ORIGINAL ARTICLE



Psychological Aposematism: An Evolutionary Analysis of Suicide

James C. Wiley¹

Received: 13 August 2019 / Accepted: 23 April 2020 / Published online: 25 May 2020 © The Author(s) 2020

Abstract

The evolutionary advantage of psychological phenomena can be gleaned by comparing them with physical traits that have proven adaptive in other organisms. The present article provides a novel evolutionary explanation of suicide in humans by comparing it with aposematism in insects. Aposematic insects are brightly colored, making them conspicuous to predators. However, such insects are equipped with toxins that cause a noxious reaction when eaten. Thus, the death of a few insects conditions predators to avoid other insects of similar coloration. Analogously, human suicides may increase the credibility of future suicide threats and attempts from others, conveying an evolutionary advantage to the phenotypic expression of suicidal behavior in low-fitness contexts.

Keywords Aposematism · Cluster · Evolution · Green beard · Suicide

Introduction

Inference on the evolutionary function of psychological phenomena can be made by comparing them to physical characteristics found naturally in other organisms (Nesse 1999, 2019). From an evolutionary perspective, suicide is perplexing (Soper 2018). It is difficult to see how self-inflicted death could prove adaptive. However, in nature physical traits exist that facilitate the death of one organism so that others possessing similar characteristics receive an increased chance of survival (Guilford 1988, 1990). For instance, poisonous insects are often brightly colored, making them immediately noticeable to predators. After killing and eating such an insect, the predator endures its prey's toxic effects and learns to avoid insects of similar conspicuous coloration. This phenomenon, known as aposematism, can be compared with suicide in humans, providing novel insights on the subject.

Aposematic organisms overtly signal to predators that they are unprofitable to hunt. For instance, bright yellow and black wasps (*aculeate Hymenoptera*) possess a potent venom highly effective against vertebrate predators, such as birds (Schmidt 1990). Their coloration renders them distinct from the green and brown backgrounds of their habitats. If

a bird is stung by a wasp during predation they may become conditioned to avoid insects with similar coloration (Guilford 1990; Schmidt 1990). Thus, the conspicuous warning colors displayed by wasps convey an evolutionary advantage. Another aposematic insect is the aptly named bombardier beetle (*Brachinus* beetles; Schaller et al. 2018), who is capable of discharging flaming toxins. This defensive concoction can reach 100 °C and be accurately aimed at assailants. Bombardier beetles sport a reddish head and limbs, and have a dark blue wing cover, making them overt to predators.

These first few examples illustrate the most direct process through which aposematism can function. In the event of an attack, the assailed harms or causes great discomfort to their assailant, thus repelling them. The assailed organism bears some distinct trait, which the assailant learns to avoid. However, not all aposematic insects have defenses that will successfully repel a predator. In fact, some defenses require the predator eat, or at least taste, the aposematic insect in order to take effect. For instance, the monarch butterfly is conspicuously colored in orange and black, and does not discharge toxins or sting (Parsons 1965). However, within its body it contains toxins (i.e., cardenolides), which are only ingested by a predator if eaten. An assailing bird may leave a monarch alone after finding its initial taste unpalatable, or the bird may eat the monarch only to regurgitate the toxic prey and feel ill. In this case, however, harm is unavoidable to the aposematic prey. While monarchs may have some capacity for

Department of Psychology, Carleton University, Ottawa, ON, Canada



escaping predators, the eggs of some ladybugs (coccinellidae) are delicate and immobile, contain toxins, and are also conspicuously colored (Rieder et al. 2008; Winters et al. 2014). At least one egg would need to be consumed or tasted to facilitate aversive conditioning. Similarly vulnerable and conspicuous, larvae of the magpie moth (Abraxas grossulariata) bear only unpalatability and internal toxins as a defense (Cott [1940]2015). If pecked by a bird, larvae such as these are likely to die, but the bird will learn that hunting such larvae is unprofitable (Wallace 1867; Guilford 1990). While some aposematic insects have immediate defenses that are capable of repelling assailants, others may die as a cause of their conspicuousness, but instill in their predator an aversion to like-colored organisms. In the latter case the evolutionary fitness (i.e., survival and reproductive potential; Darwin [1859]1956; Lessard 1997) of the individual that falls victim to predation suffers, but a benefit is conveyed to those with similar coloration, thus promoting the adaptivity of such coloration.

Aposematic insects tend to live gregariously, which has prompted speculation from theorists (Vulinec 1990). Gregariousness can offer a plethora of advantages to insects, regardless of whether they exhibit aposematic characteristics. However, within the specific context of aposematism, gregariousness could offer unique advantages (Guilford 1988, 1990; Vulinec 1990). For instance, a predator may better remember the coloration of its toxic prey if many are present when vomiting or experiencing illness. Additionally, where the cause-and-effect relationship between eating a poisonous insect and vomiting may be difficult to infer, gregariousness may help to distinguish what caused the noxious reaction. If a predator were to capture non-aposematic prey after eating an aposematic insect, it may be difficult to infer which piece of prey was responsible for the subsequent noxious experience. Gregariousness solves this problem by overwhelming the predator with aposematic meals, so that if the first meal does not induce a noxious reaction, the second or third will. Thus, the theory of aposematism yields the hypothesis that, when the relationship between a warning and the consequence for ignoring the warning are difficult to infer, increasing exposure to warnings and subsequent consequences in both temporal and geographical space may be advantageous.

Theorists have also speculated over how aposematic characteristics could have been selected for through the evolutionary process. A basic assumption of evolutionary theory is that characteristics are heritable (Darwin [1859]1956; Fisher 1930). If heritable, characteristics that help an organism survive and reproduce will become more and more common among newer generations. Under the assumption of heritability, one can formulate theories about how evolution selects for particular *phenotypes*. This last term refers to a

set of traits and behaviors that are believed to be hereditary. This heredity is attributable to a *genotype*, which comprises the specific genes underlying a phenotype.

Guilford (1988, 1990) suggests that green beard selection, originally a thought experiment posited by Hamilton (1964a, b) and popularized by Dawkins (1976), helps explain the existence of aposematism. Green beard selection suggests that organisms possessing a conspicuous trait may recognize each other and provide each other with fitness benefits, while denying non-green beards such benefits. While green beard genes exist, they are rare, and suggestions of their utility in evolutionary processes is often met with skepticism (West et al. 2011). This is because green beard selection requires phenotypic expression of (a) an overt trait (e.g., a green beard), (b) the capability to recognize others with this trait, and (c) the tendency to benefit those that are recognized (Hamilton 1964a, b; Guilford 1990). Additionally, such a process is susceptible to cheaters, who express the conspicuous trait but do not provide any benefit to others. Thus, cheaters would receive benefits from true green beards but provide none in return. However, the nature of aposematism solves the issue of cheating, given that predation acts as the governing mechanism to control and extinguish cheaters. Batesian mimics are those that express the aposematic warnings of other insects but do not have any real defense from predation (Bates 1861; Runtz 2012). For example, hoverflies (Syrphidae) have the same yellow and black warning coloration as wasps, but are harmless to predators (Rashed et al. 2009; Runtz 2012). If too many Batesian mimics exist predators will learn that hunting insects of that particular coloration is profitable, making mimicry unprofitable (Guilford 1988, 1990). Because predators mediate how altruism functions in aposematic insects and their mimics, cheating becomes moderated. Additionally, the condition that green beards must be able to recognize one another is nullified by the learning and conditioning capabilities of their predators. It is this latter group that must learn to avoid conspicuous noxious prey if they are to survive, whereas their prey can remain ignorant of one another's conspicuousness.

