Suicidal altruism under random assortment

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ABSTRACT

Questions: Can there be a selective explanation for suicide? Or are all suicides evolutionary mistakes, ever pruned by natural selection to the extent that the tendency to perform them is heritable?

Model: A simple variant of trait group selection (where a population is divided into mutually exclusive groups, with the direct effects of behaviour limited to group-mates), employing predators as the mechanism underlying group selection. Predators evaluate groups to avoid potentially suicidal defenders (which, when present, limit a predator's net return), thus acting as a group selection mechanism favouring groups with potentially suicidal altruists.

Conclusion: The model supports contingent strong altruism (depressing one's direct reproduction – absolute fitness – to aid others) without kin assortment. Even an extreme contingent suicidal type (destroying self for the sake of others) may either saturate a population or be polymorphic with a type avoiding such altruism. The model does not, however, support a sterile worker caste, where sterility occurs before life-history events associated with effective altruism; under random assortment, reproductive suicide must remain contingent or facultative.

Keywords: contingent strong altruism, correlated strategy, predation, random assortment, suicidal altruism, trait group selection, weak altruism.

> *Independent thought calls for courage, because it dispenses with the protection and comfort of consensus-creating prejudices.* [Rüdiger Safranski, on Martin Heidegger's Party allegiance and assumption of rectorship in Nazi Germany (Safranski, 1998, p. 245)]

> *How many deaths make this life? How many lives this death? A complementarity principle we assiduously avoid.* (Benjamin Suzuki)

INTRODUCTION

We do have an explanation for why only one individual reproduces in many ant colonies: kin selection. We do understand self-sacrifice for relatives, for family. But suicidal altruism among non-relatives? Well, it also happens, most noticeably in warfare, perhaps even in the mind of the suicide bomber.

Suicide is cultural taboo in the United States, as is rape. Sociobiologists speaking of rape must always preface with the apology that explanation is not advocacy (e.g. Thornhill and Palmer, 2000). Curiously, sociobiological constructs of murder are not so guilt ridden as those of rape. Perhaps this is because murder is so widespread among other species that it is difficult to view murder as a special human behaviour. For example, langur males practise infanticide (Hausfater and Hrdy, 1984; van Schaik and Janson, 2000).

Suicide is taboo beyond murder and rape. Suicide we frame as utterly inefficacious, the sole exceptions, as remarked, among relatives and the strange case of war. Suicide outside these is, *a priori*, an impossible, monstrous deviation (Atran, 2003; Asad, 2007) – caused by mistake, ever pruned by natural selection.

There are evolutionary models for murder and rape, but not for altruistic suicide among non-relatives. We provide one herein. We do it not to explain phenomena such as the suicide bomber, but to plumb the essence of suicidal altruism among non-relatives with a very simple evolutionary model. We do claim that the cultural taboo against efficacious, adaptive suicide among non-relatives has no place in present evolutionary thought. Our model is biological, abstract, unrelated to political process. Our goal? To enable others to approach the malaise of irrational death.

