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Genetic bandwagoning: natural selection for quality-dependent altruism

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ABSTRACT

Background: In separate literatures, biologists have marshalled theoretical and empirical support for theories that a variant (i.e. allele, epigenetic mark, or combination thereof) can be selected to (1) induce suicide by a moribund or otherwise stressed individual, (2) induce suicide by an individual with low productive or reproductive potential, (3) impose senescence upon a chronologically old individual, and (4) reduce the yield of an individual with low genetic heterozygosity. High stress, moribundity, low productive and reproductive potential, high chronological age, and low genetic heterozygosity all indicate an individual with low genetic quality – that is, comparatively few advantageous genetic variants for acquiring prey, territory, or mates, or surviving predators and parasites. Therefore, an unappreciated commonality between these theories is that a variant can be selected that actually reduces the fitness of an individual of low genetic quality.

Bandwagoning: The fitness losses induced by the variant in low-quality individuals allow fitness gains for nearby individuals, some of which hold a copy of the variant. The heritable elements (alleles, epigenetic marks, etc.) within a single individual which can lead to such losses are collectively termed a 'bandwagoning variant' because the variant gains frequency by hitchhiking along with ('jumping on the bandwagon' of) higher-quality individuals (and their lineages) that have copies of it.

Questions: What parameter values (e.g. population size, relatedness, heritability of reproductive success) might allow natural selection for genetic bandwagoning?

Features of the model: The model is an individual-based Moran process. Each individual's quality value is randomly chosen at birth from a normal distribution that has a mean equal to the quality value of its parent.

Ranges of parameters: N (the total number of individuals in the population) varied from 50 to 500. Assortment ('relatedness') in the population varied from 0.05 to 0.15. Recorded values for the heritability of reproductive success varied from 0.024 to 0.132.

Conclusions: A variant can be selected to respond to various indications that the individual holding it has low genetic quality by inducing that individual to further reduce its fitness by forfeiting some or all of the resources (e.g. food, territory, mates) it could otherwise have used. Natural selection for genetic bandwagoning can occur even when values for N, relatedness, and heritability of reproductive success are low enough to be in line with reported values for humans and other species. Therefore, genetic bandwagoning theory might explain why indications of an organism's low genetic quality induce behaviour by that organism, or biological processes within it, that reduce that organism's fitness.

Keywords: programmed ageing, heterosis, depression, Hankshaw effect, evolution of cooperation, acceleration of adaptive evolution.

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INTRODUCTION

In various literatures, biologists have argued that natural selection has shaped a conditional tendency to forfeit resources (e.g. food, territory, mating opportunities) so that they can be utilized by any nearby individuals. The individuals that utilize them are unaware that the resources were even relinquished; therefore, such forfeitures are not explained by direct or indirect reciprocity (Nowak, 2012). In all these theories, the individual that forfeits has a lower genetic quality[1] than its neighbours. However, biologists advancing these theories have seldom explicitly stated a condition of low genetic quality.

For example, many biologists have hypothesized that if an individual is moribund due to a parasite infection or some other malady, it might commit suicide, thereby relinquishing the individual's resources to nearby individuals, whether the individuals benefitting are kin (e.g. Dawkins, 1976) or not (Refardt *et al.*, 2013). Additionally, some biologists have argued that programmed cell death occurs in unicellular organisms such as *Escherichia coli*, *Caenorhabditis elegans*, amoebas, and yeasts on the condition that the cell is stressed, even if the stress itself does not suggest imminent death (Skulachev, 1999, 2001, 2002; Thompson and Kay, 2000; Hazan *et al.*, 2004; Herker *et al.*, 2004; Pestov *et al.*, 2011). Individuals that have less advantageous heritable traits than their neighbours are more likely to be moribund and to incur various other stressors.

Furthermore, for de Catanzaro (1981, 1984), depression and its associated suicidal thoughts occur in individuals with low reproductive and productive potential in order to leave resources to more productive kin. He argued that 'the death of individuals with seriously impaired reproductive and productive potential might actually benefit their inclusive fitness by conserving resources for kin not experiencing such impediments' (1984, p. 77). Low reproductive and productive potential can have a genetic basis, in which case the depression would be incurred by low-quality individuals.

Others have argued that natural selection can result in a tendency for an individual to forfeit resources even if the forfeiting individual is not moribund or closely related to neighbouring individuals. For example, recent years have seen a resurgence of Weismann's (1889) theory that natural selection has occurred for senescence in conjunction with chronological age, i.e. programmed ageing (Mitteldorf, 2004, 2006; Longo *et al.*, 2005; Goldsmith, 2008, 2014; Pepper *et al.*, 2013; Skulachev and Skulachev, 2014; Mitteldorf and Sagan, 2016). Some authors hold that programmed ageing occurs because aged individuals can be expected, due to their chronological age, to be of low genetic quality (Skulachev, 1997; Goldsmith, 2004; Travis, 2004; Martins, 2011; Yang, 2013).

Additionally, Semel *et al.* (2006) noted that, in populations of tomato, rice, and maize, overdominance occurs primarily in reproductive traits. They argued that this constitutes evidence for natural selection for heterosis itself – that is, natural selection in favour of the association between hybrids and higher fitness – in order to promote heterozygosity in populations in a manner analogous to a plant's self-incompatibility system. This implies that natural selection has favoured the association between outbred individuals and yield improvements because heterozygous individuals are of higher genetic quality.

