolonged or complicated grief (Macias et al., 2004; Melhem et al., 2004).

Although these findings suggest the intensity of grief is tracking, to some degree, the extent to which the bereaved truly need additional support and resources, other patterns cast doubt on this expectation. As noted above, grief responses are heightened among those who lose children, compared to those who lose a spouse or parent (Maccallum, Galatzer-Levy, & Bonanno, 2015; Middleton et al., 1998). If individuals receive more support and resources from a parent or spouse than from a child, then these patterns do not comport with grief's functioning as an honest display of need. Moreover, among bereaved caregivers, those who experienced greater caregiving burden prior to the loss and those who cared for more cognitively impaired loved ones reported heightened grief symptoms (Schulz, Boerner, Shear, Zhang, & Gitlin, 2006). This finding suggests grief is intensified among those most burdened by the

deceased—the exact opposite pattern one might predict if grief signals a need for support following social loss. However, further tests of the bargaining perspective of grief are needed to adjudicate whether the intensity of grief corresponds to the amount of foregone support and resources previously provided by the deceased, as noted in Table 1.

6.3. Prevention theory of grief

Randolph Nesse (2005) forwarded another adaptationist account of grief, arguing that the psychological pain experienced by the griever may serve as a learning mechanism to prevent recurrence of the circumstances that contributed to the loved one's death. Just as physical pain may prevent further damage or future injury (Vertosick, 2000), so too might emotional pain reduce the likelihood of a similar future loss (Thornhill & Thornhill, 1989). Consider an individual who experiences the physical pain of a sunburn. This immediate pain may motivate the individual to seek shade, preventing further damage to the skin. The memory of this pain may also decrease the probability the individual again engages in prolonged sun exposure. According to Nesse, grief may function similarly to the recalled experience of physical pain, by reducing the probability the individual engages in the actions that led to the death. If, for example, parents permitted their child to roam far away from their watch and their child died during this excursion, the psychological pain the bereaved parents experience may serve as a reminder to themselves and a warning to others to keep a closer watch on their children.

Consistent with Nesse's (2005) psychological pain account, guilt and self-blame are common symptoms of intense grief, in which the bereaved reflect and ruminate over what could have been done to preclude the death (Stroebe et al., 2014). Self-blame may be especially heightened among bereaved parents compared to other bereaved individuals (Zetumer et al., 2015). These patterns suggest parents may attempt to extract lessons from the death of their child, supporting the contention that grief serves as a learning mechanism. Further support comes from the finding that parental grief is heightened when a child dies violently or accidentally, as opposed to by natural causes (Scholtes & Browne, 2015; Wijngaards-de Meije et al., 2008). This pattern suggests that grief tracks, to some degree, the controllability (and thus preventability) of a loved one's death.

However, parents' grief symptoms tend to be amplified when they have no or few remaining children (Dyregrov et al., 2003; Stroebe et al., 2013; Wijngaards-de Meije et al., 2005). These findings may cast doubt on the prevention theory because parents should presumably grieve longer or more intently to extract lessons to prevent the loss of remaining children. On the other hand, grief may be intensified because the potential inclusive fitness costs of each child's death are magnified when parents have fewer, compared to more, children. Yet, if the intensity or duration of grief parallels the value of extracting lessons from the death, then it is unclear why parents would grieve so profusely when they have no remaining children (Dyregrov et al., 2003). It is possible that this augmented grief partially explains the practice effect, whereby later born children are less likely to perish than firstborn children (Mathews & MacDorman, 2007). That is, perhaps parents who grieve more intensely following the loss of their first child are better prepared for their subsequent ones. Whether the intensity of parents' grief buttresses their remaining or subsequent children from peril is an open question for future research (as noted in Table 1).