SUICIDAL ALTRUISM AMONG NON-RELATIVES THROUGH GROUP SELECTION

Classical evolutionary thought views true altruism – foregoing reproduction while augmenting the reproduction of another – as unsupportable under random assortment (Wilson, 1975, 1977b, 1980; Cohen and Eshel, 1976; Matessi and Jayakar, 1976; Nunney, 1985; Hadany *et al.*, 2006). But altruism may also be 'weak' *sensu* Wilson (1979), and that can be supported under random assortment. A weak altruist is one that may aid others but in so doing also enhances its own absolute fitness. Darwin's (1859) 'special difficulty', the sterile social insect worker caste, and similarly extreme, reproductively suicidal altruism (e.g. Wickler, 1976; McAllister and Roitberg, 1987; Stern and Foster, 1996; Shibao *et al.*, 2004), remain the purview of kin assortment and will not be treated here. We present a simple variant of trait group selection (Wilson, 1975, 1977b, 1980) supporting reproductive suicide, but not a fully formed sterile caste, under random assortment. Prior, more restrictive conclusions have been constrained by how behavioural strategies were defined. Instanced altruistic strategies are usually assumed to be behaviourally independent of one another; individuals are autonomous in realized strategy play. We, however, will employ correlated strategies, which allow intra-group behaviour to be correlated across individuals (Rosenthal, 1974; Hammerstein, 1981; Aumann, 1987; Rissing *et al.*, 1989; Cripps, 1991; Myerson, 1991; Pollock, 1994b, 1995, 1996; Pollock *et al.*, 2004; Hadany *et al.*, 2006), so that the expression of a trait in one individual suppresses similar expression among group-mates (Kukuk *et al.*, 1998; Rissing *et al.*, 1989, 1996; Pollock *et al.*, 2004; Hadany *et al.*, 2006). Abandoning such intra-group individual autonomy in behaviour significantly expands the scope of altruism under trait group selection. Yet the conclusions of foundational trait group selection are necessary for the construction of the present suicide-supporting model. In prior terminology, 'strong altruism' (harming one's absolute fitness to aid another) under random assortment requires, in a sense, concurrent 'weak altruism' (*sensu* Wilson, 1979). Kin selection, in contrast, supports strong altruism (of which reproductive suicide is the most extreme kind) even in the absence of concurrent weak altruism.

THE MODEL

A trait group population is an infinite haploid, asexual population subdivided into an infinite number of trait groups (wherein behavioural effects are expressed), each with K individuals assorting randomly from the entire population at group formation (Wilson, 1975, 1977b, 1980). These groups are ephemeral; after social interaction, individuals disperse, again randomly, reproduce, and die. Their offspring begin the cycle anew.

We focus on the strongest form of altruism possible, suicidal defence against predators that enhances the survival of others. A model supporting such altruism will clearly support weaker forms where the altruist is allowed positive fitness. Consider two haploid types: a contingently suicidal S that *may* defend its group-mates to the death, thereby augmenting the latter's chances of survival; and a null N-type that avoids such behaviour. We will also consider, briefly, variants of N that – though they remain fundamentally self-oriented – try to mimic the S-type.

The contingent nature of suicide in S is crucial. S has the capacity to commit suicide in defence of others but need not do so. An inevitably suicidal S would clearly fail to persist (cf. Pollock *et al.*, 2004).

Our model supposes that trait groups are subject to predation. If a predator appears, one and only one S in a group always becomes suicidal, thereby retarding the predator's net success. All others, both S-types and N-types, attempt escape. So S is a 'correlated strategy' (Rosenthal, 1974; Aumann, 1987; Cripps, 1991; Myerson, 1991; Pollock, 1994b, 1995, 1996; Pollock *et al.*, 2004): some external event, beyond the control of individual S's, determines which S becomes suicidal. Moreover, the actions of S's within groups are inversely correlated (e.g. Pollock and Rissing, 1995; Kukuk *et al.*, 1998; Rissing *et al.*, 1989), with the intra-group frequency of suicide often less than the intra-group frequency of S (in fact, always so when a group contains two or more S, because only one becomes suicidal). For example, S's might forage or otherwise display/ roam near the boundary of the group; the coordination event determining suicide would then be the (random) invasion path taken by a predator. The S closest to that path would be the one to hinder the predator by means of a suicidal attack.

Our model is abstract, and assumes that such a mechanism inversely correlating the phenotypic expression of S exists. Whatever the details of this mechanism, S's expose themselves to predation risk conspicuously, while N's do not. In addition, an S's self-exposure is real, reducing its chance of survival if it attacks.

At first we assume that an S not attacked has the same fitness as a group-mate N (risk is probability of attack, not realized attack); we relax this condition later. We also assume that realized suicides are always effective for group-mates; that is, if a predator encounters a suicide, the probability that other group members (both N and S) survive is ρ_S, whereas if there is no suicidal attack during predation, all members experience survival probability ρ_N, with $\rho_S > \rho_N$.