Here, I introduce the term 'genetic bandwagoning'[2] to refer to cases in which an individual forfeits some or all of its resources (e.g. food, territory, mates) on the condition that the individual's quality is sufficiently low compared with that of its neighbours. The heritable elements (e.g. alleles, epigenetic marks) within a single individual that are responsible for genetic bandwagoning are to be collectively considered a bandwagoning variant. A bandwagoning variant would not 'know' which neighbours hold a copy of the same variant, so some of the resources forfeited in bandwagoning would be used by individuals that do not have a copy. However, even if neighbours that hold a copy of the variant use only a fraction of the forfeited resources, they can gain more descendants by doing so than the forfeiting individual could have by using all of the resources. The reason is that genetic quality is, by definition, heritable.[3] Therefore, descendants of the higher-quality individuals are likely to be better at surviving and reproducing than the descendants of the forfeiting individual.

Bandwagoning is an example of the Hankshaw effect – by which 'a property of an allele increases its likelihood of hitchhiking' (Hammarlund *et al.*, 2016, p. 1376) – because when copies of a bandwagoning variant induce low-quality individuals to forfeit resources, higher-quality individuals gain resources, which facilitates hitchhiking by copies of the variant held by the higher-quality individuals. Moreover, the hitchhiking capacity of a bandwagoning variant is less likely to be reduced by sex and recombination than some other forms of hitchhiking, since the bandwagoning variant hitchhikes with not just one allele but a multiplicity of alleles and epigenetic marks responsible for an individual's higher quality. Consequently, after sex and recombination, the bandwagoning variant is likely to continue to be located with half of the alleles to which the individual's high quality was originally attributable. And the parent that contributes the other half of the alleles is also likely to be high-quality due to assortative mating by quality that may result from sexual selection by both sexes (Bos *et al.*, 2009; Griggio and Hoi, 2010; Holveck and Riebel, 2010; Holveck *et al.*, 2011; Dakin and Montgomerie, 2014; Veen and Otto, 2015; Schultzhaus *et al.*, 2017).

A MODEL

Consider that a low-quality individual would produce C_1 offspring if it does not relinquish resources. But if it relinquishes resources, they are used by n recipients; the i^{th} recipient gains B_{i1} offspring and is related to the low-quality individual by r_i. A strategy of relinquishing resources on the condition of an individual's low quality is quality-dependent altruism (i.e. bandwagoning). In terms of Hamilton's (1964) rule, natural selection can increase the frequency of bandwagoning after one generation if:

$$C_1 < \sum_{i=1}^{n} r_i B_{i1} \tag{1}$$

Inequality (1) is consistent with most analyses of the evolution of social behaviour, which have examined the costs and benefits that result from a behavioural act solely in the first generation following the act (Hunt *et al.*, 2004). However, Inequality (1) underestimates the likelihood that bandwagoning evolves. On average, higher-quality individuals produce more offspring. But also, since genetic quality is heritable (by definition), these offspring themselves are likely to be, on average, of higher quality. Thus, the offspring of the low-quality individual and their descendants may also be, on average, low-quality themselves compared with the offspring of the recipients and their descendants.

In sum, natural selection can increase the frequency of bandwagoning by generation v if:

$$\prod_{t=1}^{v} C_t < \sum_{i=1}^{n} r_i \prod_{t=1}^{v} B_{it} \tag{2}$$

where C_t is the average quantity of offspring produced by the descendants of the low quality individual during generation t, and B_{it} is the average quantity of offspring produced during the same generation, t, by the descendants of the i^{th} recipient.

Bandwagoning can evolve by natural selection in the same way that a person who pays an expert investor to invest his capital can make more money overall over a number of years than if he invests his own capital – even if he has to pay the investor a high percentage of his capital up front – because the expert investor earns a higher rate of return on capital. The evolution of bandwagoning occurs because of the higher fitness per descendant of the higher-quality individuals, just as the investment is successful because of the higher percentage per year earned by the expert investor.

To create a model for simulation, I used a Moran (1958) process. Moran processes are simple and quite commonly used in evolutionary theory (Lieberman *et al.*, 2005; Nowak, 2006a; Proulx, 2011; Shakarian *et al.*, 2012). The Moran model's fundamental characteristic is that during each time-step, one individual in the population is randomly chosen to produce a single offspring and one individual is randomly chosen to die. Therefore, the number of individuals in the population remains a constant N from one time-step to another.

Each individual, i, in the population is characterized by a number, denoted Q_i, that represents that individual's quality. In the initial time-step, the quality value, Q_i, of each of the N individuals in the population is randomly generated from a normal distribution with a mean equal to 10 and a standard deviation of $Q_{\acute{o}}$. (The random generation of quality values for individuals born after the first time-step is described below.)

There are two types of individuals in the population: cooperators and defectors. Cooperators are of the type that bandwagons. A cooperator relinquishes its opportunity to reproduce in a time-step if its quality is below the P percentile of all individuals (regardless of type) in the population. Defectors are individuals that do not bandwagon.

Other individuals benefit from fitness forfeited by low-quality cooperators

An individual, i, in the population (whether the individual is a cooperator or defector) has fitness equal to that individual's quality, Q_i, plus its share of fitness forfeited by cooperators with quality below the P percentile. (A cooperator with quality below the P percentile has fitness of zero irrespective of its quality; its forfeited fitness is defined to be equal to its quality.)

A higher share of the forfeited fitness goes to other cooperators due to the assumption of positive assortment. Additionally, other individuals in the population gain a share of forfeited fitness in proportion to their quality. (Precise calculations of fitness are given in Appendix A1: evolutionary-ecology.com/data/3186Appendix.pdf.)

Birth and death

In each time-step, one individual in the population is randomly chosen for reproduction and one individual in the population is randomly chosen to die. (The same individual may be chosen for both reproduction and death.) The probability of being chosen for reproduction is proportional to fitness. The individual chosen to die is determined by randomly choosing $N - 1$ individuals for survival. The individual not chosen for survival is the one that perishes. The probability of being chosen for survival is proportional to quality.

