

Suicide as a Derangement of the Self-Sacrificial Aspect of Eusociality

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Building upon the idea that humans may be a eusocial species (i.e., rely on multigenerational and cooperative care of young, utilize division of labor for successful survival), we conjecture that suicide among humans represents a derangement of the self-sacrificial aspect of eusociality. In this article, we outline the characteristics of eusociality, particularly the self-sacrificial behavior seen among other eusocial species (e.g., insects, shrimp, mole rats). We then discuss parallels between eusocial self-sacrificial behavior in nonhumans and suicide in humans, particularly with regard to overarousal states, withdrawal phenomena, and perceptions of burdensomeness. In so doing, we make the argument that death by suicide among humans is an exemplar of psychopathology and is due to a derangement of the self-sacrificial behavioral suite found among eusocial species. Implications and future directions for research are also presented.

Keywords: suicide, eusociality, eusocial, burdensomeness, agitation

In what follows, we describe eusociality, including that aspect involving self-sacrificial behavior, and we suggest that, at least regarding some definitions of eusociality, humans are a eusocial species—claims that, though not without problems, are relatively straightforward and uncontroversial. Next, we make the more complicated and controversial argument that death by suicide in humans is without exception a derangement and that this derangement is specifically of the self-sacrificial aspect of eusociality.

We have three initial points about our general argument. First, this conceptualization views suicide as pathological—indeed an exemplar of psychopathology—and thus our position offers no support for suicide itself as adaptive or as anything other than a pathological derangement involving (and producing) great misery. We acknowledge other positions on this issue later in the article. Second, we do not claim to establish our more controversial ideas conclusively. Rather, we aim to describe and integrate several disparate lines of thought and scholarship, and in so doing, derive the conceptual framework on human suicide to which we think they may point. We acknowledge the somewhat speculative character of some of the article’s ideas and attempt to limit speculation wherever possible; we strive for sufficient plausibility to merit further consideration and research. Third, a key point of departure

for our conceptualization is the perfect correlation between whether or not a species is eusocial and whether or not specific individuals of that species engage in very clear and direct self-sacrifice, the kind that is always lethal or nearly so (as opposed to frequently nonlethal defensive behaviors that occur in noneusocial species; e.g., mobbing, alarm calling). That there is no exception to this rule of nature may represent a clue to understanding and demystifying suicide in humans, which in turn may aid in its prevention.

What Is Eusociality?

Eusociality, a term first used by Batra (1968) to describe nesting behavior among bees, is a system of social organization that can be roughly understood as “colony life.” More precisely, eusocial systems show the following characteristics: (a) multigenerational care of the young; (b) relatedly, cooperative care of the young; (c) division of labor (often reproductive division of labor, also known as “reproductive skew”); and (d) a form of labor involving defense of a communal locale (in which food and shelter are coincident; e.g., nest, hive, campsite). This defense risks (and regularly takes) the individual’s life at a benefit to the group (the benefit being prevention of predation or contagion, or alerting others to the possibility of predation via alarm signaling; Crespi & Yanega, 1995; Crespi, 1994; Michener, 1969; Wilson, 1971, 1990; Wilson & Hölldobler, 2005).

Eusociality has evolved infrequently. Depending on the criteria used, approximately 20 species are consensus examples of this form of social structure. Consensus species include snapping shrimp, naked mole rats, and several social insects (Choe & Crespi, 1997; Duffy, 1996a; Gadagkar, 2001; Hölldobler & Wilson, 1990; Jarvis & Bennett, 1993; Michener, 1974). Despite its rarity, eusociality is a stunningly successful strategy (Wilson & Hölldobler, 2005). As one reflection of this, species of sponge-dwelling shrimp display enhanced competitive ability (as measured by higher relative abundance within a host sponge) depending on their degree of sociality, with fully eusocial species being the most successful (Duffy, Morrison, & Ríos, 2000). On a grander

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scale, eusocial insects accounted for 75% of the total biomass of fauna in a hectare of the Amazon forest, with ants alone weighing four times more than all vertebrates (i.e., mammals, birds, reptiles, amphibians) combined (Beck, 1971; Erwin, 1983; Fittkau & Klinge, 1973; see also Wilson, 2012).

As another example, under definitions of eusociality that include humans, humans represent an epic evolutionary success story, as evidenced, for instance, by the cognitive abilities and technological innovations allowing you to read and evaluate these words, so dominant and successful that we are living in an epoch named after us (the Anthropocene; Ellis & Haff, 2009; Gowdy & Krall, 2013). Even highly successful adaptations can have dysfunctions or derangements that prove harmful or lethal to specific individuals (e.g., Durham, 1991; Gilbert, 2001; Keller, 2008; Öhman & Mineka, 2001); such is the case, we argue, with human eusociality and suicide.

Stringent Versus “Loose” Eusociality

The most stringent version of eusociality includes all of the criteria enumerated earlier but limits the “division of labor” criterion to extreme reproductive division of labor, also known as extreme reproductive skew (Crespi & Yanega, 1995; Tsuji, 1992). In the clearest example of this, all reproductive activity is undertaken by just a few specific members of the group on behalf of thousands of individuals (e.g., a honeybee queen and the few males that reproduce with her; Heinze, Hölldobler, & Peeters, 1994; Hölldobler & Wilson, 1990; Wilson, 1971). In contrast, “loose” versions of eusociality relax this extreme criterion and include lesser forms of reproductive skew and nonreproductive division of labor, as is found among humans (Lacey & Sherman, 2005; Sherman, Lacey, Reeve, & Keller, 1995).

Are Humans Eusocial?

Judged by “loose” criteria for eusociality (Lacey & Sherman, 2005; Sherman et al., 1995), there is near total consensus for human eusociality (Foster & Ratnieks, 2005; Wilson, 2012). Cooperative and multigenerational care of the young is ubiquitous (see Kramer, 2010, for review). This is evident in the caregiving roles of grandparents and extended family, particularly in collectivistic cultures, as well as childcare services and the role of teachers and schools in child rearing. Division of labor is also clearly evident across all cultures, as laborers are divided up based on their skills and the needs of the community, with all individuals relying upon the work of others to some extent for their own survival (Bowles & Gintis, 2011; Johnson & Earle, 2000; Richerson & Boyd, 1998). Specialized roles for cooperative defense exist in the form of emergency responders, firefighters, law enforcement, and the military. Localities in which food and shelter are coincident and defended at their peripheries at substantial risk to the defenders include campsites, villages, palaces, fortresses, early if not recent towns and cities, and countries (Bowles & Gintis, 2011).

Wilson (2012) argued that humans are eusocial even on strict criteria. The main question regarding humans’ fulfillment of the strict eusocial criteria centers on extreme reproductive skew (Crespi & Yanega, 1995). Although the extreme reproductive specialization seen, for example, in ants and bees (Cassill, 2002; Choe &

Crespi, 1997; Hölldobler & Wilson, 1990; Langer, Hogendoorn, Schwarz, & Keller, 2006; Paxton, Ayasse, Field, & Soro, 2002; Rettenmeyer & Watkins, 1978) is not evident in humans, there is evidence for specializations that are in part biologically based. Perhaps the clearest evidence of the latter is menopause in women in the last half of life. Foster and Ratnieks (2005) wrote,

In vertebrates, young naked mole rats . . . are the workers and, later in life, some of the workers become breeders. . . . Recent data show that distinct reproductive and helping strategies also occur in a more familiar vertebrate species, but in the reverse temporal sequence to mole rats. In midadult life, half the breeders become physiologically incapable of reproducing and help their close relatives. Uniquely for a vertebrate, the helpers are permanently sterile. What species is this? It is our own. (pp. 363–364)

Incidentally, McAuliffe and Whitehead (2005) pointed out that these strategies are not unique to one specific vertebrate species (i.e., humans), as they also occur in some species of whales. Regarding humans and several whale species, they wrote, “In all these species, reproduction ceases at approximately 40 years of age, although females routinely live on for several more decades” (p. 650). Intriguingly, there is evidence that these whale species too have eusocial characteristics and that the role of whale and human grandmothers not only includes helping but also long-term keeping of cultural information (McAuliffe & Whitehead, 2005; Whitehead, 2015), facilitated, at least in humans, by longer lifespans in females as compared to males (Hawkes, O’Connell, Jones, Alvarez, & Charnov, 1998; Joiner, 2011; Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004). In this regard, it is noteworthy that of the average female life span in humans, only approximately a quarter of it involves reproductive potential. As we will see, incidentally, menopause occurs in certain insects as well (Foster, 2010; Uematsu, Kutsukake, Fukatsu, Shimada, & Shibao, 2007). The role for these female insects may include helping, but unlike in whales and humans, also includes spontaneous self-sacrificial defense. (There is other, less convincing evidence of reproductive skew in humans as well; e.g., variability in number of children; dating scenarios; Betzig, 2012; Lenton, Fasolo, & Todd, 2009).