If the pain theory is correct and grief functions as a preventative mechanism, its efficacy would be curtailed by the fact that death has already occurred. From the prevention perspective, grief might be more effective if it followed a child's illness or injury, as opposed to a child's death. That is, if grief is an important psychological signpost to preclude similar misfortunes, then parental grief should manifest when children suffer preventable harm, more broadly. If, for example, a child becomes ill from consuming poisonous berries, or is burned from playing too close to a fire, parents should suffer similarly debilitating emotional

responses in such cases. Further empirical tests of the pain hypothesis are needed to determine whether parents experience similar levels of emotional distress following a child's injury or illness as a child's death.

The protracted time course of grief also raises questions about the prevention interpretation of grief. Prolonged pain from physical injury serves valuable functions, such as preventing further injury by limiting use of the injured body part (Vertosick, 2000). The pain from a sprained ankle, for example, disincentivizes an individual from bearing weight on that leg, granting time for the ankle to heal. It is unclear what the prolonged duration of grief accomplishes. That is, if a sharp immediate pain could accomplish future avoidance of the problematic behaviors that contributed to a child's death, natural selection should have shortened rather than prolonged the human grief response. However, grief can endure for years, including among bereaved parents (Feigelman et al., 2009; Meert et al., 2011), with depression peaking at six months post-loss (Maciejewski et al., 2007). The extended trajectory of the grief response is curious from the prevention perspective because it is unclear what function the prolonged time course serves. That is, if some bereaved individuals could effectively and rapidly extract lessons from the death of a loved one, these individuals should have achieved higher fitness than those who continued to suffer for months or years. The severity of grief, however, has a more plausible ultimate function. That is, perhaps severe pain is more likely to form associative learning than is low-level discomfort.

Another issue faced by Nesse's (2005) prevention theory of grief is whether the same preventative measures could be accomplished through means that less substantively harm an individual's fitness than profound grief, such as through cultural transmission (Boyd & Richerson, 1995). Because prolonged and severe grief is an especially costly mechanism by which to extract lessons about how to preclude a child's death, cultural transmission of practices that reduced child mortality should have been more readily favored. Social learning might allow individuals to reach similar lessons without incurring the immense costs of extensive grief. To the extent that childhood mortality was an obstacle often faced by human ancestors and substantively harmed fitness, there should have been sufficient selective pressure to favor parent behaviors or cultural practices that preemptively reduced this risk. A prolonged post-mortem grief response is presumably less effective in promoting child survival than behaviors expressed while the child was still alive.

6.4. Social signaling theory of grief

Recently, researchers have offered an explanation of human grief which proposes fitness advantages to griever as well as accounts for both the severity and duration of grief. The social signaling theory of grief contends that grief functions as a signal to potential social partners of the griever's capacity to form committed and longstanding interpersonal bonds (Reynolds, Winegard, Baumeister, & Maner, 2015; Winegard et al., 2014). As human ancestors gained control over ecological exigencies through hunting, constructing dwellings, etc., the hostile forces of nature became less predictive of survival and reproduction, whereas the behaviors and preferences of fellow humans became increasingly consequential (Alexander, 1990; Flinn, Geary, & Ward, 2005). Early humans who successfully formed cooperative alliances would have gained relatively better access to aid and socially-mediated resources than those unable to form such social bonds (West-Eberhard, 1979). However, cooperation with non-kin is difficult to foster and sustain. Absent shared genetic interests, cooperation with unrelated individuals is fraught with the potential for defection, betrayal, cheating, and abandonment (Boyd & Richerson, 1988; Cosmides & Tooby, 1992). Individuals who more accurately discerned and preferred cooperative proclivities in potential social partners would, all else equal, form alliances with more reliable and loyal individuals compared to those who could not discern potential partners' cooperative inclinations.

