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Explaining Social Behavior in Response to Death-Related Threats: The Conspecific Loss Compensation Mechanism

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Exposure to death-related threats, thoughts and cues (actual or anticipated death of conspecifics, including oneself) remain powerful stressors across primate species, including humans. Accordingly, a pervasive issue in psychology pertains to the kind of social-cognitive responses exposure to deadly threats generates. To this day, psychological models of reactions to death-related threats remain underspecified, especially with regards to modern evolutionary theory. Research on both humans and nonhuman primates' reactions to death-related threats highlights a general tendency of human and nonhuman primates to "cling to the group" and to display increased social motivation in the face of death and deadly events (predator attacks, disasters, terror attacks. . .). Given the adaptive value of social networks, which provide individuals with resources, mating pool and support, we propose the existence of an evolved mechanism to explain these affiliative responses. In particular, we propose a "conspecific loss compensation mechanism" (CLCM) that actively keeps track of and compensates for threats to the integrity of one's social network. In the face of death-related cues signaling a danger for one's social network, or actual conspecific loss, CLCM triggers proportional affiliative responses by a process labeled *compensatory socialization*. After reviewing existing evidence for the CLCM, we discuss the plausibility, parsimonious character, and explanatory power of the diversity of behavioral and cognitive responses observed among threatened and grieving individuals. We also formulate clear and novel predictions to be tested in future research.

Public Significance Statement

Research on responses to death-related threats (loss or anticipated loss of conspecifics, including oneself) among humans shows increased bonding within one's social network and derogation of outgroup conspecifics. Based on ethological observations reporting similar behavioral patterns and on the adaptive value of social networks, we hypothesize the existence of an evolved "conspecific loss compensation mechanism" (CLCM) that keeps track of and compensates for threats to the integrity of one's social network. The CLCM parsimoniously explains a wide variety of empirical findings and allows the testing of novel predictions regarding human social cognition and behavior.

Keywords: evolutionary thanatology, death-related threats, social networks, primates, loss compensation, humans

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By contrast to many of their primate cousins living in the wild, contemporary humans face little threat from predation (Isbell, 1994; Ritchie & Roser, 2019). Cardiovascular and respiratory diseases, cancer and transportation accidents are (or at least are perceived as) major threats to one's life (Ritchie & Roser, 2019). Exposure to corpses, associated funeral and bereavement practices differ cross-culturally (Eisenbruch, 1984a, 1984b; Littlewood, 1992; White, Marin, & Fessler, 2017) but sights or thoughts highlighting the actual—or anticipated—death of conspecifics—including oneself in the case of humans—probably remain a constant and powerful environmental stressor.

What changes does exposure to death-related cues or thoughts cause to human social cognition? To this day, research (which we shall review here) points at a general tendency to “cling to the group” and to experience increased social motivation in such circumstances. These patterns are likely observed among humans and other primates, while their mechanisms have started to be unveiled. Beyond detailing behavioral mechanisms, the explanation of behavior also relies on other levels of analysis, including when a given behavior emerged in evolution, how it develops through ontogeny, and why it has been selected for (what the biological function of a given behavior or trait is; Tinbergen, 1963).

In this article, we propose an evolutionary solution to explain the biological function of behaviors such as ingroup bonding and outgroup derogation, behaviors which are commonly observed in response to death-related threats. We propose the existence of an evolved mechanism (labeled “conspecific loss compensation mechanism” [CLCM]) that actively keeps track of and compensates for any threat to the integrity of one's social network. This framework is parsimonious and helps explain the various behavioral and cognitive responses observed in people facing deadly danger.

To present our theoretical proposal, we structure our argument as follows. In the first section, we review the literature pertaining to human social networks and their positive effects on individual survival and reproductive fitness. We also remind readers of the importance of social network in other species. Building upon this observation, we then review the literature on humans' reactions to death-related threats and

offer—again—a comparison with those of non-human primates. The reviewed empirical evidence shows a general tendency across species to strengthen one's bonds with ingroup members/allies after being exposed to death-related threats (or related cues). Given that (a) social networks bear adaptive value and (b) individuals strengthen their social bonds under death-threats, we argue for the existence of an evolved mechanism that helps protect the integrity of one's social network. We describe this mechanism in a fourth section and explicit novel hypotheses derived from our model (as well as available evidence regarding these) in a fifth section.

The Adaptiveness of Social Network

Primates are highly social animals, and some primate species enjoy social bonds (i.e., relative strong social ties) with other members of their groups. Human social networks typically consist of “a hierarchically organized series of grouping levels” (Stiller & Dunbar, 2007, p. 93). Research shows that, on average, human social networks are comprised of approximately 150 individuals (but see de Ruiter, Weston, & Lyon, 2011, vs. Dunbar, 2012, for debates). This upper limit is an evolutionary trade-off between the benefits (dilution of predation risk, territorial defense, access to hierarchical positions, discovery of foraging opportunities, mating opportunities) and costs (conflicts and competition, access to reproduction, pathogen prevalence) of sociality (Dunbar, 2009; Reader & Laland, 2002; see also Dunbar, 2014).

The adaptive value of belonging to a social group has established evolutionary underpinnings. As Leary (2010) put it,

In tracing the origins of human sociality, theorists have proposed that affiliation and group living enhanced our prehistoric ancestors' chances of survival and reproduction, as well as the survival of their offspring (Ainsworth, 1989; Kameda & Tindale, 2006). [. . .] Group living is characteristic of our closest primate relatives—the chimpanzees, bonobos, and gorillas—suggesting that it might have evolved before the human lineage split from that leading to other modern great apes (De Waal, 2005). (p. 865)

Accordingly, research has shown that the number and intensity of social bonds favor late survival and reproductive success (e.g., Silk et al., 2009, for one of numerous articles).

As it stands, findings point at the functionality of social networks in terms of wellbeing (Ryan & Deci, 2000), material-physical safety (Navarrete, Kurzban, Fessler, & Kirkpatrick, 2004; Pickett & Gardner, 2005), sharing of information relevant to one's survival (Lakin, Jefferis, Cheng, & Chartrand, 2003), and anxiety reduction (Buss & Shackelford, 1997). Thus, social interactions and integration to social networks are considered crucial to human individuals' survival (Caporael, 2001; Maslow, 1943; Postmes & Jetten, 2006; Ryan & Deci, 2000). Indeed, across human individuals' life span, the presence of conspecifics and allies (sometimes more than material resources) is needed to ensure survival, whether to facilitate infants' growth and normal functioning (Beckes, Simpson, & Erickson, 2010; Nysten, O'Hara, & Engeldinger, 2013) or for sustaining older individuals' autonomy and survival (e.g., Blazer, 1982). This obvious adaptive value of network integration has shaped human psychology to the point that social belonging has become one fundamental need driving many of our everyday behavior (e.g., Echterhoff, Higgins, & Levine, 2009; Leary & Baumeister, 2000; see Bonetto & Monaco, 2018).