There are three ways to interpret ρ_X. A successful predator might destroy the whole group, with $(1 - \rho_X)$ the probability of group extinction. Alternatively, ρ_X might be each group member's independent probability of survival (*sans* suicide) – a predator might get all, none or anything in between. Lastly, $(1 - \rho_X)$ might be the exact proportion of members culled by the predator. In the latter two cases, predation need not be independent across group-mates. In particular, those nearest the predator would more likely fall victim concurrently. If such are disproportionately S-types, we would have to reinterpret terms a bit, but our qualitative conclusions would remain.

We assume that a predator (or group of predators) prefers capture of multiple prey when attacking a group. Thus the rest of the prey group would not be guaranteed escape during the predator's first attack. But an attack forced to occur on the periphery (periphery defined as entry point(s) of the predator(s)) by a suicide (who must be an S-type) provides others greater opportunity for escape; in effect, a suicide throws itself at the predator, slowing it down. An N on the periphery would not do this, but try to escape. In fact, and this will be important shortly, an N prefers to avoid the periphery in the first place, shielded within the relative safety of the group's interior, or at least reducing its distance from group-mates.

Our predator is an active selection agent. It 'knows' all about S's, and would prefer to avoid them. Such an active selective agent is essential to the model. More passive selection will support neither suicide nor weaker forms of strong altruism under random assortment.

Since groups are of size K, a predator attacking a group lacking S-types gets a pay-off (group members killed) of $K(1 - \rho_N)$. Groups with an S-type (remembering that exactly one S goes suicidal) yield $1 + (K - 1)(1 - \rho_S)$, the suicide for certain plus some group-mates. Predators prefer to avoid S-types only if

$$K(1 - \rho_N) > 1 + (K - 1)(1 - \rho_S)$$

or   (1)

$$K(\rho_S - \rho_N) > \rho_S.$$

If a predator cannot differentiate groups by number of S's, then we shall show shortly that S cannot persist under random assortment. But in our model, a predator may indeed have information about the presence of S, because S's inherently tend to occur on the periphery of groups. We shall see that such foreknowledge may allow S to persist in evolutionary time.

If a predator detects an S, it may go elsewhere. If the group has several such S's, it is more likely to detect one, increasing the probability that it goes elsewhere. But a predator must decide to attack some group sometime, so a group may be attacked even though a predator has detected an S.

To model predator choice across groups, we impose a bit more structure on the population. Not only are groups formed randomly, they are paired randomly against predators who must decide to attack only one of each pair. Group selection is zero sum within predator pairings; one group will be attacked, the other not. Alternatively, one group is attacked precisely because the other – paired – group is not. Standard trait group selection has each group contribute independently to the reproductive pool. Here, however, one group's full contribution to that pool is purchased through the reduced success of its pair (which is preyed upon). Such 'strong group selection' (e.g. Pollock and Rissing, 1995; *sensu* Wilson, 1990) will be essential.

A group with peripheral S's signals the presence of potential suicides. The more S's there are, the stronger the signal and the more likely the predator detects it. For simplicity, we assume a predator either detects a signal or not. It does not evaluate the strength of signals across paired groups. (Relative evaluation of signal quality would skew selection in favour of S, as predators would then preferentially avoid that group with more S. The detect/ non-detect dichotomy thus provides a conservative bias against finding cases in which S persists.) Choice is random if no signal is detected. When one group is silent (a group may be perceived silent while containing S's) and the other is not, the predator pounces on the silent group. If both groups emit a signal, the predator is indifferent, again choosing randomly, for it cannot then avoid the suicidal defence.

Since predation events are paired across groups in a zero-sum way, selection is directed to a proper subset of groups throughout the population – as already noted, a deviation from foundational trait group selection (Wilson, 1975, 1980) that is essential for our results. Such 'truncated (trait) group selection' (*sensu* D.S. Wilson, personal communication) intensifies selection locally based on group phenotypic differences. Groups with some lesser sampled attribute endure reduced fitness relative to other sampled groups (here, sampled in pairs). The former groups are truncated, either removed from the population or their contribution to the future reproductive pool is depressed, while the latter are untouched. Original trait group selection posits that all selection occurs after group dispersal, selection then measured as population relative fitness of morphs summed across all groups. In our model, however, groups without some (sampled) attribute are differentially eliminated or have their fitness reduced relative to those exhibiting the (sampled) attribute. In standard trait group selection, the absolute fitness of a group (however composed) is solely an intra-group affair; in truncated trait group selection, the absolute fitness of one group may differ depending on the attributes of other groups, mediated by predator avoidance of recognized peripheral S's. Wilson's (1975, 1977b, 1979, 1980) advocacy of group selection began, as was fitting, with the weakest form of group selection possible. Here we augment group selection in trait groups by employing what we believe to be a plausible mechanism – predators that are concerned with making their own living and need to evaluate prey susceptibility to do so.