The social insects together represent the paradigmatic case for eusociality. Within the category of eusocial species, some are more centrally situated than others (e.g., social insects are more centrally situated than humans, or than whales, to take another possible example). If eusocial creatures are categorically different from others, it should be noted that that does not preclude variation within the category, with some examples more clearly fulfilling criteria than others. This point was convincingly made in another context by Paul Meehl’s thought and work on taxometrics (e.g., Meehl, 1995; Waller & Meehl, 1998). This work has been misconstrued as a procategorical and anticontinuum effort, when, in reality, Meehl frequently asserted that most things in nature represent dimensional entities, and that when a true category is found, marked variation within the category is the norm. If, by contrast, eusociality is a noncategorical continuum (e.g., Keller & Perrin, 1995; Sherman et al., 1995), there is consensus that humans rank highly on it, though not as highly as social insects, snapping shrimp, and naked mole rats. On either view, then, our perspective on human eusociality is plausible. We reiterate that many workers in this field see humans as eusocial (Foster & Ratnieks, 2005; Wilson, 2012). For example, Crespi (2014) wrote,

I contend that humans have evolved convergently to eusocial insects with regard to key selective pressures and genetic substrates. . . . As a result of this convergent evolution, humans are actually more similar to eusocial and cooperatively breeding insects than to most social vertebrates for a suite of interacting social and reproductive traits. (p. 7)

He continued, “Hunter-gatherers and other small-scale human groups can be viewed with fresh conceptual eyes as overgrown insects” (p. 8). We are seeking to document convergence between humans and consensus eusocial nonhumans. Conceptualizations of human societies as superorganisms are consistent with this perspective as well (e.g., Auger & Greenland, 2014; Kesebir, 2012).

Our focus in this article is on the self-sacrificial aspect of eusociality, but in this context, it is important to emphasize that humans’ self-sacrificial nature alone does not demonstrate eusociality; many noneusocial species show elements of, but not full eusociality (Keller & Perrin, 1995). Eusociality represents the simultaneous conjunction of several features; others and we are persuaded that this conjunction in humans clears the threshold for eusociality (Crespi, 2014; Foster & Ratnieks, 2005; Wilson, 2012), but there is debate in the field on this point.

In summary, a considerable amount of evidence is consistent with human eusociality. This is certainly so for “loose eusociality” and may even hold for strict versions as well, given some evidence of reproductive skew in humans (cf. work on reproductive opportunity leveling; e.g., Alexander, 1979; Foster & Ratnieks, 2005; Wilson, 2012).

Is a Self-Sacrifice Behavioral Module a Feature of Eusociality?

Given the “fortress defense” models of eusocial life and the requirement within successful eusocial communities for self-sacrifice for the sake of other members of the community, unsurprisingly, we are aware of no examples of clearly eusocial species that lack a behavioral repertoire for highly lethal self-sacrifice under conditions of inclusive fitness, and we are aware of no noneusocial species that clearly has one (Hölldobler & Wilson, 2009; Wilson, 2012). That is, in eusocial species, Hamilton’s (1964) rule $rB - C > 0$, in which B is benefit, C is cost, and r is degree of genetic relatedness, holds, with individuals submitting to great cost (e.g., death) for even greater genetic benefit (i.e., survival of multiple copies of the individual’s genes in surviving kin).

Just as it is possible to view eusociality as on a continuum from clearly noneusocial species on up to the exemplars of eusociality represented by the eusocial insects, so it is possible to regard self-sacrificial defensive behavior as on a continuum from noneusocial, typically nonlethal behaviors on up to clearly eusocial, virtually always lethal behaviors. In any species that congregates, individual behaviors that protect the aggregate are common—prototypical examples of which are alarm signaling and mobbing (e.g., Zuberbühler, 2009). Unlike many eusocial self-sacrificial defense behaviors (e.g., autothysis and nest sealing, which will be described in more detail), alarm calling and mobbing may provide a direct benefit to the caller’s own survival because they either induce scattering (which provides cover to the caller) or they enlist other members of the species in mobbing counterattack (e.g., Hollen & Radford, 2009). Zuberbühler (2009) wrote, “In many cases, the initial costs of alarm calling are quickly outweighed by

other individuals’ antipredator responses” (p. 279). In this way, noneusocial defense behaviors are but one of a basic array of individual survival strategies, along with foraging, predation, and fight-flight-freeze reactions (Gray & McNaughton, 2003), among others. These kinds of noneusocial behaviors benefit the propagation of an individual’s genes *because* they help ensure the individual’s survival and thus the individual’s ability to reproduce. By contrast, eusocial self-sacrificial behaviors benefit the propagation of an individual’s genes *despite* virtually ensuring the individual’s death and thus ensuring no future reproductive behavior. Another important difference between noneusocial and eusocial defensive behaviors is that the former tends to be performed by all or most members of a species, whereas the latter tend to be behaviorally and/or morphologically specific to certain subsets of a species (Zuberbühler, 2009).

As noted, just as the eusociality of species may be arrayed along a dimensional continuum, so may the nature of self-sacrificial behaviors. Our view is that some self-sacrificial behaviors are more prototypically eusocial than others, and we conceptualize human suicide as a derangement of prototypic eusocial self-sacrifice. Although it is not our view, we acknowledge that it is possible to see suicide in humans as a derangement of self-sacrifice, whether eusocial in nature or not. Under this interpretation, much of what we state here about self-sacrifice in nature holds, though much of what we emphasize regarding eusociality would recede in importance. We retain the eusocial perspective because (a) there is very wide consensus that some species are eusocial whereas others are not, (b) there is some consensus that humans are a eusocial species, (c) some self-sacrifice behaviors in nature are prototypically eusocial whereas others are not, and (d) the self-sacrificial behavior in humans that we focus on here—namely the derangement that is suicide—much more clearly resembles eusocial self-sacrifice than it does noneusocial behaviors like alarm signaling and mobbing.

Consider in this context the self-sacrificial behavioral array of the eusocial insects. Shorter and Rueppell (2012) summarized five categories of self-sacrificial behavior in these species: (a) sting autonomy, (b) autothysis, (c) gall repair and nest-burying self-sacrifice, (d) “death grip” biting behavior, and (e) self-removal. These are discussed in turn in the following sections in order to convey a sense of the kinds and variety of self-sacrificial behavior in nature. In later sections, we will draw parallels between some features of these eusocial self-sacrifice behaviors and human suicide.

Sting Autonomy

This phenomenon occurs when, following an insect stinging a target, the stinger as well as associated glands separate from the insect and remain pierced to the target (Hermann, 1971, 1984). The stinger can deliver venom for up to a minute after separation and can inject venom in amounts equivalent to numerous separate stings (Cunard & Breed, 1998; Hermann, 1971). Moreover, the stinger not only affects the individual target, but it also releases a pheromone which signals other insects to the area for swarm defense (Breed, Guzmán-Novoa, & Hunt, 2004; Cassier, Tel-Zur, & Lensky, 1994; Grandperrin & Cassier, 1983; Millor, Pham-Delegue, Deneubourg, & Camazine, 1999; Sledge et al., 1999; Wager & Breed, 2000).

Sting autonomy, which evolved mostly as a defense strategy to ward off vertebrates (e.g., bears, humans; Shorter & Rueppell, 2012), is lethal to the insect because it removes much of the insect's abdomen. Nonetheless, immediate death does not always occur. For example, although roughly half of honeybees die within hours of delivering a sting, some live on for several days (Hydak, 1951). Those that survive for days continue to participate in colony defense; however, instead of stinging, they bite or harass potential colony intruders. Interestingly, among honey bees, stinging defenders appear to differ in allozyme frequencies from foragers and guards, suggesting a strict division of labor within this self-sacrificial behavioral suite (Breed et al., 2004; Breed, Robinson, & Page, 1990). Versions of self-sacrificial division of labor exist in other species as well, and we will ponder in a later section whether behavioral specializations are involved in human suicide.

Autothysis

Autothysis refers to the spontaneous, internal, and fatal rupturing of a sac that releases a noxious or caustic substance externally, which evolved mostly to deter other insects (Jones et al., 2004; Shorter & Rueppell, 2012). The rupturing is accomplished via the sudden and violent contraction of abdominal or other muscles. The specific chemical agents and internal structures involved vary, but their commonality is the release of a substance that quickly congeals, is adhesive (especially to other insects), and causes invaders pain, impairment, or death (Bordereau, Robert, Van Tuyen, & Peppuy, 1997; Davidson et al., 2009; Davidson, Kamariah, & Billen, 2012; Jones et al., 2004; Sobotkin, Bourguignon, Frantisek, & Yves, 2010). An added benefit of the internal sac is that it makes the insect inedible, thus providing an additional means of deterring predation (Sands, 1982). Here again, the rupture is not necessarily immediately lethal, allowing the insect to fight on for minutes before dying.

