Evolutionary Perspectives on Suicide

C. A. Soper and Todd K. Shackelford

Abstract A scientific answer to suicidology's central question, "Why do people kill themselves?" can take two forms, and they are complementary, not competing. A proximate explanation addresses mechanistic causation—psychological experiences, interactions of risk factors, and suchlike. An ultimate explanation speaks to the behaviour's evolution in the human species. A coherent understanding of suicide requires integration of the two levels of analysis. However, suicidology has traditionally focussed on the proximate and neglected the ultimate, thereby missing half the explanatory story and hobbling the research effort. This chapter encourages a healthy rebalancing of priorities. The publication of this chapter marks a breakthrough in that it indicates an emerging rapprochement between suicidology and human evolutionary science. The two fields need each other. "Why do people kill themselves?" is a key question for evolutionists too: how could natural selection, powered by the Darwinian "Struggle for Existence", have produced an animal that wilfully and voluntarily deselects itself from the struggle? Seeking to resolve the paradox are more than a score of evolutionary hypotheses, advanced from diverse disciplines. The chapter outlines, critiques, and organises the various ideas into a conceptual map, intended to mark out the most promising throughways. The hypotheses are set out in five sections reflecting different genres of theory: non-reproductivity theories, kin and group selection theories, pathology theories, communication theories, and escape theories. The authors find the last of these most promising: "escape"-type evolutionary theories broadly align with several existing proximate theories in suicidology, but they raise important new questions for researchers. The primary obstacle to an evolutionary suicidology may be more psychological than technical, because an evolutionary view may require suicide to be understood as a universal feature of our species: there is potentially a suicidal person in us all.

C. A. Soper (✉)
Lisbon, Portugal
e-mail: contact@soper.pt

T. K. Shackelford
Center for Evolutionary Psychological Science, Oakland University, Rochester, MI, USA
e-mail: shackelf@oakland.edu

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The rapprochement of suicidology and evolutionary science is an exciting development because each holds a key to the other's advancement (Soper, 2019a, 2019b, 2022).

For evolutionists, suicide ("intentional self-inflicted death"; Farias & Plutarco, 2019, p. 1) poses a fundamental and longstanding problem (Confer et al., 2010; deCatanzaro, 1980). Wilful self-killing ought to be a non-starter in the Darwinian "Struggle for Existence" (Darwin, 1859, p. vi). Any genetic mutation that led an animal to opt out of the competition ought to be eliminated, the variant gene removed along with the animal's soma (Skinner, 1969). But clearly such a mutation did not just survive: it propagated across the human population.

Just as curiously, having emerged and spread, suicide has remained in place, today ending more than one in every 100 human lives around the world (W.H.O., 2021). The behaviour's persistence and ubiquity need explaining because all three necessary and sufficient conditions are in place for its rapid elimination: heritability, variability, and a differential impact on survival and reproduction (Darwin, 1859). The offspring of the less suicidal ought to outbreed the offspring of the more suicidal, thereby pushing the behaviour out of the breeding population. Obviously, this has not happened.

In our view, this apparent biological anomaly has implications that run wider and deeper than are yet widely recognised (Soper, 2018). Suicide, or rather, the fitness imperative to *avoid* suicide, impacts diverse research domains, including psychiatry and clinical psychology, positive psychology, and social psychology. A solution to the puzzle may afford a basis for integrating these and other fields of human psychological science (Soper, 2021, 2023b; Wong, 2022).

As for suicide research, due attention to evolution would allow progress on two legs instead of one. In common with many other domains of psychological science, suicidology has been lopsidedly concerned with proximate considerations—social, experiential, and other immediate conditions and developmental patterns—to the neglect of an ultimate, evolutionary line of inquiry.

The problem is not that a proximate analysis is wrong; it is that the proximate can only tell half the story. This limitation has long been understood and embraced by researchers in nonhuman behaviour (Alcock, 2013). The question, say, "Why do brown bears hibernate?" Can be answered at a mechanistic level: shortening days, cooler weather, and reduced food availability trigger seasonal endocrine changes, which precipitate bears' denning. But, to paraphrase Dobzhansky (1973), this proximate account makes sense only in the light of an ultimate counterpart: across their ancestral history, bears that conserved energy during mid-winter gained a *fitness* advantage—differential survival and reproductive success—leading to the spread and fixation of hibernation across the species. Hibernation is an *adaptation*, a trait shaped by random mutation and selective retention over an evolutionary timescale to serve a fitness-enhancing function. Suicidology has neglected this ultimate mode of

analysis and will remain handicapped if it "continues to ignore half of the explanatory equation" (Al-Shawaf, 2020).

So, suicidology's central question, "Why do people kill themselves?" (Leenaars, 1996, p. 221), calls for an ultimate as well as proximate explanation. In this chapter, we discuss no fewer than 23 evolutionary theories of suicide, with the hope that suicide researchers may find fruitful connections with their own work. The hypotheses, summarised and collected in Box 2.1, emerge from a variety of disciplines and span diverse ideas. They are not all mutually exclusive; some overlap, or are extensions of others. All are plausible insofar as they claim empirical support and have attained scholarly publication. However, some look to us more plausible than others. We aim to offer a road map that distinguishes the likely throughways from the dead ends.

Our review of evolutionary models is organised into five sections (A to E, above), reflecting genres of thinking. **(A) Non-reproductivity** theories suggest that suicide might occur in situations in which there appear to be negligible prospects for reproduction in any event; thus, the behaviour may persist for a lack of selective pressure against it. **(B) Kin & Group Selection** theories look for fitness gains from the act of suicide, benefits that might cause the behaviour to propagate among a suicide's kith and kin despite the costs. **(C) Pathology** theories argue that suicides result from malfunctions of ancestrally adaptive evolved systems. **(D) Communication** theories hold that suicidality is an evolved means of signalling need and getting that need met. **(E) Escape** theories offer an evolutionary perspective on suicide as an escape from psychache. As we will explain, we find the last of these genres the most promising, connecting as it does to established (proximate) escape theories in suicidology, although it also poses new challenges for researchers.

The list could be extended, but to keep our survey manageable we make two exclusions. First, we do not discuss various loose ethological analogies that scholars have drawn between animal behaviours on one side and, on the other, human self-harm (Goldney, 2000; Lester, 2014) and depression (Gilbert, 2006). Although Williams (2014), for example, draws inspiration from such comparisons, referencing these inputs as an "evolutionary approach" (p. 245), his "cry of pain" model of suicide is not built within an explicitly evolutionary framework. Second, we focus on explanations of ordinary, solo, suicide; discussions of special cases, notably suicide terrorism, can be found elsewhere (Lankford, 2015; Liddle & Shackelford, 2014).

A. Non-reproductivity

Some theorists suggest that susceptibility to suicide may arise if the individual lacks sufficient prospects for begetting offspring. If there is no hope of reproduction, then there is no biological value in survival.