Let i denote the number of S in a group and h_i be the probability that the predator detects the S signal in that group. Then, $h_i \geq h_j$ for $i > j$. $h_0 = 0$. If the paired groups have i, j potential suicidals respectively, the probability that the former group escapes attack when matched with the latter, $\alpha_{i,j}$, is

$$\alpha_{i,j} = (1 - h_i)(1 - h_j)/2 + h_i(1 - h_j) + (h_i h_j)/2. \tag{2}$$

We can now present simple emergence and stability conditions for S.

Emergence of S

Consider an individual S in a large population consisting almost entirely of N-type individuals. S almost always experiences a group where its $K - 1$ group-mates are all N, while its paired group contains only N. To persist, its expected fitness must be greater than that of the average N individual (Nunney, 1985; Pollock, 1988, 1994b, 1996). If the predator chooses the group with the S, that S must die. S has positive fitness only if both its groups avoid the predator. So its fitness is $\alpha_{1,0} = (1 - h_1)/2 + h_1 = (1 + h_1)/2$, since $h_0 = 0$ (equation 2). As the population is assumed large, to a first approximation average N experiences a group of all N, with its group similarly paired against another all N group. The predator is indifferent between two all N groups so a focal N in such a pairing enjoys an expected pay-off of $(1 + \rho_N)/2$.

Rare S may be thought of as a focal N mutating to S, with this S increasing in frequency if it does better than its pre-mutation state (e.g. Nunney, 1985; Pollock, 1988, 1994b, 1996). S is thus successful only if $(1 + h_1)/2 > (1 + \rho_N)/2$ or just $h_1 > \rho_N$. The latter inequality says that the probability of being detected must exceed the no-suicide probability of survival during an attack. *The greater the predation threat, the less conspicuous S need be*. If the predator is always indifferent to the S-signal, S will fail because its success then requires $\frac{1}{2} > (1 + \rho_N)/2$ or $0 > \rho_N$. The predator is therefore a mechanism of group selection. Individual selection on the predator determines group selection on its prey.

Predator sensitivity to *S*

How can the predator know that peripheral display by prey produces an obstacle worth avoiding? Before *S* evolves, what supports predator signal discrimination? We give two answers. The periphery may be unavoidable for some (Hamilton, 1971), with our predator subject to selection for discrimination independent of the existence of *S*. That is, the predator has already learned that stragglers should be avoided for maximal return. Rare *S* would then appear just to be another case of an unfortunate lot, with the predator primed for wariness. But *S* chooses the periphery rather than being forced there via intra-group competition (Hamilton, 1971; West Eberhard, 1978; Pollock, 1994b, 1996; Reeve, 2000); it actively engages the predator just prior to defeat. Such an *S* voluntarily assumes 'weakness' to discourage predators, so periphery display is weakly altruistic (Wilson, 1979), helping group-mates more than self, if predators sometimes detect the signal and avoid the group. Somewhat strangely, group competitive inferiors, if forced to the periphery, can transform themselves into weak altruists by becoming conspicuous failures (Pollock, 1996).

