The Evolution of Genetic Bandwagoning

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Abstract

Background: In separate literatures, scholars have recently theorized that a variant can be selected to (1) induce suicide by moribund or otherwise stressed holders; (2) impose senescence upon a chronologically old holder; or (3) reduce the yield of a holder with low genetic heterozygosity. The unappreciated commonality between these theories is that a variant can be selected to reduce the fitness of a low-quality holder. Herein, it is proposed that a variant can be selected that reduces its holder's fitness in response to not just these indications but also other indications of low genetic quality and a corresponding low outlook for lineage fitness. The fitness losses induced by the variant in low-quality individuals would allow fitness gains for nearby individuals, some of which would hold a copy of the variant. The variant would gain frequency by hitchhiking along with ("jumping on the bandwagon" of) higher-quality individuals (and their lineages) that have copies of the variant; therefore, it is called a "bandwagoning" variant.

Questions: What parameter values (e.g., relatedness, heritability of fitness, heritability of quality) allow natural selection of genetic bandwagoning? What forms of genetic bandwagoning can be selected?

Features of the model: The model is individual-based and designed to test a combination of two forms of bandwagoning: resonation and reservation. In resonation, a bandwagoning variant sequentially 1) evaluates its holder's quality and lineage fitness outlook and 2) reduces its fitness if these evaluations are unfavorable. In reservation, a bandwagoning variant accomplishes these two steps simultaneously.

Results: Genetic bandwagoning that combines resonation and reservation can be selected even when values for relatedness, heritability of quality, and heritability of fitness are low enough to be in line with reported values for humans and other species.

Conclusion: Genetic bandwagoning can account for numerous empirical paradoxes that apparently involve 1) fitness losses incurred in response to indications of low quality or 2) fitness gains occurring in response to an increase in conditions severity. Evolutionary paradoxes discussed as potential examples of bandwagoning include depression, differential nurturing, honest signaling, reproductive suppression, stress-induced production of anthocyanins, hormesis, and overcompensation.

Keywords: programmed ageing; heterosis; handicap principle; honest signaling; depression; reproductive suppression; hormesis.

1. Introduction

Multiple scholars have discussed circumstances that might lead a lower-quality[1] individual to make an uncoerced forfeiture of resources (e.g., food, territory, mating opportunities) in such a manner that they are not directly bestowed; rather, the resources are left to be utilized by any nearby individual(s) and the individuals that utilize them are often unaware of the forfeiting individual's identity or, indeed, that the resources were even relinquished. (Therefore, such forfeitures are not explained by direct or indirect reciprocity: Nowak, 2012.) For example, multiple scholars have hypothesized that if an individual is in moribund condition 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 benefiting are kin (e.g., Dawkins, 1976) or not (Refardt et al., 2013). Additionally, scholars have offered empirical support for the natural selection of a variant that leads a stressed actor to commit suicide even if the stress itself does not suggest imminent death, provided that relatedness to neighboring individuals is high (Hazan et al., 2004; Herker et al., 2004).

Other scholars have argued that a forfeiture of resources by a lower-quality individual to nearby individuals can be naturally selected to occur in numerous contexts that do not involve either moribundity of the lower-quality individual or close relatedness to neighboring individuals. For example, recent years have seen a resurgence of Weismann's (1889) old theory that there has been natural selection of senescence to occur in conjunction with chronological age, i.e., programmed ageing (Mitteldorf, 2004, 2006; Longo et al., 2005; Goldsmith, 2008, 2014; Pepper et al., 2013; Skulachev, M. & Skulachev, V., 2014; Mitteldorf & 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, V., 1997; Goldsmith, 2004; Travis, 2004; Martins, 2011; Yang, J., 2013). The implication is that low genetic quality is associated with an unfavorable lineage fitness outlook and that the natural selection of senescence occurs to reduce the reproductive success of these individuals with unfavorable lineage fitness outlooks to allow more resources for individuals with more favorable outlooks. Additionally, Semel et al. (2006) noted findings that demonstrated that, in multiple species, heterosis occurs primarily among reproductive traits, which, they argued, constitutes evidence that heterosis itself

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[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 typically used in the sense of "good genes," that is, "an individual's intrinsic propensity or ability to achieve fitness in an average environment" (Wang et al., 2017). An individual's condition may also be used to indicate its genetic quality (i.e., "good genes").

was selected to promote heterozygosity in populations in a manner analogous to a plant's self-incompatibility system, with the implication being that there has been natural selection of the yield improvements to outbred individuals that occurs in heterosis for the same reason that there has been natural selection of sex: Genetically heterozygous individuals are of higher genetic quality and have a higher long-term fitness outlook.

The term genetic "bandwagoning" is introduced herein to refer to a variant that induces the individual in which it is located to forfeit resources accessible to the individual (and the individual's lineage) if that individual's lineage fitness outlook is low. The heritable elements (e.g., alleles, epigenetic marks) within a single individual that are responsible for bandwagoning are collectively considered a "bandwagoning variant." Each of the theories reviewed above—1) selected suicide by moribund or stressed individuals; 2) selected senescence by aged (i.e., low-quality) individuals; 3) selected reduced yield[2] for individuals of low heterozygosity (i.e., low quality)—is an example of a theory of genetic bandwagoning.

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 favorable outlook for success prior to the investment 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 has a favorable lineage fitness outlook 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 copies of the bandwagoning variant in the population have more resources spent by those of its holders that have favorable lineage fitness outlooks. The latent copies of the bandwagoning variant benefit as they hitchhike upon these individuals with favorable lineage fitness outlooks.

In this manner, genetic bandwagoning is an example of the Hankshaw effect—by which "a property of an allele increases its likelihood of hitchhiking" (Hammarlund et al., 2016, pg. 1376)—because when copies of a bandwagoning variant induce forfeitures of resources in low-quality individuals, higher-quality individuals gain resources, which facilitates hitchhiking by copies of the variant held by higher-quality individuals. Moreover, this hitchhiking capacity is also less likely to be reduced by sex and recombination than some other forms of hitchhiking

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[2] To clarify, the mere observation that genetic heterozygosity is associated with increased yield is not a theory of bandwagoning, but the theory that there has been natural selection of this association—that is, natural selection of heritable elements that act in a manner that increases yield if, and only if, an organism is of high heterozygosity because such organisms can expect higher long-term fitness—is a bandwagoning theory.

since the bandwagoning variant hitchhikes with not just one allele but a multiplicity of alleles and epigenetic marks responsible for an individual's high quality. Consequently, after sex and recombination, the variant is likely to continue to be located with some alleles to which its quality advantage was attributable and it is also likely to be located with other alleles associated with high quality, insofar as there is positive assortment by quality (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).

1.1 How bandwagoning theory builds upon the recent discussion about genetic hitchhiking as a facilitator of cooperation

In recent years, genetic hitchhiking has been modeled as a facilitator of the evolution of cooperation (Santos and Szathmary, 2008; Morgan et al., 2012; Quigley et al., 2012; Waite and Shou, 2012; Asfahl et al., 2015; Hammarlund et al., 2016). In this modeling, environmental changes (which may be abiotic and/or biotic) cause individuals to be less adapted to their environment than they had been prior to the changes. Consequently, it is more likely that a variant that is adaptive in the new environment would be under strong selection. Under such circumstances, there may be an "adaptive race" (Waite and Shou, 2012) among genotypes to generate such an adaptive variant by mutation, since this would allow the winner to hitchhike with such a variant and gain frequency (and perhaps fixation). Insofar as populations are spatially structured, cooperators can gain frequency and by gaining frequency, they gain more opportunities (relative to selfish mutants) to win the adaptive race by generating an adaptive variant (Hammarlund et al., 2016).

The preceding paragraph is a somewhat simplified representation of an adaptive race. As other authors have suggested, the biotic and abiotic factors in the environment encountered by an organism are in continuous flux, as they change both because of the organism's actions (i.e., niche construction: Odling-Smee et al., 2003) and independently, which means the adaptive race also occurs continuously (Morgan et al., 2012; Hammarlund et al., 2016). Moreover, this continuous adaptive race is typically not for a sole adaptive variant but for a multiplicity of them, as there is commonly significant heritable variation in quality (Pomiankowski and Moller, 1995; Rowe and Houle, 1996; Bonilla et al., 2016). Low-quality individuals can be considered laggards in the adaptive race. They are unlikely to win and gain fixation because other individuals are ahead (that is, other individuals already have more adaptive variants than they do). Low-quality individuals and their lineages are likely to stay behind in the race, for reasons explored in section 6, so

the opportunity cost of foregoing resources may be lower for low-quality individuals than the utility of those resources to higher-quality individuals. If so, genetic bandwagoning can be selected.

There is a parallel here to the differential allocation literature, in which a parent's investment of more resources into higher-quality offspring is considered adaptive because higher-quality individuals can typically offer a higher "rate of interest" on the investment (Sheldon, 2000). However, a difference between a parent that favors quality offspring and a bandwagoning variant that favors quality holders is that for a bandwagoning variant to be selected, this difference in utility (or the difference in "rate of interest") must compensate for some fraction of resources relinquished by lower-quality individuals that are used by conspecifics that lack a bandwagoning variant or even by individuals of other species. This situation can be interpreted in terms of Hamilton's (1964) rule for determining whether there can be natural selection for a social act. If a low-quality individual's lineage fitness outlook is sufficiently low that its cost, C, of forgoing its lineage fitness is lower than the product of the benefit, B, received by individuals that would use the resources times the relatedness, r, between that low-quality individual and those benefiting, then Hamilton's rule is satisfied.

2. Two ways of bandwagoning: Resonation and Reservation

In this section, two ways of bandwagoning—resonation and reservation—are introduced. A bandwagoning variant may conceivably practice one or the other or both. The focus in this manuscript is upon a strategy that combines resonation and reservation.

2.1 Resonation

Resonation is a form of bandwagoning in which a bandwagoning variant accomplishes the two steps of bandwagoning sequentially: 1) Evaluation of its holder's lineage fitness outlook and then 2) Inducement of resource relinquishment to nearby individuals if this outlook is low compared to other individuals. The term "resonation" is chosen to represent this way of bandwagoning because the variant's direct impact upon that holder's fitness "resonates with" that holder's lineage fitness outlook prior to the forfeiture: It responds to a holder's low lineage

fitness outlook by lowering it further. A variant's ability to accomplish these two steps is based on premises offered in section 5.

A bandwagoning variant may assess its holder's lineage fitness outlook (which is, as noted above, the first step of bandwagoning) on the basis of the degree to which it has managed to, for example, evade predators, resist parasites, obtain food, and manage temperatures. Such an assessment would rely not only upon the holder's successes or difficulties in accomplishing these tasks but also upon indications regarding the severity of the conditions to which the individual has been exposed, since an individual's successes (or difficulties) in evading predators, resisting parasites, obtaining food, or managing temperatures could be because the individual has (or lacks) "good genes" or because of the ease (or severity) of conditions faced by the individual. Severe conditions may be characterized by, for example, a proliferation of well-adapted predators or parasites, a dearth of available prey, or temperature extremes. Ceteris paribus, the more it is indicated that conditions faced by the individual have been severe, the higher the lineage fitness outlook indicated for that individual.

The conditions may vary widely within a single generation and from one generation to another. In a particularly vivid depiction, the Red Queen Hypothesis (Van Valen, 1973) envisions coevolution between a species and a natural enemy, such that each may alternate having an advantage over the other owing to newly-evolved adaptations. As adaptations gain frequency in a natural enemy population, the conditions faced by a focus population become more severe and start what Waite and Shou (2012) refer to as an "adaptive race" within that focus population. If conditions are easy and many individuals are able to survive to reproductive age without difficulty, this may be because, in terms of the Red Queen, there are adaptations that give a natural enemy (e.g., a predator or parasite) an advantage, but they are at low frequency. Under such circumstances, many individuals in a focus population are able to survive to reproductive age, even if they have poor lineage fitness outlooks because they lack the "good genes" required to survive natural enemies that have these adaptations. (The offspring or grandoffspring of these individuals would likely not survive to reproductive age as the better-adapted natural enemies proliferate.) However, in the midst of easy conditions, it is difficult to distinguish between the individuals that have good lineage fitness outlooks and individuals that have poor lineage fitness outlooks because both find it easy to survive to reproductive age. The solution to this problem is reservation, which is a second way in which bandwagoning can occur.

2.2 Reservation

Reservation is a form of bandwagoning in which, in the midst of easily manageable conditions, a bandwagoning variant induces the individual in which it is located to "reserve" from (i.e., withhold) some of its ability to manage one or more potential sources of stress (such as natural enemies, like predators or parasites) for the purpose of better enabling the evaluation of that individual's lineage fitness outlook. Reservation can be considered simultaneous bandwagoning (as opposed to the sequential bandwagoning of resonation) because it allows the two steps of bandwagoning—1) evaluation of a holder's lineage fitness outlook and 2) inducement of a holder to forfeit resources if it has an unfavorable lineage fitness outlook—to be accomplished simultaneously. This is explained as follows.

In the Red Queen example, reservation may involve inducing an individual to increase its exposure to parasites or predators and/or increase its susceptibility to the parasites or predators to which that individual is exposed. If an individual survives with little difficulty in spite of the reservation, it can be more securely determined that its descendants would have the "good genes" necessary to survive if conditions become more severe. Alternatively, if a holder is killed, wounded, or infected or otherwise loses resources as a consequence of the reservation it has been induced to undertake, this allows the evaluation that the holder has an unfavorable lineage fitness outlook and that its descendants probably would not have had the "good genes" necessary for survival if conditions had become more severe. This perishing, wounding, or infection also results in a fitness loss to the individual evaluated to have a low lineage fitness outlook, thereby rendering it unable to use some or all of the resources that it otherwise could have. In this manner, the evaluation (of a holder's low lineage fitness outlook) and the forfeiture (of that holder's resources) occur simultaneously.

Resonation can (but does not necessarily) follow reservation. For example, if a holder undertakes reservation and subsequently becomes infected or wounded and consequently is evaluated to have an unfavorable lineage fitness outlook, but manages to survive the infection or wounding, a bandwagoning variant may then induce resonation. In resonation, the holder would relinquish more resources in addition to those lost as a result of the infection or wounding. Keen readers may notice similarities between the concept of reservation and the handicap principle (Zahavi, 1975; Grafen, 1990). These similarities, as well as differences, are discussed in section 2.6.

2.3 A bandwagoning variant is expected to downregulate resonation and/or reservation in response to indications of conditions severity

Natural selection would act on multiple aspects of resonation and reservation. In section 2.1, it was noted that the more severe conditions that individual has faced, then, ceteris paribus, the higher the lineage fitness outlook that is suggested for that individual. Therefore, if conditions are more severe, then a bandwagoning variant would be expected to do less resonation.

Additionally, a bandwagoning variant that induces its holder to reserve too little runs the risk of allowing its holder to survive and reproduce, even though its genes may not be "good" enough to allow its offspring or grandoffspring to survive more severe conditions, when better-adapted natural enemies are more prevalent. Alternatively, a bandwagoning variant that induces too much reservation runs the risk of inducing the death of every holder of a bandwagoning variant in the population, as even the individuals with the "better genes" would not be able to survive the reservation, whereupon there would be no individuals with a bandwagoning variant left to utilize resources forfeited by the perished individuals. However, what constitutes an appropriate degree of reservation may vary from generation to generation, since, as noted in section 2.1, in the absence of reservation, the quantity of individuals in the population that perish prior to reproduction may vary widely from one generation to another. The more individuals that have perished during a generation and the greater alacrity with which they have perished, the more severe the conditions that are indicated and, consequently, the less an individual would have to be induced to reserve in order to demonstrate it has "good genes." Natural selection would, therefore, act upon a bandwagoning variant to vary the degree of reservation it induces during a generation, such that it would reserve more if conditions have been easy and less if conditions have been severe.

By imposing resonation and reservation under easy conditions, but downregulating both resonation and reservation under severe conditions, a bandwagoning variant acts in a manner that: 1) reduces the quantity (but increases the mean quality) of the individuals in which it is located when conditions are easy and there are more likely to be many individuals in which it is located and 2) refrains from reducing the quantity of the individuals in which it is located when conditions are severe and there are likely to be few individuals in which it is located. In doing so, a bandwagoning variant smooths the variance from generation to generation in the offspring produced by

individuals with the bandwagoning variant, in accordance with theory that holds that long-term natural selection favors a genotype with a lower net variance of offspring produced by individuals with the genotype across time (Schreiber, 2015).

2.4 Varying the degree of reservation from individual to individual

As suggested above, reservation occurs to help identify whether or not an individual has a favorable lineage fitness outlook if that individual has faced easy conditions. However, the severity of conditions can change within a single generation. For example, well-adapted predators or parasites can rapidly proliferate. Therefore, a bandwagoning variant that induces all of its holders to engage in reservation at the same time and to the same degree runs the risk of leading to the death of all of its holders if the predator or parasite threat suddenly intensifies. If this were to occur, there would be no bandwagoning variant holders left to utilize the resources forfeited by the perished individuals. Consequently, it is likely that there would be natural selection of a bandwagoning variant that hedges against the possibility that conditions rapidly intensify by varying the timing and/or degree of the reservation it induces its holders to undertake. In doing so, a bandwagoning variant reduces the correlation of offspring produced between two individuals with the variant during the same generation, in accordance with theory that holds that long-term natural selection favors a genotype with a lower correlation of offspring produced between two-randomly selected individuals with the genotype from the same generation (Schreiber, 2015).