As previously alluded to, in some insects autothysis is specific to postreproductive females, who begin to produce and store the noxious agent only after reproduction has stopped (Uematsu et al., 2007; Uematsu, Kutsukake, Fukatsu, Shimada, & Shibao, 2010), at which point they begin to gather on the periphery of the home structure (Foster, 2010). Shorter and Rueppell (2012) stated, "age-related menopause may not be due to senescence but part of an age-based division of labor, with the individuals of the lowest residual [reproductive] value fulfilling the most dangerous task" (p. 4). Additionally, as with stinging behaviors in honey bees, among certain termites, autothysis appears to be a unique specialization present in specific worker termites (Costa-Leonardo & Kitayama, 1991; Sands, 1982; Sobotnik et al., 2010).

Gall Repair and Nest-Burying Self-Sacrifice

Social aphids inhabit the galls of plants, and any damage to the gall structure threatens the colony by allowing pathogens, parasites, or predators to enter (Foster, 1990; Kurosu, Aoki, & Fukatsu, 2003; Kurzfeld-Zexer, Wool, & Inbar, 2010; Pike, 2007). Aphids that specialize in gall repair use bodily secretions for the repair of gall walls (Kutsukake, Shibao, Uematsu, & Fukatsu, 2009; Stern & Foster, 1996). The secretions compose approximately a third of individuals' body weight and thus saps them to the point of death. Moreover, some individuals use their entire bodies as part of the plastered repair of the gall (Kurosu et al., 2003).

In nest-burying ants, the nest is sealed from the outside by a few workers to protect the nest from nocturnal predation (Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990; Tofilski et al., 2008). Researchers have determined that these individuals are not outside the nest because they returned late from foraging, nor do they attempt to tunnel back into the nest. The chances of these ants surviving the night are vanishingly small; virtually all are blown away by the wind or are preyed upon in the nest vicinity (Tofilski et al., 2008). These nightly self-sacrificial behaviors by worker ants have been deemed to be of negligible cost to the colony given that a scant number of lives are sacrificed daily for the survival of thousands (Bourke, 2008).

"Death Grip" Biting

The least well characterized of the self-sacrificial behavioral repertoire in eusocial insects, "death grip" biting has nevertheless been observed across multiple species (Shorter & Rueppell, 2012). The behavior occurs in some stingless bees, for example (Buchwald & Breed, 2005; Grüter, Menezes, Imperatriz-Fonseca, & Ratnieks, 2012; Shackleton et al., 2015). As its name implies, in "death grip" biting, the bee permanently locks its jaws onto an intruder in order to immobilize it, resulting in the eventual death of both the bee and the attacker via predation, dehydration, or starvation. Consistent with the calculation that the relative cost of individual self-destruction decreases with an increase in colony size, the most aggressive and self-sacrificial stingless bees belong to the largest colonies (Shackleton et al., 2015). Notably, "death grip" biting differs from some other forms of self-sacrificial defense in that it does not involve a morphological mechanism that ensures death (cf. sting autonomy; Shackleton et al., 2015).

Self-Removal

Thus far, we have considered defense mostly against predation, which is, of course, a major threat to survival. However, there is another class of threat that is perhaps even more dangerous than predation because it can destroy an entire colony in one fell swoop. That threat is infestation from a pathogen or parasite (Shorter & Rueppell, 2012; Oi & Pereira, 1993). Heinze and Walter (2010) wrote,

Leaving one's group to die in seclusion might be an efficient way of minimizing the risk of infecting kin. Anecdotal observations of moribund individuals deserting from their groups exist for several species, including humans . . . but have rarely been substantiated by quantitative analysis. (p. 249)

To remedy this, they showed that in worker ants of the species *Temnothorax unifasciatus* self-sacrifice under conditions of lethal fungal infection occurs. When researchers introduced the fungus into ants (consequently threatening not only their survival but that of their nestmates—and their genes in their nestmates), these ants left their nest hours or even days before death. For an ant, there could be no more certain way to ensure death than leaving the nest. These researchers considered and ruled out alternative possibilities that this behavior was the result of the fungus affecting the ants' nervous system or that the ants were carried away or otherwise forced out of the nest by other ants (Heinze & Walter, 2010).

Similar experiments have been conducted on honeybees and wasps, producing comparable results: Infected insects, even those

showing no outward signs of illness or impairment, decreased their food intake, stopped behaviors such as foraging and distributing food to others, and made immediate moves to abandon the hive (Hughes, Kathirithamby, Turillazzi, & Beani, 2004; Rueppell, Hayworth, & Ross, 2010). Here, too, no antagonistic behaviors from other bees to the infected individual were observed, ruling that out as an alternative explanation (Rueppell, Hayworth, & Ross, 2010). As described in a later section, human suicide also frequently involves behaviors such as cessation of activities, decreased food intake, and withdrawal from others.

Self-Sacrificial Defense Behaviors in Eusocial Noninsects

Insects display the clearest (as well as the most varied and astonishing) behavioral suite of inclusive-fitness-motivated self-sacrifice, but instances have been observed in other eusocial species as well. For example, snapping shrimp live in colonies of a few dozen to several hundred individuals; the colonies reside inside of sea-sponge hosts and therein spend their entire lives feeding on the sponge's secretions and tissues (Duffy, 2007; Erdman & Blake, 1987; Rios & Duffy, 1999). The colony's very few reproductively active members can be found in a central area of the sponge (Duffy, 1992, 1996b; Erdman & Blake, 1987). These individuals need protecting, as do the young and the food and shelter coincident within the sponge. This activity is accomplished by nonbreeding patrols at the periphery of the sponge that use a fighting claw to snap at potential intruders (Duffy, Morrison, & Macdonald, 2002; Tóth & Duffy, 2005). These defenders are larger than average, as are their claws. As Duffy (2007) wrote,

... observations and experiments suggest that a group of behaviorally specialized and morphologically distinct large individuals in *S. regalis* [snapping shrimp] shoulder the burden of colony defense, leaving small juveniles free to feed and grow and the queen free to feed and reproduce. (p. 393)

In an intriguing example of an entire society pulling together to ward off a threat, there are occasions in which the defenders' snaps are insufficient and fail to deter intruders. In response, more than half of the colony joins in a spontaneous community-wide snapping spell, producing a distinctive crackling noise lasting tens of seconds that is particularly effective at warding off potential intruders by signaling that the area is populated by a cooperative colony willing to mount a defense (Tóth & Duffy, 2005).

As is the case with snapping shrimp, so it is with naked mole rats. The clearest instance of vertebrate eusociality, naked mole rats—hairless, bucktoothed creatures, 3 to 6 in. in length at maturity, and found in the hot, dry regions of Ethiopia, Somalia, and Kenya—live in underground tunnel systems and feed on bulbs and tubers (Bennett & Faulkes, 2000; Jarvis, 1981; Sherman, Jarvis, & Alexander, 1991). Just as in snapping shrimp, body size correlates with periphery defense activity, with larger, nonbreeding individuals more likely to participate (Sherman, Jarvis, & Alexander, 1991). Further ancillary support for this view is derived from the fact that these same individuals do most of the “volcanoing,” a burrowing activity accomplished by digging with the front teeth and kicking dirt backward with the hind legs, producing a small volcano-shaped mound (Gennelly, 1965; Jarvis & Sale, 1971). The openings to these mounds are eventually sealed, but in the interim

between initial volcanoing and eventual sealing, risk of predation is high because snakes and other predators can detect the digging motion as well as the mound. There are several anecdotal reports of defender naked mole rats confronting snakes to defend the colony (Bennett & Faulkes, 2000). As in all other eusocial creatures, the reason for self-sacrificial behavior in naked mole rats is propagation of one's own genes via inclusive fitness. Stated differently, under inclusive fitness scenarios, one's death can be worth more than one's life (i.e., $rB - C > 0$). Naked mole rats constitute a clear instance of vertebrate eusociality, with all criteria met including a robust suite of self-sacrificing defense behaviors (Jarvis, 1981; Sherman, Jarvis, & Alexander, 1991). We turn now to the possibility that there is another such vertebrate—humans—and furthermore, we pose the question of whether a derangement of human eusocial self-sacrifice may at least partially explain death by suicide in humans.