The apparent altruistic nature of aposematism has facilitated speculation as to whether *kin selection* (i.e., inclusive fitness; Hamilton 1964a; Marshall 2015) has played a role in its evolution (Guilford 1985, 1990). Kin selection functions on the premise that an individual shares a large proportion of their genetic makeup with relatives; thus conveying survival and reproductive benefits to relatives also conveys a benefit to the individual's own genes. This concept was originally proposed by Hamilton (1964a) as inclusive fitness theory, and aims to explain how altruistic behaviors could evolve. For instance, infertile worker bees endlessly toil for the benefit of their queen, whose reproduction promotes her and her workers' genes into the next generation (Bourke 2011). While worth speculation, it is noteworthy that aposematism

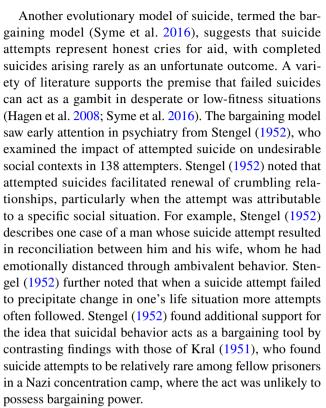


will not spread because family is benefitted, but because those with similar phenotypes are (Guilford 1985, 1990). This is observable in the context of Müllerian mimicry, wherein two different species that are well defended against predators possess similar aposematic warnings (Müller 1879; Runtz 2012). For instance, the viceroy butterfly has a similar orange and black appearance to that of the monarch butterfly, and is similarly unpalatable to predators (Ritland and Brower 1991). A predator that experiences noxious effects from eating either a viceroy or a monarch will form an aversion to both species, thus amplifying the fitness benefit of the colored pattern sported by both butterflies. While kin selection may have played some role in the initial evolution of aposematism, it does not explain Müllerian mimicry in unrelated species. Ultimately, green beard phenotypes can be obtained via multiple genetic avenues, whereas kin selection is restricted to benefits exchanged exclusively among relatives (Guilford 1985, 1990). A corollary of this conclusion is that the prosperity of green beards depends on the convergence of phenotypic expression, and that the underlying genotypes responsible for these phenotypes need not be identical. So long as green beard traits are heritable, they can proliferate through the evolutionary process without being generated by a singular genotype. Theorists agree that aposematism proves adaptive through green beard selection as well as kin and other kinds of selection (Guilford 1990). However, there remains healthy debate over which selection mechanisms were most influential in the initial evolution of aposematism.

Psychological Aposematism

Comparing Suicide to Aposematism

Through the aposematic process the death of one benefits the fitness of many. It is conceivable that, if a human threatens or attempts suicide and is ignored, a completed suicide will render future threats and attempts more believable. If the death of an aposematic caterpillar facilitates survival for those with a similar aposematic phenotype, then the fitness of that phenotype receives a net benefit despite the initial death. Similarly, if particular contexts prompt suicidal behavior in humans, then a completed suicide may increase action taken by community members to prevent suicide-prone individuals from entering said contexts. If these contexts are associated with lower fitness, then reducing the probability of entering such contexts increases overall phenotypic fitness. Thus, genotypes that prompt suicidal behavior in particular contexts could prove adaptive. I will refer to this concept of conditioning society to prevent or alleviate low-fitness contexts through suicide as psychological aposematism.



Using suicide as a bargaining tool appears to be common in many cultures (Hagen et al. 2008; Syme et al. 2016; Syme and Hagen 2019). Hezel (1984) noted that a Micronesian society had a specific word (amwunumwun) for the use of self-harming behavior as a bargaining device. Amwunumwun could refer to anything ranging from minor acts of self-harm to dramatic suicide attempts. For instance, a child refusing to eat when parents have angered them would be considered amwunumwun, as well as stabbing oneself when unwanted sexual relations are pursued by elders. Hezel (1984) suggests that the function of amwunumwun is to show that one has been harmed by those they must obey, and that despite the existing power dynamic reconciliation is necessary. In a quantitative assessment of randomly sampled ethnographic reports from across the globe, Syme et al. (2016) found that suicide attempts were often used as a bargaining tool. For example, women who were otherwise powerless often used suicide attempts to escape prearranged marriages.

Additional support for the bargaining model is found in examination of suicide risk factors, which include traumatic childhood events, bereavement, legal and financial difficulties, and sexual abuse (Turecki and Brent 2016). Accordingly, many models explain self-harming and suicidal behavior as a response to an abusive and conflict filled environment (Suyemoto 1998; Hagen et al. 2008). To consider the process dictated by the bargaining model, a victim of sexual abuse may attempt suicide to signal to others that a dangerous abuser is present and requires



eviction (Syme et al. 2016). Successfully indicating the presence of an abuser could yield a benefit to the victim and their community if their community removes the toxic individual. Alternatively, the community may be content tolerating the abuser, but will be forced to choose between taking action and the potential death of the victim, which seems more likely with ever increasing suicide attempts. Similar to aposematism, this model is prone to cheaters (Rosenthal 1993). For instance, if a community provides monetary resources and medical support to victims of sexual abuse, these resources could be acquired by convincing the authoritative entity that one has been abused, regardless of whether they were or not.

A game theoretic version of the bargaining model has been constructed by Rosenthal (1993), and suggests that sincere suicide attempters can negate the impact of cheaters by increasing the lethality of their suicide attempts, which observers will characterize as being more trustworthy. Here, lethality is conceptualized as the probability of death from a suicide attempt. It is interesting that Rosenthal's (1993) game theoretic model of suicide is remarkably similar to game theoretic models of aposematism (e.g., Leimar et al. 1986; Sherratt and Beatty 2003). Such models are signal games, wherein sincere signalers and cheaters try to convey sincerity to observers, who are trying to provide benefits to sincere signalers and deny benefits to cheaters. The major distinguishing factor is that the aposematic games treat the death of an organism as a method of conditioning predators to avoid other organisms with similar phenotypic expression. Thus, the overall fitness of their phenotype sees a benefit, despite the initially incurred death. In Rosenthal's (1993) model, the impact of a death in a previous round of play has no bearings on future observer behavior, whereas in aposematic models death functions as a conditioning mechanism and contributes to the success of sincere signalers.

If we analogize suicide victims as prey seeking to escape low-fitness contexts, suicide may act as a conditioning mechanism for society, which is the ultimate propagator of social, economic, political, and health contexts. A society will have to decide whether losing the suicide attempter is more costly than taking aid-oriented action (Syme et al. 2016). If bereavement from previous suicides has been felt, a new suicide attempter may have better success bargaining for a higher-fitness context. Thus, completed suicide may function to increase the fitness of those that share susceptibility to suicidal behavior in low-fitness contexts. The difference between psychological aposematism and the bargaining model of suicide is that the former suggests a small number of completed suicides facilitates the fitness of other suicideprone individuals, whereas the latter suggests suicide is an unfortunate outcome of the bargaining process. While the premise that suicide attempts act as signals of need is well supported, the idea that completed suicides are a maladaptive outcome of this process may be incorrect.

Interestingly, Hezel (1984) suggested that completed suicides typically achieve the committers' desired goal, in that their death forces observers to recognize the harm they caused and prompts some form of post-mortem reconciliation. While Syme et al. (2016) found distinct evidence for the bargaining model, many of the ethnographies in their study focused on cases of completed suicides, rather than unsuccessful attempts. It is interesting that ethnographers, anthropologists, and the cultures that they study consider narratives of completed suicides important, despite the fact that unsuccessful attempts are likely more prevalent (Curtin et al. 2016; Syme et al. 2016). This may be due to the role that completed suicides play in promoting the fitness of suicide-prone phenotypes. If stories of completed suicides do not spread, then suicide threats and attempts will have no bargaining power, because there will be no reason to suspect they are real.