One way such variation could be accomplished would be to vary the degree of reservation on the basis of the degree to which a holder has already been identified as being of low quality. Indeed, it was explained in section 2.2 that reservation is conducted under easy conditions in order to assess whether or not an individual's lineage fitness outlook is favorable. If an individual's quality has already been determined to be low, there is less utility in inducing that individual to engage in reservation because: 1) as long as conditions remain modest, it should be induced to engage in resonation and thereby forfeit resources, so reservation is unnecessary and 2) if conditions turn sufficiently severe that it should not engage in resonation, then it should not reserve then either due to the severity of conditions (as argued in section 2.3). Therefore, if reservation varies from individual to individual on the basis of indications about quality that have already been received, it is expected that individuals that have received

indications that they are of low quality would reserve less than individuals that have not received indications that they are of low quality.

In section A3 of the Appendix, I discuss the possibility that bandwagoning variants might also vary the reservation they induce on the basis of the sex of the individual in which they are located.

2.5 The summary so far

A bandwagoning variant is expected to:

1) induce resonation by individuals identified as low quality, reducing the fitness of these individuals so that nearby individuals can use their reproductive opportunities and other resources.

2) induce reservation particularly by individuals not (yet) identified as low quality, reserving from their ability to manage potential sources of stress in order to help identify their quality.

3) downregulate (i.e., induce less) resonation by an individual insofar as conditions faced by that individual have been severe.

4) downregulate (i.e., induce less) reservation by an individual insofar as conditions faced by that individual have been severe.

2.6 Similarities and differences between the concept of reservation and the handicap principle

The concept of reservation is similar to the handicap principle (Zahavi, 1975; Grafen, 1990) in the following respects. They both hold that there has been natural selection of a variant:

1) that imposes a burden upon its holder

2) for the purpose of helping to identify that holder's quality

3) and that the identification of quality occurs through the satisfaction of a criterion of differential costliness (which is discussed in section 5.2)

4) and that the burden is incurred conditionally (i.e., is not perfectly heritable),

5) such that individuals that are identified as low quality incur less of a burden or none at all (see section 2.3) and

6) that males would incur more of a burden than females (see Appendix section A3).

A key difference between the handicap principle and the concept of reservation is that according to the handicap principle, this burden is incurred for the purpose of helping to identify the holder's quality to other individuals, particularly potential mates (Zahavi, 1975), but also other conspecifics and natural enemies (Zahavi and Zahavi, 1997), whereas, for reservation, this burden is incurred for the purpose of helping to identify the holder's quality to the bandwagoning variant that is responsible for the burden. This distinction allows bandwagoning theory to better account for some phenomena for which the handicap principle has been invoked to explain (see section 7.1 for why and section 8 for examples of phenomena that the concept of reservation can better explain). Other differences are that bandwagoning theory predicts that 1) individuals would incur less of a burden when conditions are, and/or have been, severe (see section 2.3) and 2) the burden incurred might vary not just by quality and by sex, but also by other characteristics (e.g., birth order). The handicap principle does not make either of these statements explicitly, though the first may be implied.

3. Model

Table 1. Baseline parameter[3] values

Symbol	Description	Value
N	population size	200
N_C	starting quantity of the cooperator type	100
N_D	starting quantity of the defector type	100
Q_σ	standard deviation of distribution from which an individual's quality is generated	1
$\pi_{\mu 1}$	mean of distribution from which the quantity perishing in step #1 is generated	30
$\pi_{\sigma 1}$	standard deviation of distribution from which the quantity perishing in step #1 is generated	15
$\pi_{\mu 2}$	mean of distribution from which the quantity perishing in step #2 is generated	30
$\pi_{\sigma 2}$	standard deviation of distribution from which the quantity perishing in step #2 is generated	15
C	amount by which the ability to survive step #2 is reduced by reservation	0.5
β	percentage fecundity that an individual loses due to reservation	0.2
Y	fraction of total fecundity lost that is used by individuals in the population	0.8
r	the assortment ("relatedness") in the population	0.15
π_1	conditions cutoff for reservation	30
π_2	conditions cutoff for resonation	60
P_R	percentile cutoff for reservation in step #2	10
P_S	percentile cutoff for resonation in step #3 if no reservation occurs	10
P_T	percentile cutoff for resonation in step #3 if reservation occurs	20
T	number of generations in each run	250

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[3] Some of the model's simplifications and baseline values are discussed in Appendix section A2.

The model's parameters and their baseline values are listed in Table 1. The population is of size N at the start and end of each generation, though it drops below N in steps #1 and #2 of each generation as individuals perish, before reaching N again in step #3 as the remaining individuals reproduce. For each individual, i, in the population (regardless of that individual's type), a number is randomly generated at the beginning of that individual's life, which represents that individual's genetic quality, Q_i. For the simulation's initial generation, each individual's Q_i is randomly generated from a normal distribution with a mean of 10 and a standard deviation of Q_σ. (If the random process yields a negative value for Q_i for any individual, that individual's Q_i value is reverted to 0: $Q_i \geq 0$.) Q_i values for individuals born after the first generation are randomly produced using the Q_i value for that individual's parent (which is explained in step #3 below). The measure, Q_i, represents the sense of quality that is "an individual's intrinsic propensity or ability to achieve fitness in an average environment" (Wang et al., 2017). An individual's chances of survival of steps #1 and #2 and reproduction in step #3 are both dependent upon that individual's value for Q_i.

There are two types of individuals in the population:

1) A "defector" type practices neither resonation nor reservation. Instead, it reproduces to its capacity, irrespective of its quality.

2) A "cooperator" type combines resonation and reservation in the manner verbally summarized in section 2.5 and quantitatively described below.

Step #1: Perishing of a π_{j1} quantity of individuals

Each generation, a number is randomly produced from a normal distribution with a mean of $\pi_{\mu1}$ and a standard deviation of $\pi_{\sigma1}$. For a generation, j, this number is rounded to the nearest integer, π_{j1}, and represents the quantity of all individuals that perishes in step #1. A quantity of π_{j1} individuals perishes unless either $\pi_{j1} < 0$, in which case 0 individuals perish, or $\pi_{j1} \geq N$, in which case N - 1 individuals perish. For each individual, i, the probability of surviving this step is proportional to that individual's S_i, which is simply equal to that individual's value for Q_i. In the model, the quantity of individuals that perishes is used as a representation of the severity of

conditions and cooperators decide whether or not to do reservation in step #2, in part, on the quantity of individuals that perished in step #1.

Step #2: Perishing of a π_{j2} quantity of individuals

For step #2, a number is randomly generated from a normal distribution with a mean of $\pi_{\mu2}$ and a standard deviation of $\pi_{\sigma2}$. For a generation, j, this number is rounded to the nearest integer, π_{j2}, and represents the quantity of all individuals that perishes in step #2, unless $\pi_{j2} < 0$, in which case 0 individuals perish, or $\pi_{j2} \geq N - \pi_{j1}$, in which case all but 1 individual perishes. For each individual, i, of any type, the probability of surviving this step is proportional to that individual's S_i. For each individual, i, that does not do reservation, the individual's S_i is simply equal to that individual's value for Q_i.

The difference between steps #1 and #2 is that in step #2, some individuals of the cooperator type may do reservation. (No individuals of the defector type ever do reservation.) If the following two conditions are both true, a cooperator individual does reservation by reducing its ability to survive step #2 by C, so that its $S_i = Q_i - C$ (and if the Si value for any individual becomes negative, it is reverted to zero):

1) Less than π_1 individuals perished in step #1 and

2) The individual's Q_i value is higher than the P_R percentile of Q_i values of all individuals (regardless of type) in the population that survived step #1.

The perishing of a quantity of at least π_1 individuals in step #1 is considered to indicate that conditions have been severe, to which cooperators respond by downregulating reservation (as explained in section 2.3). However, even if conditions are not severe, cooperators do not do reservation if their quality, Q_i, is equal to or below the P_R percentile of Q_i values of all individuals. These individuals are considered low quality and their downregulation of reservation is explained in section 2.4.

Step #3: Reproduction

An individual's fecundity is denoted F_i. An individual's F_i value equals its value for Q_i except in the following cases. Changes to a cooperator's fecundity are depicted by the flowchart in Figure 1.

1) If an individual perished in step #1 or step #2, its F_i value is zero, regardless of whether that individual is a cooperator or a defector.

2) Sensu section 2, a cooperator individual does resonation if its quality is low, unless conditions are severe. In the model, the severity of conditions is indicated by the quantity of individuals (regardless of type) that perished in steps #1 and #2. If this quantity perished is less than π_2, then a surviving cooperator individual does resonation in step #3 if it identifies that its quality is low, thereby reducing its F_i value to zero.

     a) If a surviving cooperator did not reserve in step #2, then it can only identify that its quality is low if its Q_i is equal to or lower than the P_S percentile of all individuals in the population (regardless of type) that survived steps #1 and #2, in which case it reduces its F_i value to zero.

     b) If a surviving cooperator did reserve in step #2, then it can identify that its quality is low if its Q_i is equal to or lower than the P_T percentile of all individuals in the population (regardless of type) that survived steps #1 and #2, in which case it reduces its F_i value to zero. Essentially, reservation allows a higher quality percentile threshold for reproduction for individuals of the cooperator type than if resonation is practiced alone ($P_T > P_S$).

3) Alternatively, if a surviving cooperator did reserve in step #2 and its Q_i is equal to or higher than the P_T percentile of all individuals in the population, its Fi value is reduced as a residue of the reservation it undertook in step #2. The idea is that reservation in step #2 might adversely affect the fecundity of a high-quality individual, though much less so than a low-quality individual, which allows reservation to help identify individuals with Q_i values below the P_T percentile. Therefore, if a cooperator did reserve but does not do resonation, its fecundity is reduced by βC (that is, $F_i = Q_i - \beta C$), which is a cost to fecundity that occurs as a residue of the reservation, C, that the individual undertook in step #2.
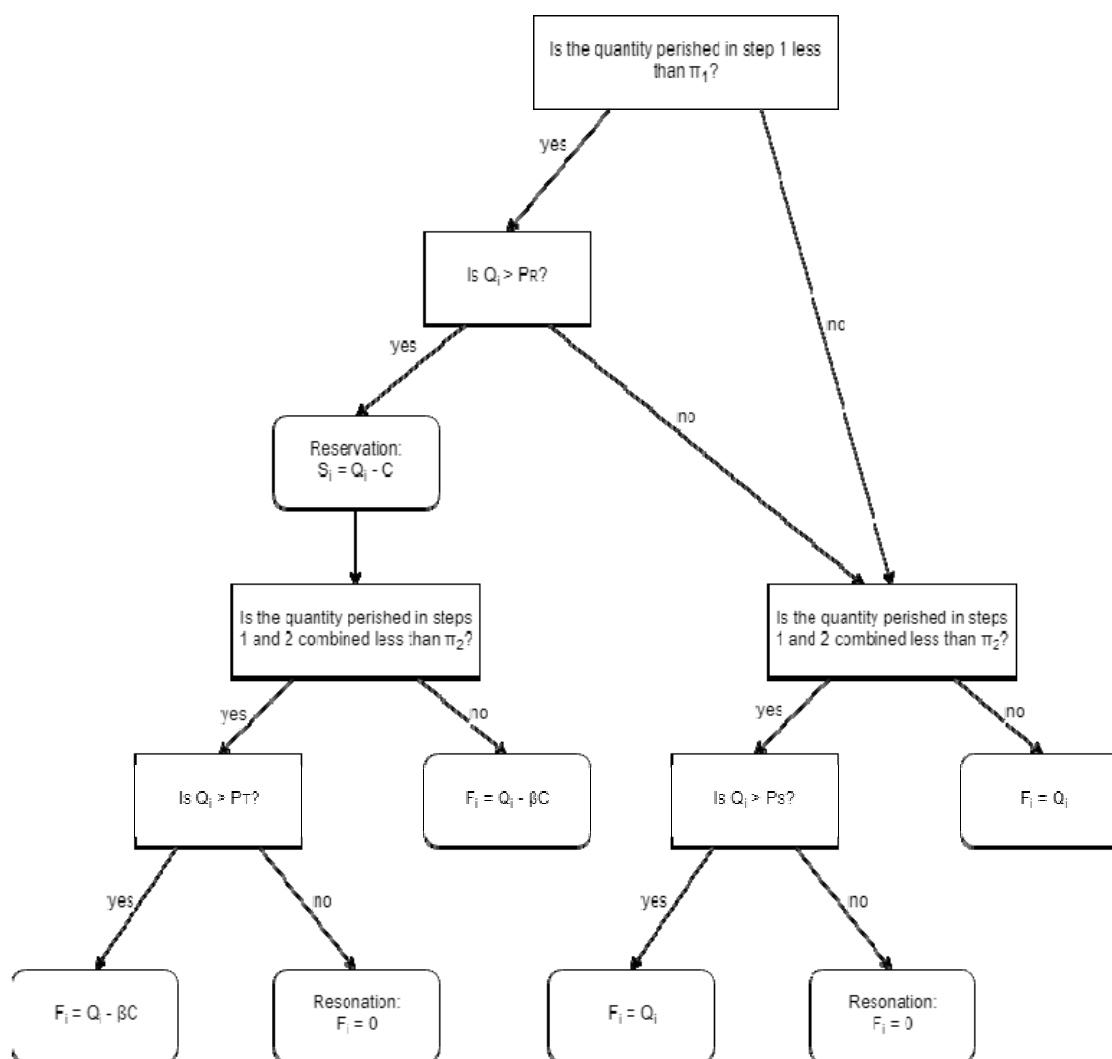
Figure 1. Flowchart of decisions for a cooperator.

The fecundity lost by individuals due to their perishing or to bandwagoning (resonation or reservation) contributes to the fecundity of each individual in the population (including the individuals that lost fecundity if they have survived) in the following manner. For each individual, i, that individual's quality, Q_i, represents the fecundity it would have attained in the absence of perishing and bandwagoning. Therefore, regardless of an individual's type, the difference between an individual's quality and that individual's fecundity calculated above (in the current step #3) is considered the fecundity lost, L_i, by that individual. For individuals for which $F_i = 0$ because they perished or did resonation, their fecundity lost, L_i, is equivalent to their Q_i value at the beginning of the generation.

For the k individuals of the defector type and l individuals of the cooperator type to begin a generation, j, the sum of the quality values for the defectors and cooperators is denoted, respectively, $Q^D =$ and $Q^C =$

$\sum_{i=1}^{l} Q_i$. The sum of the fecundity values calculated in step #3 for defectors and cooperators is denoted, respectively, $F^D = \sum_{i=1}^{k} F_i$ and $F^C = \sum_{i=1}^{l} F_i$. And the total fecundity lost by defectors and cooperators is denoted, respectively, L^D and L^C.

$$L^D = Q^D \text{-} F^D = \sum_{i=1}^{k} Q_i - \sum_{i=1}^{k} F_i$$

$$L^C = Q^C \text{-} F^C = \sum_{i=1}^{l} Q_i - \sum_{i=1}^{l} F_i$$

The percentage of an individual's fecundity lost that can be used by individuals in the same population may be considered to be less than unity, since individuals in the same population may not be able to fully use the fecundity lost and/or individuals of other species may use some of the resources that were unused by perished or bandwagoning individuals. Therefore, a variable, Y, is used below to denote the percentage of the fecundity lost due to perishing and/or bandwagoning that contributes to the fecundity of individuals in the same population. The fecundity lost by an individual, i, that is attained by other individuals in the same population is then YL_i. The total fecundity lost by cooperators and defectors that can be used by other individuals in the population is, respectively, YL^C and YL^D.

This model follows other population models by using the variable r to denote the relatedness, or assortment, of individuals in the population, where r is treated as an abstract assortment parameter without specifying how this assortment arises in three-dimensional space (Cooney, D. et al., 2016 and citations within). Commonly, an r fraction of an individual's interactions is considered to be with same-type individuals and a $1 - r$ fraction is considered to be with individuals of any type in the proportion that they occur in the population. Likewise, in the current model, an r fraction of the fecundity lost by an individual that is available to individuals of the same population is considered to contribute to the fecundity of same-type individuals and a $1 - r$ fraction is considered to go to both defectors and cooperators in the proportion that they occur in the population.

Therefore, of the fecundity lost by cooperators, given above as YL^C, a fraction, rYL^C, goes to other cooperators and a fraction, $(1 - r)YL^C$, goes proportionally to cooperators and defectors. Of the fecundity lost by defectors, given above as YL^D, a fraction, rYL^D, goes to other defectors and a fraction, $(1 - r)YL^D$, goes proportionally to cooperators and defectors.

Lost fecundity that is used by individuals of a type is added to each individual, i, of that type (including the individual that lost it) in proportion to that individual fecundity, F_i. Lost fecundity that is used by individuals in the whole population is likewise added to each individual in the population (including the individual that lost it) in proportion to that individual's fecundity. The ith defector's proportion of the fecundity gained by defectors and by the whole population is, respectively, F_i / F^D and $F_i / (F^D + F^C)$. The ith cooperator individual's proportion of the fecundity gained by cooperators and by the whole population is, respectively, F_i / F^C and $F_i / (F^D + F^C)$.