The benefits provided by one's integration to a social network has direct effects on health. In fact, social membership has a host of positive health and wellbeing outcomes. Decades of research show that social support acts as a buffer against anxiety, depression (Khaledi et al., 2014) and susceptibility to physical health (Çelebi, Verkuyten, & Bağcı, 2017; Kroenke, Kubzansky, Schernhammer, Holmes, & Kawachi, 2006). The deleterious effect of stress on depression is considerably smaller for individuals with high social support compared to those with low social support (Wang, Cai, Qian, & Peng, 2014, see also Çelebi et al., 2017). On the contrary, socially isolated people or those having relational problems have been found to display immunological and cardiovascular health problems, which leads to increased mortality rates (Stansfeld, Bosma, Hemingway, & Marmot, 1998). Furthermore, social exclusion is known to recruit brain areas otherwise dedicated to the processing of physical pain (Eisenberger, Lieberman, & Williams, 2003). Besides ensuring individuals' health and wellbeing, being socially valued by others in relationships

increases access to material and sexual resources (Williams & Zadro, 2005).

In turn, individuals' need to belong leads to the strengthening of one's social network, thereby increasing survival (through protection from predators and aggressive others; Wilson, 2005), reproductive success and successful child rearing. For instance, ostracism has been proposed as a way to reduce dominant individuals' monopolization of resources because their exclusion can lead to selection of more egalitarian traits (Gavrilets, Duenez-Guzman, & Vose, 2008). Consequently, those who do not experience an optimal level of affiliation will adjust their behavior to attain it (Baumeister & Leary, 1995). Social exclusion triggers affiliative responses, which can even lead to depression and eventually self-damaging behavior (e.g., suicide) if not properly addressed (Harterink, van Beest, Wicherts, & Williams, 2015). Social belonging increases individuals' mastery over the environment (Choi, Price, & Vinokur, 2003) and helps them efficiently cope with uncertain situations (Hogg, 2007). Social influence through norm salience provides guidance for decision-making in life-threatening situations, be it toward objects or other conspecifics (Cialdini & Trost, 1998).

Social network is so central to individual functioning that individuals are expected to possess an in-built mechanism for gauging their levels of adjustment with their social environment (Leary & Baumeister, 2000). Self-esteem has been hypothesized to act as a "thermometer" for signaling the degree of adequation between one's displayed behavior and the prescribed behavior in one's network (Leary, 2010). Evidence for this so-called sociometer theory of self-esteem lies in the finding that, when their self-esteem is threatened, people are motivated to bond with conspecifics (Vandellen, Campbell, Hoyle, & Bradfield, 2011). Also, the need to belong goes beyond short-term advantages. It is a crucial motivation that helps individuals to form long-term bonds with conspecifics, even from a very early age (Over, 2016).

As these converging findings suggest, social network integration seems to possess adaptive value and to promote reproductive fitness among humans. This observation also holds for other species. For instance, many studies have highlighted positive effects of social bonding

and social support upon anxiety reduction among both human and nonhuman primates (see [Hostinar, Sullivan, & Gunnar, 2014](#), for a review). Social integration improves reproductive success and successful child rearing to the point that social exclusion in animals could lead to a selection of prosocial behaviors which, in return, mitigates the negative effects of isolation ([Bailey & Moore, 2018](#)). Finally, the homeostatic pattern of affiliative responses observed in humans ([Zeedyk-Ryan & Smith, 1983](#)) can also be found in rodents ([Latané & Werner, 1978](#)).

Social Networks and Death-Related Threats

Accordingly, the adaptive value of social networks is at the basis of theories pertaining to the nature of reactions to death ([Jonas et al., 2014](#)). Experimental studies manipulating the salience of death-related threats consistently demonstrate that individuals react by “clinging” to members of their network (e.g., [Castano, 2004](#)), by increasing their adherence to social norms and collective beliefs ([Pyszczynski, 2015](#)) and by displaying aggressive behavioral patterns toward distant others ([Maoz & McCauley, 2008](#)). Various deadly threats (e.g., natural disasters, terror attacks) have been found to motivate individuals toward affiliating more with others ([Castano, Yzerbyt, & Palatino, 2004](#); [Dezechache, 2015](#); [Strümpfer, 1970](#)), to seek out psychological identification with relatives (or fellow citizens, see [Moskalenko, McCauley, & Rozin, 2006](#)), and even to increase accessibility in mind of attachment figures ([Mikulincer, Gil-lath, & Shaver, 2002](#)).

Human Reactions to Death

The study of individuals’ reactions to the death of conspecifics witnesses a renewal of interest among primatologists ([Anderson, 2011](#); [Anderson, Biro, & Pettitt, 2018](#); [Gonçalves & Carvalho, 2019](#)) and has been the focus of some major psychological theories regarding human behavior (e.g., Terror Management Theory; [Rosenblatt, Greenberg, Solomon, Pyszczynski, & Lyon, 1989](#)). Whether investigating human or animal behavior, and though these theories use various paradigms and methodologies the bulk of them predict a general tendency of individuals to “cling” to conspecifics when facing deadly threats.

Because of the beneficial aspects of enjoying a robust social network, it comes as no surprise that most studies regarding human reactions to deadly threats converge in demonstrating increased affiliative motivation and ingroup identification under life-threatening circumstances (see [Jonas et al., 2014](#) for a review). Other studies focusing on natural disasters have found that people experiencing such events are more likely to increase bonding with the closest peers of their social network ([Kim & Hastak, 2018](#)). Also, within work teams, increased threat (e.g., natural disasters) is associated with centralization of the communication structure ([Dunbar & Goldberg, 1978](#); [Khandwalla, 1978](#); [Smart & Vertinsky, 1977](#); [Staw, Sandelands, & Dutton, 1981](#)). Death-related stimuli increase individuals’ adherence to social norms and beliefs and—as a consequence—increased sanction of deviants ([Greenberg, Pyszczynski, & Solomon, 1990](#)). This general pattern has received a lot of empirical support, from more than three decades of research investigating and corroborating effects of death-related stimuli upon individuals’ social-cognitive and behavioral reactions ([Burke, Martens, & Faucher, 2010](#); [Castano, 2004](#); [Dezechache, 2015](#)).