This analysis leads to a worthwhile point. If one accepts the bargaining model, but insists that completed suicide cannot be adaptive, I would ask this: would suicide threats or attempts be effective bargaining tools if nobody ever killed themselves? Governments, communities, friends, and families invest numerous resources into preventing suicide (Wilkie et al. 1998; Turecki and Brent 2016), but if threats and attempts were always empty, would any of these entities continue their efforts? It seems inevitable that some suicide is needed in order for threats and attempts to be taken seriously. Thus, completed suicides provide future threateners and attempters with actual bargaining power.

Suicide Clusters Compared with Gregariousness

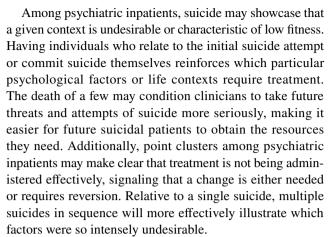
Point Clusters

A possible relation between insect aposematism and suicide becomes more tangible when observing the phenomenon of suicide *point clusters*, wherein the occurrence of one suicide prompts similar cases of suicidal behavior in temporal and geographic proximity (Joiner 1999). Aposematic insects live gregariously (i.e., in geographic proximity) so that, if preyed upon, predators will eat their noxious prey repeatedly (i.e., in temporal proximity) until experiencing noxious effects (Guilford 1990). Thus, the gregariousness of aposematic insects is designed to make clear the cause-and-effect relationship between their aposematic warning and noxious effects. Considering the exact psychological causes of suicide are impossible to determine, society may be more successfully conditioned against allowing low-fitness contexts if a series of suicides



are experienced in close proximity, both temporally and geographically. This would affirm that one particular set of factors is causal of suicide (e.g., sexual abuse, bullying), conditioning society to invest larger efforts into preventing or removing such factors.

Theoretical speculation regarding what mechanisms underlie the formation of suicide point clusters vary (Haw et al. 2013). A popular perspective is that suicide is contagious, and spreads through a population much like any disease would (Phillips 1974; Haw et al. 2013). This model suggests that members of a cluster become prone to suicide through social exposure to the initial suicide. Sacks and Eth (1981) propose that those who form social and psychological identifications with an initial suicide victim are likely to attempt suicide themselves. Their study examined a small cluster of suicidal behavior among three psychiatric inpatients. Following an initial suicide, inpatients with similar social and psychological characteristics engaged in suicidal behavior. The initial suicide and the sequential attempter were both suffering from failed careers in the performing arts. Additionally, both were prescribed psychotropic mediations, which they knew had deleterious effects on fine motor coordination. During their mutual time spent at the psychiatric ward they would collectively engage in their respective professions: the first would dance while the second played piano. After the dancer's suicide, the pianist attempted suicide by jumping out of his apartment window, suffering several severe injuries. The third member of the cluster visited the pianist while hospitalized, reporting that something had compelled her to see him. This third member had attempted suicide in a similar manner to the pianist preceding her admission to the psychiatric ward. Both she and the pianist were chronic schizophrenics. This last patient discussed being preoccupied with thoughts of suicide following the occurrence of these two events, though these thoughts remitted over the following few weeks. Crawford and Willis (1966) similarly found that psychiatric inpatient suicides occurring in the same years had remarkable similarities to each other. Three point clusters were examined, wherein suicides had similar psychological and medical pathologies and fell victim to identical lethal methods. Another case study found that three schizophrenic inpatients who shared living quarters all attempted suicide by burning themselves within a few weeks of each other (Zemishlany et al. 1987). Thus, these three studies suggest that having similar social and psychological characteristics to an initial suicide or suicide attempt may be a point cluster risk factor (Crawford and Willis 1966; Sacks and Eth 1981; Zemishlany et al. 1987). Pertaining to the clinical setting, risk factors associated with point clusters include departure of senior clinicians, influx of junior clinicians (Taiminen et al. 1992), weak organizational leadership, and demoralized staff (Rissmiller and Rissmiller 1990; Haw 1994; Haw et al. 2013).



On a somewhat larger scale, multiple point clusters involving six to eight suicides and many more attempts have occurred among Canadian indigenous communities (Ward and Fox 1977; Davies and Wilkes 1993; Wilkie et al. 1998). Pertaining investigations support the hypothesis posited by Sacks and Eth (1981) that those with similar social and psychological characteristics to an initial suicide may be more prone to becoming members of a point cluster. Many members of these indigenous point clusters were family and friends of the other suicides, had endured similar harsh contexts (i.e., incarceration, rape, sexual assault, drug abuse), and were adolescents or young adults. Another report describes a high school point cluster involving two suicides, seven attempted suicides, and 23 cases of suicidal ideation (Brent et al. 1989). Many point cluster members had at least one major psychiatric disorder and were close friends with the initial suicides. Again, those who have common personal issues to an initial suicide may be more likely to attempt suicide in the near future. Multiple suicides clumped together may reaffirm which factors were causal of low fitness, conditioning society to alleviate those factors more promptly when faced with future suicidal behavior.

Mass Clusters

Suicide point clusters require an unusually high aggregation of suicides within temporal and geographical proximity. However, clusters can also form exclusively in temporal proximity, and are referred to as *mass clusters* (Joiner 1999). These kinds of clusters have been observed following publicized suicides (Phillips 1974; Haw et al. 2013), a phenomenon sometimes referred to as the *Werther effect*. This term is derived from Goethe's 18th century novel wherein the protagonist, named Werther, kills himself after suffering unrequited love (Phillips 1974; Haw et al. 2013). Following Goethe's publication a wave of suicides occurred across multiple European countries. These suicides were similar in age and sex to the protagonist and reportedly imitated his lethal method and distinct manner of dress. Interested in the possibility that publicized suicides



can be suggestive to readers, Phillips (1974) examined more modern publications and found that suicide rates increased following newspaper reports of suicide. Furthermore, these rates appeared to increase with the degree of publicity the story received. For example, after the highly publicized suicide of the famous actress Marilyn Monroe, suicide rates increased by 12% and 10% in the United States and United Kingdom, respectively (Phillips 1974). Alternatively, a less publicized suicide was associated with only a 4% increase in American suicides. The Werther effect has been observed in recent cases, with a 10% increase in suicides occurring after the highly publicized suicide of the popular comedian Robin Williams (Carmichael and Whitley 2009; Fink et al. 2018). The effect has also been noted after the airing of movies and news stories involving suicide (Phillips and Carstensen 1986). Similar to point clusters, it is expected that those with social or psychological similarities to a publicized suicide are more likely to be influenced (Phillips 1974; Phillips and Carstensen 1986). Thus, the suggestive process may operate specifically on those who psychologically identify with the initial suicide in some way.

Again, psychological aposematism may play a role here. However, the fact that a suicide may be prompted by a previous suicide occurring beyond geographical proximity is slightly at odds with what I have proposed. Psychological aposematism provides a fitness advantage by facilitating suicides within temporal and geographical proximity, making clear which factors were causal to immediate community members. This conditions local community members to alleviate these factors as a means of preventing future suicides. Point clustering contained within that community would enhance this conditioning, but mass clustering would not necessarily impact those particular local community members. It is possible that psychological aposematism operating beyond particular geographical limits is indicative of environmental mismatch. The evolutionary process responsible for shaping suicide as an aposematic behavior would not have accounted for the spread of information via mass media. Thus, suicide as a result of contagion via publication may be a result of the vast difference between the environments within which this mechanism evolved and our modern ones. However, societies are much larger now than ever before, and may even be able to transcend cities and countries via social media (Lam 2012). If humans have transcended the geographical limits that once constrained societies within small communities, then mass clusters may still prove adaptive.