The fecundity added during the current step #3 by the ith defector individual and i^{th} cooperator individual is given below by, respectively, A_i^D and A_i^C.

$$A_i^D = F_i Y[rL^D / F^D + (1 - r)(L^D + L^C) / (F^D + F^C)]$$

$$A_i^C = F_i Y[rL^C / F^C + (1 - r)(L^D + L^C) / (F^D + F^C)]$$

The updated fecundity value of the ith defector individual and the ith cooperator individual becomes, respectively, U_i^D and U_i^C.

$$U_i^D = F_i + A_i^D$$

$$U_i^C = F_i + A_i^C$$

A total of N offspring are produced. Since the population reproduces asexually, one parent is selected randomly for each of the N offspring. An individual i's probability of producing each of the N offspring is proportional to its updated fecundity value and remains the same throughout step #3 regardless of how many offspring it has been randomly selected to produce. Each of the N offspring becomes the same type as its parent.

After the parents of N offspring are selected, the Q_i values of those parents are summed to give a value for $T_Q = \sum_{i=1}^{N} Q_i$. (If a parent produces multiple offspring, the parent's value is counted for each of the offspring it produces.) The Q_i value of each parent, i, is then multiplied by $10N / T_Q$, which normalizes the Q_i values of the parents, making the mean Q_i value for all parents equal to 10. Each offspring's Q_i value is then randomly generated from a normal distribution that has a mean equal to the new (normalized) Q_i value of its parent and a standard deviation of Q_σ (the same standard deviation that is used in step #0). Following this reproduction step, all

individuals that began the generation are eliminated from the population, leaving the N offspring to start a new generation with step #1. The run continues for T generations or until one type has gained fixation.

4. Results

The essence of bandwagoning is that when conditions are of only modest intensity, the bandwagoning variant sacrifices holder quantity for holder quality. For each generation bandwagoning occurs, the variant becomes held by a smaller quantity of holders in the next generation than if it had not done bandwagoning. However, it is not only true that the mean quality of its holders (that is, the mean quality of cooperators) is higher in the next generation after bandwagoning than if it had not done bandwagoning—it is also typically true that the quantity of high-quality holders in which it is located (that is, the quantity of high-quality cooperators) is higher than if it had not done bandwagoning. This is because high-quality cooperators are more likely than high-quality defectors to be able to use others' resources for the production of offspring, since low-quality cooperators are more likely to forfeit resources than low-quality defectors. Since there is a higher quantity of high-quality cooperators than if bandwagoning had not occurred, the cooperator type has an advantage in gaining quantity in future generations.

A pattern common to figures 2 and 3 is the drop in average cooperator quantity early in runs as the bandwagoning variant sacrifices holder quantity for holder quality. This built-up quality advantage for cooperators leads to cooperator quantity gains later in runs. (See section 6.2 for insight as to why this occurs.) The results of 10,000 runs with baseline values are depicted in figure 2A. As figure 2A indicates, average cooperator quantity remained significantly below starting cooperator quantity late in runs. For figure 2B, three variable values were more favorable to the bandwagoning variant (and the others were equal to baseline values): The cost of reservation was set lower ($C = .25$); cooperators that reserved lost less fecundity by doing so ($\beta = .1$); and the total fecundity lost that was used by individuals in the population was higher ($Y = .9$). Consequently, mean cooperator quantity significantly exceeded starting cooperator quantity of 100 late in runs. For figure 2C, no individuals perished prior to reproductive age ($\pi_{\mu 1}$, $\pi_{\sigma 1}$, $\pi_{\mu 2}$, and $\pi_{\sigma 2}$ were all set to zero). This probably benefited cooperators because it made the reproductive step a stronger determinant of fitness and higher-quality cooperators tended to have a particular advantage during the reproductive step, since they were likely to have access to more resources than higher-quality defectors because lower-quality cooperators were more likely to forfeit resources than lower-quality defectors and assortment was positive ($r = .15$). Mean cooperator quantity significantly exceeded starting cooperator quantity of

100 late in runs. As a comparison between figures 2D and 2E reveals, cooperators benefited from the lack of perishing prior to reproductive age, even when C was set to 0 (so that survival costs associated with C were inapplicable). For figure 2D, $C = 0$ and all other variable values were equal to baseline values. The mean cooperator quantity by the end of runs was 101.98 and significantly exceeded starting cooperator quantity of 100. For figure 2E, $C = 0$, there was no perishing prior to reproductive age ($\pi_{\mu 1} = \pi_{\sigma 1} = \pi_{\mu 2} = \pi_{\sigma 2} = 0$) and all other variable values were equal to baseline values. The mean cooperator quantity by the end of runs was 106.998, significantly exceeding not only starting cooperator quantity of 100, but also mean cooperator quantity by the end of runs in figure 2D.

A higher population quantity also benefited cooperators. For figure 2F, the population quantity was set to 800, with 400 starting cooperators and 400 starting defectors; C was set to zero; there was no perishing prior to reproductive age ($\pi_{\mu 1} = \pi_{\sigma 1} = \pi_{\mu 2} = \pi_{\sigma 2} = 0$); and all other variable values were equal to baseline values. In other words, the difference between figures 2E and 2F is that for figure 2F, the population quantity was four times higher. Mean cooperator quantity significantly exceeded starting cooperator quantity of 400 late in runs and was 459.86 by the end of runs, which was approximately 15% higher than starting cooperator quantity of 400. In comparison, mean cooperator quantity by the end of runs depicted in figure 2E (106.998) was only approximately 7% higher than starting cooperator quantity of 100. A higher population quantity tended to benefit cooperators because a higher total population quantity made it less likely that defectors gained fixation when the percentage of cooperators dipped early in runs, enabling cooperator percentage to recover later in runs.

C

D

E

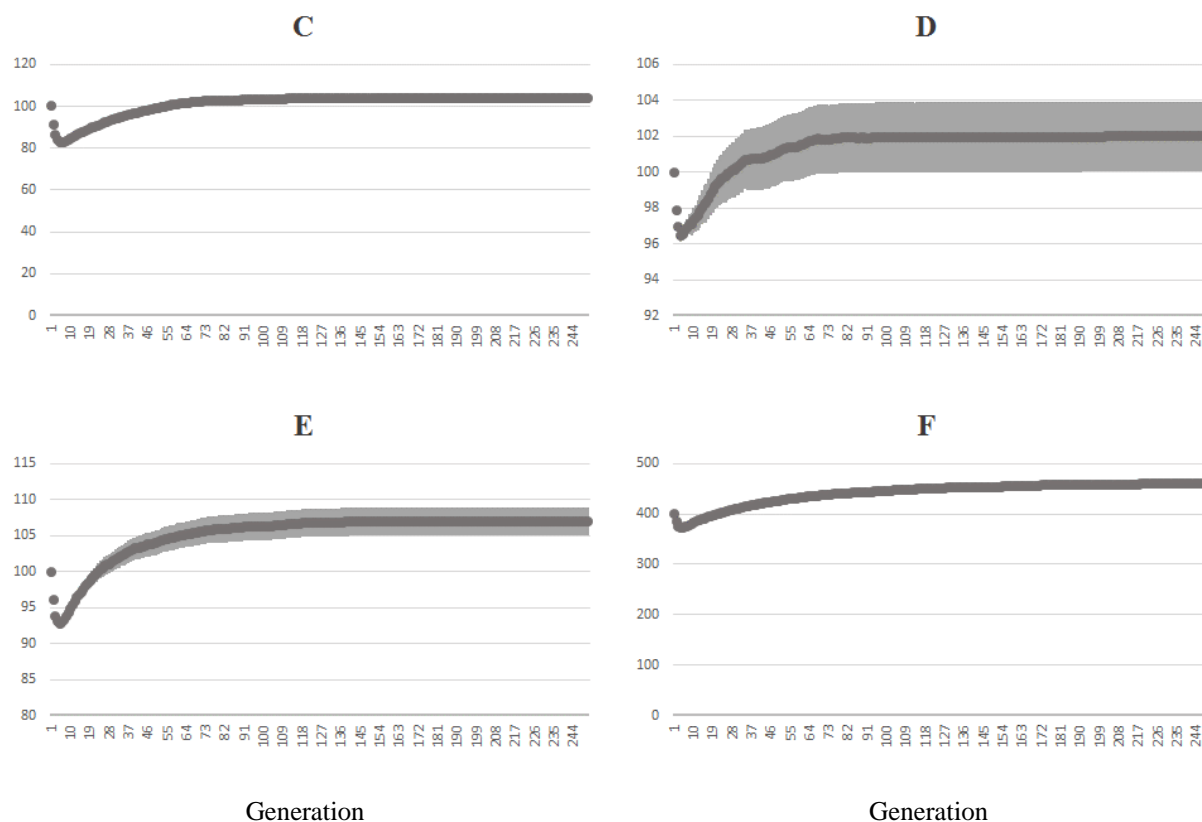**F**

Generation   Generation
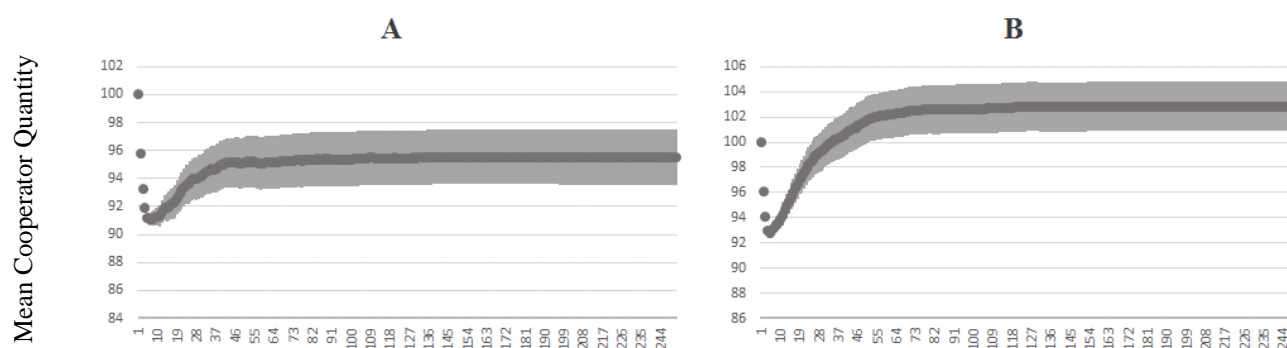
Figure 2. The average quantity of cooperators across 10000 replicate runs is indicated by the dark line. Shaded regions indicate 95% confidence intervals. For purposes of calculating these averages and confidence intervals, when defectors gained fixation during a run, then cooperator quantity was tallied as zero for each generation thereafter for that particular run and when cooperators gained fixation during a run, then cooperator quantity was tallied as N for each generation thereafter for that particular run. Heritability (h^2) values were calculated using the values generated by the program. The reported heritability values are the averages across 10000 runs. (A) With all values equal to the baseline values in Figure 1, the mean cooperator quantity by the 250th generation was significantly below the starting cooperator quantity of 100. h^2 quality: .186. h^2 fitness: .005. (B) With variable values more favorable to cooperators, such that $C = .25$; $\beta = .1$; $Y = .9$ and all other values equal to baseline values, the mean cooperator quantity by the 250th generation was significantly above the starting cooperator quantity of 100. h^2 quality: .186. h^2 fitness: .005. (C) With $\pi_{\mu 1}$, $\pi_{\sigma 1}$, $\pi_{\mu 2}$, and $\pi_{\sigma 2}$ all set to zero, so that no individuals perish prior to reproductive age, and all other values (including C, β and Y) equal to baseline values, the mean cooperator quantity by the 250th generation was significantly above the starting cooperator quantity of 100. h^2 quality: .168. h^2 fitness: .002. (D) With $C = 0$ and all other values (including $\pi_{\mu 1}$, $\pi_{\sigma 1}$, $\pi_{\mu 2}$, and $\pi_{\sigma 2}$) equal to baseline values, the mean cooperator quantity by the 250th generation was significantly above the starting cooperator quantity of 100. h^2 quality: .182. h^2 fitness: .005. (E) With $C = 0$, no perishing prior to reproductive age ($\pi_{\mu 1}$, $\pi_{\sigma 1}$, $\pi_{\mu 2}$, and $\pi_{\sigma 2}$ all set to zero), and all other values equal to baseline values, the mean cooperator quantity by the 250th generation was significantly above the starting cooperator quantity of 100. h^2 quality: .142. h^2 fitness: .002. (F)

With $C = 0$, no perishing prior to reproductive age ($\pi_{\mu 1}$, $\pi_{\sigma 1}$, $\pi_{\mu 2}$, and $\pi_{\sigma 2}$ all set to zero), starting quantities of cooperators and defectors both equal to 400, and all other values equal to baseline values, the mean cooperator quantity by the 250th generation was significantly above the starting cooperator quantity of 400. h^2 quality: .084. h^2 fitness: .001.

Moreover, the cooperator type can invade the defector type. As depicted by figure 3A, when cooperator quantity started at 1 and other variable values were equal to baseline values, cooperator quantity exceeded 1 by the end of the average run, though the margin was not significant. Cooperators gained fixation in 53 of 10000 runs. In figure 3B, defector quantity started at 1 and all variable values were equal to baseline values. Defector quantity was equal to 1 by the end of the average run. Defectors gained fixation in 50 of 10000 runs.
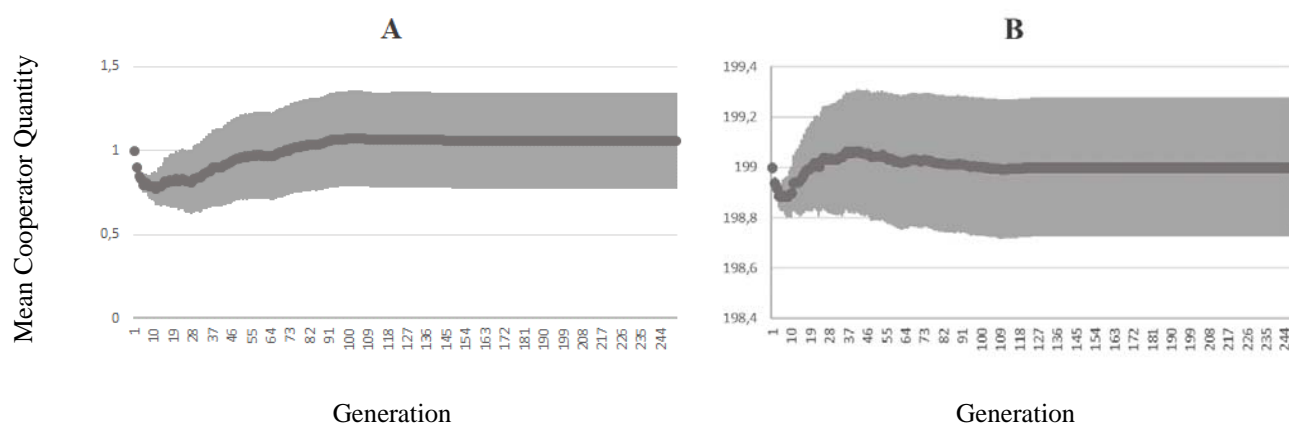

Figure 3. The average quantity of cooperators across 10000 replicate runs is indicated by the dark line. Shaded regions indicate 95% confidence intervals. For purposes of calculating these averages and confidence intervals, when defectors gained fixation during a run, then cooperator quantity was tallied as zero for each generation thereafter for that particular run and when cooperators gained fixation during a run, then cooperator quantity was tallied as N for each generation thereafter for that particular run. (A) With beginning cooperator quantity equal to 1, beginning defector quantity equal to 199, and all other values equal to baseline values, mean cooperator quantity by generation 250 exceeded beginning cooperator quantity of 1, though the margin was not significant. The cooperator type gained fixation in 53 of 10000 runs. (B) With beginning cooperator quantity equal to 199, beginning defector quantity equal to 1, and all other values equal to baseline values, mean cooperator quantity by generation 250 was exactly equal to beginning cooperator quantity of 199. The defector type gained fixation in 50 of 10000 runs.

5. Premises

5.1 Three premises that support an assumption that a variant can evolve that evaluates its holder's lineage fitness outlook and induces resonation

1) Based upon signals, cues, and/or other indications, individuals can often make an imperfect, but useful, assessment of the quality and lineage fitness outlook of another individual that has competing interests.

Numerous well-regarded theories in contemporary evolutionary biology hold that individuals can often make an imperfect, but useful, assessment of the quality and lineage fitness outlook of another individual that has competing interests, via the usage of signals, cues, and/or other indications. Choosy individuals (typically females) in many species are believed to have the ability to distinguish potential mates that would produce offspring that are "sexy sons" and/or have "good genes" from those that would not. 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 the potential mate's offspring (Kokko et al., 2002). Parents in many species are believed to have the ability to identify which of their offspring have the best genes for the purposes of allocating resources differentially to those offspring (Burley, 1986; Sheldon, 2000; Harris, W. and Uller, 2009). Parents are theorized to kill low-quality and/or less attractive offspring by practicing filial cannibalism (Klug and Bonsall, 2007) and, more generally, parental selection (Harris, J., 2006). In each of these contexts, the individual whose quality, reproductive value, and/or lineage fitness outlook are assessed and the individual making the assessment have competing interests, characterized by sexual conflict (Williams, 1966a; Parker, G., 1979) and/or parent-offspring conflict (Trivers, 1974).

2) The alignment of interests between two entities reduces the likelihood of misinformation between them.

A scholarly consensus holds that a misalignment of the interests of signaler and receiver is a factor that encourages signaling dishonesty (Maynard Smith, 1991; Hurd and Enquist, 2005; Searcy and Nowicki, 2005; Szamado, 2011). Therefore, insofar as an individual's quality and lineage fitness outlook are able to be assessed via cues and signals by other individuals that have competing interests, then, ceteris paribus, that individual's quality and lineage fitness outlook should be able to be identifiable with at least as much, or even greater, certainty by variants within that same individual that have interests that are aligned with the other variants within that individual.