To be clear at the outset, this line of thinking is difficult to square with the evidence. Generally among "higher" fauna—most reptiles, all birds, and virtually all mammals, humans included—both theory and empirical findings point to a powerful fitness advantage in staying alive under almost any realistic circumstance (Lankford, 2015). Death is genetically deleterious for most animals because it voids the advantage of *iteroparity* (Cole, 1954)—the strategy of mating and breeding in multiple cycles

Table 1 Evolutionary theories of suicide

A NON-REPRODUCTIVITY: Suicide may emerge and persist due to poor prospects for reproduction
1. Reproductive potential. Non-selected self-destructive behaviours may arise where individuals have predictably negligible reproductive prospects (deCatanzaro, 1980, 1981, 1986)
2. Sexual defeat. Suicide may follow failures to win sexual partners (Saad, 2007)
3. Life history. A present-oriented response to early life adversity may manifest in dysregulation characteristic of suicidal crises (Ziker & Snopkowski, 2020)
B KIN & GROUP SELECTION: Suicide may produce fitness benefits for the actor's kin or community
4. Burdensomeness. Self-removal may produce an inclusive fitness gain if close kin could reproduce more successfully in the individual's absence (deCatanzaro, 1980, 1981, 1986)
5. Expunged disgrace. Self-sacrifice may redeem a kinship group's social standing, (Abed, 1997)
6. Causal consciousness. A prerequisite for certain adaptations, including suicide, is the evolved human capacity for conscious self-representation (Bering & Shackelford, 2004)
7. Sacrificial victim. An individual's self-sacrifice may prevent the outbreak of lethal conflict among kin (Riordan, 2019)
8. Infection control. Removal of an infected individual may bring an inclusive fitness benefit (Tanaka & Kinney, 2011)
9. Heroic defence. self-sacrifice might bring inclusive fitness benefits if the action saves kin from a mortal attack (Abed, 1997)
10. Group selection. Suicide may produce fitness gains for the actor's community (deCatanzaro, 1980, 1981; Orbell & Morikawa, 2011)
C PATHOLOGY: Suicide is caused by a malfunction of an evolutionarily adapted system
11. Self-preservation instinct. Suicide entails overriding an instinct for survival (Soper, 2025)
12. Mismatch. Suicide may be a pathological response to modern environments (deCatanzaro, 1980, 1981)
13. Misperceived burdensomeness. Suicide is a misfiring of a eusocial self-sacrificial behavioural routine, triggered by a misperception of burdensomeness (Joiner et al., 2016)
14. Parasite manipulation. Infestation by *Toxoplasma gondii* may promote potentially self-destructive risk-taking behaviour (Amouei et al., 2020; Aubin et al., 2013)
D COMMUNICATION: Suicidality represents an evolved communication strategy, sometimes with lethal outcomes
15. Bargaining. Suicidality may be a credible, coercive signal of need. Suicidal death is an occasional maladaptive outcome (Hagen, 1999; Hagen et al., 2008; Watson & Andrews, 2002)
16. Costly apology. Attempted suicide is an evolved credible signal of remorse, functioning to aid the repair of relationships (Syme & Hagen, 2018)
17. Psychological aposematism. The credibility of suicide threats and attempts, and hence their bargaining effectiveness, is enhanced by suicidal deaths (Wiley, 2020)
18. Suffering ape. Human prosociality, offering heightened social rewards, encourages suicide attempts and other costly signals of suffering (Steinkopf, 2023)
E ESCAPE: Suicide is a learned, maladaptive, but effective means of relieving intolerable pain

(continued)

Table 1 (continued)

19. Pain relief. Suicide offers dysgenic but outstandingly effective relief from "painful tension" (Murray & Kluckhohn, 1948)
20. Social pain. Suicidogenic psychache is usually caused by fitness-relevant threats to social relations (Gunn, 2017)
21. Learning. Suicide may be a wholly learned behaviour (deCatanzaro, 1980, 1981; Skinner, 1969)
22. Pain-brain. Human intelligence by-produces suicide as a default response to pain. Evolved anti-suicide defences manage the risk (Humphrey, 2011, 2018; Soper, 2018, 2021)
23. Anti-suicide psychopathology. Emergency anti-suicide defences, triggered by chronic psychache, manifest in diverse adult-pattern psychopathologies (Himmelhoch, 1988; Soper, 2018)

across the lifespan. In the case of humans, notwithstanding declining fertility, women can conceive up to menopause and men can sire children throughout their lives. For this reason, animals usually will go to extreme lengths, sometimes even sacrificing existing offspring, to maintain themselves as reproductive going concerns (Hausfater & Hrdy, 1984). As a heuristic for genetic success, few zoologists or evolutionary psychologists would disagree that "it is bad to be dead" (Duntley & Buss, 2004, p. 107).

Nonetheless, although not claiming death is good (we will come back to that), some theorists hypothesise contingencies in which death might be tolerated.

(1) Reproductive potential. Most prominent in this territory is a creative proposal, one of many, by deCatanzaro (1980, 1981). He suggests self-destructive behaviours may not be subject to deselection if the individual has no prospect of reproduction in any event. In such conditions, selection would be unable to push any subsequently emergent trait out of the gene pool. Dawkins (1980) connects this idea to the biological principles of senescence and pleiotropy (Williams, 1957): genes express in multiple physical and behavioural traits (*pleiotropy)*—some fitness-enhancing, others not—and at different times during the organism's lifespan. Selection operates more strongly on traits expressed early in life, when more of an organism's reproductive career lies ahead, than on traits expressed later (*senescence*). So, harmful traits could emerge in later life as a price paid for gains enjoyed during youth. According to deCatanzaro (1980, 1981), this dynamic helps to explain why relatively high rates of suicide occur among the elderly, although he suggests that reproductive prospects could be impaired for other reasons, such as disease, lack of access to mates, and other setbacks.

(2) Sexual defeat. In a similar vein, Saad (2007) argues that, because past sexual failures could be taken to predict a future of more of the same, some suicides may reflect combined reproductive and psychological resignation—"the most extreme form of defeatism in the context of mating competition" (p. 693).

(3) Life history. Drawing on life history theory, Ziker and Snopkowski (2020) suggest that the disregarding of future reproductive opportunities may be a costly but ancestrally adaptive response to unpropitious circumstances. Suicide might be

understood in the context of a biological trade-off between longevity and reproductive vigour (Wilson, 1980), the best compromise solution differing from individual to individual depending on the fruitfulness of the environment. Those born into more adverse conditions may be best served by *present orientation*—a strategy of vigilance and impulsivity geared to capturing immediate gains at the expense of delayed returns (Frankenhuis & Del Giudice, 2012). Ziker and Snopkowski (2020) suggest that this beneficial-on-average short-termism is displayed in the dysregulation of executive functions that characterises suicidal crises. The authors provide longitudinal epidemiological evidence to argue that such a cognitive adjustment could explain why people who suffered childhood adversities respond to stressors with suicidal ideation.

These are ingenious ideas. They match some aspects of the empirical picture to an intriguing extent: adverse life experiences are a prominent (albeit weakly predictive) risk factor for suicidal outcomes (Franklin et al., 2017), which have been found to associate inversely with measures of reproductive status (Brown et al., 1999, 2009; deCatanzaro, 1995).