In addition, individuals confronted with death display a host of defensive reactions. For instance, death-related stimuli increase positive evaluation of conspecifics praising one’s cultural values ([Greenberg et al., 1990](#)) and promote less aggressive behavior toward those who share similar ones. Symmetrically, targets who criticize one’s culture or share a different set of values are more negatively evaluated by threatened participants, leading to increased aggression toward them ([McGregor et al., 1998](#)). There is also evidence for greater support of “hawkish” international policies (e.g., war) following death-threats ([Hirschberger & Ein-Dor, 2006](#); [Pyszczynski et al., 2006](#)). The effects of death awareness extend to individuals’ mating behaviors: they get more attracted to romantic partners ([Mikulincer, Florian, & Hirschberger, 2003](#)) and desire more intimate social relations ([Mikulincer & Florian, 2000](#)). More generally, death-related stimuli render individuals more willing to engage in social interactions ([Taubman-Ben-Ari, Findler, & Mikulincer, 2002](#)). They increase positive associations with one’s parents and allocation of resources to stay linked with attachment figures ([Cox et al., 2008](#)).

along with increased desire for children (Wisman & Goldenberg, 2005).

But what are the processes at play behind these various empirical findings? Psychological theories have proposed to link human reactions to death awareness with a general uncertainty coping mechanism involving both the behavioral inhibition system and error monitoring activity from the anterior cingulate cortex (see Tritt, Inzlicht, & Harmon-Jones, 2012). Yet, these explanations have not yet provided a clear evolutionary account of the general tendency to “cling to the group” in troubled times. Evolutionary psychologists have pointed that social psychological models of reactions to death lack integration with evolutionary biology (such as inclusive fitness theory, Hamilton, 1964; see Buss & Shackelford, 1997; Kirkpatrick & Navarrete, 2006). These critics did provide an alternative account of these effects in terms of evolved coalitional psychology (sticking to others for safety), though it has remained largely unspecified.

Recent research approaching the effects of threat (at large) on parochiality and intergroup behavior under an evolutionary lens was carried out by Whitehouse et al. (2017). These researchers were indeed puzzled by the function and emergence of sometimes costly behaviors (e.g., self-sacrifice for a cause) among humans attributable to feelings of group fusion (i.e., strong feelings of identification with one’s ingroup; see Swann, Gómez, Huici, Morales, & Hixon, 2010). To explain this phenomenon, they demonstrated that groups undergoing “fitness-decreasing experiences” (i.e., threats, including death-related) are more likely to display future progroup behavior, which then enhances individual and group fitness. Whitehouse et al. (2017) concluded that humans have evolved the tendency to cooperate more under threat because it helps to solve problems related to free-riding for instance. Seen in this light, group-fusion under threat functions as a psychological tool for thwarting kin recognition processes, thus allowing one to engage in costly prosocial behavior benefiting nonkin. However, this mechanism remains very general and still cannot account for the range of behaviors observed in reaction to death-related threats specifically (e.g., grieving, nonprosocial ingroup behavior).

To deal with this problem, we will try to highlight a specific mechanism at play which

serves the observed pattern of seeking of social support in times of danger. In this regard, many models point at the mediating role of anxiety generated by death-related stimuli and the buffering function of self-esteem on this anxiety. These assumptions draw on the sociometer theory of self-esteem (Baumeister, Twenge, & Nuss, 2002; Leary & Baumeister, 2000) which posits self-esteem is a psychological gauge for assessing how integrated the individual is among a given network. This buffering function explains why self-esteem is correlated with social identification (Tajfel, 1982), why it is negatively linked with depression/anxiety (Sowislo & Orth, 2013) and why it is bolstered by social acceptance (Blackhart, Nelson, Knowles, & Baumeister, 2009). Moreover, whenever death awareness is triggered, individuals will be motivated to suppress death-related thoughts. Because self-esteem is linked with social values (collective norms, beliefs, ideologies), threatened individuals may increase their self-esteem by reinforcing their adherence to cultural beliefs. In fact, many experimental findings support this prediction (see Pyszczynski, 2015 for an exhaustive review). Whenever reminded of their own death or exposed to death-related stimuli (both explicit and subliminal), individuals’ death thought accessibility increases, and so does their adherence to a range of cultural values. These effects were found to be moderated by individuals’ self-esteem levels (Greenberg et al., 1993).

Some of the above-mentioned effects can be triggered by different kinds of death threats, (e.g., terrorism, Landau et al., 2004; natural disasters, Dezechache, 2015). However, we must bear in mind that most psychological theories explain individuals’ reactions to death by appealing to its existential character. According to these theories, death-related thoughts following death reminders do affect people because they remind them of their own finitude, an assumption that, to our knowledge, has never directly been tested and which we propose to challenge. In fact, there is ample evidence showing that humans also react to immediate deadly dangers (e.g., during a terror attack or a natural disaster) by increasing their social connectedness with conspecifics and clinging to peers (increased prosociality and helping behavior; Dezechache, 2015). It is thus unlikely that existential concerns always motivate reactions to death-related

stimuli. Also, we may wonder whether those effects are solely found in humans. In fact, some of the behavioral correlates of death-related thoughts can be observed in nonhuman animals, notably nonhuman primates, suggesting they represent ancestral traits.

Nonhuman Primates Reactions to Death

The field of how nonhuman animals react to death is old (Forbes, 1813; see Gonçalves & Carvalho, 2019 for a review in primates), vast and growing, but it also has long been disparate (Anderson et al., 2018; Forbes, 1813; Palombit, Seyfarth, & Cheney, 1997). The bulk of observations related to how nonhuman animals experience the death of their conspecifics have been relatively anecdotal, observational and appeared as case-studies (but see Swift & Marzluff, 2018 for an experimental approach; see Watson & Matsuzawa, 2018 and Sugiyama, Kurita, Matsui, Kimoto, & Shimomura, 2009, for more systematic approaches). In primates, earliest observations were made in captive settings, with field reports (presumably made in circumstances where social dynamics are not artificially maintained) appearing relatively later (Goncalves & Carvahlo, 2019).