Once an individual is chosen for reproduction, an offspring of the same type is born; it replaces the individual chosen to die. The quality value of its offspring is randomly selected from a normal distribution with a mean equal to its parent's quality and a standard deviation $Q_{\acute{o}}$ (the same standard deviation of the normal distribution used to generate the quality values of the N individuals at the beginning of the simulation). This random generation of an offspring's quality models the effect of germline mutation because the quality values for offspring vary randomly about their parent's value. Since an offspring's quality value is drawn randomly from a normal distribution centred at its parent's value, it can potentially be either lower than, equal to, or higher than that of its parent's value, which would represent, respectively, a negative, neutral (Kimura, 1968), or positive (Waite and Shou, 2012) net influence of mutations upon quality. Quality is, therefore, partly but not completely heritable.

After the birth of one individual and the death of one individual, the quality value of each individual in the population is multiplied by a normalizing factor,[4] $10N/Q_T$, where Q_T is the sum of the quality values of all the individuals in the population.

A simulation run continues for T time-steps or until one type has gained fixation. The next section reports the results based on 10,000 replicate simulation runs for each set of variable values.

RESULTS

I show the results graphically in Figs. 1, 2, and 3. A pattern common to these figures is the drop, on average, of cooperator quantity early in runs, as the bandwagoning variant essentially sacrifices the quantity of individuals for their quality. This occurs as low-quality cooperators forfeit reproduction, which enhances the fitness of other individuals in the population. The fitness gained by other cooperators from this forfeited reproduction is less than the fitness lost from it by low-quality cooperators – partly because defectors also gain fitness from the forfeited reproduction, and partly because the factor, Y, is less than unity, so that not all forfeited fitness is recovered by other individuals. Therefore, the number of cooperators is likely to be lower in the following time-step. However, since assortment is positive, it is likely that each higher-quality cooperator gains more fitness from the forfeited reproduction than does each defector with similarly high quality. Therefore, the likelihood that a cooperator produces a high-quality offspring increases compared with the likelihood that a defector produces a high-quality offspring. A higher number of high-quality offspring for cooperators leads to increases in the number of cooperators later in simulation runs because high-quality individuals tend to have more descendants. We also observe these increases in Figs. 1, 2, and 3.

With variables equal to baseline values (Table 1), the average number of cooperators grows beyond 100, the starting number, later in runs (Fig. 1A). This result was relatively robust to changes in the quality percentile cut-off for reproduction. As Figs. 1B and 1C show, when cooperators reproduced only if their quality percentile was, respectively, at least 5 and at least 15, the average number of cooperators exceeded 100 later in runs. In all three cases, the increase above 100 later in runs was significant. This demonstrates that the success of a

Table 1. Baseline parameter values

Symbol	Description	Value
N	total number in population	200
N_{C}	starting number of the cooperator type	100
N_{D}	starting number of the defector type	100
$Q_{\acute{o}}$	standard deviation of the normal distribution from which an individual's quality is generated	1
Y	fraction of fitness lost that is used by other individuals in the population	0.8
r	the assortment ('relatedness') in the population	0.15
P	quality percentile cut-off for reproduction	10
T	number of time-steps in each run	5000

Note: Some of the model's baseline values are discussed in Appendix A2 and some simplifications included in the model are discussed in Appendix A3.