Phenomenological Similarities Between Eusocial Self-Sacrificial Behavior and Death by Suicide in Humans

Consider the following brief excerpts from Robins' (1981) in-depth study of 134 suicides in the St. Louis, Missouri, area. Regarding the first case, Robins wrote,

He became very agitated . . . restlessly pacing from room to room. At other times he would sit almost motionless for prolonged periods. His speech diminished greatly. . . . He began to lose weight and to say that he was a burden on his family and would never get well. He developed insomnia. . . . (p. 90)

Regarding the second, Robins recorded that “He stopped eating and lost 25 pounds . . . and said that he was a burden to his family . . .” (p. 85). A third: He experienced “insomnia, weight loss (he lost 20–30 pounds in the last months of his life) . . . outbursts of rage . . . he had often paced the floor, crying and wringing his hands” (p. 65). A fourth:

Severe insomnia developed. . . . He ruminated about being a burden on his family, about the family spending all their money on him, and about his wife having no money for the future. He lost weight. . . . He lost interest in everything, showing a diminution in affectionate relationships with his family and in his usual social and recreational activities. . . . He paced the floor in agitated fashion. (p. 96)

The clinical picture that emerges from these case studies and numerous other sources as well (e.g., Fawcett et al., 1990; Goldstein, Bridge, & Brent, 2008; Styron, 1992) is of the final hours and days prior to death by suicide being characterized by overarousal (e.g., agitation, insomnia), psychological and social withdrawal (and consequences thereof, such as weight loss), and pre-occupations with themes of burdening others. Indeed, our research group has proposed and identified several acute indicators of risk for suicide that may constitute a new mental disorder that we have termed acute suicidal affective disturbance (Joiner et al., 2015; Tucker et al., in press): (a) a geometric increase in suicidal intent or planning (e.g., gathering of materials for an attempt) over the course of hours or days; (b) alienation, demonstrated by withdrawal, disgust, or perceptions that one is a burden; (c) belief that suicidal intent and alienation are intractable; and (d) overarousal symptoms, including agitation, marked irritability, nightmares, and insomnia. In sections to come, we consider the phenomenological

overlap between human suicide and eusocial self-sacrifice in non-humans, focusing on overarousal states, withdrawal phenomena, and death-worth-more-than-life calculations.

A guiding theoretical heuristic for these sections is the interpersonal theory of suicide (Van Orden et al., 2010) and the considerable and growing empirical work inspired by it. The theory is explicit about two points. First, the chains of causation in suicide deaths can be dizzying in their variety. Documented risk factors number in the hundreds and range from molecular genetic to cultural levels (see Nock et al., 2008b and Van Orden et al., 2010 for review). Individual trajectories toward suicide can look very different from one another. Second, the essential claim of the theory is that all of these varying trajectories travel through a final common pathway to death by suicide. The model defines the final common pathway as the conjunction between an intractable sense of burdensomeness, an intractable sense of loneliness, and fearlessness/pain tolerance regarding physical ordeal; empirical evidence supports the model (Van Orden et al., 2010; Hagan, Podlogar, Chu, & Joiner, 2015; Smith et al., 2012; Bender, Gordon, Bresin, & Joiner, 2011; Bryan, Cukrowicz, West & Morrow, 2010). In sections to come, we will point out the relevance of these three factors for overarousal states, withdrawal phenomena, and death-worth-more-than-life calculations.

Overarousal States

Among nonhumans, colony defense reactions often involve high states of arousal. The previous example of autothysis illustrated that “very excited” insect workers contract violently and release a substance through the ventral side of their thorax to deter other insects (Bordereau et al., 1997; Davidson et al., 2009; Sobotkin et al., 2010). Such states of arousal and their subsequent release of toxic chemicals also ultimately result in the death of those workers. Similarly, self-sacrificial stinging defense behaviors often involve a state of elevated arousal and irritability, with the alarm pheromones released by defender bees inciting agitation and aggressive behaviors among other bees in the hive (Breed et al., 2004; Grandperrin & Cassier, 1983; Millor et al., 1999; Wager & Breed, 2000).

Qualitatively similar states of physical and psychological overarousal have also been observed among humans at elevated risk for suicide. For instance, in Robins’ (1981) aforementioned accounts of individuals’ suicides, he identified a sense of agitation, restlessness, and a feeling of wanting to crawl out of one’s skin as highly prevalent across the individual case studies presented. Research studies have also found support for the association between agitation and increased risk for suicide and/or suicidal ideation (Busch, Fawcett, & Jacobs, 2003; Conrad et al., 2009; Fawcett et al., 1990; Hall & Platt, 1999; Jobs, Jacoby, Cimboric, & Husted, 1997; Ribeiro, Silva, & Joiner, 2014; Way, Miraglia, Sawyer, Beer, & Eddy, 2005). For example, Busch and colleagues (2003) conducted a retrospective chart review of inpatients who had died by suicide and found that nearly 80% of these individuals had experienced marked agitation in the week leading up to their deaths. Thus, within clinical practice, agitation and irritability are considered to be important warning signs for suicide and serve as signals of acute risk (Rudd et al., 2006).

Decreased rest and greater difficulties sleeping (e.g., insomnia, nightmares) have also been associated with an elevated risk for

suicide. Robins’ (1981) accounts note that insomnia was also common among the decedents he evaluated, with 58% of individuals experiencing notable sleeping difficulties prior to their deaths. Additional findings from the literature support these observations, with a growing body of work suggesting that insomnia confers risk for suicide attempts and death by suicide (Bernert, Turvey, Conwell, & Joiner, 2014; Goldstein et al., 2008; Kodaka et al., 2014; Liu, 2004; Nadorff, Nazem, & Fiske, 2013; Wojnar et al., 2009; Wong & Brower, 2012), even when controlling for other symptoms, such as depression and hopelessness (Ribeiro et al., 2012). There is also an emerging literature on nightmares, with a number of studies finding a significant association between nightmares and suicide attempts (Li, Lam, Yu, Zhang, & Wing, 2010; Liu, 2004; Nadorff et al., 2013; Sjöström et al., 2009; Tanskanen et al., 2001), and a handful of other studies finding a link between nightmares and increased risk for suicidal ideation (Bernert, Joiner, Cukrowicz, Schmidt, & Krakow, 2005; Nadorff, Nazem, & Fiske, 2011; Sjöström, Waern, & Hetta, 2007; Wong, Brower, & Zucker, 2011).

In sum, these states of agitation, arousal, and decreased sleep in humans at elevated risk for suicide mirror the elevation in activity witnessed among insects on the verge of carrying out eusocial self-sacrificial behaviors (and may represent precursors of self-removal). For insects, an increase in arousal is an essential component of their ability to violently and aggressively attack predators (Breed et al., 2004; Grandperrin & Cassier, 1983; Millor et al., 1999; Wager & Breed, 2000). As a parallel in humans, because death by suicide is often physically painful and always fearsome (Holm-Denoma et al., 2008; Van Orden et al., 2010), it may be that these elevated levels of agitation and arousal contribute to an individual’s ability to overcome his or her innate biological instinct for survival and to ultimately enact lethal self-harm. Indeed, Ribeiro et al. (2014) specifically predicted that, in the presence of fearlessness of death, agitation would act as a facilitator of heightened suicidality; results were consistent with this prediction. Another reason overarousal is so characteristic of the moments and hours before suicide is that soon-to-be suicide decedents act and feel as if someone is about to kill them, because someone *is* about to kill them—and it may not matter, in terms of triggering an antipredator mindset (e.g., Blanchard, Hynd, Minke, Minemoto, & Blanchard, 2001), that their killer is they. Indeed, that their killer is they may trigger antipredator defensive reactions (including overarousal) all the more because their killer is close at hand and inescapable.

Withdrawal Phenomena

In instances where a pathogen or parasite, rather than a predator, may be a threat to a colony, withdrawal behaviors emerge among eusocial species. For example, when insects become infected with a pathogen, withdrawing to a location away from the rest of the colony to die has the function of preventing the pathogen’s spread (Heinze & Walter, 2010; Rueppell et al., 2010; Shorter & Rueppell, 2012). Interestingly, this type of withdrawal appears to have a willed aspect, rather than being the result of explicit banishment from other colony members (Heinze & Walter, 2010).

In humans, too, exposure to pathogens triggers behavioral responses such as social withdrawal and anxiety (Goehler, Lyte, & Gaykema, 2007). It is not our view, however, that pathogen exposure causes human suicidal behavior (though this perspective

has been proposed and defended, especially with regard to the *Toxoplasma gondii* parasite; e.g., Ling, Lester, Mortensen, Langenberg, & Postolache, 2011). Rather, we suggest that suicidal individuals view themselves as social toxins; this view is central to both their decision to withdraw socially and their conclusion that their deaths would be more valuable than their lives.

Distinct and extreme withdrawal behaviors are seen among human individuals who may be at acute risk for suicide. For example, past studies have revealed marked patterns of social withdrawal and isolation among individuals who experience suicidal ideation (Bearman & Moody, 2004; Cheatle, Wasser, Foster, Olugbodi, & Bryan, 2014), make a suicide attempt (Conwell, 1997; Cui, Cheng, Xu, Chen, & Wang, 2011; Trout, 1980), or die by suicide (Appleby, Cooper, Amos, & Faragher, 1999; Chynoweth, Tonge, & Armstrong, 1980). Among suicidal individuals, social withdrawal may have scaffolding relationships with related acute risk factors, such as “thwarted belongingness” (a sense of unmet social needs that may confer risk for suicidal ideation; Van Orden et al., 2010). At-risk individuals may isolate themselves, which exacerbates feelings of disconnection from others (Trout, 1980). Further still, as touched on already, perceived burdensomeness may also promote social withdrawal. At-risk individuals may withdraw and die by suicide specifically because they believe doing so will spare others the burden that these suicidal individuals perceive in themselves (Brown, Comtois, & Linehan, 2002; Joiner et al., 2002), in clear parallel to the self-removal behaviors of eusocial insects. In this way, patterns of distancing oneself from others are evident not only among infected eusocial insects but also among humans, especially prior to death by suicide. Taken together, it is well-established that withdrawal from friends, family, and/or society is an important acute warning sign for suicide (Rudd et al., 2006), and social withdrawal in the form of thwarted belongingness is an essential aspect of prominent theories of suicidal behavior (e.g., O'Connor, 2011; Van Orden et al., 2010).