According to the social signaling account, grief functions as a signal of the bereaved individuals' cooperative tendencies and loyalty because

the griever sacrifices time and resources to a social partner who can never repay the devotion (Winegard et al., 2014). Grief thus demonstrates an interpersonal commitment that transcends concerns about reciprocity (Frank, 1988). According to the social signaling theory, grief is prolonged and costly precisely *because* those features reliably demonstrate griever's unwavering commitment to the deceased. The immense costs associated with the experience and display of grief, such as lost time, effort, health, and social opportunities, discourage faking and thus ensure that the intensity of the grief response honestly signals a griever's prosocial inclinations (Zahavi & Zahavi, 1999). Consistent with these contentions, bereaved individuals who report lesser grief also report poorer social functioning than those who report prolonged grief (Ginzburg, Geron, & Solomon, 2002), suggesting that those who form less committed social bonds also display lesser grief. Moreover, grief is most intense over bonds that are close, supportive, enmeshed, and confiding (Lobb et al., 2010), congruent with the argument that the intensity of grief parallels the strength of the commitment pre-loss.

If the length and intensity of grief are diagnostic of individuals' cooperative nature, then potential social partners should attend to others' grief responses and select partners accordingly. Roughly 20% of grievers espouse the belief that grieving less would indicate that they are uncaring, cold, or heartless (Skritskaya et al., 2017). Supporting these beliefs, empirical investigations reveal individuals assume the intensity of others' grief response is diagnostic of griever's trustworthiness (Reynolds et al., 2015). Moreover, people use the duration and intensity of others' grief responses to inform their cooperative decisions, preferring more (versus less) intense grievers as allies. If human ancestors exhibited similar preferences over evolutionary history, the social benefits accrued to markedly distressed grievers may have maintained and amplified the intensity of the human grief response. That is, competitive marketplaces for cooperative and reliable social partners could have generated runaway selection for costly displays of unwavering loyalty (Nesse, 2007), including protracted grief.

If the social signaling theory of grief is accurate, then parental grief may signal prosocial attributes of bereaved parents. Parents who grieve profusely over their deceased child should be perceived as more devoted and nurturing parents, and perhaps, more trustworthy social partners, compared to parents who exhibit less distress over the death of a child. And, indeed, complicated grief is positively correlated with parents' attentive caregiving (Meert et al., 2011), suggesting more devoted parents function worse after losing a child compared to less devoted parents. The social signaling theory of grief predicts that parents stricken by grief at the loss of a child were selected and preferred as social partners, relative to parents who did not grieve as profusely. Indeed, bereaved parents who perceived their spouse to experience similar levels of grief as themselves experienced higher relationship satisfaction compared to those who perceived dissimilar grief severity from their spouse (Buyutkcan-Tetik et al., 2017). This pattern supports that perceptions of others' grief contribute to subsequent relationship closeness. Furthermore, if individuals prefer cues of parenting ability or prosociality when selecting long-term mates (Buss & Schmitt, 1993; Little, Burriss, Jones, DeBruine, & Caldwell, 2008), such displays of grief may also enhance a bereaved parent's desirability as a long-term partner. Although these predictions have not been tested empirically, such romantic preferences suggest that if the intensity of grief is used as an indicator of parents' nurturance or devotion to their child, then parents who more intensely grieved the loss of a child may have enhanced their desirability as romantic partners compared to parents who grieved less intensely. However, some data suggests the intensity of parents' grief corresponds to lower, rather than higher romantic relationship satisfaction (Buyutkcan-Tetik et al., 2017). Future research is needed to address how parental grief corresponds to one's likelihood of being selected as a relationship partner or retaining ongoing relationships.

The social signaling theory of parental grief is also coherent with a life history theory perspective. In environments characterized by more controllable extrinsic mortality risk, long-term romantic pair bonds