Theoretical Mechanisms

I would not say that there is conclusive evidence that the exact mechanisms underlying aposematism also underlie suicide. However, I have noticed parallels between these very different bodies of literature and felt compelled to bring them to attention. Having discussed some empirical support for the concept of psychological aposematism, I will expand upon the precise theoretical mechanisms that must operate for the concept to hold.

Integration with Evolutionary Mechanisms

The theoretical adaptivity of psychological aposematism is primarily based on green beard selection. Accordingly, I will reiterate and discuss the requirements for this type of selection in regard to the phenomenon of suicide. Green beard selection operates under the assumption of heritability and requires phenotypic expression of (a) an overt trait, (b) the capability to recognize others with this trait, and (c) the tendency to provide fitness benefits to those that are recognized (Hamilton 1964a, b; Guilford 1990).

In order for suicidal behavior to prove adaptive it must be heritable. A variety of studies suggest suicidal behavior is heritable, but specifically accountable genes are elusive (Turecki and Brent 2016). The first requirement of green beard selection suggests that suicides and equally susceptible attempters must be conspicuous. If society cannot recognize what contexts elicit suicides, then no conditioning to alleviate these contexts can occur. The literature appears to support this requirement at a macro-sociological level. Syme et al. (2016) found reports of suicide prevalent across the globe, and others describe a high degree of publicity and societal reactivity to the phenomenon (e.g., Phillips 1974; Hezel 1984; Wilkie et al. 1998; Syme et al. 2016; Fink et al. 2018; Carmichael and Whitley 2019). However, at a microsociological level there is some controversy (Hagen et al. 2008). For instance, Sourander et al. (2006) found parents' awareness of their children's suicidal and self-harming behavior to be quite low (16% and 22% for parents of girls and boys, respectively). Alternatively, Hawton and Rodham (2006) found that around 80% of self-harming youth reported that somebody else knew of their self-harming behavior. Accordingly, Hagen et al. (2008) suggest that selfharmers may not necessarily be bargaining with parents for higher fitness contexts, but with peer groups. Regardless, further research is needed to confirm whether or not this first condition required for green beard selection is met.

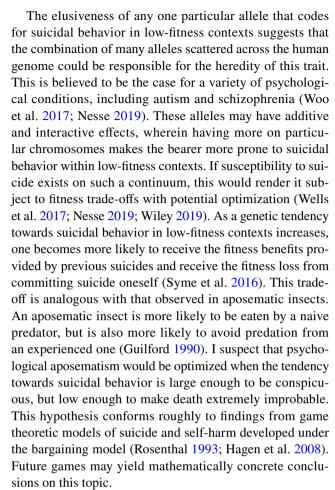
Interestingly, the last two conditions for green beard selection appear moderated through community members, and not through suicides or suicide attempters themselves. This is similar to aposematism, wherein these last two conditions are moderated through predators, not through the aposematic prey. Predators must learn through experience that aposematic prey will cause them to vomit and are thus unprofitable to hunt. Societies must learn that imposing low-fitness contexts on particular individuals results in suicide, which is a loss of a human resource. Thus, it is not



required that suicides or attempters recognize or directly benefit each other, but that society recognizes and benefits them. The literature on this topic is mixed. Many articles suggest that societies attempt to benefit suicide-prone individuals (e.g., Wilkie et al. 1998; Turecki and Brent 2016). These publications are morally oriented towards preventing and treating suicide. The efficacy of intervention programs and the value findings provide to clinical practice permeate discussion in this body of literature. Alternatively, varying cultures view victims of suicidal behavior negatively (Syme et al. 2016). Some even enforce sanctions in order to deter suicide attempts. For example, a Papua New Guinea society was found to punish suicide attempts by administering harsh beatings (Pospisil 1958).

Psychological aposematism suggests that high suicide rates amplify the bargaining power of suicide attempts. Alternatively, societies with low suicide rates will more aggressively test the legitimacy of a suicide attempt. Thus, psychological aposematism posits a few joint hypotheses that may explain this inconsistency in the literature. First, in societies where suicide rates are high, punishments deterring suicide attempts will be mild or nonexistent. Second, in societies where suicide rates are low, punishments for attempting suicide will be severe. Taken together, it is expected that as suicide rates increase punishment severity for attempting suicide will decrease. Future research investigating these hypotheses may confirm whether or not the last two conditions for green beard selection are met.

Green beard selection typically requires pleiotropic expression of traits that, in combination, achieve a fitness benefit (Guilford 1990). For example, it is expected that one gene codes for an aposematic caterpillar's warning coloration and toxicity. If these traits were coded for separately, a caterpillar might inherit warning coloration without toxicity, or vice versa. While the aposematic phenotype could still be converged upon in this situation, it appears much less likely from a theoretical perspective. Interestingly, psychological aposematism does not require pleiotropic expression, because only one trait is required of the bearers: that they are susceptible to suicidal behavior in low-fitness contexts. While aposematic insects require simultaneous inheritance of two traits, psychologically aposematic humans only require the inheritance of one. Thus, pleiotropy does not appear necessary for psychological aposematism to prove adaptive. It is often suggested that the three conditions for green beard selection must be pleiotropically expressed to prove adaptive (Guilford 1990). However, aposematism in general solves this issue by having two of these conditions operate remotely through teachable observers (Guilford 1988, 1990). Psychological aposematism takes it one step further by having the remaining condition only require one phenotypically expressed trait.



Psychological aposematism suggests that an aposematic mechanism could evolve as a defense against members of one's own species. This phenomenon is observable in the insect world. Ladybug eggs, which were used as an example earlier, express aposematism in order to defend from other unrelated ladybugs (Rieder et al. 2008; Winters et al. 2014). Ladybugs are believed to attack the eggs of unrelated ladybugs as a method of improving food availability for their close relatives (Agarwala and Dixon 1993; Joseph et al. 1999). The fewer unrelated ladybugs there are in the ecosystem consuming food, the more food there will be for family members. Thus, attacking unrelated ladybug eggs conveys an inclusive fitness benefit. Accordingly, ladybugs have evolved aposematism in their eggs to deter these attacks.

The rendition of aposematic theory described in the present article does not account for nuanced differences that exist between differing aposematic species and their predators. For example, some predators may learn which prey should be avoided by observing the feeding habits of more experienced members of their species (Thorogood et al. 2017). Other predators will either avoid or carefully taste prey that they have never before encountered (Cott [1940]2015; Wiklund and Järvi 1981). To incorporate any one of these nuances would yield a more precise



understanding of aposematism within a specific predator—prey relationship, but would not be generalizable to other species. Thus, in order to preserve generality I have refrained from incorporating any such nuances into the theory of psychological aposematism. If psychological aposematism is believed to exist, further analysis is required in order to judge if comparable nuances exist in humans.