3) A variant's bandwagoning activities would be expected to align with the interests of variants on other loci of the same individual.

If an individual's lineage fitness outlook is sufficiently low compared to nearby individuals that Hamilton's (1964) rule ($C < rB$) is satisfied if it forfeits resources to nearby individuals, it is not only true that a bandwagoning variant is expected to gain in frequency in ensuing generations as a result of bandwagoning, but it is also true that any variants at other loci on the same genotype can be expected to gain in frequency in ensuing generations as a result of bandwagoning, even if the variants at those other loci do not do bandwagoning. For example, if Hamilton's rule is satisfied by the forfeiture of resources by an individual, a variant that is responsible for the blood type of that individual and does not do bandwagoning at all can be expected to gain in frequency as a result of the bandwagoning done by other loci within the same individual. The applicable value for relatedness, r, is, in theory, the same for both variants. That is, for a bandwagoning variant and a blood type variant within the same individual, the prevalence of copies of the bandwagoning variant among neighboring individuals is, in theory, the same as the prevalence among neighboring individuals of copies of the blood type variant. Additionally, the lineage fitness outlook of an individual compared to neighbors determines the cost, C, and the benefit, B, associated with resource relinquishment by that individual. Since the bandwagoning variant and the blood type variant are part of the same individual, these values are also the same for both variants. Therefore, I assume that there is no particular evolutionary pressure upon variants at other loci to prevent a bandwagoning variant from accessing information about its holder's lineage fitness outlook or from inducing resource forfeitures by a holder that has been evaluated to have a low lineage fitness outlook.

This does not mean, however, that a mutation cannot arise—either at the loci of bandwagoning alleles or at other loci—that would prevent bandwagoning. A mutation at any locus that prevents other genes from accessing and acting upon information about the holder's quality would turn the holder into a defector—even if that locus had nothing to do with (that is, neither promoted nor prevented) bandwagoning until the mutation occurred. However, insofar as bandwagoning satisfies Hamilton's rule, the mutation would be expected to lose frequency.

Conclusion: A bandwagoning variant would be expected to be able to evaluate its holder's quality to a reasonable approximation, as well as evaluate its holder's lineage fitness outlook. Additionally, it is likely that a bandwagoning

variant would be unimpeded by genes at other loci in inducing the forfeitures of its holder's resources if its evaluation suggests that its holder's lineage fitness outlook is unfavorable.

5.2 One premise that supports an assumption that reservation can help identify an individual's quality

1) An individual's quality can be demonstrated via the imposition of a burden (i.e., a handicap) upon that individual due to the satisfaction of a criterion of differential costliness, such that it is costlier to lower-quality individuals than to higher-quality individuals.

The handicap principle was unpopular among evolutionary biologists for the first decade and a half after its advancement by Zahavi (1975). Grafen's (1990) emphasis upon a criterion of differential costliness–which is that in order for a signal to reliably indicate quality to individuals with conflicting interests, it has to be costlier to maintain for lower-quality individuals— and his inclusion of a model showing how the criterion might be satisfied instantly transformed (per Grose, 2011) the biological community's view of the handicap principle some fifteen years after Zahavi (1975). Subsequently, Getty (1998, 2006) demonstrated that signaling can reliably reflect quality even if the costs of signaling are not higher for lower-quality individuals, provided that higher-quality individuals receive a benefit from the signaling that sufficiently exceeds the benefit that lower-quality individuals would receive. However, the model in section 3 depends upon Grafen's original differential costliness criterion; therefore, it is notable that, per Grose (2011), many in the biological community agree that the satisfaction of this criterion is plausible. In the model (section 3), it was assumed that an individual that reserved and had quality at or below the P_T percentile could be identified by a bandwagoning variant within it as having low quality, either because the individual perished due to the reservation or because the individual experienced stress (e.g., wounding or infection) due to the reservation that an individual with quality above this level could avoid. The reservation, therefore, was assumed to exert a differentially costly influence upon an individual with low quality, which allowed the identification of an individual with low quality. (Similarities and differences between the concept of reservation and Zahavi's handicap principle are noted in section 2.6.)

6. Why the likelihood of natural selection of genetic bandwagoning is stronger than some might anticipate

Some scholars might be surprised by the results of simulations that show increases in the quantity of individuals that do genetic bandwagoning (i.e., the cooperator type in the model), with parameter values (e.g., population quantity; relatedness; heritability of fitness) that are roughly in line with reported values for some species. This section explores why the likelihood of natural selection of genetic bandwagoning is stronger than some might anticipate.

6.1 Discussion regarding heritability values of quality and fitness

Insofar as an offspring produced by higher-quality and fitter individuals is more likely to be of high quality and fitness than an offspring produced by other individuals, then the natural selection of a bandwagoning variant that induces lower-quality individuals to forfeit resources is also more likely. Historically, theory has predicted the heritability of fitness to be minimally low—that is, that variation in fitness between individuals has been predicted to be far less attributable to genetic differences than to chance—because any alleles substantially contributing to fitness would be expected to gain fixation (thereby reducing genetic variance) far more rapidly than mutations would replenish variation at their loci (Borgia, 1979; Taylor and Williams, 1982). However, this prediction is evidently contradicted by the appearance in many species (e.g., birds of paradise, fish, frogs, insects) of "leks," which are groups in which males congregate to display signals of their quality to females (Kirkpatrick, 1982; Kirkpatrick and Ryan, 1991). Even though the lekking males contribute little to the females besides sperm, the females often exhibit a preference for the same male and incur costs to mate with that male, which suggests their preference occurs to ensure that their offspring have better genes (Kirkpatrick and Ryan, 1991; Rowe and Houle, 1996). This apparent contradiction between theory and empirical observations is known as the lek paradox (Borgia, 1979; Taylor and Williams, 1982; Kirkpatrick and Ryan, 1991; Kotiaho et al., 2001).

A well-received resolution to the lek paradox has emerged over the past several decades (Pomiankowski and Moller, 1995; Rowe and Houle, 1996) and is based on two premises: 1) An individual's ability to display for mates (e.g., with ornaments, dances, songs) depends upon that individual's condition and 2) There is substantial genetic variance in condition because condition is influenced by alleles at many different loci—enough loci that, each generation, there is a substantial amount of mutations at those loci, so variation is replenished each generation. The conclusion, therefore, is that a variance in display reflects a variance in condition. In recent years, scholars have also pointed to

epigenetic marks as a source of heritable differences in condition, particularly since epigenetic marks tend to be subject to a higher mutation rate than genes (Bonilla et al., 2016).

The heritability of fitness has been reported to be significant but low—approximately 10% (reviewed in Burt, 1995 and in Merila and Sheldon, 2000). In natural populations, heritability values for condition are sometimes substantially higher than heritability values for fitness (Kotiaho et al., 2001; Parker, T. and Garant, 2004; Birkhead et al., 2006), though the heritability of fitness is believed to occur through the "capture" of heritable condition (Pomiankowski and Moller, 1995; Rowe and Houle, 1996). As noted in section 1, "quality" in this manuscript is defined as an individual's ability to achieve fitness in an average environment, which distinguishes it from condition and fitness. Heritability of quality (by this definition) is likely to be higher than heritability of condition or heritability of fitness due to reversion to the mean. For example, in the results (section 4), higher values were calculated for heritability of quality than for heritability of fitness. In the model, an individual's quality was a determinant of the quantity of offspring it produced and also served as the mean to the normal distribution from which any offspring's quality value was randomly generated. Unsurprisingly, higher values of reproductive success tended to be disproportionately obtained by individuals that, out of luck, produced a fraction of the total offspring produced that generation that exceeded the proportion of their quality to the population's total quality—that is, individuals that had reproductive success above the value predicted by their quality—and the lower values of reproductive success were obtained by individuals that underperformed the proportion of their quality to the population's total quality. Yet, the quality values for any offspring—which wound up partly determining the offspring's reproductive success—were randomly generated from a mean equal to the parent's value for quality. In other words, an individual's reproductive success may have exceeded the value predicted by its quality, but the mean quality of that individual's offspring was still expected to be equal to the individual's quality and that partly determined the probability of the offspring's reproductive success. Consequently, the offspring of the individuals with the highest values of reproductive success were likely to have lower reproductive success than their parents and the offspring of the individuals with the lowest values of reproductive success were likely to have higher reproductive success than their parents. This is different from the calculation for heritability of quality: If a very high quality value—a value that significantly exceeded that of its parent—was generated for an individual, that value became the mean from which the quality of the individual's offspring was generated. For the same reason, the heritability values for fitness and condition that are reported in studies of natural populations likely underestimate the heritability value for quality that would be calculated in a

study upon the same populations using parent-offspring regression: As an individual's fitness (or condition) outperforms or underperforms the "goodness" of its genes (i.e., the individual's quality), the fitness (or condition) of each offspring is determined partly by the parent's quality and not by the parent's fitness (or condition), while the quality of each offspring is also determined partly by the parent's quality. This insight offers useful context in which to consider the heritability values for quality and fitness calculated using parent-offspring regression in section 4 with respect to the heritability values for condition and fitness that have been reported in natural populations: Values for heritability of condition and fitness would tend to correspond with higher values for heritability of quality.

6.2 An increasing difference between two lineages' expected quantities of descendants

Waite and Shou (2012, pg. 19084) wrote in a study of bacteria that "the probability of either type eventually dominating a co-culture is related to its initial abundance in the population because a larger population is more likely to sample better mutations." The same statement applies to lineages: A fitter individual's offspring are collectively more likely than a less fit individual's offspring to sample better mutations, so that not only does the fitter individual have a higher quantity of offspring, but the best mutations generated are likely to be obtained by the offspring of the fitter individual. Consequently, when the heritability of genetic quality is positive, the margin by which the expected quantity of descendants of a higher-quality individual's lineage would typically exceed the expected quantity of descendants of a lower-quality individual's lineage tends to increase from one generation to another. This is explained as follows.

Suppose that a high-quality individual produces s offspring and a low-quality individual produces r offspring, with $s > r$. Suppose this difference in fitness is partially because the high-quality individual has quality of value a and the low-quality individual has quality of value b, with $a > b$, so that the high-quality individual's offspring are expected to, on average, have a mean quality of a and the low-quality individual's offspring are expected to, on average, have a mean quality of b. Due to germ-line mutation and recombination, different offspring from the same parents are assumed to inherit different mutations and genetic combinations, some of which have a positive effect upon quality and some of which have a negative effect. Consequently, there is variation in the quality of the offspring about these mean offspring quality values. The variation in quality of the higher-quality

individual's offspring can be modeled as s random choices from a distribution that has a mean of a and the variation in quality of the lower-quality individual's offspring can be modeled as r random choices from a distribution that has a mean of b, with $s > r$ and $a > b$. Generally, if s random numbers are chosen from a distribution that has a mean of a and r random numbers are chosen from the same form of distribution (e.g., normal, Poisson) that has a mean of b and the same standard deviation and $s > r$, then the difference between the expected ith highest number chosen after s choices, E[Xis], and the mean of the distribution from which those s choices are drawn, a, exceeds the difference between the expected ith highest number chosen after r choices, E[Xir], and the mean of the distribution from which those r choices are drawn, b: E[Xis] - a > E[Xir] - b. Rearrangement provides: E[Xis] - E[Xir] > a - b. In other words, for every offspring produced by the lower-quality individual, it is expected that there is an offspring produced by the higher-quality individual that has a quality that is higher by more than a - b. The mean quality of the higher-quality individual's grandoffspring is, therefore, expected to exceed the mean quality of the lower-quality individual's grandoffspring by a margin that exceeds a - b, which is the margin by which the mean quality of the higher-quality individual's offspring is expected to exceed the mean quality of the lower-quality individual's offspring. In the same manner, the quality advantage of the higher-quality individual's lineage can be expected to increase with each generation in which the lineage has more fitness and the lineage is expected to have more fitness in each generation in which it has a quality advantage. As quality is a determinant of fitness, this serves to illustrate that if the heritability of quality is positive, the difference between two lineages' expected quantities of descendants, ceteris paribus, increases as the projection becomes increasingly long-term. This difference between the two lineages' expected quantities of descendants would continuously increase from one generation to another in an infinite population or continuously approach an asymptote from one generation to another in a finite population. The increases in expected lineage fitness of higher-quality individuals with increases in time of projection correspond to the average cooperator quantity increases with time that are observable in Figures 2 and 3: An advantage in quality predicts an advantage in quantity.

7. Applying bandwagoning theory to empirical phenomena

Like any model, this model uses numerous simplifications (see Appendix section A2). In the model, at a single time step, an individual has the binary decision to do reservation or not and then, subsequently, at a single

time step, the individual has the binary decision to do resonation or not. In the wild, there may be numerous gradations in the timing and magnitude of resonation and reservation practiced, upon which selection can act. It was suggested in section 2.3 that a reserving individual would downregulate reservation as conditions become more challenging. An individual may be able to modify its reservation in response to the degree of intensity of the conditions, so that if conditions elevate in intensity but fall short of being severe, an individual may continue to reserve, but less than before (see Appendix section A2.3 for more about this simplification). Additionally, a lower-quality individual may be able to do resonation in different time steps, forfeiting some fraction of its resources at different time steps, instead of relinquishing all of its resources at a single time step. This would be advantageous because the individual's lineage fitness outlook may change over the course of time, since individuals which formerly had higher lineage fitness outlooks might: 1) perish, while the focus individual does not due to luck or 2) no longer have higher lineage fitness outlooks because the changing environment has led different genes to be associated with a higher lineage fitness outlook. Insofar as an individual's lineage fitness outlook is low but is likely to change, that individual might use just enough resources to keep itself and/or its lineage alive and relinquish remaining resources unless, or until, its lineage fitness outlook changes. As resonation and reservation may occur in a more gradated manner, the downregulation in resonation and reservation that occur under more challenging conditions may also occur in gradations.

7.1 Explaining a focus herein upon reservation of abilities used against parasites

In the model, an individual's quality was unidimensional (see Appendix section A2.2 for a discussion about this simplification): A single number represented an individual's quality. However, in the wild, an individual may be better than conspecifics at one component of fitness (e.g., evading predators), but not as good at another (e.g., capturing prey). Reservation of abilities used against natural enemies is more likely to be selected than reservation of abilities used in other ways because the rapid coevolution of populations and their natural enemies (sensu the Red Queen's scenario: Van Valen, 1973) means that the association between any particular variant involved in combating natural enemies and fitness is likely to change faster from one generation to another than the association between any particular variant used in other ways and fitness. This makes it more likely that reservation against natural enemies is selected because there is more of a purpose in incurring a cost to identify whether an individual compares

favorably to conspecifics in a particular component of fitness if that individual is likely to differ from the rest of the population in that component. Or, put another way, there is no purpose in incurring a cost to evaluate an individual's trait if it does not differ from the rest of the population.

Additionally, an individual's reservation of abilities used against predators and parasites are more likely to be selected than reservation of abilities used against prey because an individual is more likely to be able to evaluate its abilities to capture prey if it does not do reservation. This is because an individual is likely to make many pursuits at prey throughout its life and is more likely to survive a failed attempt at prey than a failed attempt to evade a predator or a failed attempt to resist a parasite. Put another way, a surviving individual is more likely to know through the usage of honest signals how its success at capturing prey has compared to conspecifics than it is to know how its success at evading predators or parasites has compared to conspecifics because surviving individuals are more likely to have been perfectly successful at predator evasion and parasite resistance than at prey capture.

Many empirical phenomena for which the handicap principle is invoked are candidates for explanation by bandwagoning in the form of reservation. The focus below (section 8) is on examples of reservation that involve susceptibility to parasites, not predators. This is because empirical phenomena characterized by susceptibility to parasites (examples below) that can serve as examples of reservation are commonly not well-explained by the handicap principle. They often involve the suppression of some immunity factors within the body of the individual and as such, conspecifics usually have no way to directly verify this suppression, which raises the possibility that stepwise mutation can occur that allows the associated signal to be exhibited favorably, while also eliminating the susceptibility. By contrast, phenomena characterized by, for example, bright or weighty ornaments or the otherwise absence of camouflage can be interpreted as examples of reservation involving susceptibility to predators, but can also be explained by the handicap principle because the ornaments are directly viewable by the individuals that are, according to the handicap principle, the intended recipients of the signals. The more unique ability of bandwagoning theory to explain susceptibilities to parasites is why these phenomena are featured in the empirical reports considered below, but bandwagoning theory can also potentially explain many empirical phenomena characterized by susceptibility to predators.

7.2 Patterns consistent with bandwagoning

The following (section 8) are persistent empirical paradoxes that are potentially explained by genetic bandwagoning theory. They are characterized by: 1) indications to an individual that it is of lower quality, which appear to be followed by an underperformance by that individual in competition with conspecifics, e.g., for mates, food, and territory (which is consistent with resonation, sensu section 2.1); 2) indications to an individual that it is of lower quality, which appear to be followed by an increase in that individual's ability to survive parasites (which is consistent with a downregulation of reservation, sensu section 2.4); 3) indications of severe conditions faced by an individual that appear to be followed by that individual's increased ability to procure mates, food, and territory (which is consistent with a downregulation of resonation, sensu section 2.1); and 4) indications of severe conditions faced by an individual that appear to be followed by that individual's better performance in surviving parasites (which is consistent with a downregulation of reservation, sensu section 2.3). (Most of the empirical reports in section 8 include all four of these aspects.) Additionally, these empirical phenomena are considered paradoxes because it appears that the underperformance could have been avoided at a cost lower than that associated with the underperformance, which means they are not well explained by existing theory. Future work can further assess whether the underlying phenomena are suitable for explanation by genetic bandwagoning theory.