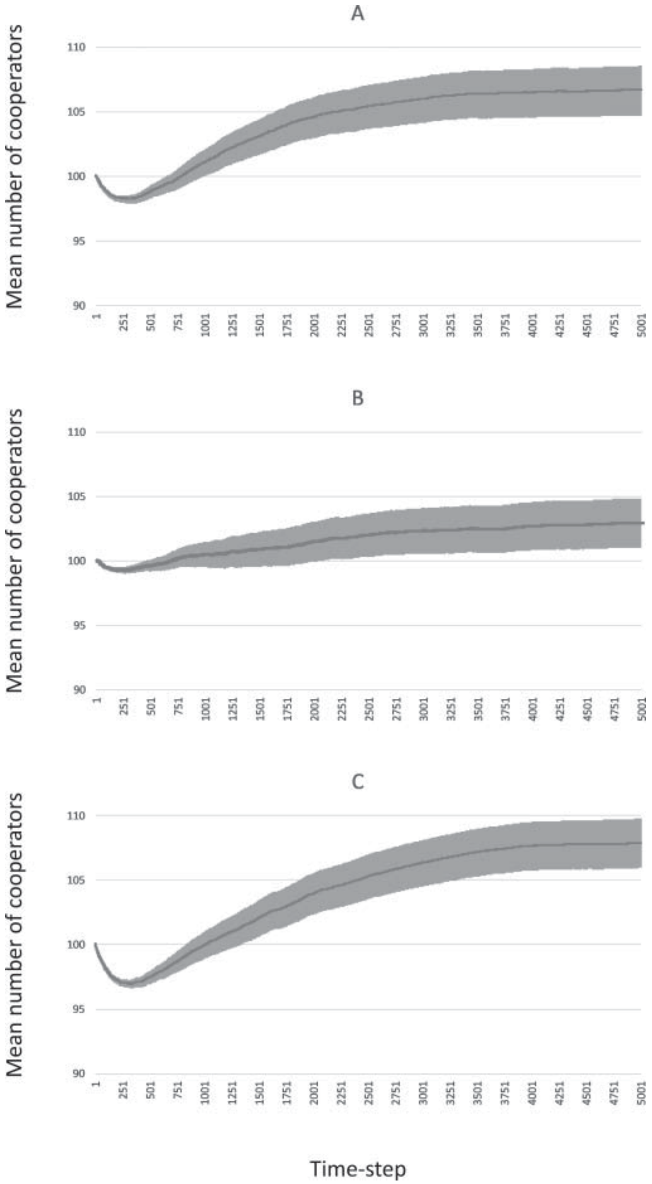


Fig. 1. The dark line indicates the average number of cooperators during 10,000 replicate runs. Shaded regions indicate 95% confidence intervals. When defectors gained fixation during a run, the number of cooperators was tallied as zero for each time-step thereafter in that run. When cooperators gained fixation during a run, the number of cooperators was tallied as N for each time-step thereafter in that run. Heritability (h^2) values for reproductive success (RS) were calculated using the values recorded as the program ran. The reported h^2 RS values are the per-run values averaged across 10,000 runs. In (A), all values were set equal to the baseline values in Table 1. h^2 RS = 0.086. In (B), all values were set equal to baseline values except $P = 5$. h^2 RS = 0.085. In (C), all values were set equal to baseline values except $P = 15$. h^2 RS = 0.087. In all three cases, the average number of cooperators was significantly greater than the initial number of cooperators (100) by the 5000th time-step.

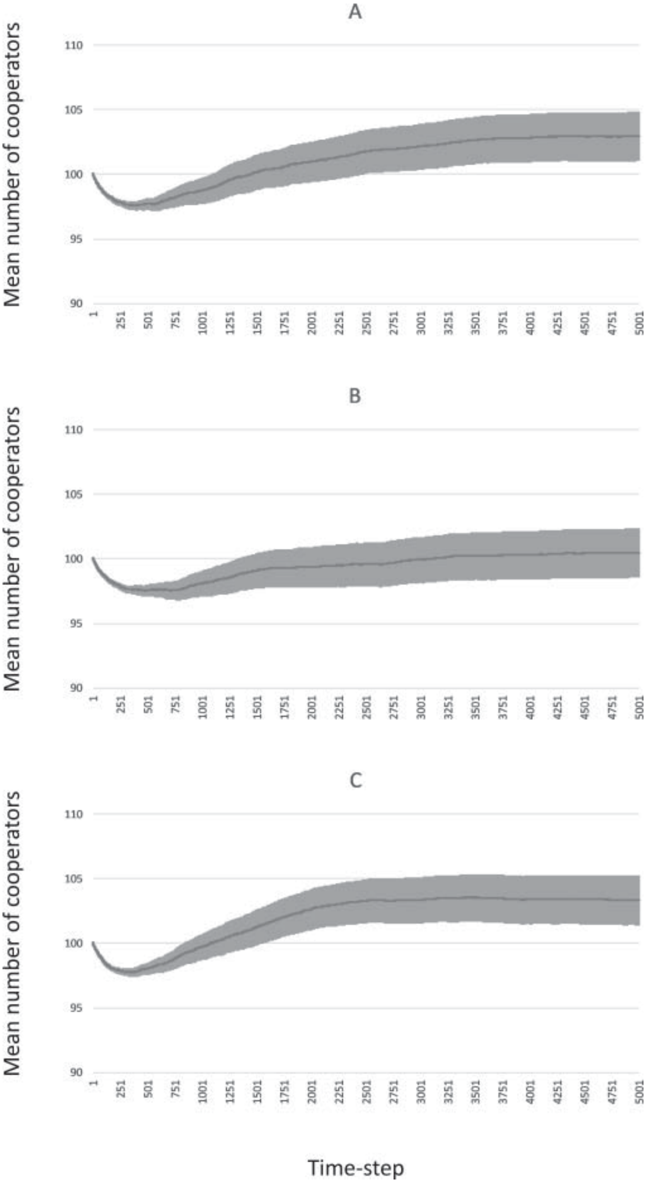


Fig. 2. As in Fig. 1, the dark line indicates the average number of cooperators during 10,000 replicate runs, and shaded regions indicate 95% confidence intervals. Calculation of averages, confidence intervals, and heritability values as for Fig. 1. Also, as in Fig. 1, heritability (h^2) values for reproductive success (RS) were calculated using the values recorded as the program ran, and the h^2 RS values reported are the per-run values averaged across 10,000 runs. In (A), all values were set equal to baseline values except for $r = 0.1$, and the average number of cooperators was significantly greater than the initial number of cooperators (100) by the 5000th time-step. h^2 RS = 0.085. In (B), all values were set equal to baseline values except $r = 0.05$, and the average number of cooperators was greater than the initial number of cooperators (100) by the 5000th time-step but the difference was not significant. h^2 RS = 0.086. In (C), all values were set equal to baseline values except for $Y = 0.5$, and the average number of cooperators was significantly greater than the initial number of cooperators (100) by the 5000th time-step. h^2 RS = 0.086.