Psychological aposematism suggests that the causal mechanisms underlying suicide clustering are distinct from other imitation and learning mechanisms. This I am unsure of. It is worth comparing suicide clustering to other phenomena that can spread through learning and imitation to see if suicide truly appears special in some way. For instance, what underlying mechanisms make mass clusters distinct from increased religiosity following the publicized promotion of Christianity (Phillips 1974)? Suicide clusters could have nothing to do with benefiting the fitness of others who are prone to suicide in low-fitness contexts. Rather, individuals may simply observe and thus try to implement a new way of addressing their life problems. For example, the three schizophrenics who attempted to burn themselves to death (Zemishlany et al. 1987) may have been sensitized to this activity by their peers' attempts. Perhaps this appeared to them as a potential solution to their suffering (Soper 2018), which they had not previously imagined. While the parallels I have drawn between suicide clustering and aposematic gregariousness exist, it is unclear if suicide clusters result as a malfunction of human learning capabilities or if they are selected for through the evolutionary process.

Integration with Bargaining Model Mechanisms

The bargaining model asserts that suicide attempts sincerely convey that the attempter is willing to sacrifice their life if a bargain is not achieved (Rosenthal 1993; Syme et al. 2016). Thus, the probability of death (i.e., costliness) associated with the attempt is what makes it credible. Alternatively, cheap signals (e.g., verbal threats of suicide) are expected to be ineffective as bargaining tools. Psychological aposematism posits that completed suicides will lower the costliness required by suicide attempters to achieve their bargain. If psychological aposematism is integrated with the bargaining model, the new focus of this synthesized model would be the costliness threshold that requires surpassing if a bargain is to be achieved. Psychological aposematism suggests that increasing suicide rates will cause this threshold to lower, permitting cheaper signals to achieve bargains. Hypothetically, if suicide rates were high enough, this costliness threshold could be shifted low enough to allow verbal suicide threats to achieve bargains. This topic in its entirety requires further investigation. As a starting point, it may be interesting to examine whether suicide rates within cities moderate the relationship between suicidal behavior and direct fitness (i.e., offspring counts; Marshall 2015). Data for such a study may be obtainable from open access datasets and government data sources (e.g., Health and Retirement Study 2016). If increasing suicide rates are associated with an increasing correlation between suicidal behavior and fitness, this may indicate that higher suicide rates help victims of suicidal behavior bargain for higher fitness contexts.

Additionally, the bargaining model implies that some might try to fake suicidal behavior in order to acquire the fitness benefits that are being conveyed to sincere suicide threateners or attempters (Rosenthal 1993). Within the context of psychological aposematism, this concept is synonymous with Batesian mimicry. Naturally, lowering the costliness threshold required in order to obtain a bargain through suicidal behavior would also make obtaining a bargain easier for mimics. However, I would like to caution against the idea that the psychologically aposematic and their mimics could ever be parsed from each other. The empirical literature has found that even the subtlest expression of suicidal ideation has resulted in suicide (e.g., Johansson et al. 2006). While it is tempting to believe that those who engage in cheap suicidal behavior (e.g., suicide threats) could be mimics, the empirical literature suggests this would not provide a perfect split (Franklin et al. 2017). There would naturally be false negatives, who might then go on to commit suicide after not receiving the appropriate aid. I will stress that, in nature, Batesian mimics must be excessively rare relative to their truly aposematic models (Guilford 1990; Harper and Pfennig 2007). If Batesian mimics are too common, then predators will learn that hunting organisms of similar coloration is profitable, thus making Batesian mimicry unprofitable. Accordingly, if Batesian mimics of the psychologically aposematic exist, I would expect them to be rare.

The bargaining model (Hagen et al. 2008; Syme et al. 2016) and psychological aposematism both suggest that the evolution of suicide is dependent on social relationships. Queller (2011) lists three mechanisms through which social relationships can convey a fitness benefit. The first is labelled the kin effect and corresponds to Hamilton's (1964a) original formulation of inclusive fitness, being the impact that an organism has on its own fitness through reproduction and altruistic behavior towards genetic relatives. The second is labelled the kith effect and represents fitness benefits obtained from mutually beneficial relationships between unrelated organisms. For example, humans and canines have provided mutual benefits to each other, thus evolving together (Catanzaro 2003). The third is called the kind effect and corresponds to fitness benefits conveyed to those who share some trait but have no familial relationship (e.g., green beard selection).

In its original formulation, the bargaining model operates through kin and kith effects. For example, family and friends will consider aiding a suicide attempter seeking to escape



a prearranged marriage, but those without vested interest in the victim will be indifferent (Syme et al. 2016). Family endures a fitness detriment from the death of a genetic relative and friends may endure a fitness detriment from the death of a potentially collaborative social partner. As an additional alternative, I have proposed that psychological aposematism operates at the societal level, potentially transcending familial and interpersonal relations. This is explicable through the kind effect. If suicides inflict severe fitness losses throughout familial and social networks, then changing societal norms to be aid-oriented towards suicidal behavior will increase fitness for members of these networks. This will also provide a fitness benefit to suicideprone individuals as a whole, regardless of which networks they belong to. This highlights the green beard component of psychological aposematism. However, much like insect aposematism (Guilford 1990), psychological aposematism appears to be intertwined with multiple forms of selection. This green beard effect can only be achieved by influencing kin and kith effects.

Furthermore, psychological aposematism may be entangled with other human tendencies that appear to have evolved through kind selection. In particular, conforming to and enforcing norms may enable societal-wide cooperation that yields otherwise unobtainable fitness benefits (Boyd 2018; Stanford 2019). To illustrate, an individual's fitness is directly impacted if family members or collaborative social partners are murdered, but a person may be indifferent to the killing of unrelated or unacquainted individuals. Nevertheless, murder is often punitively sanctioned at the societal level (United Nations Office on Drugs and Crime 2019). Certain behaviors may be so detrimental to fitness that society-wide costs for prevention outweigh their costs of occurrence. People will inevitably care less about the murdering of those who do not provide some benefit to their own fitness, but may recognize that societal regulations punishing murder are worthwhile. This kind of societal-wide norm enforcement is believed to have played a crucial role in the evolution of human cooperation (Boyd 2018; Stanford 2019). Perhaps similar underlying mechanisms facilitate societal investment in the prevention of suicidal behavior. I would not restrict this to prevention approaches that are aidoriented. As discussed previously, norms that are punitive towards suicidal behavior may be favored if suicides occur in insufficient numbers to render threats and attempts sincere.

While bargaining model theorists (Hagen et al 2008; Syme et al. 2016) imply that the larger society will be indifferent towards victims of suicidal behavior, I believe that the bargaining model could still operate beyond immediate familial and interpersonal relationships. An often-overlooked property of kin selection is that it can yield a high degree of genetic relatedness between seemingly unrelated individuals (Cornwallis et al. 2009; West et al. 2011). If two

parents are unrelated to each other, then their offspring are expected to share half of their genetic material with each parent (Hamilton 1964a). However, if parents have some degree of genetic relation to each other, then their child can share more than half of their genetic material with each parent, because there is overlap in the parents' genetics (Hamilton 1964a, b, 1970, 1972; West et al. 2011). Genetic relatedness between distant family members (e.g., first, second, and third cousins) also amplifies through this property. If mating is largely confined within a population due to limited migration, then genetic relatedness among members will increase as new generations are born. Iterating through many generations permits kin selection to function on a larger scale than is typically assumed (Gardner and West 2006; Kümmerli et al. 2009; West et al. 2011). Accordingly, a more generalized sympathy towards suicidal behavior may evolve, permitting suicide attempters to appeal to the broader society for aid. While it is tempting to dismiss this aspect of kin selection as irrelevant to modern human societies that are genetically diverse, pertinent research suggests similar mechanisms still play an important role in the continued evolution of human cooperation (Figueredo and Wolf 2009). However, a full treatment of this topic is beyond the scope of the present article. Additionally, there are complexities to this property of kin selection that I have not detailed; interested readers should consult Gardner and West (2006) and Kümmerli et al. (2009) for more thorough considerations.