Alternatively, imagine two prey species linked by a common predator. One species may undergo regular kin assortment, supporting some sort of suicidal defence in the usual kin selective sense. The predator entrains on prey signalling, detecting potential suicides engendered by kin selection. Kin assortment need not be absolute, but might be mediated by distance (Mitteldorf and Wilson, 2000). The second species assorts randomly but – enduring the same predators – is thereby exposed to latent group selection, realized upon a mutation to *S*. Even more simply, a population originally under kin assortment might switch to random assortment and retain contingent suicide, assuming that the condition $h_1 > \rho_N$ (or something a bit weaker – see below) is met, ensuring at least polymorphism in *S* and *N*. Spatial proximity employing kin selection (Mitteldorf and Wilson, 2000) can become simple trait group selection (altered for spatial dispersal) if pedigree distance increases through dispersal and invasion. Alternatively, generalization away from kin selection might be no more than an extension of parental care. Consider bird mobbing. Parents will attack potential predators near their young. This aggressive display might be generalized to display irrespective of nestlings, providing benefit to a non-kin group. What we call 'periphery display' might already be employed in natural history, the predator thus familiar with its effect. Predator sensitivity to a previously evolved prey defence seems a reasonable pre-adaptation for our model. Finally, many predators are able to learn. Sensitivity to *S*-display in a long-lived, localized predator can then be instantaneous in evolutionary time.

Saturation of *S*

Suppose rare *N* appears in a population that is otherwise *S*. The average *S* experiences a world where predators are indifferent. If its group is attacked, it becomes suicidal with probability $1/K$. It escapes predation with probability ρ_S when one of its group-mates has become suicidal. Average *S*'s expected fitness is therefore

$$(1 + (\rho_S)(K - 1)/K)/2.$$

Rare *N*'s expected fitness is (from equation 2)

$$\alpha_{K-1, K} + (1 - \alpha_{K-1, K})\rho_S.$$

So N can persist when

$$\alpha_{K-1,\,K} + (1 - \alpha_{K-1,\,K})\rho_S > (1 + (\rho_S)(K-1)/K)/2$$

or (3)

$$2\,\alpha_{K-1,\,K} > 1 - \rho_S/(K(1-\rho_S)).$$

So S may resist invasion by N even when survival after realized suicide (ρ_S) approaches zero. Resistance succeeds so long as $K(\rho_S - \rho_N) > \rho_S$ is satisfied (equation 1). There is here a tension between group size, K, and these two conditions. Larger group size makes equation (3) less likely, but predator discrimination more likely (equation 1). Smaller group size makes S saturation more likely, while predator discrimination becomes less likely. The condition for S success, $h_1 > \rho_N$, may hold although saturation fails, and that combination ensures polymorphism in S and N. We thus expect S to succeed over a greater parameter space in larger groups but often only polymorphically so.

Recall that rare S survives only when avoiding predation, thereby refraining from suicide. Under true polymorphism, some S in a preyed group will not become suicidal as there is only one sacrificial S per group preyed upon. The condition $h_1 > \rho_N$ is thus overly stringent for sustained polymorphism once the initial hurdle is surpassed.

Polymorphism may predominate for an additional reason. Continual predator scanning involves a cost. So predators should be less willing to scan once S is near saturation. High-frequency S may then select for predator indifference, allowing N to persist when rare. Overall, polymorphism seems to be the most likely evolutionary outcome.

Suicide requiring kin selection

Our suicide model requires a coordination event (e.g. direction of predator attack) that differentiates S into two forms, and a mechanism (predator choice) that differentiates groups by probable frequency of S (revealed by pre-suicide periphery display), imposing a zero-sum outcome (predator choice) correlated inversely with this intra-group frequency. Prior models allow differential genotypic response under kin selection. Wilson (1977a) provides an excellent example of coordination under kin selection leading to contingent suicide in the trematode parasite *Dicrocoelium dendriticum* (Wickler, 1976). At one point in its life cycle, the parasite is ingested by ants. Up to 50 parasites are ingested at once; but only one ultimately goes suicidal to alter the behaviour of the ant, causing the host to 'spend large amounts of time fastened by its mandibles onto the tips of grass blades, a location that obviously facilitates being eaten by livestock [the next step of the parasite's life cycle]' (Wilson, 1977a).