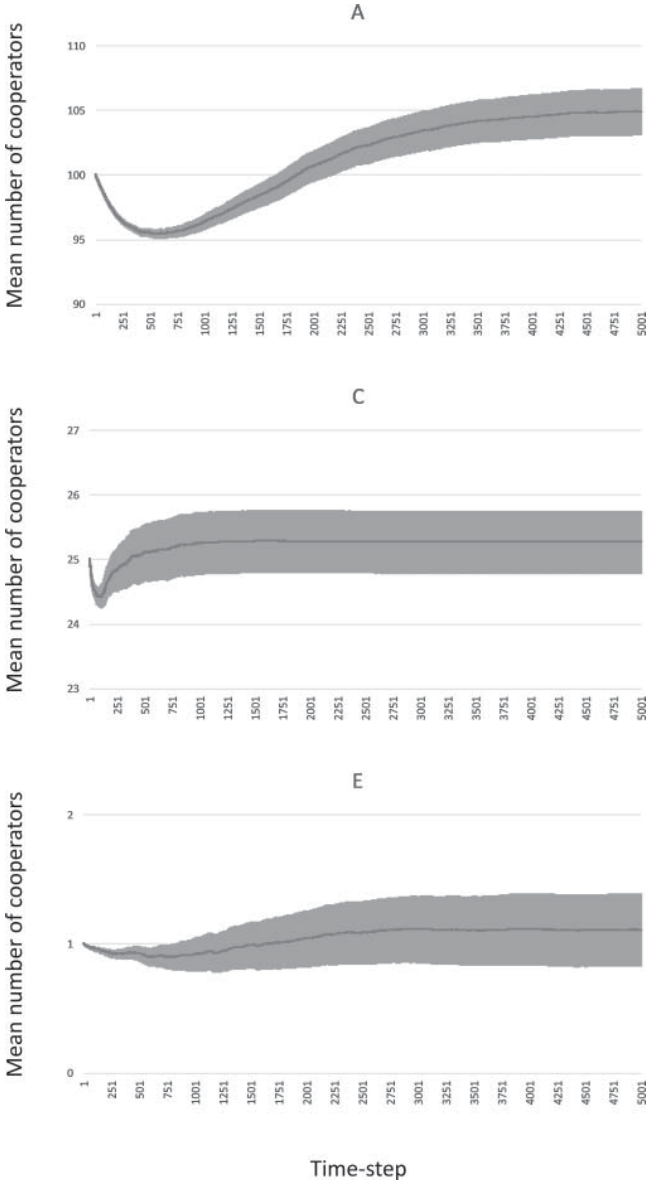
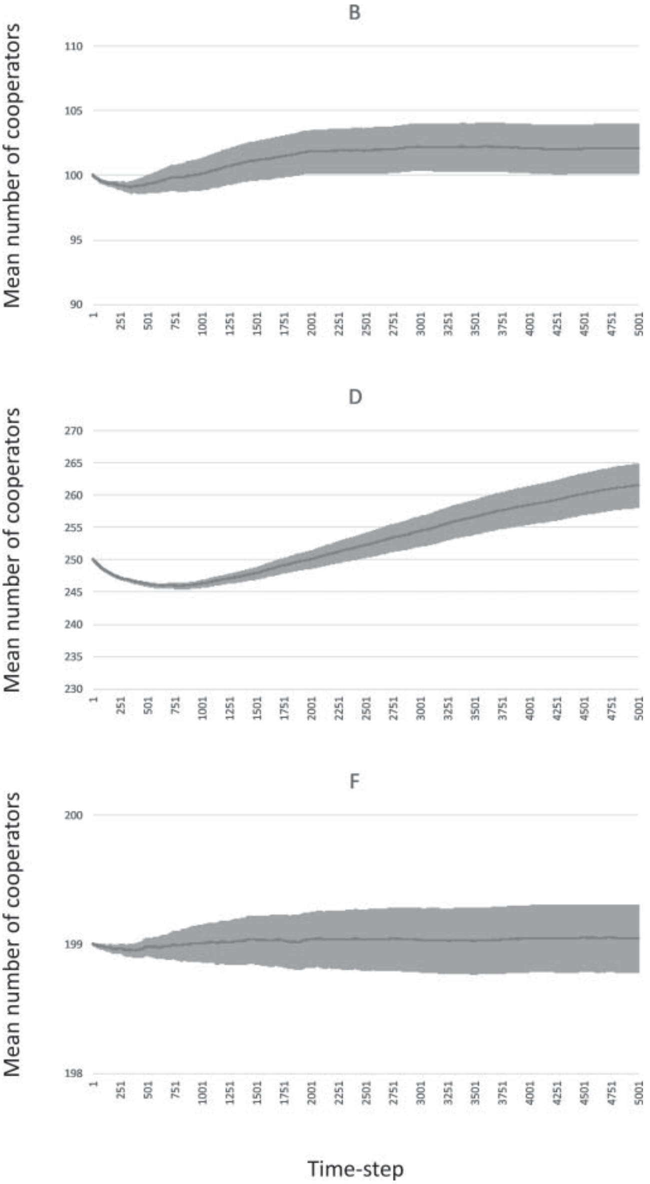


Fig. 3. In each of the six graphs, the dark line indicates the average number of cooperators during 10,000 replicate runs, and shaded regions indicate 95% confidence intervals. All statistics are calculated as in Fig. 1. In (A), all values were set equal to baseline values except $Q_{\acute{o}} = 0.3$, and the average number of cooperators was significantly greater than the initial number of cooperators (100) by the 5000th time-step. h^2 RS = 0.032. In (B), all values were set equal to baseline values except $Q_{\acute{o}} = 3$, and the average number of cooperators was significantly greater than the initial number of cooperators (100) by the 5000th time-step. h^2 RS = 0.132. In (C), all values were set equal to baseline values except $N_C = N_D = 25$, and the average number of cooperators was greater than the initial number of cooperators (25) by the 5000th time-step, but the difference was not significant. h^2 RS = 0.053. In (D), all values were set equal to baseline



values except $N_C = N_D = 250$, and the average number of cooperators was significantly greater than the initial value (250) by the 5000_{th} time-step. h^2 RS = 0.099. In (E), $N_C = 1$, $N_D = 199$ and all other values were set equal to baseline values. The average number of cooperators was less than the initial number (1) by the 5000th time-step, but the difference was not significant. h^2 RS = 0.024. The cooperator type attained fixation in 47 of 10,000 runs. In (F), $N_D = 1$, $N_C = 199$ and all other values were set equal to baseline values. The average number of cooperators was greater than the initial number (199) by the 5000th time-step, but the difference was not significant. h^2 RS = 0.026. The defector type attained fixation in 41 of 10,000 runs.

bandwagoning strategy does not require an individual to identify with absolute precision whether its quality is below a particular percentile.