In addition to social withdrawal, research has revealed that other forms of withdrawal from life, specifically a loss of appetite and marked weight loss, are also characteristic of individuals at elevated risk for suicide. As an example, Robins' (1981) analysis found withdrawal from eating to be the single most commonly reported symptom among individuals who later died by suicide, with 60% endorsing notable weight loss. Other studies have also found a significant decrease in appetite and/or weight loss among suicide decedents (McGirr et al., 2007). Dramatic weight loss is additionally a key feature of major depressive disorder and anorexia nervosa (American Psychiatric Association, 2013), both of which are strongly associated with increased suicide risk (Cavanagh et al., 2003; Herzog et al., 2000; Keel et al., 2003).

Death-Worth-More-Than-Life Calculus

Among nonhumans, there are numerous cases of the lives of a small minority being sacrificed to ensure the survival of the rest of the colony. Previously mentioned cases illustrating this include nest-burying ants who seal their nest against predation but ultimately perish themselves (Bourke, 2008; Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990; Tofilski et al., 2008) and stingless bees who use a “death grip” to permanently lock their jaws on intruders, which results in their death but

protects the rest of the colony (Buchwald & Breed, 2005; van Zweden, Grüter, Jones, & Ratnieks, 2011). Put simply, in these instances, within the broader context of species and colony survival, these insects' deaths are viewed as being worth more than their lives. In line with Hamilton's (1964) rule (i.e., $rB - C > 0$), there is an even greater genetic benefit to these few insects' dying rather than surviving, as their deaths ensure that the colony as a whole is able to survive.

For humans seriously considering suicide, a similar mindset emerges, with at-risk individuals believing that their death will be worth more to others than their life. Findings from numerous studies implemented across a wide range of populations and settings confirm that perceptions of burdensomeness on others play a significant role in conferring risk for suicidal ideation (Batterham, Calear, & van Spijker, 2014; Christensen, Batterham, Soubelet, & Mackinnon, 2013; Cukrowicz, Cheavens, Van Orden, Ragain, & Cook, 2011; Cukrowicz, Jahn, Graham, Poindexter, & Williams, 2013; Fink-Miller, 2014; Jahn, Cukrowicz, Linton, & Prabhu, 2011; Jahn, Poindexter, & Cukrowicz, 2015; Kanzler, Bryan, McGeary, & Morrow, 2012; Monteith, Meneff, Pettit, Leopoulos, & Vincent, 2013; O'Keefe et al., 2014; Opperman, Czyz, Gipson, & King, 2015; Tucker & Wingate, 2014; Van Orden, Lynam, Hollar, & Joiner, 2006). Perceived burdensomeness has also been shown to differentiate those with a history of suicide attempts from those without an attempt history (Brown, Dahlen, Mills, Rick, & Biblarz, 1999; Van Orden et al., 2006). These findings align with established patterns of suicide risk revealing that individuals who are unemployed (Borges et al., 2010; Brown, Beck, Steer, & Grisham, 2000; Kposowa, 2001) or chronically ill (Druss & Pincus, 2000; Juurlink, Herrmann, Szalai, Kopp, & Redelmeier, 2004; Marzuk et al., 1988; Smith, Perlis, & Haythornthwaite, 2004) may be at elevated risk for suicide. These individuals may believe that they are causing undue burden on family members, friends, and society as a whole. This may then lead them to tragically conclude that others would be better off without them and consequently attempt or die by suicide (Filiberti et al., 2001). Scenarios in which people die by suicide specifically because they believe their physical status (e.g., chronic illness) burdens others parallel self-removal phenomena in eusocial insects.

The primary purpose of eusocial self-sacrifice among nonhumans is to save the lives of others within the same colony or with close genetic relatedness. If suicide is, as we hypothesize, a derangement of this behavioral suite, it would follow that humans who die by suicide perceive their own deaths to benefit family members (i.e., those with highly shared genes) and other friends or loved ones (i.e., colony mates). As outlined earlier, there is a vast body of literature connecting a sense of perceived burdensomeness with suicidal ideation and risk for suicide attempts and death (Joiner, 2005; Van Orden et al., 2010).

Suicide as a Derangement

Derangement can be medically defined as a disturbance of regular order (American Heritage Dictionaries, 2004). Etymologically, the noun is derived from the French word *dérangement* (circa early 18th century; origin *déranger* and Old French *desreg-*

*nier*¹) and was first used in reference to mental order in the late 18th century (e.g., Crichton, 1798). In this context, derangement was used to refer to a divergence from normal soundness or reason (Baldwin, 1911).

Our view is that suicide is an exemplar of a derangement (i.e., disturbance of regular *mental* order), even more so than florid psychosis or mania. The latter are clearly derangements (altered states of mind), yet most people with these conditions live on. Suicide, however, is in direct opposition to a fundamental biological imperative (i.e., strong instinct for self-preservation). This imperative can serve as a considerable obstacle to enacting even very fervent wishes to die, as regularly happens when desperately suicidal people instinctually save themselves at the last moment (Barber, Marzuk, Leon, & Portera, 1998; Joiner, 2014). How people manage to overcome this imperative is a major feature of prominent models of suicide for this reason (e.g., O'Connor, 2011; Van Orden et al., 2010).

Some past conceptual work has advanced an evolutionary account of suicide. Aubin, Berlin, and Korreich (2013) summarized this area; the most relevant aspect of their review was what they termed the “altruistic suicide hypothesis” (see also De Catanzaro, 1986, 1991, 1995), which is that suicide was and still can be adaptive under conditions of low reproductive potential and high burden on kin. There are compatibilities between that account and ours, especially as regards perceived burdensomeness, but there are at least three important differences. First, our perspective emphasizes distorted perceptions of burdensomeness, whereas the “altruistic suicide hypothesis” points to actual burden on kin. Second, our framework sees suicide as a derangement of an adaptation, whereas the “altruistic suicide hypothesis” views it as an adaptation under certain conditions. Third, in the modern context, our perspective does not require that perceived burdensomeness is with regard to genetic kin, whereas the “altruistic suicide hypothesis” sees burdensomeness on genetic kin as essential.

Relevant to suicide as a derangement, there is wide agreement among suicide researchers that, at a minimum, 90% of all suicides involve mental disorders (e.g., Harris & Barraclough, 1997). The debate is regarding which figure from 90% to 100% is correct; our position is that it is 100%, for the following reasons. First, suicide involves the unsanctioned and frequently brutal killing of an innocent; the state of mind that one's own death has inviting properties; the potential deaths of others via suicide contagion (Hecht, 2013), not to mention the occasional actual deaths of bystanders (e.g., those landed upon by suicidal people jumping from a height in an urban setting, those killed by chemical exposure; Joiner, 2014); the deprivation of choice and life to one's future self (Hecht, 2013); the deprivation of choice and future care and comfort to loved ones; and the willingness to devastate dozens of people into a shocked state of bereavement (Cerel, 2015), not infrequently without warning and certainly without their consent. Any one of these is suggestive of psychopathology; their conjunction is a clear exemplar of psychopathological functioning.

Second, it is true that eventual suicide decedents and/or their relatives sometimes deny that they have a mental disorder. Given the continued stigmatization of mental disorders (Corrigan & Watson, 2002; Hinshaw, 2006), it is unsurprising that some people deny that they or theirs have them, even people who themselves clearly do or whose family members clearly do (Corrigan & Rao, 2012; Hinshaw, 2005). Moreover, among those with mental dis-

orders, those who die by suicide tend to have more serious conditions than those who do not die by suicide (Cavanagh, Carson, Sharpe, & Lawrie, 2003; Nock et al., 2008a). The more serious the disorder, the more insistent the denial of it can be.

Third, psychological autopsy studies of suicide decedents regularly return rates of mental disorders well into the range over 90% (e.g., Robins, 1981; Cavanagh et al., 2003), and this without talking to the person in question at all. This could mean that the true rate is over 90% but less than 100%. It could also mean, however, that the true rate is 100% and that studies are returning underestimates because people deny and/or conceal mental disorders (especially subclinical forms of major depressive disorder; Corrigan & Rao, 2012; Hinshaw, 2005), so that no one knew of them except the eventual decedent and perhaps a nonfamily confidant (e.g., family physician, clergy).

Fourth, the most common scenario that occurs to people in discussions of putative “rational” suicide is physician-assisted suicide in the context of terminal illness. However, although it is controversial, there is evidence that what differentiates terminally ill patients who seek such services versus those who do not are subclinical manifestations of mood pathology (Ganzini et al., 2003). Fifth, and finally, it is a fairly common clinical experience to observe those whose suicidality plainly stems from an unmistakable mental disorder, who are nevertheless resolute that their suicidality is “rational” (see, e.g., Werth & Cobia, 1995, for a perspective contrary to ours).