augment parenting effort, and social cooperation reduces mortality risk and enhances inclusive fitness (Figueredo, Vásquez, Brumbach, & Schneider, 2007). The environments that favor slower life history strategies should thus offer higher social rewards for individuals who signal their prosocial inclinations through grief than environments that favor faster life history strategies. Applying life history theory to the social signaling theory of grief generates the prediction that slower life history parents should grieve more intensely upon the death of their child than faster life history parents. That is, slower life history strategists would reap larger social returns from signaling their cooperative dispositions and parenting effort through a heightened grief response, compared to faster life history strategists. If social cooperation is a more predominant and efficacious strategy for slower life history individuals (Figueredo et al., 2005), then slower strategists should also preferentially select more distressed bereaved parents as social and romantic partners. Slower life history individuals, who must form reliable and cooperative social partnerships for cooperation and parenting, should also benefit more substantively from selecting social partners and mates based on the intensity of their grief responses, relative to faster life history individuals, whose less controllable environments constrained the payoffs to cooperation and high parenting effort. Whether parents' grief responses differ as a function of life history speed has yet to be tested empirically. Future research may thus examine: 1) whether parents' life history strategy corresponds to the intensity of their grief responses, and 2) whether social choosers' life history strategy shapes their perceptions of and preferences for more versus less intensely grieving parents (see Table 1).

7. Reconciling the various explanations

In the preceding pages, we reviewed the extant evolutionary theories of grief, which can be applied to understand patterns of parental grief. As noted above, a complete evolutionary explanation of grief must account for the immense costs endured by griever from their protracted dysfunction. Without such compensatory advantages to grievers, natural selection should have favored parents who experienced limited grief and thus suffered few fitness costs following their child's death. The social signaling account of grief fills this task by contending that prodigious grievers are preferentially selected as social partners because their enduring debilitation reliably signals a capacity to form long-standing and devoted bonds. The bargaining perspective also proffers adaptive advantages to grievers by contending that displays of grief reliably signal need (e.g., foregone resources or support), which compels investment and aid from remaining social partners. However, the bargaining explanation becomes slightly less tenable in the case of parental grief, whereby parents were often primarily provisioning resources to children (rather than receiving) prior to the death, and are therefore less likely to require compensatory aid. Nonetheless, evidence suggests relative to those who lost other social partners, bereaved parents generally experience greater dysfunction and are at an elevated risk for developing complicated grief.

Although we have emphasized heavily the importance of accounting for the costs suffered by grievers, it is possible that the various explanations of grief are not mutually exclusive. That is, grief may have served numerous functions, which offer different advantages at particular stages. For example, human grief may have originated in a much simpler form with a shorter duration, similar to the inquisitive behavior of our close phylogenetic relatives, the chimpanzees. Upon the immediate absence of a social partner, enhanced vigilance may have been adaptive due to the costs of too quickly abandoning a fitness-promoting relationship, as the by-product account contends. Thus, the benefits of heightened vigilance or search behaviors may have favored a brief period of some grief symptoms, such as yearning or false recognitions. Likewise, if the death were potentially preventable, then emotional suffering in the form of rumination may have been favored due to the lessons the griever (or their kin) extracted about preventing similar

losses in the future, as the prevention theory would contend. Alternatively, if the deceased were a critical source of social support for the bereaved, then elongated grief may have been favored to reliably signal the griever's impaired fitness and need for compensatory support in such circumstances. Last, to the degree that the intensity of grief signaled honestly the griever's capacity to form enduring and loyal commitments, then social partners who selectively allied with more intense grievers would have reaped the long-term payoffs of reliable alliances. These social preferences may have further intensified and lengthened the grief response by favoring more versus less intensely grieving individuals as trusted social partners. If slower life history strategists accrue greater benefits from cooperation and high-investment parenting, then modern manifestations of parental grief may be most protracted among slower, compared to faster, life history strategists.

It is possible then that some combination of these functional explanations favored the current pattern of parental grief. To disentangle the relative merits of these hypothesized selective forces, future research may benefit from examining the extent to which the grief trajectory comports with predictions from these extant evolutionary explanations, as outlined in Table 1. Alternatively, certain grief symptoms may be present in non-death circumstances that presented similar adaptive challenges as death. From the prevention perspective, parents may experience rumination or depression when their children suffered preventable illness or injury. Likewise, from the by-product account, the symptoms of grief that most closely approximate vigilance should manifest in other contexts when a loved one is absent, beyond death. Comparative models with cooperative non-human animal species may also prove useful in adjudicating the strength of the various evolutionary arguments. For example, among species whose conspecifics depend heavily on one another, then the bargaining model might predict these animals emit similar grief-like behaviors (e.g., distress calls, lethargy) following the loss of a valued partner to evoke compensatory aid. Future research can thus adjudicate whether the emergent pattern of evidence lends support to these predictions.