The bargaining process inevitably requires the victim of suicidal behavior to communicate what it is they wish to bargain for (Hagen et al. 2008; Syme et al. 2016). This communication could occur explicitly through written or spoken language. Alternatively, implicit forms of communication could be used (e.g., immediately threatening or attempting suicide after an argument with a spouse). The potential for suicide may then activate evolved reactions within those that the bargain is directed towards (e.g., fear of bereavement). Alternatively, the observer may use certain logical deductions to judge whether the suicide threat or attempt is sincere. These deductions may be based on personal observations or information communicated through others (e.g., friends report that this was the victim's third and most lethal suicide attempt and should therefore be taken seriously). Psychological aposematism is governed by similar underlying mechanisms. For instance, the process through which previous suicides adjust the costliness threshold required to obtain a bargain occurs through culturally transmitted information (e.g., spoken language, novels, newspapers, social media). This transfer of information may play upon evolved reactions (e.g., feeling bereaved after hearing about a suicide) or logical deductions (i.e., loss of revenue due to an employee taking bereavement leave) in order to achieve a fitness benefit. Additionally, suicide clusters may be similarly triggered through culturally transmitted information. Feeling



empathetic towards a recently communicated suicide may encourage one to engage in suicidal behavior.

Suicide has been suggested to be a uniquely human phenomenon (Preti 2007; Soper 2018). There are no known examples of nonhuman species that consciously take their own lives. While some nonhuman species exhibit social transmission (Laland and Brown 2006; Thorogood et al. 2017), the extensive capacity that humans have for this factor may be what makes suicide unique to humans (Soper 2018). Thus, suicide itself may arise from a mixture of evolved traits and culturally transmitted concepts. This is not to say that the ability to engage with culturally transmitted information is not itself an evolved trait (Heyes 2018; Stanford 2019). However, culturally transmitted information is not coded within one's genetic makeup (Laland and Brown 2006).

Despite this, evolutionary theorists suggest that culturally transmitted information is ultimately still driven by evolution (Richerson and Boyd 1989; Laland and Brown 2006; Laland 2008; Eberhardt 2010; Boyd 2018; Heyes 2018; Andersson and Törnberg 2019; Buskell 2019; Stanford 2019). While culture is more malleable than genetic composition, evolution will still select for cultural traits that benefit fitness. Thus, culture may deviate from its evolutionary path more quickly than genetic makeup, but will always be pulled back towards some fitness-optimizing trajectory. This suggests that a combination of ordinarily evolved traits and culture could be responsible for the evolution of unique human qualities, such as suicide.

Towards a Comprehensive Evolutionary Theory of Suicide

A caveat of the bargaining model is that one must have the potential for higher fitness in order to be alleviated from a low-fitness context (Syme et al. 2016). Accordingly, the bargaining model specifically aims to explain suicide in populations whose high fitness is constrained purely by their context. For example, a healthy young man who is denied access to a mate of choice may attempt suicide as a method of bargaining to alleviate these constraints. A corollary of this is that the bargaining model does not explain suicidal behavior in those that possess low reproductive potential and are burdensome to their kin (Syme et al. 2016). Thus, the bargaining model and psychological aposematism do not comprehensively explain suicide.

Other evolutionary theories have been proposed that, when brought together, begin to form a comprehensive understanding of the phenomenon. However, there are still gaps to be filled. For example, deCatanzaro (1980, 1981) proposes that burdensome individuals may kill themselves to free up resources for their family members. This could

potentially convey a fitness benefit to kin, who share a large proportion of the suicide victim's genetic makeup. DeCatanzaro's (1981) theory coincides with findings that suggest higher perceived levels of burdensomeness are associated with suicidal ideation (McPherson et al. 2007; Syme et al. 2016). Additionally, national-level statistics indicate that the likelihood of committing suicide increases with age, confounding it with an increasing likelihood of terminal illness and decreasing probability of reproduction (Curtin et al. 2016; Syme et al. 2016). DeCatanzaro's (1981) theory has received numerous criticisms (Soper 2018; Nesse 2019). For instance, why would individuals not disperse from their family, thus eliminating an imposed burden on kin and maintaining their own reproductive potential (Syme et al. 2016; Nesse 2019; Syme and Hagen 2019)? While synthesizing the concept of psychological aposematism with other evolutionary perspectives of suicide is the next natural analytical step, it is beyond the scope of the present article. Suffice to say, if accepted, psychological aposematism will be only a small part of a larger explanation of suicidal behavior.

Conclusion

Many parallels exist between insect aposematism and human suicide. This article suggests that the processes governing both phenomena facilitate a small number of deaths in order to benefit the fitness of many. The death of an aposematic insect conditions a predator to avoid alike insects in future (Cott [1940]2015; Guilford 1990). Similarly, a suicide may condition society to take future threats or attempts of suicide more seriously. Aposematic insects live gregariously so that when preyed upon exposure to their warning coloration and noxious effects is maximized (Guilford 1990). This expedites aversive conditioning in predators. Likewise, suicide clustering may occur because it more strongly affirms which social and psychological factors are causal of suicide relative to a single suicide. In turn, this motivates community members to alleviate these specific factors when faced with future threats and attempts. This concept of psychological aposematism suggests completed suicides increase the overall fitness of the suicidal phenotype, whereas previous models have dismissed completed suicides as maladaptive. While psychological aposematism cannot be considered a valid scientific concept until it has received further empirical and game theoretic scrutiny, I hope that its hypotheses are of interest to researchers.

Acknowledgments I am grateful to Samantha Carlucci, Tom Wiley, Aaron English, and two anonymous reviewers for providing helpful comments on this manuscript.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Agarwala BK, Dixon AFG (1993) Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). Eur J Entomol 90:45–50
- Andersson C, Törnberg P (2019) Towards a macroevolutionary theory of human evolution: the social protocell. Biol Theory 14:86–102. https://doi.org/10.1007/s13752-018-0313-y
- Bates HW (1861) Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Trans Linn Soc Lond 23:495–566. https://doi.org/10.1111/j.1096-3642.1860.tb00146.x
- Bourke AFG (2011) The validity and value of inclusive fitness theory. Proc R Soc B 278:3313–3320. https://doi.org/10.1098/rspb.2011.1465
- Boyd R (2018) A different kind of animal: how culture transformed our species. Princeton University Press, Princeton
- Brent DA, Kerr MM, Goldstein C, Bozigar J, Wartella M, Allan MJ (1989) An outbreak of suicide and suicidal behavior in a high school. J Am Acad Child Adolesc Psychiatry 28:918–924. https://doi.org/10.1097/00004583-198911000-00017
- Buskell A (2019) Reciprocal causation and the extended evolutionary synthesis. Biol Theory 14:267–279. https://doi.org/10.1007/s13752-019-00325-7
- Carmichael V, Whitley R (2009) Media coverage of Robin Williams' suicide in the United States: a contributor to contagion? PLoS ONE 14:1–13. https://doi.org/10.1371/journal.pone.0216543
- Catanzaro TE (2003) Section introduction: human-animal bond and primary prevention. Am Behav Sci 47:29–30. https://doi.org/10.1177/0002764203255209
- Cornwallis C, West SA, Griffin AS (2009) Routes to cooperatively breeding vertebrates: kin discrimination and limited dispersal. J Evol Biol 22:2245–2457. https://doi.org/10.1111/j.1420-9101.2009.01853.x
- Cott HB ([1940]2015) Adaptive coloration in animals. Facsimile Publisher, Delhi
- Crawford JP, Willis JH (1966) Double suicide in psychiatric hospital patients. Br J Psychiatry 112:1231–1235. https://doi.org/10.1192/bjp.112.493.1231
- Curtin SC, Warner M, Hedegaard H (2016) Increase in suicide in the United States, 1999–2014. National Center for Health Statistics, pp 1–8. https://www.cdc.gov/nchs/products/databriefs/ db241.htm
- Darwin C ([1859]1956) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 6th edn. Oxford University Press, London
- Davies D, Wilkes TCR (1993) Cluster suicide in rural western Canada. Can J Psychiatry 38:515-519. https://doi. org/10.1177/070674379303800709
- Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