In this context, it is noteworthy that approximately 78% of inpatients report at least some regret about attempting suicide in the days immediately after their suicide attempts (Henriques, Wenzel, Brown, & Beck, 2005). This underscores our claim that the desire for suicide is contrary to our inherent self-survival instinct, which often is quickly reestablished after or even during a suicidal crisis. In sum, although some suicide decedents are resolute that they do not have a mental disorder before or at the time of their death, most suffer from a clinically diagnosable mental disorder at the time of their death (Cavanagh et al., 2003), and it is our view that the remainder experienced undiagnosed/subclinical forms of mental disorders (we will return to the role of mental disorders in a later section). Mental disorders, in our view, contribute substantially to the derangement of human eusociality that is suicide.

Indeed, as discussed earlier, suicide can be characterized as an acute disturbance preceded by a geometric increase in suicidal intent in the hours and days before an attempt, along with marked alienation and overarousal states. Consistent with this perspective, in one study, clinicians indicated that suicide decedents experienced acute and intense affective states (most often desperation) immediately preceding their death compared to current seriously depressed (but not suicidal) patients (Hendin, Maltsberger, Haas, Szanto, & Rabinowicz, 2004). Despite suicidal behavior being the most prominent psychiatric or primary care emergency, suicidality has often been diagnostically delegated to a medical complication or symptom rather than an actual, distinct disorder (Aleman & Denys, 2014)—a peculiar state of affairs, in our view, for a phenomenon that is an exemplar (arguably *the* exemplar) of psychopathology.

¹ From *des* (i.e., to do the opposite; from Latin *dis*) and *ranger/rengier* (i.e., to put in order; from *reng* “line, row,” from German *rank*).

Suicide is the tenth leading cause of death in the United States (Centers for Disease Control and Prevention [CDC], 2013a), yet it stands in striking diagnostic contrast to other leading causes of death (e.g., heart disease, cancer). For example, Alzheimer's disease—the only other mental condition among the top 10 leading causes of death—is characterized by a derangement of mental faculties and is given prominent diagnostic status (American Psychiatric Association, 2013). In fact, all leading causes of death, except for accidents, can also be medically viewed as derangements of the physical body (i.e., disturbance of regular order) and can be independently diagnosed. We assert that suicide should similarly be viewed as a derangement of a regular mental order—specifically that of the human state of eusociality.

Of What Is Suicide a Derangement?

Humans are certainly self-sacrificial beings. This has been integral to our ability to succeed as a species on a grand scale (Gintis, 2000; Fehr & Fischbacher, 2003; Wilson, 2012). Examples of this are evident across all cultures and time periods and include parents who provide for their children despite not being able to sufficiently care for themselves; charitable institutions, such as hospitals, medical clinics, and schools; military recruits who volunteer to defend their nation; and firefighters and law enforcement officers. This proneness toward self-sacrifice, characteristic of all eusocial creatures, ensures the survival of our communities on levels ranging from the nuclear family to national safety to the health of the planet. However, it is imperative to emphasize that a self-sacrificial calculation of the value of one's own death exceeding the value of one's life—which is often valid in the case of ants, bees, aphids, and so forth—represents a tragic, flawed, and sometimes fatal miscalculation (i.e., a derangement) among modern humans when made and acted upon in the context of suicide.

Tragically, this miscalculation among eventual suicide decedents includes beliefs, for example, that money provided through life insurance will be of greater worth than their lives, or that they will be removing from others the financial, physical, and emotional costs of managing medical needs, debts, or general expenses and hardships that might be the result of unemployment or disability. That we view suicide as a derangement of eusocial self-sacrifice does not mean we view suicide as selfish. Indeed, we are convinced—and the evidence supports—that suicide often, if not always, includes elements of “others better off” calculations, which are incompatible with selfishness (Joiner, 2010).

Our stance in the current work was influenced by the interpersonal theory of suicide (Van Orden et al., 2010), including its emphasis on perceived burdensomeness as a prominent feature of the suicidal mindset. A revealing angle on this state of mind is that many suicide decedents are aware of the aftermath of their deaths and many apologize (e.g., in notes) for this reason (Foster, 2003; Ho, Yip, Chiu, & Halliday, 1998). What this should not obscure, however, is that these very same notes *also* regularly state that the deaths will represent a net benefit overall, not just to the decedent (e.g., an end to misery) but to everyone (Brown et al., 2002; Joiner et al., 2002). That this is distorted thinking is putting it mildly and is reflective, in our opinion, of the severity of the psychopathology involved.

One example of potentially lethal self-sacrificial behavior in humans, paralleling the behavior of other eusocial creatures, is an

individual engaging in an activity that will most likely result in death in order to save others nearby (e.g., covering a live grenade with one's own body). Interviews with individuals who have carried out such behaviors to save comrades (i.e., colony-mates) nearby, but who have fortunately survived, have revealed that they did not engage in these behaviors with any desire to die (Lankford, 2013). Rather, they forced themselves to do something they had no desire to do (i.e., die or be seriously injured) in order to do something they valued greatly (i.e., saving those around them). In prominent systems of suicide-related nomenclature (e.g., Silverman, Berman, Sanddal, O'Carroll, & Joiner, 2007; Crosby, Ortega, & Melanson, 2011) intent to die is viewed as integral to the concept of suicide. Thus, by definition, these individuals were not suicidal because they did not possess a desire to die. These individuals' great sacrifice represents a clear instance of the self-sacrificial suite of behaviors of eusociality in humans. We view suicide as one step removed from exactly this kind of behavior, the step being the derangement we emphasize here.

By contrast, although suicide terrorists display similar behaviors to nonsuicidal, truly altruistic self-sacrifice, deeper analysis reveals these similarities to be superficial. These individuals extensively plan and engage in lethal activities at least in part (by their evaluation) to benefit their families and society (Reuter, 2006). Interviews with individuals who planned to engage in suicide terrorism but who experienced a bomb malfunction or another impediment to enacting their plan suggest that these individuals feel as though they are a burden to their families (Baer, 2008; Berko, 2012)—a similar sentiment expressed by individuals at elevated suicide risk (Brown et al., 2002; Joiner et al., 2002). Crucially, these interviews also reveal that a substantial portion of these suicide terrorists report a history of depression, past suicidal thinking, and/or suicide attempts prior to making the decision to engage in suicide terrorism (Lankford, 2013; Merari, Diamant, Bibi, Broshi, & Zakin, 2009; Merari, 2010). This stands in contrast to assertions that suicide terrorists are not psychologically impaired in any way, are entirely mentally healthy, or are even above average in functioning. To further underscore this important point, interviews with violent terrorists who do not participate in suicide attacks, and even those who train and dispatch suicide terrorists, have revealed that the majority of these individuals would not be willing to carry out a suicide attack themselves, despite being willing to fight and possibly die to defend their cause (Lankford, 2013; Merari et al., 2009; Merari, 2010). This suggests that there is a distinct quality to suicide terrorist activity and provides support for the idea that this type of deliberate, lethal self-harming act represents a derangement of humanity's self-sacrificial tendencies. This is in marked contrast to the willing but undesired self-sacrifice described earlier.

The aforementioned perceptions of burdensomeness common among those who desire and ultimately die by suicide are central to our argument, but they do not constitute our full argument. An account focusing only on burdensomeness leaves several issues unaddressed, issues for which our eusocial framework has explanatory reach (e.g., a eusocial perspective is explanatory regarding overarousal phenomena, whereas a burdensomeness-only account is not; unlike a burdensomeness-only model, a eusocial approach situates human suicidality within an evolutionary biological framework, which may spur future theoretical and empirical work; e.g., animal models of human suicide).

Nonetheless, perceptions of burdensomeness are an essential aspect of our perspective. Regarding this construct, the often perseverative misperception of oneself as a burden is so ubiquitous that it is one of the key components of leading theories of suicidal behavior (O'Connor, 2011; Van Orden et al., 2010), and, in clinical settings, is unmistakable if patients are queried about it capably. Those who die by suicide are spurred, at least in part, by the opinion that their deaths will be worth more to others than their continued lives. More explicitly, these individuals act in response to a misperception of Hamilton's (1964) rule, believing that their own lives must be sacrificed in order to benefit surviving family members and loved ones, as well as society as a whole (and perhaps themselves, a point to which we will return). This misperception is itself the derangement that is at the core of the argument we present here.

Implications and Future Directions

Our perspective is that human suicide is a breakdown—a dysfunction—of that aspect of eusociality involving self-sacrificial behavioral characteristics. If this perspective holds explanatory power, a possible implication is that suicide is more likely among that subset of the population who are well above average in the relevant behavioral parameters. Just as breakdowns are more likely in engines that are run at high power and for lengthy durations, we reason that suicide may be more likely in those with tendencies that are highly self-effacing or self-sacrificial. We do not, however, postulate that suicide occurs only in this group. We believe that individual differences in the relevant parameters are fluid and dynamic; a prevalently nonsacrificing individual can experience states of high altruism and self-sacrifice. It is a dysfunction of this state that we theorize is present in the minds of those who die by suicide.