However, there are empirical and theoretical problems (for other critiques, see Ayres, 1982; Gunn et al., 2021; Rubinstein, 1986; Soper, 2018). Empirically, suicide is not limited to people who lack reproductive prospects. For example, many suicides occur among adolescents and young adults, especially in non-Western countries (Phillips et al., 2002). At the same time, post-menopausal women—people with no possibility of direct reproduction—are not especially suicidal (Usall et al., 2009). The life history notion has similarly mixed support: trait impulsivity, putatively a marker for present orientation (Ellis & Del Giudice, 2019), associates only weakly with suicidality (Anestis et al., 2014), and there are wider doubts as to whether life history theory, which originated to explain differences between species, sheds useful light on differences between individuals of the same species (Van de Walle et al., 2023).

A theoretical difficulty is a logical gap between explanans and explanandum. Sexual defeat, present orientation, and the lifting of selective pressure might open the door to any number of non-adaptive traits, from which death may incidentally ensue. But it is nowhere explained why non-selection should lead to suicide in particular, rather than some other behaviour. Suicide is puzzling because, biologically, where there is life there is hope. However unpromising one's reproductive outlook, it is not improved by killing oneself (Dawkins, 1980; Lankford, 2015). Suicide requires a special explanation.

B. Kin and Group Selection

To address the origin of suicide specifically, other hypotheses suggest that, under certain conditions, not only might death not be bad, on balance, for genetic success, it might even be good. Wilful self-destruction may be positively selected due to the survival and reproductive benefits that the act delivers to the actor's friends and family, provided that these indirect gains outweigh the direct cost to the actor.

Again, to be clear at the start, this notion too swims against a tide of evidence. As Gunn et al. (2021) document, the biological downsides of suicide are so extreme

that it is difficult to imagine an upside that would credibly tilt the balance the other way. Fitness harms arise at multiple levels. We already have discussed the direct cost of death: the complete forfeit of future reproduction (Section A). However, the costs go even beyond that, damaging the reproductive prospects of the deceased's kin as well, in two ways.

First: by whatever cause, death is usually detrimental for the bereaved family (Duntley, 2005). The dead can no longer protect their offspring and other relations, or help with those relations' child-raising. Genetic collateral damage follows the principle of *inclusive fitness* (Hamilton, 1964): an individual's genetic kin are prospective vehicles for the individual's reproduction by proxy, inasmuch as those kin can propagate shared genes. The closer the deceased's kin genetically, the greater the loss of this potential indirect reproduction. Thus, by exposing children to new danger and deprivation, the death of a parent may inflict particularly severe inclusive fitness harm (Geary, 2000). The loss of the elderly also has an inclusive fitness cost: even post-menopausal women—given their accumulated experience, *especially* post-menopausal women—may have valuable opportunities to aid the raising of grandchildren (Hawkes et al., 2000). Thus, as deCatanzaro (1981) notes, contra his "reproductive potential" hypotheses discussed above, even individuals that are entirely excluded from direct reproduction can still "promote their inclusive fitness by working toward the benefit of reproducing relatives" (p. 161). Wider still, death deprives the community of the deceased's labour and knowledge and may disrupt social and power relations (Duntley, 2005).

Second: not only, as discussed above, is it "bad to be dead" (Duntley & Buss, 2004, p. 107), but also, measured by inclusive fitness, suicide looks to be an especially bad way to die. The world over, close families of suicides incur additional costs in the form of stigmatising treatments meted out to people bereaved in this way (Fedden, 1938; Mugisha et al., 2011). Genetically speaking, since these special punishments cause inclusive fitness harm above and beyond the impact of bereavement by other causes, suicide is, literally, a fate worse than death (Gunn et al., 2021).

Nonetheless, several theorists have sought to explain the evolution of suicide by hypothesising countervailing upsides for kith and kin that might be sufficient to tip the scale. DeCatanzaro (1980, 1981) again leads the way, suggesting that "altruistic suicide" might deliver benefits to close family and/or the wider community, perhaps overriding the costs to the actor.

(4) Burdensomeness. The first of these proposals leans on a corollary of inclusive fitness: the idea of *kin selection*, whereby a trait may spread due to fitness benefits accruing to the genetic relations of those who possess it (Maynard Smith, 1964). DeCatanzaro (1980, 1981) suggests if people become such a burden that their families would be better off without them, then kin selection may drive the propagation of a tendency for burdensome people to remove themselves. In evidence, deCatanzaro cites feelings of burdensomeness as a recurring theme in suicide notes, and occasional ethnographic accounts that report assisted suicides by frail or elderly members of certain nomadic tribes. A study of ethnographies by Syme et al. (2016) offers further tentative support. Abed (1997) offers a comparable idea, that altruistic self-killing might have improved the fitness of the kinship group in ancestral settings

in which the act eases competition for resources, such as in starvation conditions. DeCatanzaro (1986) developed a mathematical formula that specifies the parameters under which, so he argues, self-destruction might occur, combining the notions of burdensomeness with reproductive potential (discussed earlier, in section 2). Survey findings by deCatanzaro (1995) and Brown et al., (1999, 2009) accord with this composite formulation.

Other theorists have advanced other variations on the inclusive fitness/kin selection theme.

(5) Expunged disgrace. Another suggestion by Abed (1997) is that if a suicide serves to erase a kinship group's shame, the sacrifice may improve the social standing, and thereby the survival prospects, of surviving family members.

(6) Causal consciousness. Bering and Shackelford (2004) argue that the operation of certain adaptations, suicide included, requires a phylogenetically novel capacity for shame and other conscious self-representations. On this basis, ancestrally adaptive suicide could have evolved only in the human species.

(7) Sacrificial victim. Riordan (2019) argues that an individual's voluntary self-sacrifice could produce an inclusive fitness gain by keeping the peace. At times of familial tension, a single death may be less costly than the internecine conflict that might otherwise ensue.

(8) Infection control. Tanaka and Kinney (2011) advance the idea of suicide as an adaptation for disease control: an inclusive fitness benefit could arise from the self-removal of an infectious individual. In support of the hypothesis, they cite higher suicide rates among professions exposed to infectious disease.

(9) Heroic defence. Abed (1997) suggests a heroic self-sacrifice might bring inclusive fitness benefits where that defence saves kin from a mortal attack.

These are inventive ideas, but they face a slew of objections (Soper, 2018). Here are two.

First, noting limitations of his own proposal, deCatanzaro (1981) gives a two-fisted reason why kin selection "probably could not explain the majority of cases of suicide" (p. 269). Punching from one side, an unfeasibly large reward would have to concentrate among close kin to produce a selective effect, because shared genetic interest falls away exponentially with relational distance, quickly approaching zero. A famous quip by J. B. S. Haldane—that he would not lay down his life for his brother, but he would to save two brothers or eight cousins (Maynard Smith, 1964)—illustrates how genetic mathematics limits the hypothesis's reach. Based on realistic levels of relatedness in ancestral hunter-gatherer bands, Bowles and Gintis (2011) estimate that an altruistic behaviour could take hold by kin selection only if it delivered a benefit to others at least an order of magnitude greater than the cost to the altruist: but there is no obvious fitness payoff to be had from self-killing that would come close to matching the cost, let alone exceeding it by this required multiple. Punching from the other side, closest relations seldom experience suicide as a blessing, despite accruing the lion's share of any supposed inclusive fitness gain (Azorina et al., 2019).