Figures 2A to 2C show results when one variable's value was changed to be less favourable to cooperators while all other variables were set equal to baseline values. With $r = 0.1$ (Fig. 2A) or $Y = 0.5$ (Fig. 2C), the average number of cooperators significantly exceeded 100 later in runs. When $r = 0.05$ (Fig. 2B), the average number of cooperators later in runs exceeded 100, but the margin was not significant.

To generate Figs. 3A and 3B, I changed the standard deviation of the normal distributions from which offspring quality values were generated. I increased it to obtain Fig. 3A and decreased it to obtain Fig. 3B. All other variable values were set equal to baseline. In both Figs. 3A and 3B, the average number of cooperators significantly exceeded 100 later in runs.

To generate Figs. 3C and 3D, I changed the total number of individuals in the population. All other variable values were set equal to baseline. In Fig. 3C, the average number of cooperators exceeded 25 (the initial number) later in runs, but not significantly. In Fig. 3D, the average number of cooperators significantly exceeded 250 (the initial number) later in runs. A higher total number of individuals probably tended to benefit cooperators because a higher total number of individuals made it less likely that defectors reached fixation when the percentage of cooperators dipped early in runs and that enabled the percentage of cooperators to recover later in runs.

The results demonstrate that the cooperator type can invade the defector type. In Fig. 3E, the initial number of cooperators equalled 1, the initial number of defectors equalled 199, and the other variable values were set to baseline values. The cooperator type gained fixation in 47 of 10,000 runs. In Fig. 3F, the initial number of cooperators equalled 199, the number of defectors equalled 1, and the other variable values were set to baseline values. The defector type attained fixation in 41 of 10,000 runs.

DISCUSSION

My model shows that bandwagoning can evolve when parameter values are on a par with those that have been documented for a number of species, including humans (see Appendix A2). The results demonstrate that to succeed, a bandwagoning strategy does not require an individual to identify with absolute precision whether its quality is below a particular percentile. Additionally, the success of bandwagoning was not materially influenced by whether the standard deviation of the normal distribution from which each individual's quality was generated was relatively high or low. That insensitivity demonstrates that bandwagoning can evolve whether an offspring inherits many or few mutations that raise or decrease its quality. Each offspring's quality was drawn randomly from a normal distribution with a mean equal to the quality value of the offspring's parent. In other words, mutations exerting a positive influence upon quality were simulated to be as likely as those exerting a negative influence upon quality; but this simplification did not significantly influence results (I. Solon, unpublished findings). Some of the model's simplifications and their influences on the results are discussed in Appendix A3.

The evaluation of an organism's quality

The assumption that a variant can make a useful approximation of an organism's quality pervades evolutionary theory. For example, both the 'sexy son' (Fisher, 1930; Weatherhead and Robertson, 1981; Andersson, 1994) and 'good genes' (Andersson, 1982, 1994; Iwasa and Pomiankowski, 1994; Moller and Alatalo, 1999; Byers and Waits,

2006) hypotheses of sexual selection involve an assessment by the female about the reproductive value of a male's offspring (Kokko *et al.*, 2002). Furthermore, parents in many species are believed to identify which of their offspring have the best genes and allocate more resources to them (Burley, 1986; Sheldon, 2000; Harris and Uller, 2009). Moreover, parents are theorized to kill low-quality and/or less attractive offspring by practising filial cannibalism (Klug and Bonsall, 2007) and, more generally, parental selection (Harris, 2006).

In the above contexts, the organism whose quality is assessed and the organism making the assessment have competing interests, due to sexual conflict (Williams, 1966; Parker, 1979) and/or parent–offspring conflict (Trivers, 1974). However, prevailing theory holds that such assessments can be made accurately, primarily on the basis of honest signals of quality (Andersson, 1994; Nowicki *et al.*, 1998; von Schantz *et al.*, 1999; Duffield *et al.*, 2017), even though a misalignment of the interests of signaller and receiver encourages signalling dishonesty (Maynard Smith, 1991; Hurd and Enquist, 2005; Searcy and Nowicki, 2005; Szamado, 2011). By contrast, a variant's bandwagoning is compatible with the interests of the variants at other loci of the same individual. The variable values that determine whether a bandwagoning variant can gain frequency by natural selection (Inequality 2) are the same as those that apply to determining whether a variant at another locus within the same individual gains frequency through the bandwagoning done by the bandwagoning variant, even if that other variant does no bandwagoning. In other words, consider that a copy of a bandwagoning variant is located within an individual that also holds a copy of a variant responsible for blood type (for example). The likelihood that a neighbour holds a copy of the bandwagoning variant is, in theory, the same as the likelihood that a neighbour holds a copy of the blood-type variant. If a lower-quality individual with copies of both the bandwagoning variant and the blood-type variant forfeits resources and the bandwagoning variant gains frequency because copies hitchhike on neighbouring, higher quality individuals that use some of the forfeited resources, the blood-type variant also figures to gain frequency by hitchhiking – even though the blood-type variant does no bandwagoning itself. This suggests that information (e.g. hormonal, physiological) received by the variant about its holder's quality is at least as reliable as information about an organism's quality that is received through honest signals of quality by potential mates or parents of that organism. Yet bandwagoning theory does not require a variant, when evaluating the quality of the individual in which it is located, to have any particular foresight or to make an evaluation with any more precision than established theory assumes individuals have when they evaluate another individual's quality.