The division of these phenomena into categories is in accordance with how they are represented in the various literatures as paradoxes and should not be taken to suggest they do not cooccur in the same individual. Indeed, I do suppose that in numerous species, several of these phenomena would be represented in the same individual simultaneously, so that, for example, a low-quality individual might exhibit depression, might suppress reproduction, and might also signal honestly but unfavorably, despite apparent opportunities to cheat and a high-quality individual might incur a susceptibility to both predators and parasites, despite apparent opportunities for stepwise mutation to allow the avoidance of this susceptibility at a cost lower than that associated with the susceptibility.

7.3 Does stress indicate lower quality or more challenging conditions?

In numerous experiments, some of which are discussed in section 8, scholars have imposed a variety of stressors upon an individual in order to assess the effect of the stressor upon the stressed individual's fitness compared to controls. The results have varied by species, type, and dosage of the stressor, as well as by other

factors. Phenomena such as hormesis and overcompensation are characterized by favorable effects of stress upon fitness, which have particularly vexed scholars (see sections 8.6 and 8.7, respectively). These varying influences of stressors upon fitness are consistent with bandwagoning theory since stressors can indicate (1) the stressed individual's low quality, (2) challenging conditions, or (3) both. Bandwagoning theory would predict resonation in response to low quality and a downregulation of resonation in response to challenging conditions.

Certain stressors (such as rejection by a parent or mate or subjection to bullying) often result from an evaluation made by a conspecific (the parent, mate, or bully, respectively) that the stressed individual's quality compares unfavorably to others. Bandwagoning theory would, therefore, predict that an individual would respond to these kinds of psychological stressors imposed by a conspecific by being more likely to do resonation (and downregulate reservation).

Physical exercise can simulate challenging conditions associated with predator evasion, as physical activity can be both a cause and an effect of an increased predator threat (Sih et al., 2004). More specifically, it simulates a *successful* predator evasion unless it cooccurs with wounding. Consequently, bandwagoning theory would predict a downregulation of resonation in response to physical exercise.

It may be more complicated for a scholar to assess whether some other physical stressors indicate the stressed individual's low quality or challenging conditions (or both). Some factors that may influence the indication are as follows.

1) Context. Have other individuals been exposed to the same stressor or not and is the stressed individual capable of assessing via communication or honest signaling the degree to which neighbors have successfully managed the stressor? The more neighbors have been afflicted, the more conditions are to blame.

2) Type of stressor. It may be difficult to assess the degree to which other individuals have been exposed to the same stressor because the condition of some other individuals may not be knowable. Additionally, because of luck, one individual may be exposed to a parasite or predator threat, whereas another in the same population may not. Therefore, a bandwagoning variant may be selected to respond differently to different physical stressors. If there is typically low genetic variation with respect to managing a particular stressor, a bandwagoning variant may be selected to downregulate resonation in response to that stressor, since an individual's affliction with the stressor does

not indicate that individual's low quality (as other individuals would not be expected to be able to manage the stressor successfully). For example, for some plant populations ravaged by herbivory, survival may have more to do with luck than quality, so a bandwagoning variant in these populations would be selected to respond to herbivory by downregulating resonation. In the same way, though physical activity has been suggested above to simulate a successful predator evasion, the success may conceivably be relative. Hypothetically, if in some populations there were individuals in evolutionary time that could have evaded a predator by discouraging it through signaling, without expending substantial energy, then predator evasion through physical activity would have indicated a lower degree of success, due to an unnecessary energy expenditure, in which case there may have been natural selection of a bandwagoning variant that responds to physical activity by inducing resonation. Alternatively, under the assumption that it was rare in evolutionary time that there were individuals that could avoid a predator without expending energy, then the energy expenditure associated with predator evasion would not indicate low quality and then there may have been natural selection of a bandwagoning variant that responds to physical activity by downregulating resonation.

3) Success in management. If there is genetic variance in ability to manage a stressor, then the imposition of that stressor could result in a response that depends upon the degree to which that individual was successful in managing that stressor. For example, if an individual is infected, that individual's immune response could indicate that the individual has "good genes" for resisting that parasite, even if that individual's condition is lowered by the infection.

In sum, if an individual holds a bandwagoning variant, certain psychological stressors such as social defeat stress or rejection by a mate or parent are typically more suggestive of low quality rather than challenging conditions and can, therefore, be expected to result in a greater likelihood of resonation. However, if a stressor suggests challenging conditions rather than low quality, resonation is downregulated and fitness may increase. Certain physical stressors in particular contexts may cause a downregulation of resonation, though if the stressor is severe, the effect on fitness of a downregulation of resonation may be exceeded by the effect on fitness of the stressor itself. The more severe the stressor, the more likely the effect on fitness of the downregulation of resonation is exceeded by the effect on fitness of the stressor itself. Therefore, an inverted-U-shaped relationship between stressor intensity and fitness may be observed.

8. Paradoxes potentially explained by genetic bandwagoning theory

8.1 Depression

Report: Chronic bouts of stress lead, in many species, to anhedonia; diminished libido; and sadness, self-loathing, and/or self-neglect (Seligman, 1975; Weiss, J. et al., 1982; Sapolsky, 1998; Austin et al., 2001; Franklin et al., 2012; Anders et al., 2013; Sun et al., 2013). These symptom clusters indicate depression in humans (Austin et al., 2001; Anders et al., 2013; Sun et al., 2013) and learned helplessness in other species (Seligman, 1975; Weiss, J. et al., 1982; Sapolsky, 1998; Franklin et al., 2012). In humans, these symptoms often carry considerable costs, including risk of suicide and other causes of mortality (Hagen, 2003). Depression is also among the top five causes of disability throughout the world (Caspi et al., 2003) and thirty percent of lost productivity worldwide is believed to be caused by stress-precipitated psychiatric pathologies, such as depression, anxiety and schizophrenia (Nestler, 2012). Depression is also associated with increased physiological resistance against parasites (Kinney and Tanaka, 2009; Anders et al., 2013; Raison and Miller, 2013).

Paradox: There probably were mutations in evolutionary time that allowed individuals to avoid the evidently-costly depressive moods in response to stress. However, depression is prevalent during ages in which natural selection is strong (Medawar, 1952). Consequently, depression has long been considered an evolutionary paradox (Hagen, 2003; Nettle, 2004; Kinney and Tanaka, 2009; Varga, 2012; Raison and Miller, 2013). A set of recently-advanced hypotheses hold that depression was selected in conjunction with the prevention of infection by parasites and pathogens, in order to encourage energy preservation and solitude during times of high parasite risk (Kinney and Tanaka, 2009; Anders et al., 2013; Raison and Miller, 2013). Such a view dates to at least Hart (1988), but has become popular more recently due to evidence suggesting genetic and physiological links between parasite resistance and depression, wherein inflammatory immune responses can predict subsequent depression; depressive symptoms evidently resulting from a wide range of stressors are associated with stronger inflammatory immune responses, increased body temperature, and hypoferremia; and the few allelic variants that have been implicated in increasing depression risk are also involved in immunity, particularly inflammatory immune responses (Anders et al., 2013; Raison and Miller, 2013). However, while many causes of depression might have, historically, suggested an increased infection risk, other common ones (e.g., the death of kin or the loss of a mate without combat) may not have imposed enough of an infection risk to make depression beneficial to the individual or to kin, especially since kin can be adversely affected by an individual's depression (Ramchandani et al., 2005; Shen et al., 2016). That many forms of chronic stress precipitate a

costly depressive response tailored to parasite resistance seems very inefficient, which contrasts with the precision associated with other aspects of the stress response (Sapolsky, 1998). Indeed, depression is caused by numerous non-infectious diseases, even if the individual is unaware that he or she is diseased (Yirmiya et al., 1999; Dowlati et al., 2010; Irving and Lloyd-Williams, 2010; Parker, G. and Brotchie, 2017; Pryce and Fontana, 2017). Additionally, depression is a costly way of exerting a preference for solitude. As non-depressed individuals can exhibit a preference for solitude (Burger, 1995), there probably could have been mutations over evolutionary time scales that would have led a sick individual to prefer solitude without requiring that individual to incur the costs of self-loathing.

Potential explanation by genetic bandwagoning theory: Sources of chronic stress that cause an individual's depression—such as rejection by a parent, bullying by a conspecific, rejection by a mate, infectious or noninfectious disease, a parent's depression from the same sources (Yirmiya et al., 1999; Widom et al., 2007; Dowlati et al., 2010; Kaltiala-Heino and Frojd, 2011; Anders et al., 2013; Raison and Miller, 2013; Nestler, 2014)—are typically the sort that would suggest the individual is of low quality. When individuals experience chronic stress from these sources and subsequently incur the costs of depression, they act in a manner consistent with resonation. The lowered resistance to parasites by non-depressed individuals is consistent with reservation by individuals not identified as low quality. The increased resistance to parasites by depressed individuals is consistent with a downregulation of reservation by individuals identified as of low quality.

Notably, de Catanzaro (1981, 1984) independently arrived upon a similar evolutionary interpretation of depressive moods without accounting for the associated parasite resistance. He held that depression, with the associated suicidal ideations, occurs to increase inclusive fitness by offering an individual's resources to more productive individuals. He explained (1984, pg. 77) 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." I consider it appropriate to classify de Catanzaro's theory of depression as a bandwagoning theory of depression. However, bandwagoning theory does not require kin to benefit preferentially from the resources that are relinquished. This allows the bandwagoning theory of depression to better respond to a classic rejoinder to de Catanzaro's theory, which is, "why wouldn't a burdensome individual simply leave their kin" instead of committing suicide (Syme et al., 2016, pg. 189)? The answer is that the relatedness among human populations (Harpending, 2002) can be sufficiently high to allow natural selection of the forfeiture of resources by a significant

segment of low-quality individuals (according to the results in section 4). Therefore, even if a person with a low reproductive outlook 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 would still be likely to satisfy Hamilton's (1964) rule. The explanation offered by bandwagoning theory for depression also differs from de Catanzaro's theory because it: 1) places more of an explicit emphasis upon long-term fitness considerations and 2) offers an explanation for the enhanced resistance to parasites that tends to be associated with depressive moods.

Evolutionary explanations that maintain that the sole purpose of depression is to prevent infection risk fare poorly in explaining the finding that depression tends to result not from a single incidence of stress but from a prolonged (i.e., chronic) bout with stress and that the likelihood of developing depression is higher if an individual has a history of it (Ghaziuddin et al., 1990; Kendler et al., 2000; Solomon et al., 2000; Brilman and Ormel, 2001). Indeed, a history of chronic stress that has not yet resulted in an infection would suggest that further incidents of stress are less likely to be caused by infection. However, in the context of genetic bandwagoning theory, a history of chronic stress is more indicative than a single instance of stress that the stress was due not to luck but to the individual's genetic quality. Therefore, a bandwagoning variant would be more likely to induce its holder to completely forfeit its current resources and the resources it might subsequently obtain (i.e., via suicide) if the holder has had a history of chronic stress.

Moreover, according to theories holding that depressive mood occurs to promote isolation in order to prevent infection (Kinney and Tanaka, 2009; Anders et al., 2013; Raison and Miller, 2013), males should be more susceptible to depression than females, since, in evolutionary time, they were more likely to participate in hunting, escaping predators, and fighting conspecifics—activities implicated by Raison and Miller (2013) in imposing infection risk. Instead, males are significantly less likely to develop depression than females (Nolen-Hoeksema, 1990; Hopcroft and Bradley, 2007; Andrews and Thomson, 2009; Seedat et al., 2009), but have significantly greater parasite loads than females (Folstad and Karter, 1992; Klein, 2000). This sex disparity in depression is, however, explainable by a bandwagoning theory interpretation of depression. Bandwagoning theory offers that males would likely do more reservation, while females are more likely to do resonation (see Appendix section A3). Since bandwagoning theory would explain that depression is an example of resonation and the associated elevation in inflammatory immunity is a downregulation of reservation, females would be predicted to be more likely to be induced to experience more depression.

Additionally, if depression is an example of bandwagoning, there is evidence consistent with downregulation of both resonation and reservation under challenging conditions. Physical exercise occurred in evolutionary time as both a consequence and a cause of a predator threat (Sih et al., 2004) and, therefore, simulates challenging conditions. Numerous meta-analyses have found that physical exercise reduces depression incidence (Craft and Perna, 2004; Stathopoulou et al., 2006; Cooney, G. et al., 2013; Schuch et al., 2016; but see Krogh et al., 2017). If depression is an example of resonation, the reduction in depression incidence with exercise is consistent with a downregulation of resonation under challenging conditions. Physical exercise is also found in multiple species to raise resistance to infection (Davison et al., 2014; Bortolini et al., 2016). Insofar as the lowered parasite resistance that is associated with an absence of depression is an example of reservation, the raised parasite resistance that follows exercise is consistent with a downregulation of reservation under challenging conditions. The diminished depression that occurs with physical exercise is also more difficult to explain with a theory that depression occurs to reduce the risk of infection spreading, as it simulates hunting, escaping predators, and fighting conspecifics—all behaviors assumed by Raison and Miller (2013) to carry the most significant infection risk.

8.2 Differential nurturing

Report: In numerous rodents and primates, higher levels of maternal nurturing (e.g., licking and grooming) lead to more growth (Denenberg and Karas, 1959; Field, T. et al., 1986; Schanberg, 1995; Field, T., 1998), greater cognitive function and memory (Field, T., 1998; Korosi and Baram, 2009; Zhang and Meaney, 2010), higher alertness (Field, T. et al., 1986; Field, T., 1998), greater behavioral maturity (Field, T. et al., 1986), and lower mortality risk (Denenberg and Karas, 1959; Field, T. et al., 1986), while lower levels of maternal nurturing lead to a depressed-like phenotype, which includes depression (Franklin et al., 2010, 2011; Weiss, I. et al., 2011), anxiety (reviewed in Korosi and Baram, 2009; Weiss, I. et al., 2011), and greater tendencies to resign to stressful sources (Nestler, 2012). Despite the costs incurred by offspring that are nurtured less than others, mothers that are chronically stressed exhibit diminished nurturing across the aggregate of their offspring in comparison to mothers that are not chronically stressed (Bosch et al., 2007; Zhang and Meaney, 2010; Heiming et al., 2011; Mansuy et al., 2013). A mother's nurturing practices tend to remain consistent through her lifetime and her offspring are likely to impart the same levels of nurturing to their offspring that they received from their mother—within-lineage

consistency of maternal nurturing which is mediated epigenetically (Meaney, 2001; Zhang and Meaney, 2010; Mansuy et al., 2013; Drury et al., 2016).

Paradox: The popular evolutionary explanation for diminished nurturing by stressed mothers is that it acts as a signal to offspring regarding the level of vigilance required in the environment, particularly versus predators (Champagne et al., 2003; Pittet et al., 2012; Drury et al., 2016). However, maternal effects (e.g., licking, grooming) are dependent upon the father's experiences, even if the offspring share the same mother (and evidently the same formative environment) and even if the fathers have no postpartum interaction with the offspring. That is, even in the postpartum absence of fathers, offspring of fathers subjected to social defeat stress are induced via maternal effects to exhibit a depressed-like phenotype (Dietz et al., 2011; Dietz and Nestler, 2012), while offspring of enriched-reared fathers are nurtured more than other offspring (Mashoodh et al., 2012). Additionally, exposure to predator odor during gestation has often been found to stimulate postpartum maternal affection—the opposite of what would be expected if reduced nurturing were intended to increase vigilance toward predators (McLeod et al., 2007; Coutellier and Wurbel, 2009; Mashoodh et al., 2009; St-Cyr et al., 2018; but see St-Cyr and McGowan, 2015 for less nurturing by predator-odor-exposed mothers and see St-Cyr et al., 2017 for no differences in nurturing). Moreover, work by Sapolsky (1998) and Suomi (1997) suggests that reduced maternal nurturing results in offspring that become subordinates in groups and, therefore, achieve lower reproductive success. They independently documented what they considered inefficient stress responses in, respectively, baboons and rhesus monkeys. This condition, which Sapolsky (1998) and Suomi (1997) each considered maladaptive, is both a cause and an effect of reduced maternal nurturing.

Potential explanation by genetic bandwagoning theory: According to bandwagoning theory, a stressor can either indicate the stressed individual's low genetic quality, in which case resonation and a downregulation of reservation are expected to result, or challenging conditions, in which case a downregulation of both resonation and reservation are expected to result. Stress imposed on an individual would be expected to lead a bandwagoning variant within the individual's offspring to induce the same effects as it induces within the parent, insofar as quality is heritable and conditions are also inherited: A stressor that indicates a parent's lower quality also suggests its offspring's lower quality. In experiments on maternal nurturing, the types of chronic stress inflicted upon parents that have caused diminished nurturing to offspring have typically been bullying or restraint stress (Smith et al., 2004; Champagne and Meaney, 2006; Bosch et al., 2007). While restraint stress does not have a close analogue to wild conditions, stress from bullying indicates that the bullied individual's quality compares unfavorably to that of conspecifics insofar as a

subordinate status indicates lower quality (as suggested in Georgiev et al., 2015). Insofar as these experimental stressors have indicated low maternal quality, the resulting reduced maternal nurturing and consequent lowered offspring reproductive success are consistent with resonation by the offspring in response to the reduced nurturing. Additionally, reports that reduced nurturing causes increased vigilance to predators (Champagne et al., 2003) and that restraint stress causes increased resistance to parasites (Iwakabe et al., 1998) are each consistent with a downregulation of reservation by lower-quality individuals. Furthermore, as noted above, predator odor has frequently been found to increase maternal nurturing, which is consistent with a downregulation of resonation under challenging conditions.