A recent collection of articles has been published that tried to unify this disparate work and provides a framework to study the evolutionary history of behaviors surrounding the death of conspecifics under the name “evolutionary thanatology” (Anderson et al., 2018). Our own endeavor is more modest, as we seek to evaluate the extent to which primates other than humans display reactions that are similar in nature (notably increased social motivation) to humans when being exposed to death. We shall also take it for granted that primates (and particularly apes) possess a capacity to detect so-called animacy detection malfunction (Gonçalves & Biro, 2018) and unusual behavior, along with a capacity to react to specific olfactory cues emitted by corpses. We believe this assumption to be generally warranted (Anderson, 2018; see Gonçalves & Carvahlo, 2019, for a lengthy discussion).

In a recent and authoritative review, Gonçalves and Carvahlo (2019) have provided much of the materials needed to examine primates’ reactions to death. Obviously, species difference exists, but our summary will remain

general enough. Part of the available reports, focusing on the loss of infants due to accident or infanticide, show that, in some species, mothers carry the deceased infants for periods of times that can exceed a week (though typically not more than a few days; Altmann, 1980; Schaller, 1963; Van Lawick-Goodall, 1968), with a progressive abandonment of the corpse (likely depending on the climatic conditions, favoring or not the preservation of the corpse), and manipulations that suggest awareness of the nonanimacy of the deceased infant (e.g., dragging infants by the tail, Gonçalves & Carvahlo, 2019; leaving them underwater when drinking from water sources, Perry & Manson, 2009; or cannibalism, Fedurek et al., 2019; see also Watson & Matsuzawa, 2018 for a review). Beyond carrying (and in some species, even when carrying does not occur), mothers can engage in cleaning and grooming of the corpse (Biro et al., 2010; Kaplan, 1973), a behavior which may serve learning (Cronin, Van Leeuwen, Mulenga, & Bodamer, 2011). Besides mothers, other group members may show interest in corpses of infants, although much more limited in scope and intensity as compared to that of the mother.

Caring and grooming responses may also occur toward other group members, a behavior which is seemingly mediated by the strength of social bonds between the focal and the deceased individual (Gonçalves & Carvahlo, 2019; Yang, Anderson, & Li, 2016), and which may consist in inspections (Van Leeuwen, Mulenga, Bodamer, & Cronin, 2016), shaking (Stewart, Piel, & O’Malley, 2012), poking, dragging, grooming and even cleaning the corpse (van Leeuwen, Cronin, & Haun, 2017). Interestingly, guarding has also been observed (Koerth-Baker, 2013), a behavior which may target a close kin of the deceased (typically the mother: Mori, Iwamoto, & Bekele, 1997) and which may reflect and help foster the stability of coalitions. Finally, proximity maintenance (also known as “vigils”; Gonçalves & Carvahlo, 2019) is also reported, particularly among the closest kin of the deceased.

Besides behavioral reactions, psychosocial reactions have also been tentatively identified in primates noticing the death of conspecifics. States such as grief were attributed, consisting in protest behaviors (e.g., Fashing et al., 2011; Goodall, 1990), sudden withdrawal from social activities (reviewed in Gonçalves & Carvahlo,

2019; see also Anderson, 2016) and which severity may be associated with the conspecifics loss (i.e., proportional to the social bond that existed between the individuals). For infants “grieving” their mother, social withdrawal may even lead to death caused by the complete interruption of feeding and foraging activities (Goodall, 1990; Hinde & Spencer-Booth, 1971). In mothers losing infants, similar behaviors have been observed (Gonçalves & Carvahlo, 2019). Loss of a group member can also be associated with lesser activity in groups of great apes (Less, Lukas, Kuhar, & Stoinski, 2010).

Is social withdrawal the main and only response of primates experiencing the death of a conspecific? Studies indicate that death in a primate troop can lead to high stress levels in the group, against which a suite of behaviors can be deployed to help buffer the stress. These include social activities such as grooming and activities which are in turn likely to foster social bonds with remaining partners. Such a pattern has been evidenced in female chacma baboons, in which the death of a close relative is both associated with transient elevated levels of stress and increased investment in allogrooming (higher rate of allogrooming and diversity of grooming partners), suggesting that females may compensate for the loss of a social partner by the fostering of existing grooming partners, or by recruiting new grooming partners (Engel et al., 2006). This pattern may, however, be subjected to interindividual differences in personality (Seyfarth & Cheney, 2013). Higher investment in allogrooming following death of a group member is also suggested in rhesus macaques, particularly in individuals that were close to the corpse (Buhl et al., 2012).

In sum, the literature on primates suggests that exposure to death may cause withdrawal of social activities (a pattern which may in fact be confined to dependent individuals, such as young infants, upon losing their mother) but may also increase social activity. The role of social support in buffering stress is however undeniable. Future work should yet clarify whether reliance on social partners when experiencing death is a species-dependent phenomenon.

Toward a Conspecific Loss Compensation Mechanism

The Compensatory Socialization Hypothesis

So far, we have seen that there is a general tendency in humans to “cling” to conspecifics when facing death-related stimuli. The “coalitional” aspect of human psychology is so ingrained that, in troubled times, individuals will automatically seek out to gather with similar others as a way to cope with and survive a threatening situation (Romero, Uzzi, & Kleinberg, 2016). We have also argued that all theories pertaining regulation processes to such threats converge in predicting and providing evidence for a general tendency to stick to others (i.e., to engage in a form of “hypersocial” coping under symbolic or realistic threats including death-related ones), which likely extends to nonhuman primate species. While these adaptive reactions to death-related threats (Wilson, 2005) are now well empirically supported and understood in terms of both proximal (e.g., anxiety regulation) and distal factors (evolved coalitional psychology), there is a current lack of specification concerning their exact evolutionary underpinnings. It is a known fact that conspecifics help individuals in dangerous times, but no research has yet investigated the existence of potential modules (sensu Cosmides & Tooby, 1994; Fodor, 1985) to explain individuals’ reactions to death-related threats. In fact, specifications regarding the mechanisms and the function (Tinbergen, 1963) of such reactions have been largely overlooked from an evolutionary perspective, an issue we propose to address.