Indeed, established theory holds that organisms can approximately evaluate the fitness they would obtain for the purpose of practising fitness-dependent sex (Hadany and Beker, 2003; Hadany and Otto, 2007; Ram and Hadany, 2016). Empirical support has come so far from studies of microbes, fungi, and plants, but the theory is thought to be applicable to other species (Ram and Hadany, 2016).

Information that allows an individual to estimate its own quality might come from a variety of sources. For example, other individuals rely upon honest signals to assess an individual's quality and these signals indicate quality because they are diminished when organisms experience various stressors, such as hunger, infection, thermal or psychosocial stressors (Andersson, 1994; Nowicki *et al.*, 1998; von Schantz *et al.*, 1999; Duffield *et al.*, 2017). A bandwagoning variant could conceivably use biochemical, endocrinological, and physiological indications of the same stressors (Pickering and Pottinger, 1995; Sapolsky, 2001; Schneiderman *et al.*, 2005) as well. Additionally, established theory holds that an organism is aware of its position in a dominance hierarchy and that this position is partly determined by the organism's quality (Hsu *et al.*, 2006; Georgiev *et al.*, 2015).

Other phenomena noted above – mate choice, differential allocation, and parental selection – are also potential indicators to an organism of that organism's quality. Indeed, when parents and prospective mates give an organism more or less resources or attention, they wind up communicating information to that organism about how its quality compares with conspecifics. Additionally, in some phenomena offered as examples of bandwagoning (in the Introduction), a variant uses an organism's older age or low genetic heterozygosity to indicate that the organism is of lower quality.

An individual is less likely to commit suicide if its quality and lineage-fitness outlook are likely to change

As the foregoing suggests, a variant's evaluation of the quality and lineage-fitness outlook of the individual in which it is located develops continuously as more and more information becomes available in the form of, for example, competitive bouts, different types of stressors, and interest from potential mates. Such an evaluation is subject to change as new information becomes available.

Whether a bandwagoning variant might evolve to induce an individual with a low lineage-fitness outlook to relinquish some or all of the individual's resources ought to depend upon how likely it is that the individual's lineage-fitness outlook will change. For example, other individuals that are of higher quality might wind up perishing due to luck. Or the individual's quality might change because a natural enemy evolves so that the individual becomes less susceptible to the natural enemy compared with conspecifics. Or the individual's offspring might be born with a favourable mutation while the offspring of conspecifics are not as lucky. If the individual's lineage-fitness outlook is unlikely to change, it is more likely that a bandwagoning variant would induce the individual to forfeit all of the resources it might have obtained (i.e. induce that individual to commit suicide). If the individual's low lineage-fitness outlook is more likely to change, then it is more likely that the variant would induce that individual to forfeit only some resources so that the individual can remain alive in case its fitness outlook improves. This partial forfeiture of resources could involve resource forfeitures over multiple time-steps, each contingent upon the holder's continued low lineage-fitness outlook. However, for simplicity, the decision to induce relinquishment of resources (or not) occurs only once in the model.

CONCLUSION

The thesis of this paper is that blind altruism (that is, altruism done anonymously and without preference to related individuals) can evolve by natural selection, provided that the altruistic individual is of low quality. A variant (allele, epigenetic mark, or some combination thereof) responsible for this altruism is, herein, called a bandwagoning variant. The altruism would temporarily reduce the number of individuals with the variant. But if assortment is sufficiently positive, the altruism should lead to more offspring being produced by the higher-quality individuals with a bandwagoning variant than offspring produced by higher-quality individuals that do not have a bandwagoning variant. This change, in turn, increases the likelihood that the highest-quality offspring in the population have the bandwagoning variant, which increases the likelihood that the bandwagoning variant will attain fixation. It boils down to a short-term sacrifice of the quantity of bandwagoning-variant holders in return for a higher quality of bandwagoning-variant holders. This higher quality leads to advances in the number of bandwagoning-variant holders in future generations.

The model is based upon assumptions that are generally supported by prevailing evolutionary theory. Also, the model is somewhat conservative – that is, some of the model's simplifications are unfavourable to bandwagoning. (Some simplifications are discussed in Appendix A3.) The results demonstrate that bandwagoning can evolve when parameter values are in line with those found in the natural populations of some species (see Appendix A2 about how baseline variable values were chosen).

Furthermore, in the Introduction I document that a number of scholars have advanced support for theories involving altruism that is done anonymously and that is not directed to kin. They hold that altruism can still evolve by natural selection on the condition that the altruist is characterized by high stress, high chronological age, low reproductive or productive potential, or low heterozygosity. The (heretofore) underappreciated link between these literatures is that these characteristics are all indications of low quality. Thus, the theoretical and empirical support these scholars have garnered for their theories adds credibility to the notion that in populations of numerous species, parameters are suitable for the evolution of bandwagoning.

Several theories reviewed in the Introduction can even be re-interpreted as special cases of bandwagoning theory: the theory of heterosis and the theories holding that programmed ageing evolved because aged individuals can be expected to be of low genetic quality. Evidence that bandwagoning can evolve by natural selection in the specific forms of programmed ageing and heterosis lends credibility to the theory that bandwagoning in whatever form can evolve by natural selection.

Support for the theories of stress-induced suicide and depression reviewed in the Introduction is also consistent with bandwagoning theory, but these do not constitute special cases of bandwagoning theory because their authors have not suggested that they are induced by low genetic quality. In a departure from de Catanzaro's theory of depression (see Introduction), bandwagoning theory does not require that relinquished resources go to kin. That allows a response to a classic rejoinder to de Catanzaro's theory of depression: 'Why wouldn't a burdensome individual simply leave their kin' instead of committing suicide? (Syme *et al.*, 2016, p. 189). The answer is that even if relatedness between the relinquishing individual and those benefitting is equal to (or lower than) the relatedness among human populations estimated by Harpending (2002), the results demonstrate that bandwagoning can still evolve. Therefore, even if a person with low quality were to venture away from his or her family to a different location in the same population, that individual's forfeiture of resources at that location can still increase the frequency of the bandwagoning variant.