Second, the "Burdensomeness" (4, above) and similar hypotheses suffer from multiple gaps in their logic. Even if (a big "if") family members stood to gain from an individual's removal, removal need not entail a killing: among other sublethal

solutions, the individual would do better by just walking away, thereby preserving reproductive capability (Wright, 1994). Even if (another big "if") the individual needed to be killed, that would still not call for suicide: the killing would more logically be done by the act's most direct beneficiaries (Skinner, 1969). Accordingly, problems of burdensomeness are resolved among animals (humans included) by infanticide or fratricide ahead of suicide (Hausfater & Hrdy, 1984; O'Connor, 1978). In sum, we agree with Nesse (2019) that a kin selection hypothesis of suicide is "almost certainly wrong" (p. 91).

(10) Group selection. Recognising that inclusive fitness leaves an explanatory shortfall, deCatanzaro (1980) speculates that a genetic gain from "altruistic" suicide might extend beyond close kin. If an advantage accrues to the wider community, then lethal self-sacrifice could be selectively promoted at a between-groups level, rather than between individuals. In this vein, Lester (1988) suggests that self-eliminating behaviour may have evolved as a mechanism for controlling population size and/or for removing the less fit from the breeding pool. The latter idea echoes the Social Darwinism of nineteenth-century essayists such as Morselli (1881) and Strahan (1893)—and, indeed, a passing comment on suicide by Darwin (1879/2004) himself. Orbell and Morikawa (2011) offer a group selection version of Abed's (1997) notion of heroic defence (9, above), arguing that an evolved willingness to sacrifice oneself in dire circumstances to save a coalition of kinship groups may explain the psychology of Japanese "kamikaze" attacks during WWII. The general problem with this line of explanation is that, as Williams (1966) explains, in nature the tragedy of the commons generally prevails: a heritable, variable trait that inflicts an inclusive fitness disadvantage will be deselected, regardless of its benefit to the group. There might be exceptions under special hypothetical conditions (Sober & Wilson, 1998), but theory weighs against the idea, as deCatanzaro (1980) acknowledges, and few mainstream evolutionists contend that group selection could be so powerful a force as to induce deliberate self-killing.

In sum, there is no obvious way to explain suicide as a fitness-serving adaptation, whether by kin selection or, even more improbably, group selection. In other words, the evolutionary dynamic that caused suicide to arise and persist in our species was almost certainly not powered by supposed benefits to be won from the act.

C. Pathology

Other theories suggest that suicide may not have evolved as a fitness-promoting adaptation, but occurs instead due to the pathological failure of an adaptation to perform its evolved function. Although at first blush this may look like a less demanding kind of solution, it is not. A coherent theory of this type has to identify not only the original functional adaptation, but also explain the dysfunction; why the dysfunction should result in suicide as opposed to some other outcome; and why the process of selection has not promoted effective countermeasures. Most of these components are missing from the extant proposals.

(11) Self-preservation instinct. A pervasive faux-evolutionary idea in this genre is that suicide violates a *self-preservation instinct* (or *survival instinct*, *life tendency*, *life instinct*, and suchlike expressions)—defined by the American Psychological

Association (2018) as "the fundamental tendency of humans and nonhuman animals to behave so as to avoid injury and maximize chances of survival (e.g., by fleeing from dangerous situations or predators)".

The self-preservation instinct is a figment of "folk" biology. It feels intuitively correct and has the aura of an evolutionary principle, but it is the stuff of myth and tradition. It stems from an ages-old vitalist notion of life as a transcendent material that exists independently of the organisms it enervates, and from the creationist belief that life is divinely imbued. The survival instinct idea was rendered redundant in 1859 with the publication of Darwin's great realisation that life perpetuates by a "blind" automatic process. Unfortunately, the profound implications of that redundancy have yet to be absorbed into suicide science. As a result, today's researchers tend to view suicide in essentially the same way as their predecessors did before 1859. Esquirol (1845) thought suicide was "most opposed to natural laws, and the instinct of self-preservation" (p. 272). So did Durkheim (some "force is always necessary to offset the fundamental instinct of self-preservation"; 1897/1952, p. 6) and Freud (How does it become "possible for the extraordinarily powerful life instinct to be overcome?"; 1910/1957, p. 232). Modern-day researchers—such De Leo et al. ("Suicidal behaviour clashes with the survival instinct"; 2021, p. 622), Joiner and colleagues (Suicide "is in direct opposition to a… strong instinct for self-preservation"; 2016, p. 242), and Nock et al. ("All organisms are imbued with a survival instinct"; 2019, p. 258), and many others—presume the same premise.

That suicide research has long struggled to make progress may be largely due to this paradigmatic misconstrual. The "Self-Preservation Instinct" paradigm impedes scientific understanding because it sets up the expectation that the human organism's default track is not suicide. Therefore, the intervention of some extraordinary suicidogenic event or circumstance—the mysterious "X" in Fig. 1a—is presumed necessary to throw someone off course. Generations of researchers have duly tried to identify "X", the putative special contingency. That no trace has been found (Belsher et al., 2019; Franklin et al., 2017) should be no surprise: as the self-preservation instinct, which suicide allegedly transgresses, is unreal, then so are the conditions that cause the transgression. Later in this chapter (22 and 23, below) we point to reasons to believe that the opposite biological scenario is more likely: a "Self-Preservation Instinct Not" paradigm (Fig. 1b). Counterintuitively, suicide is the adult human organism's default path, which is nearly always blocked by the intervention of evolved anti-suicide adaptations. If this analysis is correct, the research focus ought to seek instead to identify, understand, and capitalise on these special-purpose defences.

For discussion of the self-preservation instinct in suicide research, see Soper (2018, 2025).

(12) Mismatch. DeCatanzaro (1980, 1981) posits, more as a heuristic than a model, that suicide may result from cognitive systems that were functional in our species' ancestral environments, when humans lived as hunter-gatherers in small bands in Pleistocene Africa, but are not functional now. There may not have been time for the human mind to evolve ways of coping with modern lifestyles.

Environmental mismatch is a good way to make sense of certain human problems: for example, the human appetite for sweet and fatty foods, shaped by an ancestral

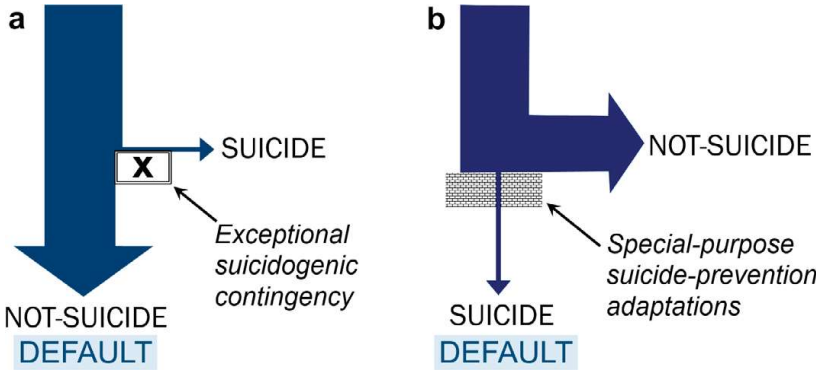

Fig. 1 Comparison of "Self-Preservation Instinct" (Fig. 1a) vs. "Self-Preservation Instinct Not" (Fig. 1b) paradigms of suicide. *Source* Proposed by author

scarcity of high-energy nutrients, makes us prone to obesity in twenty-first-century conditions of plenty (Nesse & Williams, 1994). But the idea is not as helpful as a way to understand suicide. It is unclear what exactly has changed to produce suicide now, when it supposedly did not in our ancestral past. This supposition is anyway contraindicated: among nineteenth-century hunter-gatherer societies—the closest we have to a window into deep prehistory—suicide was reportedly at least as prevalent as it is in the modern West (Steinmetz, 1894; Zilboorg, 1936).