This state of affairs leads us to hypothesize the existence of a more general CLCM for social network maintenance, that may be triggered by death-related threats. The idea behind the CLCM is very simple, yet generates various deductible consequences. Cues of conspecifics’ death (visual, olfactory), we argue, constitute aversive stimuli that are stressful to individuals (among primates but also in nonprimate species, see Chakraborty et al., 2019) insofar as they signal the potential loss of a conspecific and thus, of a part of their social network. Because of the importance of the integrity of the social network, the void left by the dead conspecific needs to be filled (i.e., compensated for). The

CLCM therefore predicts that death of conspecific should lead to affiliative responses. A potential difference between humans and other species might be that humans do not need to directly perceive the death of a conspecific for the CLCM to be activated. Our capacity for abstract thinking means remote perception or imaginations linked to the potential death of a conspecific (perceptions of insecurity due to crime, news of natural disasters or an ongoing war, territorial loss. . .) may be themselves sufficient to activate CLCM and trigger anticipatory affiliative responses. In other words, it is possible that the inputs of the CLCM are different between species, particularly for species capable of abstract thinking (which may not require the direct perception of a corpse to infer the loss), while the output of the mechanism (affiliation) would be similar across species.

The main hypothesis behind the CLCM is that, whenever threatened, the integrity of an individual's social network should have to be restored (compensated for) because it is central to individual survival and reproductive success. To do so, individuals of a given species will seek to interact positively and recreate bonds with still living network members (i.e., display affiliative responses). We call this process compensatory socialization. More specifically, and in line with Hamilton's (1964) principle of inclusive fitness, this compensatory socialization would bear reproductive advantage. Indeed, socialization, through access to resources and social support should positively impact the likelihood of one's successfully transmitting its genetic makeup directly through improved survival (and thus likelihood of sexual encounters) and/or indirectly enhancing offspring survival as well.

Accordingly, we argue that, among humans, social networks have double implications for fitness. First and obviously, close conspecifics in one network are made of genetically related individuals (e.g., kin). There is thus a fitness implication of compensatory socialization so that any loss among these should be compensated to improve support on other kin, increasing their chances of survival and reproduction. This relationship is reciprocal: investing compensatory time on one's kin also directly improves one's own fitness. Also, humans have unusual levels of prosociality which means that nonkin (besides one's partner, friends, col-

leagues; Queller, 1985) are also an important part of one's social network. In that case also, compensatory socialization would bear *indirect* fitness implications, due to increased support gained from extended kin but also to the maintenance of a network guaranteeing access to potential mates.

The compensatory socialization hypothesis was combined with recent work derived from the social brain hypothesis and the structure of primate social networks (e.g., Dunbar, 2014), which highlights the evolutionary trade-off between the maintenance of large social networks and constraints in terms of time-budget and associated costs of sociality (such as potential increased competition for foraging or mating resources). This latter framework allows us to predict that compensatory socialization—if measured in terms of time spent interacting with conspecifics—would be a direct function of at least three parameters: genetic relatedness of the threatened conspecific, social relatedness (closeness in the network) of conspecifics available to interact with and, in the case of a dead conspecific, the proportion of interaction time with that individual in the whole network.

Though we might debate specific patterns of compensation due to differences in biological kin and other (not genetically related) close individuals among humans, compensatory socialization should preferably be exerted proportionally to the amount of time budget an individual allocates to a threatened or deceased target conspecific, because of the implications in terms of direct support and access to resources as indicated by interaction time. Thus, the CLCM predicts that, under threat, there should be a positive correlation between interaction time with the threatened (or deceased) target and magnitude of compensation (e.g., time allocated to another conspecific which bears similar social network characteristics in terms of closeness, etc.). Conversely, we expect a negative correlation between social distance with the deceased conspecific and magnitude of compensatory socialization effects.

We consider that the CLCM offers a distal explanation (along with a more specific mechanism) to integrate current empirical findings from the psychology of death-related threat regulation. For instance, grief is an ubiquitous phenomenon among humans (Bonanno & Kaltman, 1999) and is theorized as a costly behavior

enabling individuals to signal their levels of commitment to a group (or a cause), as well as their capacity to form strong nonutilitarian social bonds (see Winegard, Reynolds, Baumeister, Winegard, & Maner, 2014) to conspecifics. At the same time, noncostly grief-like behavior is seen in nonhuman primates (e.g., refusal to leave the corpse of a familiar individual) and is thought to facilitate reunification with a lost social partner, a behavior which is particularly maladaptive when the lost individual is dead (see White & Fessler, 2017). From a CLCM perspective, both explanations can be tied together. Seemingly maladaptive grief behaviors could stem from compensatory socialization and constitute incidental cues for strength of prior bonding with the deceased partner (because compensation should be proportional to prior time spent with the conspecific). This cue could be interpreted and picked up among species with abstract social judgment capabilities, yielding fitness gains. This gain in turn would facilitate the evolution of this behavior into a more costly and functional one among these species but not others.

Human reactions can thus seem more complex than nonhuman primates' at first glance (involving ideology, social norms and cultural values), though they might really stem from common basic processes. That is why we will now discuss how the CLCM can highlight aspects of human behavior and cognition that are not so qualitatively different from nonhuman primates'. Moreover, compared to previous theories of threat regulation which rely on homeostatic accounts of human cognition and behavior (e.g., Jonas et al., 2014; Rosenblatt et al., 1989), the CLCM offers to consider individual reactions as proactive (and not reactive), in line with an allostatic model of biological phenomena (see Sterling, 2012). The very concept of compensatory socialization in reaction to anticipated loss of conspecific is much in line with the notion that adapted organisms anticipate needs and prepare for their satisfaction before disturbing events arise.

What Triggers Compensatory Socialization?

Compensatory socialization could be triggered by various cues including mortality salience or social exclusion (and isolation) but

also cues related to animacy that help individuals detect the living condition of an organism (see Barrett & Behne, 2005). Because compensatory socialization is hypothesized to occur proportionally to interaction time with the lost conspecific, we predict that the recoverable character of the loss (temporary, such as one leaving its relative to study abroad or permanent such as death) should not matter. In fact, according to that time-proportional principle, compensatory socialization should occur to "fill-in" the vacuum left by decreased interaction time. For instance, military personnel in operations are still allowed conversations with their family, and compensation should be of magnitude to fill the gap between current interaction time (a few hours per week) and prior time (tens of hours each week). From a CLCM perspective, this is different but quantitatively almost equivalent to compensation after the death of closed ones.