As we noted in the sections on various self-sacrifice behaviors in social insects and other noninsect species, these behaviors tend to be morphologically and/or behaviorally specialized; that is, only a subset of group members enact these behaviors. For example, Shackleton et al. (2015) wrote,

. . . many social insects, including stingless bees, exhibit age polyethism (Sommeijer, 1984), where the risky tasks such as guarding are performed by the older workers with shorter life expectancies (Tofilski, 2002). These factors can lead to a very high investment in defense and, potentially, the decision to commit self-sacrifice (Brown et al., 1999; De Catanzaro, 1986). Eusocial insects could thus be described as having an exaptation for self-sacrificial behavior. (p. 279)

Earlier, we described a similar scenario involving aphids in which dangerous defense duties were disproportionately handled by older insects (Kutsukake, Shibao, Uematsu, & Fukatsu, 2009; Stern & Foster, 1996). Therefore, we might expect that self-sacrifice, and the suicides that result from dysfunctional self-sacrifice, may not be evenly distributed in humans. Rather, there should be clustering in subgroups defined by basic, biologically relevant parameters such as age and gender, and perhaps other additional parameters, such as occupation. In line with this expectation, death by suicide is in fact disproportionately likely in older males (CDC, 2013b), and certain occupations have been shown to be associated with both high suicide rates and high levels of dangerous service to others (e.g., firefighters; Milner, Spittal,

Pirkis, & LaMontagne, 2013; Stanley, Hom, Hagan, & Joiner, 2015).

Relevant to sex differences, we noted earlier that a key role for grandmothers, both in humans and whales, is the keeping of valuable cultural information (McAuliffe & Whitehead, 2005; Whitehead, 2015; Joiner, 2011). Based on this, and the low rate of death by suicide in older women as compared to older men (CDC, 2013b), we conjecture that the keeping of cultural information may be a protective buffer against suicide. This idea may hold clinical utility, in that a focus of psychotherapy for older at-risk women should be to make this role explicit and to strengthen it (the same approach would be unlikely to harm, and may actually help, older at-risk men as well). In this approach, the existence of grandchildren is not a prerequisite; the same function can be triggered by nieces, nephews, and so forth, as well as by more abstract groups such as “future generations” (though the less abstract, the better).

Earlier, we also noted that there exists for some species a relationship between colony size and the aggressiveness of self-sacrificial behavior, with larger colony size associated with more aggressive defense (Shackleton et al., 2015). Extrapolating to human suicide, this could be viewed as a suggestion that there is a positive association between indices such as city size and suicide rates. However, the preponderance of evidence indicates that death by suicide is more likely in rural rather than in urban settings (Jagodica, Agius, & Pregelj, 2012). Stockard and O'Brien (2002) examined macrolevel sources of decreased social integration for birth cohorts and found that a key source was larger size of the cohort relative to the rest of the population. Stockard and O'Brien (2006) subsequently applied the same methodology to birth cohorts (from 1875 to 1985) in 19 modern nations and observed very similar findings. The key variable thus may not be urban versus rural, but rather the degree to which individuals feel themselves to be faceless, anonymous, and insignificant parts of a larger community or cohort. “Putting a face” to things (including future generations) may thus have therapeutic effects.

There is a significant genetic component to death by suicide in humans (e.g., Brent & Melhem, 2008), and an important point is that whatever the constellation of genes that confers risk for suicide may be, it is a constellation that is distinct from that which confers vulnerability for major depressive disorder (Brent & Mann, 2005; Brent et al., 2004). What is being genetically transmitted? One possibility is aggression, as the genetic risk for suicide is particularly notable for violent forms of suicide (Brent et al., 2004; Bondy, Erfurth, de Jonge, Krüger, & Meyer, 2000; Bellivier et al., 2000). Based on the current conceptualization, another possibility is tendencies toward self-effacement or self-sacrifice. In fact, there is evidence that there are strong genetic effects on altruism, empathy, and pro-social behavior (Knafo, Zahn-Waxler, Van Hulle, Robinson, & Rhee, 2008; Rushton, 2004).

That there are strong genetic effects on both suicide and altruism-related behavior can be viewed as consistent with our claim that suicide represents a derangement of eusocial self-sacrifice. In eusocial insects, the self-sacrificial tendency is under total genetic control and is entirely a product of kin selection (Foster, Wenseleers, & Ratnieks, 2006). It should be acknowledged that, in addition to genetic factors, self-sacrifice in humans is shaped by nongenetic factors as well (e.g., religion, culture; Cohen, 1972; Fehr & Fischbacher, 2003).

Our view is that the ancient origins of self-sacrifice in our human ancestors were specific to genetically related kin, and that genetically related kin are still powerful triggers of the behavior (and thus of its derangement in suicide). We are reluctant to state that only kin can trigger the behavior, however, because increasing cognitive and cultural complexity has increased the size of potential in-groups so dramatically (Gintis, 2000; Fehr & Fischbacher, 2003; Wilson, 2012). Consistent with this, it is not uncommon to observe in clinical settings the derangement being triggered by nongenetic sources (e.g., "I'm a burden on society").

In the context of altruism-related behaviors, it is intriguing to consider whether one facet of the suicidal process may be understood as pathological generosity. This phenomenon clearly exists (e.g., people who regularly donate all or most of their salary, and in the process impoverish themselves and any dependents), and is seen most commonly in the aftermath of neurological insult (e.g., stroke; Ferreira-Garcia, Fontenelle, Moll, & de Oliveira-Souza, 2014) or as a facet of the manic phase of bipolar disorder (a condition, of course, associated with a high rate of death by suicide; American Psychiatric Association, 2013; Jamison, 2000). These cases tend to show extreme forms of self-abnegation, and frequently create substantial problems and burdens for themselves and their families (cf. perceived burdensomeness). We again underscore the speculative nature of this possibility; one potential value of exploring this further, however, is that some of the instances of strokes spurring pathological generosity involve highly localized brain damage (e.g., clear pathological generosity developed in an individual whose stroke was localized in the medial forebrain bundle; Ferreira-Garcia et al., 2014). These localized brain areas and processes may serve as candidates for potential biomarkers of suicide risk.

It is also possible to consider suicide as a distorted form of restorative justice. A sense of restorative justice for others is a basic element of human nature (e.g., Riedl, Jensen, Call, & Tomasello, 2015, showed that 3-year-old children intervene against cheating, and they are as likely to do so when a third-party is a victim as when they themselves are the victim). The psychopathology underlying suicidality may be such that eventual decedents view their burdensomeness on others as so extreme as to render them deserving of death. This can be particularly evident in major depressive disorder, especially when the symptom of guilt is very prominent or even psychotic in its expression (e.g., the belief that one is guilty of all the world's evil; Gaudiano, Young, Chelminski, & Zimmerman, 2008; Park et al., 2014). Like pathological generosity, restorative justice has been linked to specific brain regions (e.g., the right temporoparietal region; Güroğlu, van den Bos, Rombouts, & Crone, 2010; Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010), which in turn may be candidates for biomarkers of suicide risk.

Regarding mental disorders, that they play a role in death by suicide is incontrovertible; our view is that 100% of suicide deaths are spurred by mental disorders. It would be a mistake, however, to single out any one disorder (with the possible exception of acute suicidal affective disturbance, a provisional diagnosis described earlier that our team has proposed and defended), as deaths by suicide are a fairly regular occurrence in schizophrenia (Hor & Taylor, 2010), anorexia nervosa (Keel et al., 2003), borderline personality disorder (Black, Blum, Pfohl, & Hale, 2004), bipolar disorder (Jamison, 2000), and major depressive disorder (Bostwick

& Pankratz, 2000), among others. Our view is that these conditions can significantly contribute to the qualitative break that we postulate here: namely, the perseverative misperception that one's death by suicide unburdens others. This, in combination with our view that all suicides involve some form of mental disorder, leads us to suggest that at least one mental disorder is necessary for death by suicide, but that none are sufficient. This view is consistent with the basic facts that mental disorder at the time of death is detected in all or nearly all suicide decedents (Cavanagh et al., 2003), but that most people with mental disorders do not die by suicide.

A specific mental disorder, major depressive disorder, deserves further consideration. Its lethality combined with its high prevalence produces the most overall suicide mortality of any condition (Cavanagh et al., 2003). Many of the phenomena that we emphasize here (e.g., "shutdown" phenomena, insomnia, etc.) are features of major depressive disorder (American Psychiatric Association, 2013), as are aspects of the theory which substantially guided our work (Van Orden et al., 2010; the concept of perceived burdensomeness can be seen as a specific example of the worthlessness symptom of major depressive disorder) and aspects of other conceptual models (e.g., Nesse, 2000 proposed that depression's "shutdown" aspect may be adaptive when goals are unreachable or when it inhibits futile challenges to a dominant figure). While it is true that both overarousal and "shutdown" phenomena like social withdrawal can stem from an array of factors including major depressive disorder, it is also intriguing that the one tends to suppress the other. That is, aroused people tend not to be shut down, and people who are shut down tend not to be aroused. A unique aspect of the hours and days preceding death by suicide is that these two processes, usually in opposition to one another, co-occur (Robins, 1981). That versions of these processes are also typically in opposition in nonhumans, but regularly co-occur in eusocial nonhumans before self-sacrifice, just as they do in humans before suicide, is suggestive that the perspective we articulate here may have merit.