That said, although environmental mismatch does not comfortably explain the origin of suicide, it might help us to understand individual variations in susceptibility to suicide, and in at least two ways. First: if the chief driver of suicide is pain, especially emotional pain, as argued in the "Escape"-type models outlined later in this chapter, then, debatably, some aspects of modern lifestyles could be more emotionally painful, and therefore more suicidogenic, than was the case for our distant ancestors (Baechler, 1979). Second: following one "Escape"-type model (pain-brain; section 20 below), Soper (2021) argues that human psychological defences against suicide were shaped in an environment in which wilful self-killing was generally not quick or easy to accomplish. The restriction of access to quick and easy means of suicide may have a powerfully protective effect (Chen, et al, 2016) because it buys time for the organism's evolved anti-suicide systems to mobilise.

(13) Misperceived burdensomeness. Inspired by deCatanzaro's "burdensomeness" theory (4, above), Joiner et al. (2017) offer a "sociobiological extension" of Joiner's (2005) interpersonal theory of suicide (IPTS)—a theory founded, it should be noted, on the doubtfully tenable premise of the "survival instinct" (11, above). Based on their classification of humans as *eusocial* (comparable, that is, to colonial insects), Joiner and colleagues speculate that suicide may reflect a pathological misfiring (triggered by a faulty self-appraisal of burdensomeness) of a hypothesised cross-species "self-sacrificial behavioral suite" (2016, p. 235) which, so the authors also speculate, may characterise eusociality.

This proposal represents an ingenious, well-intentioned, and rare effort to find evolutionary footings for one of suicidology's mainstream (proximate) frameworks.

However, it mistakes a description ("eusocial") for a substantive explanation. Self-sacrificing behaviours of colonial insects and other caste-forming species arise from algorithms of inclusive fitness that are driven by these species' familial and genetic configurations. In a colony of honeybees, for example, where only one member (the queen) procreates, helped by a caste of sterile, genetically-similar workers, a worker bee can be sacrificed in defence of the queen and colony with no loss of genetic material (Alexander et al., 1991)—in contrast to (human) suicide. Even if humans were deemed loosely "eusocial" by some debatable criteria (Gintis, 2012), the gulf between humans' and colonial insects' reproductive strategies makes a theory of suicide based on the behaviour of the latter, in Bering's (2018) words, "just kind of a non-starter" (p. 71). For a biological critique of IPTS and its "sociobiological extension", see Soper (2022).

(14) Parasite manipulation. Aubin et al. (2013) speculate that the microbial parasite *Toxiplasma gondii* may hijack normal cognitive systems, promoting potentially lethal risk-taking behaviour and perhaps suicidality. Suicide might reflect an adaptation that benefits the parasite, not the host. Although much has been written (Amouei et al., 2020), this line of theory falls short of useful specificity. It is not explained theoretically why *T. gondii* infestation should generate suicide in particular (as opposed to risky behaviour) and, empirically, its correlation with suicidality, although statistically significant, is weak.

These "pathology" proposals are intriguing, but none looks to us compelling or helpful as a way to explain suicide's evolutionary origins.

D. Communication

Another genre of theory views suicidality as an adaption that evolved as a means of fitness-enhancing communication, functioning for the benefit of the suicidal signaller. From this perspective, occasional suicidal death is viewed not as pathology but as an unfortunate outcome, some lethal risk being necessary for the signal to be taken seriously.

(15) Bargaining. Researchers led by Watson and Andrews (2002) and Hagen (1999, 2003; Hagen et al., 2008) view suicidal behaviour as a means by which otherwise powerless individuals elicit concessions, consciously or not, from dominant but reluctant others. The proposed explanandum is not suicide per se but a broad notion of "suicidality", encompassing ideation, threats, and non-lethal self-injury, as well as high-intent suicide attempts (Hagen et al., 2008). Broader still, the hypothesis buds from a "social navigation" hypothesis of depression (Hagen, 1999; Watson & Andrews, 2002): Hagen (1999) likens depression to "going on strike" (p. 350) insofar as debilitating symptoms of fatigue and anhedonia combine a costly (thereby honest) signal of need with what Hagen construes as a withdrawal of labour, functioning to get the need met. By this interpretation, suicidality lies at the most drastic end of a spectrum of "depressive and suicidal bargaining" (Gaffney et al., 2022, p. 245). To be credible, a suicidal gambit necessarily entails a game-theoretical balancing of risks and returns, with the possibility of a fatal outcome (Rosenthal, 1993). Suicidal death is not adaptive but, rather, a high-stakes gamble lost. Syme et al.(2016) argue that their review of ethnographic records provides empirical support for the hypothesis.

(16) Costly apology. Accepting that not all suicidal acts are easily explained by the bargaining model, Syme and Hagen (2018) offer a complementary hypothesis: that suicidal behaviour may also have evolved as a costly, and therefore credible, signal of remorse, designed to repair social relations to the actor's benefit in the wake of a severe transgression on the actor's part. Again, the target explanandum is suicidality, not specifically suicide. On the basis of their further ethnographic review, these authors argue that the hypothesis may apply to a minority of cases.

(17) Psychological aposematism. Wiley (2020) suggests that the social clustering of suicides may have an evolutionary origin analogous to the biological strategy of *aposematism*, whereby colourful displays function to caution predators that a prey animal is so distasteful or venomous that it is not worth attacking. In contrast to the "bargaining" and "costly apology" models (above), which view fatal outcomes as a maladaptive side-effect of on-average ancestrally adaptive communication, Wiley argues that a certain minimal level of mortality may be part of the adaptation, necessary for suicidal communication to be taken seriously. Suicidal deaths function to inform the community about the contexts in which suicides occur, thereby conditioning the community to ameliorate these conditions.

(18) Suffering ape. Steinkopf (2023) posits that our species' extreme sociality adds to the fitness value of issuing costly signals of suffering, suicidal behaviour included, due to the social rewards that such signals elicit. He infers that self-harm and suicidal behaviour could only have evolved in a prosocial environment.