In addition, we argue that, among humans, compensatory socialization should mostly be triggered by cues of anticipated loss. It means that mortality salience regarding a conspecific (or a group of conspecifics) should trigger cognitive responses having to do with one's anticipation of losing one's relatives, and not only concerns about one's death per se. In other words, an important threat component behind death would be the idea and anticipation of one being cut out of one's social network. This may be another reason why thinking about one's death should be specifically terrifying.

The emergent network dynamics that result from such interactions could be explained entirely by this kin selection derived hypothesis in line with the principles of coalitional psychology. Like Kirkpatrick and Navarrete (2006), we argue that there might exist such evolved reactions as a fear of death which could be adaptive, even if it can endanger the individual sometimes. This is because the cost of a temporarily debilitating death anxiety would be overrun by facilitating prosocial behavior toward close genetic relative, maximizing their survival and their chance of reproductive success, therefore improving one's reproductive fitness. The only distinction is that those reactions would have to do with the death of other, close members of one's social network. We also argue that magnitude of compensatory socialization effects under real or anticipated loss would be mediated

by stress levels. A wealth of research has been dedicated to the study of individual coping with stress and systematically highlight such strategies as social coping (reaching out to conspecifics for social support) as effective ways of reducing anxiety levels (Romero et al., 2016). Stress motivates individuals to engage in social interactions such as grooming behavior (Dunbar, 2014), which in turn, reinforces social bonds and potentially compensates for the amount of interaction time/frequency with the deceased or disappeared group member. In sum, the CLCM hypothesis proposes that reactions to loss are oriented toward social network maintenance and that the apparent “altruistic” behavioral outcome would be underlined by kin selection, guaranteeing the successful replication of the individual’s genetic contribution.

The Explanatory Power of the CLCM Hypothesis

If we want to provide the CLCM with a solid theoretical foundation, the mechanism of compensatory socialization should be able to account for the many findings of research related to the effects of death-related threats among humans (and other animals) in a coherent and simple way. The first line of findings that can be explained that way is the one which relates to death-threats’ effects upon individuals’ beliefs. More specifically, psychological theories predict that when confronted with death, individuals will increase their adherence to group related norms and beliefs to decrease death anxiety (Burke, Kosloff, & Landau, 2013). A CLCM explanation of this tendency would be that it is actually a byproduct of increased bonding under loss salience. In fact, humans are known for their homophily (see for instance McPherson, Smith-Lovin, & Cook, 2001). Individuals tend to marry, reproduce and cluster in groups with “like-minded others” (conspecifics with similar sets of norms and values; McPherson et al., 2001; Smits, 2003). Given the well-known fact that individuals conform more to values and norms to bond with others (in the case of integration in a new group, this process is called anticipatory socialization, see Merton & Kitt, 1950), it would only be logical that individuals trying to increase bonding with ingroup members under loss salience would display more adherence to ingroup’s shared norms. Support-

ing this hypothesis, studies have shown that reminders of death decrease ingroup members’ perception as threatening individuals and increase attention to ingroup members while bolstering conflict components linked with outgroup members (Dickter & Bartholow, 2007). Similarly, death-related threats increase accessibility of stereotypical in/outgroup social categorization (i.e., the tendency to think positively of ingroups and negatively of outgroups; see Henry, Bartholow, & Arndt, 2010). This could explain why aggressive intergroup behavior increases under salience of mortality-related stimuli (Greenberg, Solomon, & Pyszczynski, 1997). Increased conformity to group norms would automatically trigger more punitive behavior toward moral transgressors or outgroup members that, by definition, do not share (therefore violate by default) one’s set of norms and beliefs. It would also explain why—under mortality salience—individuals tend to be more “respectful” of cultural symbols (e.g., lesser consideration for using a crucifix in a problem-solving task, Greenberg, Porteus, Simon, Pyszczynski, & Solomon, 1995). Here, we must keep in mind that cultural norms among humans have a social bonding function (Hogg, Hohman, & Rivera, 2008).

Another class of findings are consistent with the CLCM: cultural differences in effects of death-related threats—or rather, the apparent absence of such differences. Yen (2013) meta-analysis of moderators of death-related threats’ effects shows that cultural differences masked bigger differences due to researchers and research teams (and associated differences in methodologies). Their results cast doubt on the existence of cross-cultural differences in how we react to death-related threats. This might be taken as crediting the existence of a universal evolved mechanism behind these effects. In particular, the individualistic-collectivistic orientation dimension does not seem to offer clear differences in how people react to death threats. From a CLCM perspective, this is not surprising given that offline social networks size (another dimension over which cultures may be compared) does not differ between members of individualistic versus collectivist cultures (Cardon et al., 2009).

A fair amount of social-psychological literature is also devoted to the study of cultural and ideological moderators of mortality salience ef-

fects. Most effects of such moderators as tolerance (Greenberg, Simon, Pyszczynski, Solomon, & Chatel, 1992), fatalism-karma beliefs (Yen, 2013) and political ideology can be explained by the present CLCM (because these beliefs can be considered as readily accessible social beliefs to which individuals conform under loss salience to engage in compensatory socialization). In that perspective, these effects would not be considered direct effects of death induced anxiety regulation but side effects of a more general and deeply rooted mechanism pertaining to social network maintenance.

Social Network Maintenance: Specific Mechanism or Byproduct?

When hypothesizing the existence of a novel evolved mechanism, two issues must be straightforwardly addressed. First, one needs to identify fitness-related problems relevant to the organism under consideration. Then, one needs to provide for a parsimonious (minimalistic) solution for this problem. Relatedly, it is also crucial to consider alternative solutions that could be provided for by existing mechanisms. So far, we have seen that social networks are adaptive and threats to their integrity should constitute an important (and “old”) issue for a social species like humans. This lead us to propose a minimal solution (one mechanism labeled “compensatory socialization”), with maximal implications (i.e., diverse outcomes such as intergroup aggression and increased conformism). Still, one question remains: do we need to hypothesize a novel mechanism, or could compensatory socialization effects stem from already theorized evolved modules?