The current article investigates primarily the pattern of grief among parents who have lost a child because this is one of the most intense forms of bereavement and because the loss of a child substantially impaired ancestral parents' inclusive fitness. To be sure, however, the loss of other social partners was undoubtedly a recurrent challenge faced by ancestral humans, which also impaired inclusive fitness. It is possible that the manifestations of grief differ depending upon the particular loss, in accordance with the various evolutionary interpretations. For example, the loss of a mate on whom one heavily depended may more readily amplify one's needs for social support than the loss of a dependent child. Thus, from the bargaining perspective of grief, the level of pre-loss dependence may better predict grief intensity when an individual loses a romantic partner, rather than a child. Likewise, from the social signaling perspective, social partners may make divergent inferences about grievers dependent upon the particular social loss. For example, if a warrior expressed despair at the death of a fellow soldier or the group's leader (to whom he or she was not particularly close), this distress may be taken as diagnostic of the griever's commitment and loyalty to the group more than to the particular deceased individual per se (Winegard et al., 2014). Thus, a full understanding of the evolutionary origins and adaptive advantages of grief will require deeper investigation of 1.) circumstances beyond death that posed similar adaptive challenges, 2.) non-human animal responses to death, and 3.) how grief manifests in response to various social losses beyond parental grief.

8. Mechanism of grief: Attachment severance

Although several evolutionary explanations for grief have been proposed, few have addressed the mechanism by which grief persists or diminishes over time. Boutwell, Beaver, and Barnes (2015; and elaborated by Buss, Goetz, Duntley, Asao, & Conroy-Beam, 2017) argued that

humans evolved a mental system that motivates jettisoning a mate under certain circumstances, known as “primary mate ejection”. When an individual’s mate harms his or her inclusive fitness (e.g., is physically abusive), is of lower mate value, or is unfaithful, individuals should be especially likely to jettison such partners (Buss et al., 2017). Additionally, Boutwell et al. (2015) proposed that overcoming the psychological distress of relationship dissolution, termed “secondary mate ejection”, allows the newly independent individual to return to other fitness-relevant goal pursuits, such as searching for a new mate. Boutwell and colleagues may have been too narrow in their examination of the psychology underlying mate ejection, however. Rather than possessing a mate-specific ejection system, humans might instead exhibit a more general attachment severance system, capable of reducing or eliminating attachments to both mates and children. That is, the psychological system that motivates dissolution of romantic relationships (primary mate ejection) may also motivate decreased attachment to children who compromise parental inclusive fitness (Daly & Wilson, 1981). Likewise, the mental system that underlies secondary mate ejection, or recovery from a romantic breakup, may also account for the ease with which bereaved parents overcome the death of a child.

Just as selecting a mate presents tradeoffs (e.g., one partner is physically attractive and healthy, whereas another is loyal and investing), so too does investing in children (Trivers, 1974). As noted above, parents can differ in their shared genetic interests in their children depending on their own sex, their parental certainty, and their genetic relatedness to the child’s other parent. Moreover, some children exhibit clearer cues of health, indicating a greater likelihood of survival, than do other children. Because time and resources are limited, ancestral parents who directed greater investment towards healthier children may have enhanced their inclusive fitness over those who allocated resources equally, or disproportionately to less healthy children (Trivers, 1972). Parents should therefore invest more heavily in children who more robustly contribute to parental inclusive fitness (Volk & Quinsey, 2002).