These various proposals are elegant, intuitively appealing and can claim some empirical backing, but they have problems. Few scholars, if any, would dispute that suicidal threats and behaviours may sometimes, perhaps unconsciously, be manipulative (Aldridge, 1998; Hezel et al., 1985; Stengel & Cook, 1958). However, a manipulative purpose is not a necessary or sufficient condition for suicide. It is evidently unnecessary: many self-killings are organised with apparently purposeful non-disclosure (Hallford et al., 2023). These deaths are not plausible fitness-serving signals in themselves since, obviously, death rules out a response. A manipulative agenda is logically insufficient since the coercive power of non-lethal suicidality derives, second-hand, from shared knowledge of the possibility of (lethal) suicide. In this regard, Wiley (2020) asks a pivotal question: "would suicide threats and attempts be effective bargaining tools if nobody ever killed themselves?" (p. 229). We think not. Suicide needed to come first. By definition, an act of "attempted suicide" that lacks lethal intent is not literally attempted *suicide*, but what Kreitman (1977) terms, less confusingly, *parasuicide*—"a *behavioural analogue* of suicide" (p. 3, original italics). In this light, the evolutionary genesis of suicide, the original model for the analogue, needs explaining independently of subsequent manipulative spin-offs.

It looks to us that these communication-type hypotheses confuse current utility with ancestral adaptation, a not uncommon mistake in evolutionary discussions (Tooby & Cosmides, 1992). By analogy, a well-timed cough ("*Ahem!*") can speak volumes, but this is not evidence that coughing behaviour evolved as an adaptation for communication (instead of, more likely, for clearing airways). The test of evolutionary adaptation hinges on evidence not of current utility but of special design—on whether the observed characteristics of a trait match its hypothesised function so

exactly, across a spread of criteria (typically, effectiveness; cost-efficiency; reliability; and precision), that it would be an extraordinary coincidence if the trait had come about for any other reason (Buss, 2019; Williams, 1966). By this measure, we think communication hypotheses of suicide fail. Exemplifying the evidential shortfall, the signal-to-noise ratio of putative suicidal "warning signs" is too low for these to constitute reliably detectible or actionable predictors of suicidal acts (Belsher et al., 2019; Franklin et al., 2017; Large, 2022; Mulder et al., 2016; Soper et al., 2022). See Soper and Shackelford (2023) for a critique, and Gaffney et al. (2023) for Hagen and colleagues' response.

E. Escape

The most robust ultimate models of suicide, to our minds, construe the act as an escape. Evolutionary theory accords here with a swathe of proximate "escape" theories in mainstream suicidology (Gunn, 2014). However, an evolutionary perspective reveals new and challenging implications, as we will explain.

(19) Pain relief. Almost certainly, no fitness upside is to be had from killing oneself—at least, none that comes close to the certain downside. From the perspective of the genotype (the organism's genetic code, the sole purpose of which is to reproduce), death is "The End".

However, "The End" has an entirely different cost/benefit ratio from the viewpoint of the phenotype—the living human being. For the phenotype, death promises an alluring payoff: it solves absolutely the problem of pain. Murray and Kluckhohn (1948) highlight the resulting biological conflict within the human organism:

> Suicide does not have *adaptive* (survival) value but it does have *adjustive* value for the organism. Suicide is *functional* because it abolishes painful tension. (p. 15, original italics)

"Painful tension" is a biological need state, like hunger or thirst. Pain demands a response because it is designed precisely not to be tolerated; it is meant to motivate action to reduce and preferably end the aversive stimulus (Klein, 2015). Pain is an evolved and presumably universal concomitant of animal life, enabling motile organisms to navigate their internal and external environment by steering themselves around fitness hazards. Sometimes, perhaps much of the time (Benatar, 2015), participation in the Darwinian struggle is going to hurt.

More narrowly, Shneidman's (1993) neologism, *psychache*, captures the kind of pain that is so intolerable as to induce escape by suicide: "the hurt, anguish, soreness, aching, psychological pain in the psyche, the mind" (p. 51).

(20) Social Pain. Narrower still, Gunn (2017) identified the prime source of suicidogenic psychache as social. Humans, a highly social species, are especially sensitive to threats to vital interpersonal relations. Social pain can be particularly excruciating and, like pain generally, probably has evolutionarily adapted roots (Eisenberger & Lieberman, 2005; Thornhill & Thornhill, 1989).

From this thread of ideas, the ultimate—and proximate—origin of the *motivation* for suicidal escape emerges: pain, frequently social, sets up a biological imperative to obtain relief.

However, although motivation is a necessary condition for suicide, it is not sufficient. The act of intentional self-killing presumes the *means*, which starts with a cognitive capability—knowledge of what is intended. Where does awareness of the deadly exit come from?

(21) Learning. Regarding mental access to the suicide idea, deCatanzaro (1980), yet again, offers a hypothesis: "suicide may be an entirely learned behavior" (p. 267). Here we agree.

Humans are almost certainly not born with the latent thought of killing themselves. The notion of self-accomplished death, a synthesis of sophisticated abstractions, is too convoluted a representation to be plausibly transmitted by genetic inheritance, even if selection were to tolerate such a variant (which it probably would not; Skinner, 1969). What humans are born with is nascent intelligence so promiscuous that—alongside normal social and cognitive development, rarely before the early teen years but often soon after—they will piece together the facts of life and death, and draw their own conclusion (Macdonald, 2007; Mishara, 1999; Soper, 2018). Not unreasonably, and whatever others might have to say on the matter, some cognitively mature humans will perceive death as an outstandingly efficacious solution to a painful life (Marsh et al., 2021). It may be just a short step to acting on that thought (Borges et al., 2012).

By this light, "The Lure of Death" (Humphrey, 2018, p. 1) by suicide can be understood as a noxious by-product of human sapience. By all accounts, free-floating intelligence is an adaptation: it enabled our ancestors to thrive in complex social structures and varied physical environments (Humphrey, 1976; Tooby & DeVore, 1987). The overriding fitness benefits of intelligence can be measured by the many costly downsides borne for its sake, including the enlarged brain's metabolic burden (Aiello & Wheeler, 1995), mutational load (Keller & Miller, 2006), obstetric challenges (Haeusler et al., 2021)—and suicidality (Soper, 2018).

On the face of it, the hypotheses in this "escape" section are not particularly contentious so far. A loose consensus in suicidology would rally to a conception of suicide as a learned, strongly dysgenic, but pre-eminently effective escape from psychological suffering, generally stemming from interpersonal troubles. Several prominent (proximate) suicide theories—those of Durkheim (1897/1952), Shneidman (1993), Joiner (2005), and others—are consistent with this position.

However, as we will see, the escape-type model's evolutionary implications are profoundly problematic.

(22) Pain-brain. The chief problem is that, combined, the preceding proposals in this section present necessary *and sufficient* conditions for suicide. Every normal adolescent and adult carries the motivation (pain), and the means (cognitive capability, or "brain") to intentionally kill themselves (Soper, 2018). If both the motivation and means to take a course of action are present, then that course of action ought to be taken. By this light, controverting the "survival instinct" paradigm (11, above), suicide is not an aberration or pathology: it is the expectable consequence of being human—what will happen by default, unless some counteractant intercedes. The curiosity is not why a few of us opt out of life, but why most of us do not. Logically

as well as numerically, the *non*-suicide of 98.7% of humankind is in greater need of an explanation than the suicide of 1.3% (W.H.O., 2021).