One way to address this issue is to focus on the evolutionary problem at hand, namely that of the preservation of the integrity of social networks. In a way similar to van Prooijen and Van Vugt’s (2018) argument for the existence of a specific module at play behind conspiracy beliefs (vs. conspiracy beliefs as the result of cognitive biases), we contend that a byproduct hypothesis carries a fundamental flaw: assuming that network integrity threats (e.g., death of a close conspecific) either “do not exist or did not constitute significant selection pressures influencing ancestral humans’ genetic fitness” (p. 774). This hypothesis is unlikely given the

adaptive value of social networks and their centrality to the life of social organisms. Furthermore—and to the best of our knowledge—there is a current lack of mechanisms directly pertaining to this specific problem in the field of evolutionary psychology.

Another argument in favor of a specific CLCM comes from examining mechanisms that pertain to environmental threats broadly defined and carrying the potential for lethal outcomes. Theories pertaining to hazard precautions (e.g., Boyer & Liénard, 2006) describe the way individuals engage in behaviors aimed at avoiding or palliating hazards such as crop productivity and natural disasters (which explains ritualistic behaviors for instance) and thus pertain to engagement in preventive action, especially in the case of latent (i.e., inferred) threats. However, once a threat has manifested itself and consequences appear on one’s social network, a specific subset of behaviors should be present to cope with social losses. Other mechanisms are frequently invoked to explain the “coalitional” outcomes observed among humans under threat, especially when threat pertains to pathogens and infectious diseases. As such, pathogen and disease-related threats are susceptible to trigger increased outgroup derogation and ingroup identification as part of a “behavioral-immune system” designed to protect individuals from getting sick (Schaller, 2011). Still, this mechanism can trigger responses in absence of threats that aren’t necessarily deadly and is thus not tailored to account for similar behavioral patterns in the face threats of higher lethality (e.g., war, death of one’s relatives).

It is thus likely that a CLCM could exist independently of behavioral immune system-related components, meaning that the two systems could be in conflict under some specific circumstances. As an illustration, recent experimental work among vampire bats revealed that social interactions with diseased conspecifics were largely dependent upon social network related factors (see Stockmaier, Bolnick, Page, & Carter, 2020). As the researchers put it themselves,

In general, our results indicate that sick conspecifics were not actively avoided, nor did they isolate themselves. Instead, our observations were most consistent with the simplest explanation that reduced social interactions resulted from LPS-injected bats being lethargic. Studies on banded mongoose [...]

and rhesus monkeys [. . .] also found no evidence for avoidance of sick conspecifics. In these species and the vampire bats, the overall benefits of social interactions might outweigh the benefits of avoiding sick individuals, especially in highly connected groups where indirect transmission is almost inevitable (Loehle, 1995). [. . .] In vampire bats, however, the direct and indirect fitness benefits of social interactions [. . .] likely outweigh the indirect fitness benefits of potentially preventing infections to related groupmates. (p. 10)

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Finally, hypothesizing a distinct CLCM is in line with basic principles of evolutionary psychology such as error management; which states that when on kind of error is more costly (in terms of fitness) than others, behaviors that help reduce the frequency of committing this costly error should be favored by selective forces. In our perspective, not compensating losses in one's social network indeed bears important fitness costs (e.g., impeded access to resources, mates, social support), rendering likely the presence of specific mechanisms to prevent this issue. The benefits of hypothesizing a specific CLCM also extend to discussions of other death-related phenomena such as grief. In fact, debates persist as to whether grief too would be a byproduct or stems from specific mechanisms (costly signaling; see [White & Fessler, 2017](#)). Here, we think that a CLCM perspective could inform this debate, favoring a costly signaling perspective on grief (facilitating compensatory socialization).

Novel Predictions

As we have seen, the CLCM hypothesis—as a specific evolved mechanism - is consistent with many of the findings from threat regulation theories in psychology which investigated the cognitive and behavioral effects exposure to death-related stimuli. In fact, by proposing this novel mechanism, we aimed at providing a synthetic account of these empirical outcomes, by considering that all of them might be specific byproducts of a bonding drive under anticipated loss (i.e., compensatory socialization). We will now detail some of the novel predictions that can be derived from our theory and mention existing support for those predictions, and how these could be tested in future research (see [Table 1](#) for an overview).

Social Network Effects of Threat

First of all, and as mentioned previously, a straightforward prediction from the CLCM is that compensatory socialization should be proportional to the amount of interaction time that should have been available from the lost conspecific. Evidence for a proportional relationship between those two factors has been observed among birds who were deprived of their partner ([Firth et al., 2017](#)) and among human social networks after the death one's friend ([Hobbs & Burke, 2017](#)).

These results could be replicated by using experimental methods. For instance, it is conceivable to create artificial discussion groups in the lab and then excluding one party member to assess the way the others compensate interaction with other party members depending on their prior interaction time with the departed member. If we expect that perceived reversibility of loss (e.g., death vs. moving in another country vs. moving in another neighborhood) should not be an important moderator of the effects of loss on compensatory socialization, the possibilities that exist to maintain interaction (such as social media and phone use) however should matter (possibility of contact maintenance). One way to test these hypotheses could be to explain participants that the party member is leaving for far away and does/does not consider coming back (reversibility), and that they could/could not be contacted (contact maintenance).

Priming individuals with anticipated loss of different kinds of conspecifics should lead to proportional increases in compensatory responses in terms of psychological measures such perceived ingroup entitativity, affiliative need or group identification. More specifically, and as stated earlier, we argue that compensatory socialization should preferably be exerted proportionally to the amount of interaction time with the lost social member. Yet, all else being equal, for similar interaction time proportions in an individual's network, genetically related lost targets should trigger more compensatory responses than for nonkin.

Moreover, conspecific loss priming should lead to the same proportional increases in network indices such as transitivity, closeness with group members and frequency of interaction with other members of natural networks. In

Table 1
Summary of the Conspecific Loss Compensation Mechanism’s Main Theoretical Predictions, Their Degree of Corroboration Across Study Species, and Future Potential Research Directions