Dickins and Rahman (2012) pointed to findings in some species that paternal absence and reduced maternal nurturing induce, in females, greater attractiveness to males and more indiscriminate, and earlier, sexual interest. They hypothesized that reduced nurturing serves to communicate to offspring that conditions are stressful and that, therefore, they should reproduce more indiscriminately. Dickins and Rahman (2012) did not distinguish between stressors indicating low quality and stressors indicating challenging conditions. They, therefore, predicted that indications of predator threats would result in lower levels of licking and grooming, which appears not to have been founded; indeed, as noted above, predator odor tends to stimulate higher levels of nurturing. As explained in section 2.4, a low-quality holder of a bandwagoning variant is induced to downregulate reservation in case severe conditions occur and to reproduce only insofar as severe conditions do occur. For the same reason, a low-quality holder of a bandwagoning variant might accelerate puberty in case severe conditions occur even as it reproduces only insofar as severe conditions do occur, which would explain the findings to which Dickins and Rahman (2012) refer. Indeed, females that physically develop faster often do not attain higher reproductive success (Ellis, 2004), which is consistent with the suggestion that low-nurtured females typically do resonation, even if they mature faster. (The relationship between age of pubertal development and reproductive success is not a simple one from which to draw conclusions, due to the alteration of pubertal timing by numerous factors besides psychological stress.)

The cooccurrence of hypotheses holding that depression is solely to prevent the transmission of infections (section 8.1) and hypotheses holding that a depressed-like phenotype is solely to maintain vigilance against predators (this section) lends credibility to the notion that these behaviors are not tailored to either purpose. Bandwagoning theory offers the explanation that these behaviors, which evidently impose reproductive costs upon

low-quality individuals, are, instead, examples of resonation by individuals identified to have low quality and that the associated parasite resistance and vigilance against predators are examples of reservation downregulation by individuals identified to have low quality.

8.3 Honest signaling and the susceptibility to parasites associated with sexually-selected characteristics

Report: In many species, androgens (e.g., testosterone) are evidently responsible for an association between an individual's quality and that individual's sexually-selected characteristics (e.g., strength, aggression, ornaments, songs, displays), wherein higher quality leads to higher androgen production, which leads to more advantageous sexually-selected characteristics (Nelson et al., 1989; Folstad and Karter, 1992; Johnstone, 1995; Dong et al., 2004; Muehlenbein and Bribiescas, 2005; McGraw and Blount, 2009; Ritschard et al., 2011; Lynn et al., 2015; Fedurek et al., 2016; Weaver et al., 2017). The production of androgens also appears to cause susceptibility to parasites in many species (Roberts et al., 2004; Habig and Archie, 2015). Numerous scholars have hypothesized that these phenomena owe to a tradeoff between sexually-selected characteristics and immunity, with higher-quality individuals being better able to sacrifice immunity in order to invest in sexually-selected characteristics, so they invest more in sexually-selected characteristics than lower-quality individuals (Folstad and Karter, 1992; Groothuis et al., 2005; Muehlenbein and Bribiescas, 2005). The tradeoff suspected is typically energetic (Groothuis et al., 2005), though other resources have been mentioned (Muehlenbein and Bribiescas, 2005).

Paradoxes: In particular, two paradoxes in the literature on sexually-selected characteristics are potentially explained by genetic bandwagoning theory.

1) Why do some sexually-selected exhibitions honestly reflect the exhibitor's quality despite apparent opportunities for mutations to evolve that would allow dishonestly advantageous exhibitions?

Many ornaments and other signals do not appear at all costly to produce (Husak and Swallow, 2011; Emlen et al., 2012; Simons et al., 2015), which raises the question: Why are they not faked? That is, why have there not been mutations that decouple the sexually-selected characteristics from the androgen production, allowing the advantageous characteristics to be exhibited even if the individual downregulates androgen production?

For example, carotenoid ornaments reliably reflect quality (through testosterone: McGraw and Blount, 2009; Weaver et al., 2017), even though carotenoids are evidently not limiting (Hill, 2006, 2014; McGraw and Blount, 2009; Simons et al., 2014). Simons et al. (2015) have proposed mutations that would allow an individual to cheat with a dishonestly advantageous ornament that would cost the cheater less than the cost imposed by honesty. The absence of these mutations in natural populations— and the prevalence of honest carotenoid ornaments— is difficult to explain.

Additionally, the well-studied zebra finches use song as an honest signal of quality, as song reliably indicates testosterone levels in development (Ritschard et al., 2011; Fedurek et al., 2016), even though: 1) song is metabolically cheap (Ritschard et al., 2010; Zollinger et al., 2011); 2) stressed birds incur song deficits even after a song allotment that is adequate for exact copying in other birds (Brumm et al., 2009); and 3) some nutritionally stressed populations of wild zebra finches have more complex songs than populations with greater food availability (Zann and Cash, 2008), all of which indicate that zebra finches could have evolved the ability to learn complex song irrespective of nutritional stress. The maintenance of zebra finch song as a reliable indicator of quality is, therefore, perplexing.

2) Why are sexually-selected characteristics associated with a higher susceptibility to parasites, even though the susceptibility is not well-explained in terms of an energetic tradeoff?

In a meta-analysis, Roberts et al. (2004) found no effect of androgens upon direct measures of immunity, but they did find androgens to increase ectoparasite abundance in several studies. In a larger, more recent meta-analysis, Habig and Archie (2015) replicated the finding that dominant males are consistently more susceptible to a breadth of parasites, but found that result "puzzling," since they could find no significant differences between the immune responses of dominant and subordinate males. They suggested that dominant males may suppress antibody production in response to antigens, which is an aspect of the less energetically costly Th-2 mediated immunity and which is contrary to how individuals reducing immunity to save energy would be predicted to operate (Lee, K., 2006). Consequently, Habig and Archie (2015) concluded that their results did not support the hypothesis that dominant individuals sacrifice immune function to engage in greater reproductive effort. Relatedly, Kankova et al. (2014) found that when Japanese quail offspring were subjected to moderate caloric restriction during development, the offspring with high egg testosterone content retained their growth advantage and did not suffer an immunity disadvantage, which, they concluded, contradicted a hypothesized tradeoff between growth and immunity. Interestingly, subordinate individuals do not exhibit stronger immunity responses or even greater resistance to

infections in general, though they exhibit heightened antibody responses to antigens that are representative of the immune challenges that would occur in a natural environment (Cavigelli and Chaudhry, 2012).

Potential explanation by genetic bandwagoning theory: The first paradox—the honest signaling of quality despite an apparent opportunity to cheat—is potentially explained as an example of resonation. When quality is signaled honestly, the favorability of the signal is determined by the signaler's quality, so that low-quality individuals signal less favorably. By signaling less favorably, low-quality individuals lose fitness, since mates, as well as food and territory, are more likely to go to individuals with better signals (Folstad and Karter, 1992; Hauser, 1997; Groothuis et al., 2005). The fitness costs from honest signaling of quality are, therefore, imposed differentially to low-quality individuals, which is consistent with resonation.

The second paradox—a susceptibility to parasites incurred by higher-quality individuals—is potentially an example of reservation. This explanation for the susceptibility to parasites of higher-quality individuals is supported by patterns of maternal investment of carotenoids in offspring. Scholars had predicted that maternal investment of carotenoids in offspring would be correlated with maternal investment of androgens (e.g., testosterone) so that carotenoids, which help fight infections, can compensate for androgens, which are associated with a susceptibility to infections (Safran et al., 2008). However, while androgens (e.g., testosterone), which promote growth, aggression, and sexually-selected characteristics, tend to be deposited more into offspring with higher-quality parents (reviewed in Groothuis et al., 2005), mothers tend to invest more carotenoids in offspring produced with lower-quality progenitors (Saino et al., 2002; Navara et al., 2006; Bolund et al., 2009). Additionally, females that can be expected to have the most resources and the highest reproductive success have been found to deposit lower concentrations of carotenoids into their offspring than other females (Safran et al., 2008). Moreover, offspring of progenitors that are experimentally infected with parasites—which can indicate either lower quality or more challenging conditions (section 7.3)—are allocated more carotenoids (Gil, 2008), which is consistent with a decrease in reservation that would be predicted by bandwagoning theory in response to either lower quality or more challenging conditions. These findings are consistent with an explanation offered by bandwagoning theory that there has been natural selection of bandwagoning variants that induce reservation (in the form of susceptibility to parasites) under unchallenging conditions to individuals that have not been identified as low quality. In these cases, a bandwagoning variant within a mother imposes the susceptibility upon its offspring.

There is also some evidence consistent with a downregulation of resonation under challenging conditions. Scholars have documented that individuals sometimes tend to exhibit more advantageous signals in response to being infected (reviewed in Duffield et al., 2017). These findings are typically explained in terms of the terminal investment hypothesis (Williams, 1966b; Clutton-Brock, 1984), which holds that an individual's investment in current reproduction should be inversely related to the individual's residual reproductive value. In terms of the terminal investment hypothesis, a stressor that suggests a reduced residual reproductive value would be expected to result in greater investment in current reproduction, which would explain more advantageous signaling that occurs in response to such a stressor. However, since evidence in favor of the terminal investment hypothesis is equivocal (Duffield et al., 2017), it is worth noting that imminent danger that results in more advantageous signaling is also consistent with a downregulation of resonation, as imminent danger can be indicative of challenging conditions. In studies that test the validity (and the extent of the applicability) of terminal investment theory, it is common for researchers to experimentally stress an animal (e.g., with infection, herbivory, perceived predator risk, hunger) and assess its signaling intensity, reproductive output, and longevity compared to controls. It is tricky to evaluate bandwagoning theory in terms of these studies because they have commonly been designed to test terminal investment theory, which holds that investment in present reproductive success will be higher if future reproductive outlook is lower, and which does not distinguish in its prediction on the basis of whether it will be lower because 1) the individual's quality is low or 2) conditions are challenging; therefore, scholars have generally not distinguished between the two causes of a reduction in future reproductive outlook. Alternatively, bandwagoning theory would predict that, in response to the first indication, an individual would be more likely to do resonation (and downregulate reservation) and, in response to the second indication, it would be more likely to downregulate both resonation and reservation. As discussed in section 7.3, an individual would assess whether the stressor suggests the first or the second indication on the basis of the type of stressor, the damage incurred as a result of the stressor, and the context of the stressor, for example, the degree to which it appears conspecifics have successfully managed the same stressor or indications regarding the number of predators that have threatened the population. Making such a distinction might be challenging for a researcher: An experimental infection might indicate that an individual has "good genes" for resisting a parasite afflicting the population, even if its condition is depleted in doing so.

Few clear patterns have been revealed across studies designed to test terminal investment theory. However, Duffield et al. (2017) observed that individuals exposed to low levels of infection tend to reduce reproduction,

whereas individuals exposed to high levels tend to increase reproduction. In terms of bandwagoning theory, exposure to low levels of infection may be more consistent with low genetic quality, whereas exposure to higher levels of infection may be more indicative of more challenging conditions. This may be because exposure to initial levels of infection causes resonation and a downregulation of reservation, reducing the individual's susceptibility and likelihood of further exposure. If the individual continues to be exposed despite the downregulation of reservation, it may be more suggestive of a threat of high intensity. In this interpretation, the reduced reproduction in response to low exposure would be consistent with resonation and the increased reproduction in response to higher exposure would be consistent with a downregulation of resonation.

8.4 Reproductive suppression

Report: Reproductive suppression (which has also been called "socially induced suppression," "physiological suppression," and "social contraception") occurs when subordinate individuals exhibit a diminished physiological capacity for, and/or interest in, reproduction. This has been documented in mammals, birds, fish, and invertebrates (Saltzman et al., 2009) and sometimes occurs even though subordinates show comparable body condition to dominants and overlap dominants substantially in age (Saltzman et al., 2009; Harrison et al., 2013). In some species, a group's subordinates are completely incapable of reproduction; however, their fertility and libido quickly return if the dominant group members depart the group (Sapolsky, 2001).

Paradox: There is well-established theory regarding how individuals in a group are expected to divide reproduction (Vehrencamp, 1983). However, multiple large reviews have determined that theory is not matched well by experimental and observation results (Field, J. et al., 1998; Nonacs and Hager, 2011). Indeed, a review by Nonacs and Hager (2011) reported (pg., 295) that "some individuals appear to behave suboptimally and lose fitness by either joining disadvantageous groups or not leaving them." Subordinates' reproductive suppression is considered an evolutionary paradox (Johnstone, 2000; Saltzman et al., 2009; Clutton-Brock et al., 2010).

Potential explanation by genetic bandwagoning theory: Insofar as a subordinate status indicates lower quality (as suggested in Georgiev et al., 2015), the inhibition of reproduction by subordinates and their associated fitness loss is consistent with resonation. Dominant individuals consistently have higher parasite loads across a variety of taxa

(Habig and Archie, 2015), which is consistent with their reservation and with a downregulation of reservation by subordinate individuals (see section 2.5).

Outside of the reproductive suppression literature, the hormesis literature (Calabrese, E. and Baldwin, 2001; Calabrese, E., 2005; Calabrese, E. and Blain, 2011; Calabrese, E., 2013a; Calabrese, E., 2013b) and the reproductive compensation literature (Gowaty et al., 2007; Gowaty, 2008; Ratikainen and Kokko, 2010) both document that certain stressors can increase an individual's fecundity. In particular, the hormesis literature documents that physical stressors such as insecticide, ethanol, and radiation can increase an individual's reproductive success (e.g., Ayyanath et al., 2013, 2014; Shephard et al., 2018) and strengthen antibody responses (Calabrese, E., 2005), in conjunction, apparently, with overall fitness gains. Insofar as these stressors indicate challenging conditions, the associated responses are consistent with a downregulation of resonation and reservation under challenging conditions. Hormesis and reproductive compensation are discussed in terms of bandwagoning theory in, respectively, section 8.6 and Appendix section A2.3.

8.5 Stress-induced anthocyanin production

Report: Plants of many species respond to a wide variety of stressors (strong light, UV-B radiation, temperature extremes, drought, nutrient deficiencies, bacterial and fungal infections, wounding, herbivory, herbicides, and various pollutants; Gould et al., 2009) by 1) producing anthocyanins, which imposes a photosynthetic cost (Manetas, 2006; Karageorgou et al., 2008; Gould et al., 2009) and 2) increasing production of their defensive compounds against parasites. The phenomenon is biochemically well-explained. Defensive compounds against parasites (e.g., phenols, tannins; Schaefer and Rolshausen, 2006) are produced in a common biosynthetic pathway with anthocyanins, causing plants to produce both defensive compounds and anthocyanins in response to stressors.

Paradox: An increase in defense compounds in response to stress should be possible without suffering a photosynthetic cost. That is, mutations could have evolved that would have decoupled the production of defensive compounds from the photosynthetic cost associated with the production of anthocyanins. Consequently, the production of anthocyanins during stress is an evolutionary paradox (Manetas, 2006; Gould et al., 2009; Cooney, L. et al., 2012; Kovinich et al., 2014; Menzies et al., 2016). Manetas (2006, pg. 173) echoed Haberlandt (1914) who wrote that "the general

physiological and ecological significance for the presence of anthocyanins in vegetative organs is still very obscure." The paradox is reinforced by an apparent evolutionary convergence. Plants of the order Caryophyllales do not produce anthocyanins. However, they produce betalains, which are produced by very different biosynthetic pathways, but which are considered to be a substitute for anthocyanins because, like anthocyanins, betalains evidently: 1) are produced in response to many sources of stress (e.g., UV light, drought stress, salt stress, cold temperatures, and pathogens); 2) reduce the light available for photosynthesis; and 3) participate in defense against herbivory (Steyn et al., 2002; Berardi et al., 2013; Hatlestad and Lloyd, 2015; Jain and Gould, 2015; Miguel, 2018; Polturak and Aharoni, 2018).

Potential explanation by genetic bandwagoning theory: To my knowledge, experiments involving anthocyanin production during stress have not attempted to identify whether the stress has suggested low genetic quality more than difficult conditions. Insofar as a stressor does indicate the plant's low genetic quality, then by producing anthocyanins, stressed (i.e., lower-quality) individuals incur a photosynthetic cost, which is consistent with resonation: A photosynthetic cost, ceteris paribus, reduces a plant's outlook for reproductive success (Obeso, 2002). Sunlight is different from other resources I have considered in examples of resonation because when it is relinquished by low-quality individuals, it is not as readily used by nearby individuals. A prediction associated with a bandwagoning theory explanation for the stress-induced production of anthocyanins is that other resources besides light are limiting to photosynthesis and that, in conjunction with incurring the photosynthetic cost, the stressed plant releases these limiting resources that can be used by neighboring plants. This would be an example of resonation. So why incur the photosynthetic cost? Indeed, the resonation could be conducted with solely the resource release, without incurring the photosynthetic cost. The leaf reddening itself in response to stress may be explained by the defense indication hypothesis (Schaefer and Rolshausen, 2006), the photoprotection hypothesis (Gould et al., 2018), and/or another hypothesis of adaptive function (Strauss and Whittall, 2006; Gould et al., 2009). However, bandwagoning theory can offer an explanation for why the leaf reddening is done by stressed individuals and not by unstressed individuals: Stressed individuals have less to lose from incurring a photosynthetic cost because they, in resonation, are sending to nearby individuals resources that limit photosynthesis. Consistent with this interpretation, plants have been documented to release numerous kinds of resources to neighboring individuals through mycorrhizal networks (Teste et al., 2009; Simard et al., 2012; Gorzelak et al., 2015) and the imposition of stress upon a plant has been documented to be a mediator of resource releases from that plant (Song et al., 2015). The increase in the production of defensive

compounds by stressed individuals that occurs concurrently with the anthocyanin production is consistent with a downregulation of reservation, which would be expected by individuals identified as low quality (section 2.4). Individuals not identified as low quality would not be expected to incur the photosynthetic cost of anthocyanins or betalains and, by not increasing defense compound production, they act in a manner consistent with reservation, which is also expected of individuals not identified as low quality (section 2.4).