Non-suicide, too, needs an ultimate as well as a proximate account. The ultimate reason why most people do not die this way is that our ancestors lived and died with this survival hazard over an evolutionary timescale—ever since "man discovered that he can kill not only animals and fellow-men but also himself" (Stengel, 1964, p. 1). In response to this recurrent exposure, over thousands of generations, intense selection shaped effective suicide-prevention adaptations (Fig. 1b). We are the offspring of individuals who, so protected, tended not to kill themselves.

The proposed existence of evolved anti-suicide defences may raise eyebrows in both suicidology and evolutionary science, but it is a reasonable inference. Humphrey (2011, 2018) and Soper (2018), from different starting points, converged independently at this expectation. They could both be wrong, of course, but other scholars who have examined the argument find it persuasive (Lester, 2019; Maris, 2022; Shackelford, 2021).

Not only do these defences likely exist, but they should also not be difficult to see in action. Enabling human sapience to be survivable, they presumably play a major role in human psychology. They should be conspicuous and ubiquitous in human lives.

However, at least two misapprehensions may obstruct our view of them (we will highlight a third in the closing paragraphs, below). First is the widespread misconception that humans are restrained from suicide by a unitary "survival instinct", as already discussed. A second misunderstanding is that suicide is prevented entirely as a fortuitous side-effect of adaptations that evolved for preventing *accidental* deaths. This is implausible. Suicide and misadventure are importantly distinct threats, which will have driven the evolution of distinct defensive countermeasures (Soper, 2022).

These blind spots relate to what evolved anti-suicide defences are *not*. So, what *are* they? Anticipating the question by several decades, Himmelhoch (1988) posits that "[p]owerful restraints, neurophysiological, psychological, and social, reside in us all against the completion of self-destruction", including "complex, evolutionarily determined feedback mechanisms" (p. 46). We will come back to Himmelhoch's ideas.

Humphrey (2011, 2018) argues that the maintenance of a positive reason for living is a human survival necessity. He suggests that ancestral humans constructed a "soul niche" (2011, p. xii)—a subjectively rewarding conscious experience that maintains an "appetite for staying alive" (2018, p. 4). Along similar lines, Soper (2018, 2021) envisages an array of "pain-type fenders"—evolved psychological adaptations that render the idea of suicide redundant by working reciprocal levers (Fig. 2). On one side, "upping the ups" (2021, p. 147), humans spend as much time as possible engaged in pleasures that would be "biologically frivolous and vain" (Pinker, 1997, p. 521) for any other animal, but give life-preserving meaning to human existence. On the opposite side, other adaptations "down the downs" (Soper, 2021, p. 140): the human capacity for self-serving self-deception and hopeful worldviews moderates the organism's exposure to potentially suicidogenic psychache (or "cognitive dissonance", "unpleasure", and other close synonyms). Suicide avoidance may thereby

constitute unitary biological footings for diverse aspects of human psychology, including positive psychology, psychodynamic defences, religiosity, and altruistic morality, which together maintain "Life Worth Living" (Soper, 2021). Meanwhile, culturally-propagated mores—stigma, taboo, and a fear of death—cognitively barricade the suicide exit, making the option difficult to contemplate (Humphrey, 2011, 2018; "brain-type fenders"'; Fig. 2; Soper, 2018). "brain-type fenders".

These are intriguing proposals. They have theoretical coherence and appear to align with the epidemiological record (Soper, 2018). However, if they are broadly correct, then a new problem arises. As already noted, pain is an evolved necessity of animal life. Humans cannot be kept completely pain-free. So, what holds us back when, despite the above adaptations, human lives become so painful that the suicidal exit may begin to appeal?

(23) Anti-suicide psychopathology. Himmelhoch (1988) proposes a final line of evolved defences against suicide, "the organism's 'last gasp' adaptive survival response" (p. 46) which, he argues, manifests in diverse forms of psychopathology: compulsive drug and alcohol use; manic states and bipolar disorder; severe personality disorders; psychosis; non-suicidal self-harm; and eating disorders. Developing these ideas within the pain-brain framework (section 20, above), Soper (2018, 2023a) hypothesises a set of uniquely human adaptations ("keepers") that, from adolescence onward, and in diverse permutations, activate in response to intense, chronic psychache. Emergency defences stop suicidal thoughts from escalating into lethal attempts in two ways: "pain-type" keepers deploy certain depressive and other symptoms to blunt the motivation for escape, thereby making suicide unnecessary; whereas "brain-type" keepers interfere with memory, logical thinking, and other high-level executive functions, thereby making suicidal action impracticable (Fig. 2).

The existence of evolved special-purpose defences implies that suicidal deaths are statistical residuals—scenarios that lack sufficient predictive correlates by which the organism could have foreseen and forestalled a lethal outcome (Soper, 2019b). Over an evolutionary timescale, all recurring precursors of deliberate self-killing that are detectible at the level of the organism have been subsumed into an onboard suicide-prevention algorithm. By acting on the information, stopping all suicides that can practicably be stopped, the evolved system exhausts the available cues' predictive value. This dynamic parsimoniously explains why human populations display "natural" (Yang & Lester, 2009) or "base" (Goldney, 2003) rates of suicide, and why these deaths appear to instantiate stochastically (Corke et al., 2021; Taylor et al., 2021). Suicide is unpredictable at the level of the individual not because it is an infrequent event, as is often claimed (Rosen, 1954), but the other way around: suicide's infrequency is an emergent property of its non-predictability. Suicide is not an uncommon cause of human death; it *looks* rare, thinly dispersed across any given population, because evolution by natural selection has left no usefully accurate predictors with which to narrow the field of vision to a sub-population at special risk (Soper et al., 2022; Soper, 2019b). Soper (2019a) argues that a minimal, universal, and more or less species-typical risk of dying this way resides as a "daily occupational hazard of being human" (p. 468).