General predictions	Operational predictions	Status	Species	Future direction
Compensatory socialization after threat to network integrity	Direct (increased bonding)	Well-corroborated	Humans (Hobbs & Burke, 2017) Nonhuman primates (Anderson, 2011) Birds (Firth et al., 2017)	Replications using more specific social network integrity threats
	Indirect (e.g., increased collective action)	Well-corroborated	Humans (e.g., Whitehouse et al., 2017)	Replications using more specific social network integrity threats
	No compensatory socialization after network integrity cue	Partially corroborated (with physical safety)	Humans (Napier, Huang, Vonasch, & Bargh, 2018)	Replications needed using specific social network integrity cues
Specific compensatory socialization characteristics	Proportional to prior interaction time	Partially corroborated (observational evidence only)	Humans (Hobbs & Burke, 2017) Birds (Firth et al., 2017)	Experimental studies needed
	Same for both reversible and irreversible losses	N/A	N/A	Empirical tests needed
	Stronger if no affordance for contact (when reversible)	N/A	N/A	Empirical tests needed
	Depends on genetic proximity	Partially corroborated (not among humans)	Vampire bats (Stockmaier, Bolnick, Page, & Carter, 2020)	Empirical tests needed among humans
Increased strength of compensatory socialization	According to relevant individual differences (e.g., extraversion)	N/A	N/A	Empirical tests needed
	For concrete, immediate death-related threats	N/A	N/A	Empirical tests needed
	In high relational mobility contexts	N/A	N/A	Empirical tests needed

Note. N/A = not available.

addition, these phenomena could be investigated using social–cognitive paradigms such as recognition speed of faces/names from genetically related or unrelated close or distant conspecifics. These effects should also hold under other kinds of threats (e.g., mortality salience). Finally, because network compensation relies on relative time spent with other members of one’s social network, the more members in the network, the less time spent with each, the less

people should compensate under threat. This is because it would be easier to compensate with other available people close to one’s network.

A CLCM perspective would also predict a moderation of classical threat (including mortality salience effects) by priming a collective versus individual belief in afterlife (e.g., thinking that significant others would await on the other side or not). Relatedly, it is predicted that among individuals having experienced near-

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death, the ones who experienced hallucinations about seeing relatives during their coma should also be subsequently less intensely or frequently afraid of death.

Finally, moderators of threat effects should be found with individual differences in sociality, empathy levels, sociopathy, introvert personality, agoraphobia or coping styles (e.g., seeking of social support). Moreover, if individual differences constitute potent moderators, it is likely that the nature of threat themselves may differently activate compensatory socialization processes. As such, we expect that abstract threats (e.g., cancer diagnosis vs. speeding car; see Vallacher & Wegner, 2014) would lead to slower and weaker affiliative responses. This should also be true of “long-term” and diffuse threats (e.g., human extinction due to global warming). In line with an ecological psychological framework (Gibson, 2014), we should also not neglect the potential role of environmental factors and especially of socioecological variables that pertain, for instance, to affordances for engaging in compensatory socialization. Accordingly, differences in relational mobility (i.e., the extent to which an environment affords opportunities for forming novel social relationships), which was found to moderate propensity for social risk taking (Li, Hamamura, & Adams, 2016) could affect the extent to which individuals react to social network integrity and death-related threats in terms of compensatory socialization.

Reduction of Threat’s Socially Negative Effects

A CLCM approach to deadly threat regulation posits that threatened individuals are motivated to compensate for anticipated loss in their social network. Conversely, it implies that individuals having compensated or being relatively low in death-related threat perception should display less such tendencies. In other words, the CLCM allows us to predict that if exposed to stimuli that increase perception of a dense and complete social network (e.g., false feedback on one’s social network size), individuals should display lower levels of compensatory responses, higher levels of individualistic tendencies (e.g., more individualistic self-construal; Markus & Kitayama, 1991) and reduced intentions of spending time interacting with others. This

should also lead to more tolerance of deviants and less adherence to social norms, less conformity. One clue that it might work so lies in the recent finding that priming a sense of physical safety promotes more liberal social attitudes among conservatives (Napier, Huang, Vonasch, & Bargh, 2018).

Also, evidence from evolutionary psychology shows that people are attracted to peers if interaction benefits exceed its costs, that they punish more individuals that threaten inequity of social exchanges and avoid physically threatening individuals (see Simpson & Lapaglia, 2006). Accordingly, the CLCM would predict that these tendencies could be increased/decreased according to salience of anticipated social network loss or gain (e.g., making a new friend).

Other Derived Hypotheses

Other predictions that can be derived from the CLCM have already been corroborated such as the fact that grieving individuals are perceived as more prone to engage in social interactions and that perceivers of grieving targets are more willing to engage in social interaction with them (Winegard et al., 2014).

Corroboration for the CLCM can also be found in the literature pertaining to deviance management, such as the fact that deviant in-group members are not sanctioned immediately but other members actively try to maintain them within the group at great costs before finally rejecting them (see Schachter, 1951). Under the CLCM, deviance sanction is expected to be proportional to one’s social bonds with the deviant member. The greater the bond, the less likely and less harsh the sanction because one’s maintenance of one’s social network would prevail. Deviance should be tolerated up to the point that the deviant’s behavior cost exceeds benefits from maintaining that individual within one’s network.

Finally, our model could help explain why social isolation may cause death in some monkey individuals separated from their mothers but not in those caged with conspecifics (e.g., Suomi, Collins, & Harlow, 1973). In the absence of potential network compensation through bonding, the CLCM predicts increases in stress levels not being coped with, which, over time, should lead to acquired helplessness, depression and potentially self-destructive be-

havior in the long run. This is coherent with decades of research demonstrating that social isolation among humans (i.e., network unavailability, or lack of perception one's network) can lead to feelings of meaninglessness, alienation, self-estrangement, powerlessness (i.e., feelings of anomia, see Srole, 1956; Smith & Bohm, 2008) that are predictive of suicidal, violent and antisocial behavior (Adam-Troian et al., 2019; Durkheim, 1897/1951; Teymoori et al., 2016).

Conclusion

As we have seen, a CLCM interpretation of death-related threat reactions among humans and other primates is consistent with empirical findings in the literature among both human and nonhuman primates. It also enables novel, counterintuitive predictions for expanding the threat-regulation literature, while allowing for a wider scope and perspective for understanding human behaviors usually explained by different psychological theories (e.g., social categorization, social norms). Postulating the existence of a CLCM can provide a larger picture over converging findings on coalitional psychology from evolutionary, social-cognitive and socioanthropological standpoints. Moreover, we hope that this theoretical proposition could generate a novel, finer grained understanding of evolved reactions to threat as regards a parsimonious explanation.

The compensatory socialization hypothesis allows for taking a fresh perspective on known phenomena and to synthesize literature from sociological, psychological and ethological research while being in line with modern accounts of evolutionary theory. Besides its potential usefulness, we are confident that postulating the existence of a CLCM provides a stimulating framework for future research aiming to develop more accurate predictive models of reactions to death-related threat.

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