Additionally, there is some evidence consistent with a downregulation of resonation and reservation under challenging conditions. "Plant growth promoting" bacteria and fungi have been found to increase both a plant's photosynthetic capacity and its production leaf phenols (Mucciarelli et al., 2003; Barka et al., 2006; Singh et al., 2015). Furthermore, there is evidence that a plant actively recruits these plant growth promoters when it is being subjected to stressors, such as parasites or drought (Yang, J. et al., 2011; Berendsen et al., 2012; Lee, B., et al., 2012; Kim et al., 2016; Kong et al., 2016; Naylor and Coleman-Derr, 2017). From a bandwagoning interpretation, the stressors would constitute the challenging conditions and the increases in photosynthesis and phenols would constitute the downregulation of, respectively, resonation and reservation in response to challenging conditions. The literature on plant growth promoting microbes is relatively young but future experiments can perhaps assess whether the stressors that lead to a plant's recruitment of plant growth promoting microbes are more indicative of that plant's quality or more indicative of challenging conditions. If this recruitment of plant growth promoters under stress is an example of a downregulation of resonation and reservation under challenging conditions, the latter would be true.

8.6 Hormesis

Report: Hormesis (Calabrese, E. and Baldwin, 2001; Calabrese, E. and Blain, 2011; Calabrese, E., 2013a; Calabrese, E., 2013b) is sometimes defined rather generally as a biphasic response to a stimulant, though the controversy about hormesis (Calabrese, E. and Baldwin, 2000; Forbes, 2000; Thayer et al., 2005; Cook and Calabrese, 2006; Mushak, 2009; Jager et al., 2013; LeBourg and Rattan, 2014; McClure et al., 2014) and the chief significance of hormesis to the current paper, owes to a prevalence of studies that have suggested (or concluded after experimentation) that stressors can cause the fitness of stressed individuals to be higher than controls. Numerous stressors (e.g., ethanol, radiation, insecticide, herbicide, caloric restriction, and temperature stress) have been cited (Mattson, 2008a; Rattan, 2008; Costantini et al., 2010; Rattan and Demirovic, 2010; Haddi et al., 2016; Vargas-Hernandez et al., 2017) for apparently increasing fitness in a wide variety of taxa (e.g., plants,

insects, invertebrates, humans), with the commonality being that the response is biphasic so that low doses of the stressor cause increases in fitness compared to controls and high doses of the stressor cause decreases.

Paradox: Many of the findings cited above were classified under the umbrella "paradoxical effects" before the term "hormesis" became commonly used (Calabrese, E., 2010). The "confusion and controversy" (Jager et al., 2013, pg., 263) about hormesis arises because, as McClure et al. (2014, pg., 2225) wrote, "Studies identifying beneficial influences of stress on fitness would challenge our understanding of evolution because it would imply that life histories are generally suboptimal." This apparent affront to well-established theory has inspired responses from numerous skeptical scholars (Forbes, 2000; Mushak, 2009; Jager et al., 2013; McClure et al., 2014). The most popular explanation among skeptics is that while one or more life history parameters may improve in response to stress, this occurs at the expense of one or more life history parameters and, therefore, does not increase Darwinian fitness. Historically, it has been supposed that stress-induced increases in reproduction come at the expense of longevity, though numerous reports have found the two parameters to both increase in response to stress (Costantini, 2014, pgs., 26-27). More recently, it has been argued (McClure et al., 2014) that stress-induced increases in life history parameters occur at the expense of immunity. However, numerous scholars have reported that a variety of stressors can induce an immunity improvement in conjunction with enhancements in other life history traits (Calabrese, E., 2005; Rattan, 2008; Costantini et al., 2010; Yang, G. et al., 2016; Cui et al., 2017). The longevity gains occurring commonly in hormesis appear to be partly caused by promotions of innate immunity (Gems and Partridge, 2008). The best-known examples of stress-induced benefits that do not rely upon immunity tradeoffs involve those studied in humans. Legions of doctors encourage their patients to engage in physical exercise, which is a stressor (it increases energy demands compared to controls), but at moderate doses (that is, moderate intensities and durations), it enhances immunity, longevity, and libido (Gleeson, 2007; Rattan, 2008; World Health Organization, 2010). People are similarly advised to consume the phytochemicals which are found in fruits, vegetables, and other sources. They improve immunity and overall health (Lampe, 1999; Leitzmann, 2016) and have also been argued to exert much of their favorable influences by invoking stress response pathways (Mattson, 2008a; Mattson, 2008b; Rattan, 2008; Calabrese, V. et al., 2012). Moderate caloric restriction can also improve health outcomes without impairing immunity (Youngman et al., 1992; Meydani et al., 2016). Thus, the paradox remains, heretofore, unresolved.

Potential explanation by genetic bandwagoning theory: Bandwagoning theory potentially offers an evolutionary explanation for hormesis because it does maintain that, as McClure et al. (2014, pg., 2225) put it, "life histories are generally suboptimal." That is, bandwagoning theory holds that individuals that are not undergoing challenging conditions would reserve and/or resonate and, consequently, would underperform the fitness of which they are capable. When conditions are challenging, individuals would downregulate reservation and resonation, which may lead to an increase in general functionality and Darwinian fitness. However, if conditions are too challenging, the negative influence upon fitness that is attributable to the conditions may be greater than the positive influence due to the downregulated reservation and resonation. This is consistent with the dosage-dependent nature of the fitness response to stress that occurs in hormesis and, specifically, the inverted-U-shaped relationship between stress and fitness that is often documented (Mattson and Calabrese, 2010).

Notably, the stressors documented to result in fitness gains are typically caused by, or simulate, abiotic or interspecific sources. Physical exercise has been suggested (section 7.3) to simulate a successful predator evasion. Pesticides, pollutants, and caloric restriction are the kinds of physical stressors that may suggest challenging conditions more than low quality, depending upon species, stressor, and context (as indicated in section 7.3). By contrast, to my knowledge, psychological stressors[4] such as bullying and rejection have not been found to result in hormetic fitness gains (see, for example, Van der Vegt et al., 2009), even though psychological stressors can have physiological ramifications (Sapolsky, 1998). These sorts of psychological stressors are the kinds of stressors that are most often indicative of lower quality, as explained in section 7.3.

The finding that males often experience greater benefits from hormesis than females (LeBourg et al., 2000; Sorensen et al., 2007; Costantini et al., 2010; LeBourg and Rattan, 2014) is also potentially explained by bandwagoning theory: Males would be theorized to engage in more reservation than females (see Appendix section A3). Therefore, a downregulation of reservation would result in a greater gain in ability against natural enemies for males. Females would be more likely to engage in resonation (see Appendix section A3) but a hormetic downregulation of resonation, which would be expected to lead to greater female fecundity, would typically not be identified in studies

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[4] There are some difficulties in assessing whether psychological stressors such as bullying and rejection have a favorable effect on fitness, since there is often no scholarly effort to distinguish between these stressors and other psychological stressors that are more suggestive of challenging conditions, such as how often a child was left home alone and how often a child's basic needs were not accommodated.

as a "benefit" of hormesis to females compared to males because it would also increase the reproductive success of males.

8.7 Overcompensation

Report: Numerous authors have found that grazing by herbivores or clipping by humans increases a plant's productivity or reproductive output, so that clipped or grazed plants are fitter than those that are not. This phenomenon is called overcompensation (Belsky, 1986; Paige and Whitham, 1987; Paige, 1999; Agrawal, 2000).

Paradox: As Lennartsson et al. (1997) wrote, "Overcompensation appears as a paradox because herbivory usually has negative effects on plant growth and reproduction and because overcompensating plants seem not to behave optimally in the absence of herbivory." Indeed, Belsky et al. (1993, pg. 109) wrote, "Neither life history theory nor recent theoretical models provide plausible explanations for the benefits of herbivory." Despite the development of theoretical models (Nilsson et al., 1996; Agrawal, 2000), overcompensation continues to be considered by some to be paradoxical (Juenger and Bergelson, 2000; Banta et al., 2010). A particular peculiarity is the recent finding that, in response to damage, plants can both augment chemical defenses and produce more seeds, which contradicts theory that predicts a tradeoff between resistance and fitness compensation (Mesa et al., 2017).

Potential explanation with bandwagoning theory: An increase in reproductive output in response to clipping or grazing would be consistent with a downregulation of resonation in response to challenging conditions. Overcompensation probably could be categorized as an example of hormesis (which is discussed in section 8.6), though it has not, to my knowledge, been noted yet in reviews of hormesis. Overcompensation is documented to occur more in populations that are more often grazed by herbivores (Lennartsson et al., 1997), which is consistent with bandwagoning theory since, in these populations, herbivory is more suggestive of challenging conditions characterized by the deaths of many plants. Bandwagoning theory would, therefore, predict natural selection of a bandwagoning variant that responds to herbivory in these populations by downregulating resonation.

The observed genetic variance in the degree of overcompensation (Strauss and Agrawal, 1999) is consistent with an explanation from bandwagoning theory. Low-quality individuals would engage in resonation under unchallenging conditions, so they would gain the most from forgoing resonation under challenging conditions and

insofar as quality is heritable, parents that gain the most from forgoing resonation are more likely to have offspring that gain the most. An explanation for overcompensation by bandwagoning theory also anticipates that clipping or grazing would only increase fitness at particular intensities and that at particularly high intensities, it would result in diminished fitness, which is consistent with a reported common decrease in plant fitness in response to herbivory (Belsky, 1986; Lennartsson et al., 1997). Additionally, the recent finding that some plants respond to herbivory by both augmenting chemical defenses and producing more seeds, contrary to the theorized tradeoff between the two (Mesa et al., 2017), would be explained under bandwagoning theory as a downregulation of both resonation and reservation, which would be expected to occur as conditions become more challenging.

9. Summary

The case for genetic bandwagoning that has been offered in the current paper is essentially four-fold:

1) Several fairly well-regarded theories advanced by others (section 1) are actually theories of genetic bandwagoning even though they do not invoke the bandwagoning term or metaphor.

2) The key premises (section 5) on which bandwagoning theory relies are also assumed by well-established theory.

3) A representative model (section 3) and corresponding tests (section 4) demonstrate that if parameter values are in line with reported values, a strategy combining resonation and reservation can be selected in favor of a defector strategy.

4) Bandwagoning theory offers an explanation for numerous, otherwise-paradoxical empirical phenomena (section 8). Though bandwagoning theory has not yet been experimentally tested in its ability to account for these phenomena, it may not surrender much of a head start in this respect to well-respected theories such as Trivers' (1971) reciprocal altruism and Zahavi's (1975) handicap principle, which were accepted on the basis of their plausibility and which, in the view of some scholars, have still been subjected to only minimal experimental analysis (Hammerstein, 2003; Silk, 2003; Grose, 2011).

9.1 Challenging bandwagoning theory

Even if parameter values are unfavorable to genetic bandwagoning, it is likely that some degree of bandwagoning occurs if the variation in quality is sufficiently high in natural populations. For example, even if values for relatedness are very low, some individuals are likely to have quality that is sufficiently low compared to conspecifics that a bandwagoning variant can be selected if it only induces forfeiture when located within individuals that have quality that is that low or below. (Such a bandwagoning variant might only do resonation, not reservation.) Others (see section 1) have essentially made this argument without invoking the bandwagoning term or metaphor when they have argued that resource forfeitures by moribund individuals might evolve. Such a variant itself could be quite prevalent, though relinquishment of resources might not be common because it may be that only a very low percentage of individuals in a typical generation has quality that is sufficiently low to induce the relinquishment.

Challenging that bandwagoning occurs with the prevalence suggested in the manuscript would involve not just questioning the model's resemblance to wild conditions—the model's simplifications are acknowledged (Appendix section A2)—but that the model was grossly unfair to the defector strategy and/or the parameter values used are unrealistic and that a more realistic test would demonstrate that bandwagoning is not selected with the same prevalence. The validity of genetic bandwagoning theory does not require it to be the best explanation for every (or even any) empirical phenomenon mentioned in section 8. However, the more empirical phenomena that can be explained uniquely by bandwagoning theory, the more prevalent it suggests genetic bandwagoning to be in natural populations.

9.2 Genetic bandwagoning as a mechanism for the evolution of cooperation

The evolution of cooperation is a perennial question (Hamilton, 1964; Trivers, 1971; Nowak, 2006, 2012; West et al., 2007; West et al., 2011). Cooperation is defined (West et al., 2007) as "a behaviour which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient." The resource forfeitures by low-quality individuals that result from genetic bandwagoning constitute cooperation that affords indirect genetic benefits (West et al., 2007; West et al., 2011) to the forfeiting individual. In comprehensive reviews of the evolution of cooperation, kin discrimination, green-beard discrimination, group selection, limited dispersal, and spatial selection have been offered as ways cooperation for indirect benefits can evolve (Nowak, 2006, 2012; West et al.,

2007; West et al., 2011). These are all ways of referring to a state in which cooperation evolves primarily because of a high degree of positive assortment in the population. In other words, cooperation that owes to these explanations satisfies Hamilton's rule primarily via high relatedness between the cooperating and benefiting individuals rather than a high benefit-to-cost ratio associated with the cooperation. Genetic bandwagoning is distinct from these explanations because cooperation that owes to genetic bandwagoning can satisfy Hamilton's rule even if relatedness is low, since it satisfies Hamilton's rule (which is $C < rB$) primarily via a high benefit-to-cost ratio (high B/C), which occurs due to the better abilities of "good genes" individuals to turn the resources into fitness over ensuing generations.

9.3 The evolutionary influences exerted by a bandwagoning variant

By inducing resonation and/or reservation, a bandwagoning variant potentially exerts various evolutionary influences upon the population in which the variant is selected and the natural enemies of that population. Through both resonation and reservation, a bandwagoning variant acts to direct resources from genotypes with a long-term fitness disadvantage to genotypes with a long-term fitness advantage. The bandwagoning 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 with a long-term fitness advantage, the bandwagoning variant accelerates the fixation of the alleles at other loci on these genotypes that are responsible for this long-term fitness advantage. Acceleration of adaptations that occurs this way is similar to the way that condition-dependent sexual selection can accelerate the fixation of adaptations (Lorch et al., 2003) in that both are ways by which higher-quality individuals are conferred additional fitness advantages.

By inducing reservation against natural enemies, a bandwagoning variant may exert a reverse effect upon these natural enemy populations. Just as reservation of ability against predators or parasites makes it more difficult for reserving individuals to survive against these natural enemies, it also makes the challenge of predating and parasitizing easier for the predators and parasites. This is especially true since reservation occurs when conditions are easy and there are few well-adapted predators and parasites. If reservation against predators or parasites were not undertaken and conditions were easy, individuals might be captured or infected by only the best-adapted individuals of the natural enemy population. As a consequence, the adaptations held by the few well-adapted

predators or parasites would rapidly gain fixation. However, insofar as reservation is undertaken, individuals become more easily predated or parasitized. Poorly-adapted individuals of predator or parasite populations that might have no success at predating or parasitizing an individual that does not reserve might be able to successfully predate or parasitize a reserving individual. Consequently, poorly-adapted predators or parasites are more likely to be able to reproduce, as reproductive success becomes more attributable to luck than it would have if reservation were not undertaken. Then the adaptations held by the best-adapted predators or parasites gain frequency more slowly that if reservation had not been undertaken. In this manner, a bandwagoning variant that induces reservation from ability that is used against a natural enemy population can act to slow the evolution of adaptations within that natural enemy population.

In sum, a bandwagoning variant can act to accelerate the evolution of adaptations within the population of individuals that hold the bandwagoning variant. A bandwagoning variant that induces reservation from a holder's ability that is used against a natural enemy population can also act to slow the evolution of adaptations within that natural enemy population. This may be relevant to a problem that famously baffled Wynne-Edwards (1962): What prevents the overpopulation of predators in natural populations? Scholars invoking the handicap principle have identified many more apparent handicaps to predator evasion than to prey pursuit (Zahavi and Zahavi, 1997). It has been argued here that the concept of reservation can explain many phenomena for which the handicap principle is typically invoked (see examples in section 8). Whether these burdens imposed to ability to evade predators are interpreted as handicaps (by the handicap principle) or reservation (by bandwagoning theory), the evolutionary influence is the same: In a focus population in which individuals incur a burden against their ability to evade predators, this incurred burden accelerates the evolution of adaptations used to evade predators and, in the predator populations, it slows the evolution of adaptations used to pursue prey (the prey being the focus population). This may help explain cases in which a focus population "stays ahead" of its predators (e.g., Sutrisno et al., 2014), as the predators stay ahead of their own predators.