Some degree of kin selection is needed to retain such suicide (Wilson, 1977a). For *D. dendriticum*, 'predators' are not feared, but welcomed. Moreover, in the *D. dendriticum* system, predators are passive; they do not make zero-sum choices between groups based on probable group genotypes (nor could they), they simply eat what they encounter. Changing the absolute probability of encounter (group extinction, not being eaten, measured by $[1 - \rho_N]$, $[1 - \rho_S]$) is not sufficient for our S to evolve; the predator must actively evaluate information provided by groups ($\alpha_{i,j}$; weakly altruistic signals provided by group (abstract) peripheral S's) to avoid (personally) unwanted outcomes. Because signalling potential suicide (for the parasite to attract predators exclusively) cannot be present in the parasite's natural history, kin selection is mandatory for the evolution of altruism.

There is no *a priori* reason to restrict inverse behavioural correlations (mechanisms detailing unique, divergent roles among group-mates) to kin (Kukuk *et al.*, 1998; Rissing *et al.*, 1989; Pollock, 1994b, 1995, 1996; Pollock *et al.*, 2004). Abandoning the notion that random assortment necessarily implies behavioural autonomy among individuals absent coercion (Aumann and Maschler, 1972; Rosenthal, 1974; Aumann, 1987; Pollock, 1994a), we find herein that the scope of altruism under strong, truncating trait group selection is considerably greater than heretofore considered possible. We have focused on reproductive suicide as the most stringent form of strong altruism; clearly, weaker sacrifice will fare better, and we expect, generally, these latter to be most likely revealed in nature. But empirical cases may be hard to detect when suicide or weaker forms are fundamentally contingent. Prior theory may also cloud recognition of such sacrifice among non-relatives [e.g. predator mobbing in birds (Caraco *et al.*, 1980; Rainey *et al.*, 2004)], labelling some altruism as aberrant, evolutionarily ephemeral or misinterpreted (e.g. Atran, 2003). Measures of strong, truncated trait group selection, mediated by predation, may reveal unexpected adaptation where aberrant failure now apparently resides.

Strategic suicide, not suicidal strategy

In our extreme model, S codes for two options, one actively suicidal, the other passively personally beneficial. Predators determine which is experienced, acting, from the perspective of a focal S individual, as a randomization mechanism yielding suicide or personal success. This randomization is not, however, identical to a standard randomized strategy (Aumann and Maschler, 1972; Maynard Smith, 1982; Pollock, 1994a), for the personally beneficial S outcome is possible only because the suicidal S outcome is regularly realized, entraining predators to avoid groups with 'louder' pre-suicidal commitment. Contrast a binary randomized strategy that codes for success in, say, wet versus dry years. In a wet year, randomizing to dry may cause personal death, but such death does not directly enhance the absolute fitness, present or future, of those happening to randomize to wet. 'Dry' does not suicidally aid 'wet' by being 'dry' in wet years. A standard randomized strategy may have some personally disastrous outcomes akin to suicide, but such outcomes are born solely because other outcomes are beneficial, not because the beneficial outcome requires the presence of failure in others. In a wet year, 'wet' does well whether 'dry' is present or not. Ostensible suicidal outcomes do not imply suicidal altruism; zero-sum coordination among outcomes via common strategy is key.

S, while not suicidal as a strategy, employs suicide to enhance its population-wide success. One might be tempted to say S risks suicide in the hope of the alternative passive gain. But one could equally say that S risks the passive gain in the hope of (predator randomized) suicide. Both outcomes are essential for S's stability, suicide feeding back onto passive gain, unlike the wet/dry year gamble. Here privileging personal gain confuses strategy survival with individual, contingent survival, masking the mechanism of selection (Pollock, 1988, 1994a; Pollock *et al.*, 2004). The 'selfish gene' is not the selfish individual. While a successful strategy must be selfish, encoding mechanisms that ensure its evolutionary persistence (Dawkins, 1982), these mechanisms may induce extreme sacrifice even without kin selection. And it is that extreme sacrifice that phenotypes actually experience (Aumann and Maschler, 1972; Pollock, 1994a). Strategy S is not suicidal; but this is immaterial to the S that experiences suicide.

ACKNOWLEDGEMENTS

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