Likewise, just as mourning the dissolution of a romantic relationship interferes with the rejected individual’s ability to pursue other fitness goals, so too does mourning the death of a child. Navigating the upset of a child’s death may include recovering from the emotional trauma, retaining the current relationship or finding a new mate, conceiving another child, and caring for other children or related kin, among other important tasks. Depression, illness, apathy, social withdrawal, and neglect of remaining children are costly to grievers’ fitness. If individuals experience similar responses following the dissolution of romantic relationships as they do to the death of a child, then recovery from romantic breakups should also be calibrated to fitness payoffs. Indeed, many of the symptoms following divorce mirror those of grief: strong yearning for the loved one (O’Connor & Sussman, 2014), heightened depression (Sbarra, Emery, Beam, & Ocker, 2013), lower life satisfaction (Lucas, 2015), elevated risk of illness (Björkenstam, Hallqvist, Dalman, & Ljung, 2013), and risk of early death (Shor, Roelfs, Bugyi, & Schwartz, 2012). These similar decrements in fitness following divorce suggest that, like parental grief, the costs of mourning should be calibrated to fitness payoffs.

These fitness calculations may have favored the evolution of a system that calibrated both attachment to mates and offspring, as well as grief following dissolution or death contingently based on fitness payoffs. These parental investment and grieving inclinations might be produced by the same mental mechanisms implicated in jettisoning romantic partners and recovering from dissolved partnerships (Boutwell et al., 2015). If a single system promotes detachment from a mate as well as overcoming the death of a child, then perhaps the neurological architecture that underlies recovery from the dissolution of a pair bond also underlies recovery from the loss of a child.

Although correlational, fMRI studies of bereaved women exposed to photographs of the deceased identified heightened activation of the caudate nucleus (Gündel, O’Connor, Littrell, Fort, & Lane, 2003), a brain area implicated in romantic love (Bartels & Zeki, 2000). These bereaved

women also exhibited activation of the posterior cingulate gyrus (Gündel et al., 2003), which similarly demonstrated heightened activity among women mourning romantic breakups (Najib, Lorberbaum, Kose, Bohning, & George, 2004). Moreover, compared to bereaved individuals exhibiting low levels of grief, individuals exhibiting intense grief, known as complicated grief, showed greater activation of the nucleus accumbens, a brain area associated with reward processing and addiction (Knutson, Adams, Fong, & Hommer, 2001; O’Connor et al., 2008). Stronger activation of this area was associated with more intense yearning for the deceased. These patterns suggest that the brain pathways that underlie romantic attachment and grief over romantic dissolution also play a role in the intensity of the grief response following death.

Another possibility is that genetic influences on neurotransmitter levels and brain regions provide general mechanisms through which individuals return to a state of “equilibrium” (Rowe, 2001) in the wake of the loss of a loved one, whether it be to death or relationship dissolution. Dopamine and norepinephrine levels have been linked to feelings of romantic attraction (Fisher, Aron, Mashek, Li, & Brown, 2002), which contribute to the addictive and obsessive nature of love (Fisher, Xu, Aron, & Brown, 2016). Given that the reward and addiction brain pathways underlying love also underlie grief, it is possible that these neurotransmitter systems also predict the intensity of parents’ grief. Likewise, the oxytocinergic brain system has been implicated in both maternal and romantic attachment (Bartels & Zeki, 2004; Levine, Zagoory-Feldman, & Weller, 2007). One study found that securely attached mothers showed stronger oxytocin responses and activation of oxytocinergic brain regions when looking at their infants, compared to insecurely attached mothers (Strathearn, Fonagy, Amico, & Montague, 2009). These neurohormone systems may play a role in regulating the length and intensity of distress following both romantic dissolution as well as a child’s death, suggesting a plausible shared physiological mechanism between mate ejection and the recovery from child grief.

An attachment severance system is consistent with a life history perspective. Individuals’ ability to jettison mates or recover from a child’s death may vary with life history strategy, such that faster life history individuals more quickly jettison attachment to deceased or fitness-harming children (as well as forming less intense attachments towards children generally) compared to slower life history individuals, who exhibit high parenting effort and invest heavily in fewer children. Should these two processes be facilitated by overlapping neurological mechanisms, those individuals more likely to form weaker attachments to children should also be those most likely to jettison mates swiftly and easily. That is, there should be a correlation between one’s relative ease of detachment and recovery from the loss of romantic partners or children and the intensity of both should be predicted by individuals’ life history speed. Whether individuals who show more intense distress over romantic relationship dissolution also experience more pronounced grief at the death of a child has yet to be explored empirically.