As stated earlier, we do not claim to establish our more controversial ideas conclusively. Our goal in this article is to describe and integrate several lines of thought and scholarship in order to better understand and organize a conceptual framework underlying human suicide. It is our view that a phenomenon's nature, including its randomness and noise, need not fully accord in every respect with a theory about that phenomenon in order to be useful. Theoretical accounts that explain much if not all of a given phenomenon can be useful in many ways, including spurring future theoretical advances that may lead eventually to explanation of the entirety of a phenomenon. "Fuzzy" logic, edges, and boundaries are important concepts in fields including philosophy, linguistics, mathematics, computer science, and others (e.g., Pedrycz, 1996). As with many complex phenomena in nature, the suicidal process can have "fuzzy edges," and we do not claim that our framework fully explains each and every facet of suicidality. We contend, rather, that we have advanced a conceptualization that illuminates suicide at least partially and also incrementally beyond existing accounts. We hope that our ideas will merit further consideration and investigation.

We turn now to several additional lines of research that we believe will advance our understanding of and test the claims made in this article. First, research assessing rates and reasons for suicide among military service members, law enforcement

officers, firefighters, and similar others who voluntarily place their personal safety, and even their lives, at risk to protect and improve the lives of others may be informative. Initial research is already underway in these populations and may help guide the development and refinement of our assertions (e.g., Vargas de Barros, Martins, Saitz, Bastos, & Ronzani, 2013; Nock et al., 2014; Violanti, Robinson, & Shen, 2013). For instance, a recent study found that volunteer firefighters have nearly twice the risk of suicide attempts compared to professional firefighters (Stanley et al., 2015). This finding may be explained in part by the fact that these men and women risk their lives on a purely voluntary basis rather than as part of their career (though there is of course an element of choice involved in becoming a nonvolunteer firefighter as well), and thus, may be significantly more willing to make sacrifices for the good of those surrounding them. Many volunteer firefighters serve in small towns and personally know many of the community members they serve. This may function as a protective buffer against suicide, via the “putting a face to things” process alluded to earlier and other forms of social connection. However, should these individuals experience alienation (perhaps in the wake of a mental disorder), the contrast between their internal sense of disconnection and the close-knit nature of their communities may heighten the sense of alienation. Intense alienation, combined with mental disorder, might warp their self-sacrificial nature into a belief that their deaths are worth more than their lives. (We are aware of similar scenarios and processes in military settings through our ongoing military suicide prevention research program.) These specific claims, as well as alternative ones, must be more fully evaluated before any definitive conclusions regarding our proposed framework can be drawn.

An additional line of relevant research would involve the distinction between suicidal thoughts and behaviors using animal models of activation (predator defense) and removal (infection defense). Such investigations would provide an opportunity to determine whether these distinctions are relevant to understanding types of human suicide or if (as we believe is more likely) there are no particular types of suicides and that, instead, a combination of both concerns occurs in humans considering suicide. Our views on this particular topic are discordant from those delineated in the classic work of Durkheim (1897/1951), whereas many other facets of our general arguments are resonant with Durkheim’s theorizing.

A greater delineation of the concept of derangement (i.e., as the concept of dysfunctional self-sacrifice) may be especially helpful in understanding suicidal events such as murder-suicide and, as already noted, suicide terrorism. A current theory of murder-suicide posits that this type of behavior is driven by a perversion of key human virtues: mercy, justice, duty, and glory (Joiner, 2014). Incidents that begin as planned suicides morph into murder-suicides when the perpetrators conclude that their own deaths require others to die too; this conclusion arrives in their minds based on beliefs that to not kill others would be unvirtuous (e.g., a mockery of justice, a failure of mercy). The particular tragedy of these scenarios is the simultaneity of perpetrators’ genuine belief in the virtue of their behavior and their lack of awareness that they are actually committing atrocity. Within this framework on murder-suicide, suicide is primary in the phenomenon (Joiner, 2014; Hagan, Podlogar, & Joiner, 2015); the primary derangement within murder-suicide as with suicide per se is with the misperception that one’s death is worth more than one’s life. The per-

version of virtues leading to murder follows in a small percentage of suicides (approximately 2%; Joiner, 2014), for reasons (other than perverted virtues) that are not well understood. The “perversion of virtue” model of murder-suicide implies a derangement of a derangement; that is, virtue perversion is a derangement of the primary suicidal derangement described in the current article.

Further investigation into the nature of burdensomeness among suicidal individuals may also resolve what appears, at first blush, to represent an exception to our current framework. As previously discussed, many deaths by suicide clearly include allusions to others being better off (e.g., in notes, journals; Brown et al., 2002; Joiner et al., 2002), which is consistent with the principles of eusocial self-sacrifice. Many notes left by suicide decedents also include references to one’s own self being better off, with some even seeming to be primarily focused on this (Brown et al., 2002). This suggests that perceptions of self-burdensomeness may play a role in conferring risk for suicide. Indeed, we have empirical evidence for the relationship between self-burdensomeness and suicide risk across three studies (i.e., a cross-sectional study [$N = 1,019$] and a three-wave multilevel-lagged study [$N = 4,123$] among unselected community participants, a clinical intervention study that tested for correlated-change between pre- and posttreatment [$N = 260$; Gebauer, Joiner, Baumeister, Göriz, & Teissman, under review]). In each, an index of self-burdensomeness was at least as strongly related as other-burdensomeness to suicidal ideation. This association held despite controlling for major covariates, such as past suicide attempts, weak social ties, low self-esteem, hopelessness, and depression.

How to understand this motivation (e.g., relief from one’s own misery) in light of the conceptualization we advance here, which is principally focused on suicide as a derangement of a *self-sacrificial* behavioral suite? Given human cognitive complexity, as well as increasing cultural emphasis on the self over decades and centuries, it seems plausible that the basic, original thought pattern on unburdening others is now often compounded by a highly interrelated thought pattern on unburdening of self. That is, individuals who view themselves as being a burden on others may blame themselves for their feelings of other-burdensomeness, resulting in aversive, unpleasant self-views. Thus, in humans, it is conceivable that perceptions of burdening others lead to suicidality *because* they lead to intolerably negative feelings and perceptions about oneself; in this view, suicide is perceived to primarily unburden the self but is spurred distally by perceptions of unburdening others. Consequently, additional work probing the potential complementary and interactional relationship between self- and other-burdensomeness may help to reconcile deaths by suicide that seem primarily driven by a desire to unburden oneself with the eusocial framework.

Another direction of inquiry related to these ideas includes the speculation that the increase in suicide rates observed over the past several decades (despite advances in treatment and prevention; Sullivan, Anest, Luo, Simon, & Dahlberg, 2013) might be partially related to an increase in eusociality resulting from the advent and dissemination of novel technologies allowing for an unprecedented increase in global connectedness. We emphasize the speculative character of this point; however, any potential drawback of prevailing positive trends, such as increased social harmony, is worth scrutinizing. It is also possible that this same connectedness

has paradoxically produced a greater sense of individual insignificance, which in turn may spur suicidal thinking and behavior.

Given that suicide has been difficult to prevent or even reduce, that it has a substantial genetic component, and that (in our view) it results from a breakdown in an essential aspect of our nature (i.e., eusociality), some may conclude that suicide has a quality of inevitability. We do not agree. Human eusociality is inherent and inevitable; derangements to it need not be.

On this point, we believe that the idea of the cost benefit analysis of Hamilton's (1964) rule may be useful in the context of psychotherapy for suicidal patients. Within this framework, the goal of therapy would be to shift suicidal individuals from a calculation of the value of their death being worth more than their life to a recognition that their calculation is a misperception and derangement of a valuable human characteristic they possess (i.e., proneness to self-sacrificial behavior)—a derangement that is being driven by (and that has the possibility to produce) great misery.

We reiterate that a theoretical point of departure for the current conceptualization is the interpersonal theory of suicide (Van Orden et al., 2010). The theory's empirical support is substantial; nevertheless, we acknowledge the possibility that the theory is imperfect or inaccurate, and caution that if so, our conceptualization regarding eusociality may be undermined to some degree.

To conclude, we have argued here that humans meet many if not all criteria for eusociality and that eusociality is defined in part by self-sacrificial behaviors. It therefore follows that human self-sacrifice should be salient, and we have conjectured that one of its most prominent forms—suicide—represents a derangement of an otherwise adaptive behavioral repertoire. Suicidal behavior has been viewed by many as baffling, perhaps even inexplicable. One potential contribution of our ideas is to demystify the phenomenon, and by so doing, facilitate understanding, destigmatization, and ultimately prevention of this grave form of suffering.

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