Additionally, these examples serve to show that the indications of an organism's low quality and the ways in which a low-quality organism can be altruistic can take a variety of forms. For instance, low quality can be indicated by high age, low heterozygosity, high stress, or other factors. The altruism may involve suicide or not. As discussed above, if the lineage-fitness outlook of a low-quality individual with a bandwagoning variant is more likely to change, that individual is less likely to commit suicide and more likely to relinquish some resources while also remaining alive in case its lineage-fitness outlook changes.

In this manner, a range of paradoxical empirical phenomena can potentially be explained with bandwagoning theory. These phenomena would share the characteristic that an indication of an organism's low quality induces behaviour by, or biological processes within, that organism which appear to reduce its fitness.

Bandwagoning as a source of the evolution of cooperation

The evolution of cooperation is a perennial question (Hamilton, 1964; Trivers, 1971; Nowak, 2006b, 2012; West *et al.*, 2007, 2011). Cooperation has been defined as 'a behaviour which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient' (West *et al.*, 2007, p. 419). The resource forfeitures by low-quality individuals that result from bandwagoning constitute cooperation that affords indirect genetic benefits (West *et al.*, 2007, 2011) to the forfeiting individual. In comprehensive reviews of the evolution of cooperation, authors have offered kin discrimination, green-beard discrimination, group selection, limited dispersal, and spatial selection as ways by which cooperation for indirect benefits can evolve (Nowak, 2006b, 2012; West *et al.*, 2007, 2011). These are all ways of referring to a state in which cooperation evolves primarily via high relatedness between the cooperating and benefitting individuals. Altruism due to genetic bandwagoning is distinct from these explanations because cooperation that results from bandwagoning can evolve even if relatedness is low because a higher-quality individual can expect considerably higher lineage fitness from the use of a resource than a lower-quality individual can from the same resource. (For example, a higher-quality individual and a lower-quality individual might each use resources to produce 10 offspring, but from these offspring the higher-quality individual might accrue 15 surviving grandoffspring, whereas the lower-quality individual might have only two grandoffspring that survive to reproductive age.)

Bandwagoning can accelerate the evolution of adaptations

By inducing relinquishments of resources by low-quality individuals and not by high-quality individuals, a bandwagoning variant acts to direct resources from genotypes associated with a long-term fitness disadvantage to genotypes associated with a long-term fitness advantage. The variant becomes selected as its copies 'ride on the bandwagon' of the genotypes that offer this long-term fitness advantage. In directing resources to genotypes associated with a long-term fitness advantage, the variant accelerates the fixation of the alleles at other loci that are responsible for this long-term fitness advantage. The acceleration of adaptations that can occur this way resembles the way that condition-dependent sexual selection can accelerate the fixation of adaptations (Lorch *et al.*, 2003) and also the way that condition-dependent sex hastens the rate of adaptation by imposing the cost of sex upon low-quality individuals (Hadany and Otto, 2009). In these cases, higher-quality individuals receive additional fitness advantages and/or lower-quality individuals disproportionately incur costs, both of which accelerate adaptive evolution.

NOTES

1. The term 'quality' is used often but inconsistently in evolutionary literature (Wilson and Nussey, 2010; Bergeron *et al.*, 2011; Hill, 2011). An individual's genetic quality (i.e. 'good genes') is sometimes distinguished from its 'phenotypic quality' (i.e. condition). In the current paper, 'quality' is used in the sense of 'good genes' – that is, 'an individual's intrinsic propensity or ability to achieve fitness' (Wang *et al.*, 2017) due to genetic variants that leave it more or less advantaged in prey and territory acquisition or more or less susceptible to, for example, predation or infection. Variation in genetic quality is assumed to owe to mutations or epimutations having positive – as in the Red Queen's (Van Valen, 1973; Hartung, 1981; Ridley, 1993; Liow *et al.*, 2011; Brockhurst *et al.*, 2014) and adaptive (Morgan *et al.*, 2012; Waite and Shou, 2012; Hammarlund *et al.*, 2016) races – or negative influences upon quality. An individual's condition may also be used to indicate its genetic quality (i.e. 'good genes').
2. In some English-speaking countries, a person is said to 'jump on the bandwagon' of an entity (for example, another person or a group) if his or her investment in that entity occurs on the condition that it already has a favourable outlook for success and the investment occurs in

order to benefit from that impending success. Likewise, a bandwagoning variant determines whether the individual in which it is located is of high quality and if so, it remains latent and if not, it induces the individual to forfeit resources, some of which may be used by individuals with copies of the same bandwagoning variant. Consequently, the net impact is that more resources are spent by high-quality holders. The latent copies of the bandwagoning variant benefit as they hitchhike upon (‘ride on the bandwagon’ of) high-quality individuals and their lineages.

3. Historically, theory has predicted variation in genetic quality to be low (Borgia, 1979; Taylor and Williams, 1982). However, in recent decades, it has become accepted that mutations (Pomiankowski and Moller, 1995; Rowe and Houle, 1996) and epigenetic changes (Bonilla *et al.*, 2016) can maintain variation in genetic quality.
4. This normalization is done so that the mean quality value in the population remains equal to 10 from one generation to another. That keeps the relationship between Q_δ and individuals’ values for quality approximately the same from one generation to another. It also keeps individuals’ values for quality manageable. Otherwise, individuals’ quality values are likely to grow to astronomical levels, since there is, essentially, natural selection for quality: higher-quality values are advantageous in both reproduction and survival, and quality is partly heritable.

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