- deCatanzaro D (1980) Human suicide: a biological perspective. Behav Brain Sci 3:265–272. https://doi.org/10.1017/s0140 525x0000474x
- deCatanzaro D (1981) Suicide and self-damaging behavior: a sociobiological perspective. Academic Press, New York
- Eberhardt N (2010) Cybernetic determinants in the evolution of brain and culture. Biol Theory 5:31–39. https://doi.org/10.1162/BIOT a 00013
- Figueredo AJ, Wolf PSA (2009) Assortative pairing and life history strategy. Hum Nat 20:317–330. https://doi.org/10.1007/s1211
- Fink DS, Santaella-Tenorio J, Keyes KM (2018) Increase in suicides the months after the death of Robin Williams in the US. PLoS ONE 13:1–12. https://doi.org/10.1371/journal.pone.0191405
- Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford
- Franklin JC, Ribeiro JD, Fox KR, Bentley KH, Kleiman EM, Huang X et al (2017) Risk factors for suicidal thoughts and behaviors: a meta-analysis of 50 years of research. Psychol Bull 143:187–232. https://doi.org/10.1037/bul0000084
- Gardner A, West SA (2006) Demography, altruism, and the benefits of budding. J Evol Biol 19:1707–1716. https://doi.org/10.1111/i.1420-9101.2006.01104.x
- Guilford T (1985) Is kin selection involved in the evolution of warning colouration? Oikos 45:31–36. https://doi.org/10.2307/35652
- Guilford T (1988) The evolution of conspicuous coloration. Am Nat 131:S7–S21. https://doi.org/10.1086/284764
- Guilford T (1990) The evolution of aposematism. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanism and strategies of prey and predators. State University of New York Press, Albany, pp 23–64
- Hagen EH, Watson PJ, Hammerstein P (2008) Gestures of despair and hope: a view on deliberate self-harm from economics and evolutionary biology. Biol Theory 3:123–138. https://doi.org/10.1162/ biot.2008.3.2.123
- Hamilton WD (1964a) The genetical evolution of social behaviour I. J Theor Biol 7:1–16. https://doi.org/10.1016/0022-5193(64)90038
- Hamilton WD (1964b) The genetical evolution of social behaviour II. J Theor Biol 7:17–52. https://doi.org/10.1016/0022-5193(64)90039 -6
- Hamilton WD (1970) Selfish and spiteful behaviour in an evolutionary model. Nature 228:1218–1220. https://doi.org/10.1038/2281218a0
- Hamilton WD (1972) Altruism and related phenomena, mainly in social insects. Annu Rev Ecol Evol Syst 3:193–232. https://doi.org/10.1146/annurev.es.03.110172.001205
- Harper GR, Pfennig DW (2007) Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? Proc R Soc B 274:1955–1961. https://doi.org/10.1098/rspb.2007.0558
- Haw CM (1994) A cluster of suicides at a London psychiatric unit. Suicide Life Threat Behav 24:256–266
- Haw C, Hawtson K, Niedzwiedz C (2013) Suicide clusters: a review of risk factors and mechanisms. Suicide Life Threat Behav 43:97– 108. https://doi.org/10.1111/j.1943-278X.2012.00130.x
- Hawton K, Rodham K (2006) By their own young hand. Jessica Kingsley Publishers, London
- Health and Retirement Study (2016) RAND HRS Longitudinal File 2016, public use dataset. Produced and distributed by the University of Michigan with funding from the National Institute on Aging (grant number NIA U01AG009740). Ann Arbor, MI. https://www.rand.org/well-being/social-and-behavioral-policy/centers/aging/dataprod/hrs-data.html. Accessed 23 Oct 2018



- Heyes C (2018) Cognitive gadgets: the cultural evolution of thinking. Harvard University Press, Cambridge
- Hezel FX (1984) Cultural patterns in Trukese suicide. Ethnology 23:193–206. https://doi.org/10.2307/3773746
- Johansson L, Lindqvist P, Eriksson A (2006) Teenage suicide cluster formation and contagion: implications for primary care. BMC Fam Pract. https://doi.org/10.1186/1471-2296-7-32
- Joiner TE (1999) The clustering and contagion of suicide. Curr Dir Psychol Sci 8:89–92. https://doi.org/10.1111/1467-8721.00021
- Joseph SB, Snyder WE, Moore AJ (1999) Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. J Evol Biol 12:792–797. https://doi.org/10.1046/j.1420-9101.1999.00077.x
- Kral VA (1951) Psychiatric observations under severe chronic stress. Am J Psychiatry. https://doi.org/10.1176/ajp.108.3.185
- Kümmerli R, Gardner A, West SA, Griffin AS (2009) Limited dispersal, budding dispersal, and cooperation: an experimental study. Evolution 64:939–949. https://doi.org/10.1111/j.1558-5646.2008.00548
- Laland KN (2008) Exploring gene–culture interactions: insights from handedness, sexual selection and niche-construction case studies. Philos Trans R Soc B 363:3577–3589. https://doi.org/10.1098/rstb.2008.0132
- Laland KN, Brown GR (2006) Niche construction, human behavior, and the adaptive-lag hypothesis. Evol Anthropol 15:95–104. https://doi.org/10.1002/evan.20093
- Lam WSE (2012) Literacy and capital in immigrant youths' online networks across countries. Learn Media Technol 38:488–506. https://doi.org/10.1080/17439884.2014.942665
- Leimar O, Enquist M, Sillén-Tullberg B (1986) Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. Am Nat 128:469–490. https://doi.org/10.1086/284581
- Lessard S (1997) Fisher's fundamental theorem of natural selection revisited. Theor Popul Biol 52:119–136. https://doi.org/10.1006/tpbi.1997.1324
- Marshall JAR (2015) Social evolution and inclusive fitness theory: an introduction. Princeton University Press, Princeton
- McPherson CJ, Wilson KG, Murray MA (2007) Feeling like a burden: exploring the perspectives of patients at the end of life. Soc Sci Med 64:417–427. https://doi.org/10.1016/j.socscimed.2006.09.013
- Müller F (1879) Ituna and Thyridia; a remarkable case of mimicry in butterflies. Meldola R (trans) Proclamations of the Entomological Society of London, pp 20–29. https://www.ucl.ac.uk/taxome/lit/muller_1879.pdf
- Nesse RM (1999) Proximate and evolutionary studies of anxiety, stress, and depression: synergy at the interface. Neurosci Biobehav Rev 23:895–903. https://doi.org/10.1016/S0149-7634(99)00023-8
- Nesse RM (2019) Good reasons for bad feelings: insights from the frontier of evolutionary psychiatry. Dutton, New York
- Parsons JA (1965) A digitalis-like toxin in the monarch butterfly, *Danaus plexippus* L. J Physiol 178:290–304. https://doi.org/10.1113/jphysiol.1965.sp007628
- Phillips DP (1974) The influence of suggestion on suicide: Substantive and theoretical implications of the Werther effect. Am Sociol Rev 39:340–350. https://doi.org/10.2307/2094294
- Phillips DP, Carstensen LL (1986) Clustering of teenage suicide after television news stories about suicide. N Engl J Med 315:685–689. https://doi.org/10.1056/NEJM198609113151106
- Pospisil LJ (1958) Kapauku Papuans and their law. Yale University Publications in Anthropology, New Haven
- Preti A (2007) Suicide among animals: a review of evidence. Psychol Rep 101:831–848. https://doi.org/10.2466/pr0.101.3.831-848
- Queller DC (2011) Expanded social fitness and Hamilton's rule for kin, kith, and kind. Proc Natl Acad Sci USA 108:10792–10799. https://doi.org/10.1073/pnas.1100298108