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Appendix

A1. Guidance for variable values

Literature on humans primarily guides the values used for the simulations because humans are particularly well-studied and well-represented among the paradoxical empirical phenomena that bandwagoning theory can potentially explain (section 8) and because human populations are smaller than populations of other well-studied species, which makes the simulations more manageable.

The baseline N of 200 approximates Dunbar's (1993) predicted group size for humans. Human group size probably underestimates human population size. Since a larger population size benefits genetic bandwagoning (see section 4), this baseline number of 200 is conservative.

The baseline value for the standard deviation of the distribution from which quality values are selected is 1. The mean quality value across the population is 10, making the coefficient of variation (Houle, 1992) of quality also equal to 10, which puts it in line with that of the signaling of quality in numerous species (Pomiankowski and Moller, 1995). The standard deviation influences heritability values of fitness and quality. The resulting heritability values (Figures 2 and 3) are of the order of magnitude of values reported empirically (Merila and Sheldon, 2000).

Cooperators undergo reservation if their quality percentile is above 10 and they undergo resonation if their quality percentile is at or below 10 if no reservation has occurred and at or below 20 if reservation has occurred. These values approximate the percentage of individuals in human populations that battle depression (Kessler and Bromet, 2013), as well as the percentage of individuals in monkey populations that exhibit a high-reactive phenotype, characterized by social deficiencies and inadequate care for their offspring (Suomi, 1997), which is "virtually identical" chemically to major depression in humans (Sapolsky, 1998, pg. 293).

The baseline values for the quantity perishing prior to reproductive age approximate values reported for percentage perishing prior to reproductive age in preindustrial humans (Pettay et al., 2005). The baseline value for relatedness is in line with the approximation for human populations by Harpending (2002). Values for other variables are selected more arbitrarily, so a range of values is explored, with some values more favorable to bandwagoning and other values less favorable.

A2. Notable simplifications of the model

Simplifications are, by definition, part of models. In this section, I discuss particular simplifications that may be advantageous to cooperators (that is, simplifications that increase the likelihood of selection of bandwagoning) or defectors. In the model, cooperators forego fecundity if their quality is low in order to confer fecundity to higher-quality individuals that might be of the same type. The more the lineage fitness gained exceeds the lineage fitness lost, the more likely cooperators are successful. Therefore, simplifications of the model that are advantageous to higher-quality individuals are advantageous to cooperators, while simplifications that are advantageous to lower-quality individuals are advantageous to defectors. Below, simplification 1 is of uncertain effect, simplifications 2 - 4 are probably advantageous to cooperators, and simplifications 5 - 7 are probably advantageous to defectors.

A2.1 Simplification of uncertain effect: no modeling of sex

If a higher-quality individual and a lower-quality individual are modeled to produce offspring with the same mate, the resulting offspring of the higher-quality individual would have, on average, only one-half the quality advantage over the offspring of the lower-quality individual that the higher-quality parent had over the lower-quality parent. Thus, in a simple model, sex may exert a dilutive influence upon a lineage's quality advantage over another, which would be a disadvantage to cooperators. However, in a more sophisticated model that better resembles dynamics in the wild, there may be assortative mating by quality (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), such that higher-quality individuals are more likely to have higher-quality mates. If so, a lineage's quality advantage over another is more likely to persist, which would benefit cooperators. Additionally, if sexual selection is modeled, low-quality individuals that could have reproduced asexually may not be able to find a mate, in which case a low-quality individual would have less to lose by forfeiting resources prior to this anticipated sexual selection, the modeling of which would represent an advantage to cooperators.

A2.2 Simplifications that are advantageous to cooperators

1) The likelihood that all individuals in the population perish is nil

One restriction of the model is that the maximum quantity of individuals in the population that can perish prior to reproductive age during any generation is N - 1, not N. That is, there is no generation in which all individuals in the population perish prior to reproductive age. The stricter cutoff that allows solely one individual to survive increases the likelihood of fixation of a type that has a few very high-quality individuals in comparison to another type that has a higher quantity of individuals that are not as high quality. The cooperator type is more likely than the defector type to have a few very high-quality individuals because low-quality cooperators are more likely to forfeit resources, with the reproduction of cooperators becoming more concentrated among the highest-quality individuals of the cooperator type. Therefore, the cooperator type is more likely to benefit when it is common for N - 1 individuals to perish prior to reproductive age. This simplification likely did not substantially influence the results. In a test set of 10,000 runs with baseline values, there were no runs in which every individual in the population would have perished. Indeed, cooperators actually fared better when there was no perishing prior to reproductive age (section 4).

2) The probability of being randomly selected to produce offspring is constant throughout step #4

If an individual produces an offspring, it becomes burdened with protecting and providing for that offspring. Consequently, a parent is impaired in the production of offspring in comparison to an individual that does not already have offspring. However, in the model, if an individual is chosen to produce the ith offspring in step #4, it does not diminish that individual's likelihood of producing the jth offspring in step #4 (where $i < j$). This is a simplification that is advantageous to fitter individuals (which are more likely to be higher-quality), since at any given point, they are more likely to have produced prior offspring. However, this sort of simplification is not without precedent. For example, in the popular Moran (1958) model, an individual that is randomly chosen for reproduction during a time step is just as likely to be chosen to produce the offspring in the next time step as an individual that was not chosen.

3) There is solely one dimension of quality modeled

In the model, each individual's quality is characterized solely by a single number. This departs from a wild scenario in which an individual might be, compared to conspecifics, better in one component of fitness (e.g.,

fighting conspecifics, acquiring territory) and poorer in another (e.g., resisting parasites, evading predators). The modeling of a single dimension of quality is, however, not that different from a wild scenario because an individual's deficit (or strength) in one component is assumed to influence the individual in another. An individual that is, for example, better at catching prey than another individual is expected, ceteris paribus, to have an advantage in evading predators because it does not have to take as many risks as the other individual in order to catch prey. Likewise, individuals that are better able to avoid wounding or infection are advantaged in their pursuit of prey and their competition with conspecifics, since wounded or infected individuals are impaired in these regards.

However, in a more realistic (i.e., wild) scenario, there is the possibility that in different generations, some traits may have a higher selection differential than other traits in some generations and a lower selection differential in other generations. For example, if an individual is better than a second individual at capturing prey, while the second individual is better than the first at evading predators, the first individual has more of an advantage when prey are scarce and the second individual has more of an advantage when predators have proliferated. The relevance of more than one trait to an individual's lineage fitness outlook is suggested by the exhibition of multiple signals, each apparently signaling a particular trait (McCullough and Simmons, 2016).

The model does not offer representation to the possibility that there may be genetic or phenotypic variance in multiple facets, with associated selection strengths that differ from one generation to another. This simplification probably benefits cooperators (that is, increases the likelihood of selection of bandwagoning) because it means that alleles associated with a fitness advantage in one generation are more likely to be associated with a fitness advantage in subsequent generations. However, as noted in Appendix section A1, the baseline parameter values were selected partly so that the heritability values for fitness and quality that were generated during the running of the program tended to be in line with, or lower than, reported values for multiple species.

A2.3 Simplifications that are advantageous to defectors

1) No modeling of differential allocation

In many species, parents have been documented to allocate more resources to offspring produced with higher-quality progenitors (Burley, 1986; Sheldon, 2000; Harris and Uller, 2009; Stiver and Alonzo, 2009; Ratikainen and Kokko, 2010).

By investing more resources in offspring from higher-quality mates, parents invest more in offspring that figure to "generate higher returns on investment" than others (Sheldon, 2000; Harris and Uller, 2009). These additional resources to offspring with higher-quality progenitors do not improve the genes of the offspring, but they potentially improve the offspring's likelihood of surviving to reproductive age and the offspring's fecundity; thereby, they improve the lineage fitness outlook of the higher-quality progenitor. However, in the model (section 3), offspring of higher-quality progenitors do not receive an advantage in survival or fecundity in addition to their advantage in genetic quality.

Some studies have reported negative differential allocation, by which parents invest more resources into offspring produced with lower-quality individuals (Gowaty, 2003; Gowaty et al., 2007; Gowaty, 2008; Ratikainen and Kokko, 2010; Haaland et al., 2017). Owing to the youth of the literature reporting negative differential allocation, few patterns have been identified, but one apparent pattern, by which females invest more infection-fighting carotenoids in offspring produced with lower-quality mates, is argued (section 8.3) to be consistent with genetic bandwagoning. Another potential explanatory role for bandwagoning theory with respect to negative differential allocation may be that, in some studies, when experimenters prevent females from reproducing with their preferred males, this obstacle to reproduction with preferred mates may serve as an indicator to them that conditions are difficult, which therefore, according to bandwagoning theory warrants a downregulation of resonation and reservation. Indeed, in Gowaty's reproductive compensation theory—the most popular interpretation of negative differential allocation findings—primary reasons for the inaccessibility of preferred mates include predation and parasite risk (Gowaty et al., 2007; Gowaty, 2008). Another pattern of reverse differential allocation may involve anomalously high-quality females. Though female quality or attractiveness is seldom reported, findings of compensatory female investment have disproportionately involved a female sample with anomalously high quality, whether that quality was indicated by predation avoidance (e.g., Byers and Waits, 2006), previous fecundity (e.g., Bolund et al., 2009), or size (e.g., Braga Goncalves et al., 2010). The best interpretation of this pattern in terms of both bandwagoning theory and differential allocation theory may be that even the lowest-quality offspring of high-quality females can be expected to have good enough genes that its lineage can gain fixation.

2) No modeling of honest signaling of quality

The honest signaling of quality between individuals with competing interests is prevalently reported in the empirical literature on many species (Andersson, 1982; Kirkpatrick, 1982; Andersson, 1994; Hill and Johnson, 2012; Warren et al., 2013). Honest signaling of quality benefits higher-quality individuals because they send honest signals of quality that are more beneficial to them in deciding competitive bouts, obtaining mates, and garnering resources for themselves and their offspring (Kirkpatrick, 1982; Andersson, 1994; Hsu et al., 2006; Rutte et al., 2006). In section 8.3, I argue that honest signaling of quality between individuals with competing interests is uniquely explainable by genetic bandwagoning, which is a matter yet to be decided. However, the empirical report that honest signaling of quality is widespread is a matter separate from whether bandwagoning theory explains its prevalence. The modeling of honest signaling of quality would make genetic bandwagoning more likely to be selected due to the benefit it would offer to higher-quality individuals. Yet this benefit is not modeled herein (section 3): In the model, higher-quality individuals do not receive an advantage in survival or fecundity in addition to their advantage in genetic quality.

3) An individual can only distinguish between two degrees of conditions severity in two time steps

In the model, an individual can only determine whether the quantity of individuals that perished in step 1 was under π_1 and can only determine whether the quantity of individuals that perished in steps 1 and 2 was under π_2. This may be a somewhat conservative way of representing an organism's information about the severity of the conditions that it has experienced. While it is argued in section 2.4 that reservation would be hedged across individuals with a bandwagoning variant due to incomplete information about the severity of conditions, this incompleteness would refer to the conditions to be faced in the future, not conditions evaluated in retrospect. Wild scenarios may allow an individual to distinguish between more than two degrees of severity in its conditions after each of two time steps. If so, an individual can more precisely evaluate its lineage fitness outlook and, therefore, be more appropriate about whether or not to do resonation. Additionally, in the model, a decision to do reservation is binary: An individual can respond to conditions by deciding only whether or not to do reservation. However, in the wild, an individual may be able to adjust the degree of reservation according to the severity of conditions during a generation. This may make selection of bandwagoning more likely because it means that there may be more different variations of it upon which selection can act. Therefore, the model's representation of imprecise determinations regarding the severity of conditions may be unrealistically disadvantageous to cooperators.

A3. Some empirical findings suggest that reservation may be varied on the basis of sex

In section 2.4, it was suggested that, in addition to varying the degree of reservation it induces in response to the conditions during a particular generation, a bandwagoning variant would vary the degree of reservation it induces across its holders. If the natural enemy threat facing a population rapidly intensifies before a bandwagoning variant's holders can adjust by downregulating reservation, it is more likely that most or all holders of a bandwagoning variant become killed if they are all undertaking the same degree of reservation than if some holders are undertaking less reservation or none at all. So, in essence, a variation of reservation is a hedge against a rapid intensification of conditions—particularly the intensification of the natural enemy threat against which traits are reserved.

In section 2.4, it was suggested that a bandwagoning variant might induce less reservation if it is located in a holder that has already been identified as low quality. In the current section, it is suggested that a bandwagoning variant might also, in many species, induce less reservation if it is located in the sex that undertakes the lesser reproductive investment (typically, males). This pattern of variation would co-occur with variation by quality, such that males not already identified as low quality might reserve the most and females already identified as low quality might reserve the least. The variation of reservation by sex would be expected to be characterized by lower reservation by females than males in many species because a sudden increase in the severity of conditions, characterized by a proliferation of well-adapted predators and/or parasites, might kill many individuals. This would tend to drive the population far below its carrying capacity, as there would be a surplus of food and territory resources available due to the large quantity of perished individuals. In such a scenario, the bandwagoning variant would particularly "want" to be held by the sex that engages in greater reproductive investment, since fecundity is limited by this sex. In many species, this sex is female (Lively, 2011). (This is a departure from more ordinary circumstances, in which higher fecundity may not be indicated, since food or territory resources may not be sufficient to support such fecundity.) Therefore, a bandwagoning variant would vary the reservation it induces in a manner that would spare females if conditions turn severe: Under normal conditions, it would induce less reservation by females and more by males to ensure that females, in particular, are spared if conditions suddenly intensify.

If variation of reservation were to occur in this pattern, males would be more susceptible to natural enemies. Under a presumption that there is no difference in mean quality between male bandwagoning variant holders and female bandwagoning variant holders at the beginning of a generation, the male holders that survive to reproductive age would likely have a higher mean quality and lineage fitness outlook than the female holders that survive to reproductive age. This is because males reserved more, leading more of the low-quality male holders to have perished. Because of this, the bandwagoning variant is likely to induce resonation with less frequency in male holders than in female holders.

Higher male fecundity and greater male susceptibility to natural enemies are also compatible with popular theory, which holds that 1) males are expected to be more sexually indiscriminate due to their lower reproductive costs (Bateman, 1948; Trivers, 1972) and that male susceptibility to natural enemies may result 2) from tradeoffs associated with higher investment in male-male competition (Bateman, 1948; Trivers, 1972) and/or 3) from handicaps they incur against natural enemies in order to impress females (Zahavi, 1975; Grafen, 1990). It is worth noting that the first two of these assumptions have been challenged recently on theoretical and empirical grounds (Snyder and Gowaty, 2007; Gowaty et al., 2012; Tang-Martinez, 2016), though other authors have argued in their favor (Janicke et al., 2016). (The third, the handicap principle, has been discussed in section 2.6 in terms of reservation.) While bandwagoning theory is compatible with Bateman-Trivers theory in accounting for some empirical findings of the sex differences in fecundity and susceptibility to natural enemies, there may be a more unique role for bandwagoning theory in explaining other of these findings. Indeed, bandwagoning theory is compatible with critical points raised by Tang-Martinez (2012)—that Bateman-Trivers theory fails to explain phenomena such as male choice and sperm depletion. Additionally, females are significantly more likely to experience depression than males (Nolen-Hoeksema, 1990; Hopcroft and Bradley, 2007; Andrews and Thomson, 2009; Seedat et al., 2009). In section 8.1, depression is suggested to be an example of both resonation and a downregulation of reservation. The sex differences in depression are, therefore, consistent with a greater degree of resonation by females and a greater degree of reservation by males. Moreover, in numerous species, males are more susceptible to infection than females, which is attributable to both physiological and genetic differences that cause them to be more susceptible to infection even if the settings are controlled (Klein, 2000). Male parasite susceptibility owes to their suppression of Th-2 (humoral) immunity (Zuk, 1990), which, it was noted in section 8.3, is contrary to how individuals reducing immunity to save energy would be expected to act, but which is consistent with greater reservation by males.

Additionally, in dioecious plant species, male plants significantly exhibit lower concentrations of defense compounds, and are consistently subjected to more herbivore damage, than female plants, which may cause the female-biased sex ratios in natural populations (Agren, 1999; Cornelissen and Stilling, 2005). Moreover, in monoecious plants, the male stamen tends to have lower concentrations of defense compounds than female reproductive parts of the same plant (Sadikoglu and Cevahir, 2004; Serrano-Diaz et al., 2012). Sex differences involving parts of the same plant are particularly difficult to reconcile with tradeoff hypotheses. The interpretation offered by bandwagoning theory is that a bandwagoning variant induces males to reserve by resisting herbivores less effectively than they could, while female herbivore resistance is closer to maximal capacity in case well-adapted herbivores suddenly proliferate. The greater rarity of males or male parts that is expected due to this reservation gives the average male or male part that has survived reservation a higher expected fitness than the average female or female part. In this manner, the bandwagoning variant ensures that holders (or parts) that have survived reservation have, on average, higher fitness. There is some empirical support for the notion that monoecious plants invest more in defense compounds for female reproductive parts (Sadikoglu and Cevahir, 2004; Serrano-Diaz et al., 2012), even though this greater investment would be contrary to theory holding that the greater investment should be in the rarer sex (Fisher, 1930) and contrary in a manner consistent with bandwagoning theory.

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