One area ripe for future research could examine whether physiological factors predict both grief intensity following death as well as the dissolutions of romantic pair bonds. If life history strategy predicts individuals’ investment in both mates and children (Figueredo et al., 2005), then the neural architecture underlying these attachment systems may reliably differ across individuals with different life history strategy speeds. Findings from the field of behavioral genetics lend some support to a shared physiological mechanism underlying life history speed and attachment. Genetic influences explain a significant proportion of variance in life history strategies (Barbaro, Boutwell, Barnes, & Shackelford, 2017b; Figueredo et al., 2004) as well as adult attachment (Barbaro, Boutwell, Barnes, & Shackelford, 2017a; Brussoni, Jang, Livesly, & MacBeth, 2000; Torgersen, Grova, & Sommerstad, 2007).

Altogether, these patterns support the dispositional nature of both attachment proclivities and life history strategies, thereby suggesting that similar mechanisms may underlie both. Given that life history theory describes how individuals vary in the effort they direct towards

mates and children, these findings provide tentative, indirect support for a shared physiological underpinning of the intensity of grief following the loss of a mate or a child. Variation among individuals' grief responses may operate through physiological pathways designed to maximize fitness during both instances of disinvestment and recovery.

9. Conclusion

Thanks largely to modern medicine, sanitation, and legal systems, most humans today enjoy the gift of witnessing their children grow to reproductive age. Historical analyses suggest this pattern was not the case throughout most of human evolution. Ancestral parents were often faced with the tragedy of a child's death. At first glance, profound grief seems a natural consequence of the strong parent-child bond. However, ultimate evolutionary analyses remind us that grieving parents who drowned in their distress would have not only compromised their own health and wellbeing, but also that of their remaining children (or potential future children). Given the ubiquity and extent of the human grief response, ancestral grievers must have reaped adaptive benefits to offset these fitness costs; otherwise, they would not be our ancestors.

The extant theories of grief proffer various explanations for short-term symptoms: costs of ignoring an advantageous partner's absence were high, grief allows grievers to extract lessons to preclude similar future losses, and grief signals a bereaved individual's need for compensatory support. Of the extant theories of grief, the social signaling account proposes both an adaptive advantage to grievers as well as an explanation for the protracted nature of parents' grief responses. According to this perspective, grievers signaled their latent commitment and loyalty to social partnerships through costly (and thus, honest) displays of distress. In socially competitive marketplaces, where social partners preferentially select allies, the benefits of signaling pro-sociality, such as through grief, may have elaborated the human grief response. Future research is needed to test whether bereaved parents receive social recompense for their extensive grief over their lost children.

If grief does indeed offer social benefits, these may be especially high for slow life history strategists, who tend to form strong cooperative social ties and thus stand to gain from enhancing their appeal as reliable cooperative partners. Slow life history strategists might also be especially likely to exhibit prolonged grief because they generally produce fewer children and invest heavily in each. Because life history speed accounts for variation in investment in both kin and non-kin relationships, similar physiological mechanisms may underlie individuals' attachment to both romantic partners and children. If so, then perhaps humans have evolved a general attachment severance system, which facilitates disengagement from fitness-harming mates and children, as well as recovery from both dissolved romantic partnerships and the loss of children.

Although parental grief is perhaps one of the most painful experiences a person can endure, it likely follows predictable and theoretically-consistent patterns. The theory and data reviewed here offer several profitable avenues for future research that can advance our understanding of the evolutionary origins of parental bereavement as well as account for variation in suffering. By examining the evolutionary origins of parental grief, we may better design clinical treatment for bereaved parents, or at minimum, provide ameliorating insight onto their experiences.

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Appendix A. Supplementary data

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