- Rashed A, Khan MI, Dawson JW, Yack JE, Sherratt TN (2009) Do hoverflies (Diptera: Syrphidae) sound like the Hymenoptera they morphologically resemble? Behav Ecol 20:396–402. https://doi.org/10.1093/beheco/arn148
- Richerson PJ, Boyd R (1989) The role of evolved predispositions in cultural evolution: or, human sociobiology meets Pascal's wager. Ethol Sociobiol 10:195–219. https://doi.org/10.1016/0162-3095(89)90019-8
- Rieder JP, Newbold TAS, Sato S, Yasuda H, Evans EW (2008) Intraguild predation and variation in egg defence between sympatric and allopatric populations of two species of ladybird beetles. Ecol Entomol. https://doi.org/10.1111/j.1365-2311.2007.00934.x
- Rissmiller DJ, Rissmiller F (1990) Inpatient suicide epidemics and suggestions for prevention. Hosp Community Psychiatry 41:922–924. https://doi.org/10.1176/ps.41.8.922
- Ritland D, Brower LP (1991) The viceroy butterfly is not a Batesian mimic. Nature 350:497–498. https://doi.org/10.1038/350497a0
- Rosenthal RW (1993) Suicide attempts and signalling games. Math Soc Sci 26:25–33. https://doi.org/10.1016/0165-4896(93)90009-8
- Runtz M (2012) Natural history. Kendall Hunt Publishing Company, Dubuque
- Sacks M, Eth S (1981) Pathological identification as a cause of suicide on an inpatient unit. Hosp Community Psychiatry 32:36–40. https://doi.org/10.1176/ps.32.1.36
- Schaller JC, Davidowitz G, Papaj DR, Smith RL, Carrière Y, Moore W (2018) Molecular phylogeny, ecology and multispecies aggregation behaviour of bombardier beetles in Arizona. PLoS ONE 13:1–20. https://doi.org/10.1371/journal.pone.0205192
- Schmidt JO (1990) Hymenopteran venoms: striving towards the ultimate defense against vertebrates. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanism and strategies of prey and predators. State University of New York Press, Albany, pp 387–420
- Sherratt TN, Beatty CD (2003) The evolution of warning signals as reliable indicators of prey defense. Am Nat 162:377–389. https://doi.org/10.1086/378047
- Soper CA (2018) The evolution of suicide. Springer, Cham
- Sourander A, Aromaa M, Pihlakoski L, Haavisto A, Rautava P, Helenius H, Sillanpää M (2006) Early predictors of deliberate self-harm among adolescents: a prospective follow-up study from age 3 to age 15. J Affect Disord 93:87–96. https://doi.org/10.1016/j.jad.2006.02.015
- Stanford M (2019) The cultural evolution of human nature. Acta Biotheor. https://doi.org/10.1007/s10441-019-09367-7
- Stengel E (1952) Enquiries into attempted suicide [abridged]. Proc R Soc Med 45:613-620
- Suyemoto KL (1998) The functions of self-mutilation. Clin Psychol Rev 18:531–554. https://doi.org/10.1016/S0272-7358(97)00105-0
- Syme KL, Hagen HE (2019) When saying "sorry" isn't enough: is some suicidal behavior a costly signal of apology? Hum Nat 30:117–141. https://doi.org/10.1007/s12110-018-9333-3
- Syme KL, Garfield ZH, Hagen HE (2016) Testing the bargaining vs. inclusive fitness models of suicidal behavior against the ethnographic record. Evol Hum Behav 37:179–192. https://doi.org/10.1016/j.evolhumbehav.2015.10.005
- Taiminen T, Salmenperä T, Lehtinen K (1992) A suicide epidemic in a psychiatric hospital. Suicide Life Threat Behav 22:350–363
- Thorogood R, Kokko H, Mappes J (2017) Social transmission of avoidance among predators facilitates the spread of novel prey. Nat Ecol Evol 14:1–8. https://doi.org/10.1038/s41559-017-0418-x
- Turecki G, Brent DA (2016) Suicide and suicidal behaviour. Lancet 387:1227–1239. https://doi.org/10.1016/S0140-6736(15)00234-2
- United Nations Office on Drugs and Crime (2019) Global study on homicide 2019. UNODC. https://www.unodc.org/unodc/en/ data-and-analysis/global-study-on-homicide.html. Accessed 20 Nov 2019



238 J. C. Wiley

Vulinec K (1990) Collective security: aggregation by insects as a defense. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanism and strategies of prey and predators. State University of New York Press, Albany, pp 229–250

- Wallace AR (1867) Letter no. 5416. Darwin correspondence project. https://www.darwinproject.ac.uk/letter/DCP-LETT-5416.xml. Accessed 3 March 2020
- Ward JA, Fox J (1977) A suicide epidemic on an Indian reserve. Can J Psychiatry 22:423–426. https://doi.org/10.1177/0706743777 02200804
- Wells JCK, Nesse RM, Sear RS, Johnstone RA, Stearns SC (2017) Evolutionary public health: introducing the concept. Lancet 390:500–509. https://doi.org/10.1016/S0140-6736(17)30572-X
- West SA, Mouden CE, Gardner A (2011) Sixteen common misconceptions about the evolution of cooperation in humans. Evol Hum Behav 32:231–262. https://doi.org/10.1016/j.evolhumbehav.2010.08.001
- Wiklund C, Järvi T (1981) Survival of distasteful insects after being attacked by naïve birds: a reappraisal of the theory of aposematic coloration evolving through individual selection. Evolution 36:998–1002. https://doi.org/10.1111/j.1558-5646.1982.tb054
- Wiley JC (2019) Moral orientations in psychology: contrasting theoretical perspectives. BMC Psychol 7:1–6. https://doi.org/10.1186/s40359-019-0287-y

- Wilkie C, Macdonald S, Hildahl K (1998) Community case study: Suicide cluster in a small Manitoba community. Can J Psychiatry 43:823–828. https://doi.org/10.1177/070674379804300807
- Winters AE, Stevens M, Mitchell C, Blomberg SP, Blount JD (2014) Maternal effects and warning signal honesty in eggs and offspring of an aposematic ladybird beetle. Funct Ecol 28:1187–1196. https://doi.org/10.1111/1365-2435.12266
- Woo HJ, Yu C, Kumar K, Reifman J (2017) Large-scale interaction effects reveal missing heritability in schizophrenia, bipolar disorder and posttraumatic stress disorder. Transl Psychiatry 7:1–10. https://doi.org/10.1038/tp.2017.61
- Zemishlany Z, Weinberger A, Benbassat M, Mell H (1987) An epidemic of suicide attempts by burning in a psychiatric hospital. Br J Psychiatry 150:704–706. https://doi.org/10.1192/bjp.150.5.704

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