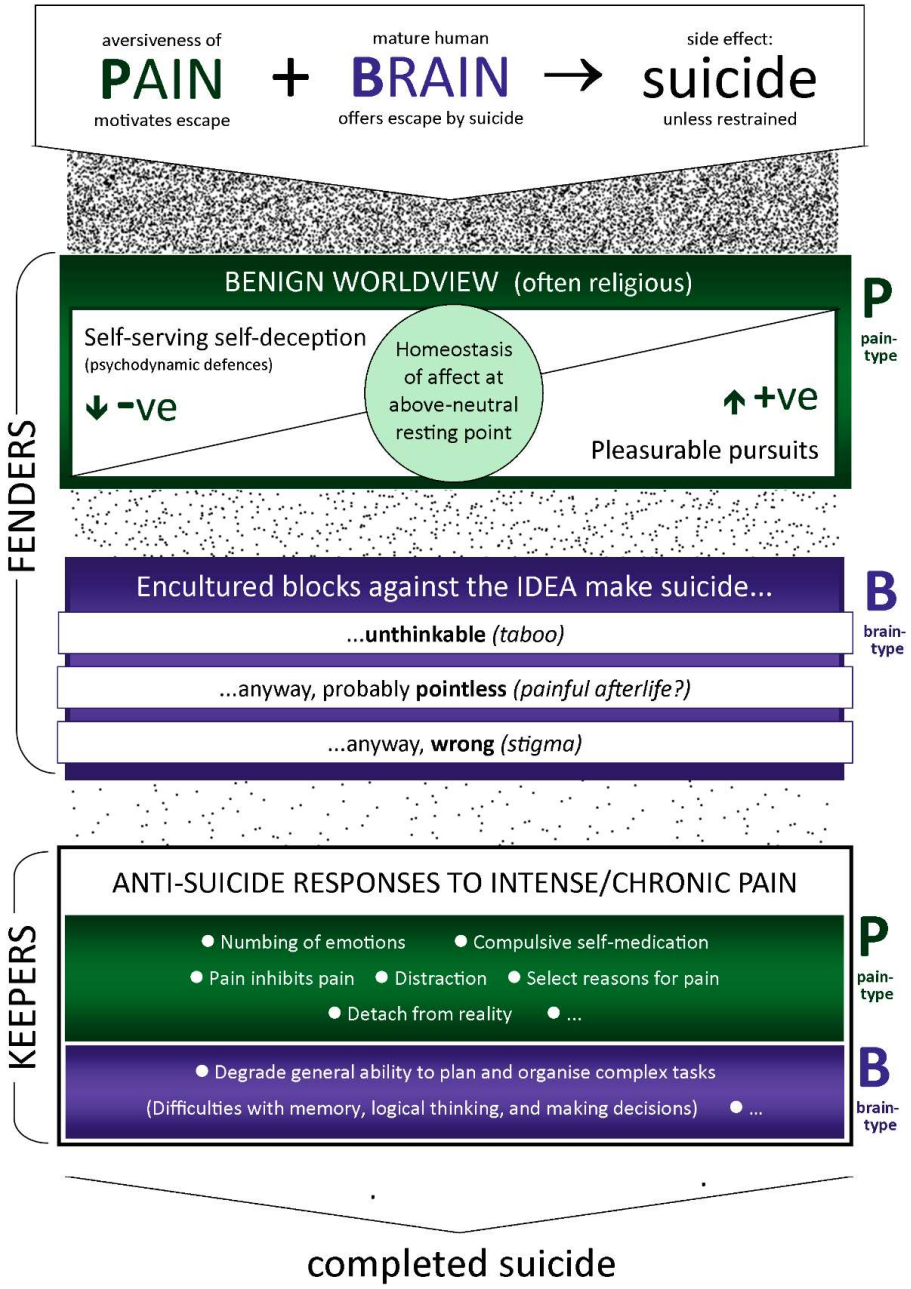

Fig. 2 Pain-brain theory: schematic of hypothesised evolved anti-suicide defences. Reading from top to bottom: suicide's twin necessary and sufficient conditions (top) "pain" and "brain" generate a mass of potentially suicidal trajectories, virtually all of which are intercepted by lines of organismic anti-suicide defences, leaving a minimal residue of completed suicides (bottom). The first barrier ("pain-type fenders"), co-ordinated by benign worldviews, deploys psychodynamic defences and motivates pleasurable pursuits to maintain affect at an above-neutral resting point, thereby making the idea of suicidal escape redundant. The next barrier ("brain-type fenders") uses encultured blocks to keep the idea of suicide unthinkable, seemingly unreliable as an escape from pain, and morally wrong. The final defences are "keepers"—emergency interventions, activated by intense, chronic psychache, which function to prevent suicidal ideas from being enacted. Keepers present as diverse symptoms of psychopathology: "pain-type keepers" use emotional numbing and other measures to lessen the necessity for suicidal escape; while "brain-type" keepers interfere with cognitive faculties usually sufficiently to make suicidal action difficult to organise. *Source* Adapted from Soper (2018)

If this conception of suicide and psychopathology is correct, then it implies a need for a radical reassessment of suicide-prevention practice and policy and has wide-ranging repercussions for mental healthcare (Soper et al., 2022).

This concludes our review. Time will tell whether any of the above formulations are on the right track, and more ideas will no doubt come forward, if and only if suicide researchers give due attention to an evolutionary mode of enquiry. There are hopeful signs in this respect. We find Joiner and colleagues' work encouraging (Rogers et al., 2018; Stanley et al., 2018), notwithstanding our aforementioned theoretical objections. Nonetheless, only the barest beginning has been made.

To return to blind spots, the main barrier to progress may be more psychological than methodological. Suicidologists may understandably baulk at an evolutionary perspective, holding up, as it does, a mirror to human nature. Evolutionary analysis lets the research domain loose from the reassuring realm of the third person, where suicidal behaviour belongs to *them* (patients, subjects, "suicidal people") and can be attributed to special conditions arising from *their* lives. A prerequisite for considering whether, as Himmelhoch (1988) asserts, evolved defences against suicide "reside in us all" (p. 46) is to conceive that there may be a "suicidal person in all of us" (Bering, 2018, p. 3).

This first-person perspective of suicide may be disconcerting, but it promises a rich reward. By seeking to integrate ultimate and proximate modes of explanation, standing on two legs instead of one, suicidology has the prospect not only of making progress in its own field, but of pioneering a coherent approach to the advancement of mental health science (Soper, 2023a). Beyond even that, by addressing this most puzzling aspect of our species' evolution, suicide researchers may spearhead a new scientific understanding of what it is to be human.

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C.A. Soper, Ph.D., is an evolutionary psychologist, psychotherapist, and independent researcher based in Lisbon, Portugal, and a leading theorist in the evolution of suicide. He holds degrees from the University of Cambridge and the University of London and won his Ph.D. with a thesis titled *Towards Solving the Evolutionary Puzzle of Suicide*, which formed the basis of a textbook, The *Evolution of Suicide*, published by Springer in 2018. A more accessible book, *The Evolution of Life Worth Living: Why We Choose to Live*, was published in 2021. He is a speaker on evolutionary perspectives of suicide at scholarly conferences and has published several articles and chapters in this field. The latter include the co-authored section on suicide in the prominent 2023 Handbook, *Evolutionary Psychiatry*, published by the Royal College of Psychiatrists and Cambridge University Press (R. Abed and P. St John-Smith, Eds.).

Todd K. Shackelford received his Ph.D. in evolutionary psychology in 1997 from the University of Texas at Austin. Since 2010, he is Professor and Chair of the Department of Psychology at Oakland University in Rochester, Michigan, where he is Co-Director of the Evolutionary Psychology Lab (www.ToddKShackelford.com). Shackelford led the founding in 2012 of Ph.D. and M.S. programs in psychology at Oakland University. In 2016, he was appointed Distinguished Professor by the Oakland University Board of Trustees. Shackelford has published over 350 journal articles and his work has been cited about 32,000 times. Much of Shackelford's research addresses sexual conflict between men and women, with a focus on men's physical, emotional, and sexual violence against their intimate partners. Since 2006, Shackelford has served as editor of the journal *Evolutionary Psychology* and in 2014 founded the journal *Evolutionary Psychological Science* as Editor-in-Chief. Shackelford is an elected Fellow of the Association for Psychological Science and the American Psychological Association.