The Evolution of Genetic Bandwagoning

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Abstract

The concept of "genetic bandwagoning" is introduced. In genetic bandwagoning, a bandwagoning allele evaluates the outlook for lineage fitness of the individual holding the allele. If its holder's lineage fitness figures to be low, the bandwagoning allele induces its holder to relinquish some, or all, of the holder's own resources (e.g., food, territory, mates), which are then used by individuals that happen to be nearby. While some nearby individuals may not possess a copy of the bandwagoning allele, it is likely, if assortment is sufficiently positive, that numerous individuals do and most of those that do have a better lineage fitness outlook than that of the individual that was induced to forfeit the resources, since the inducement is contingent upon a poor lineage fitness outlook. Due to their better lineage fitness outlook, the nearby individuals make better usage of the resources than the forfeiting individuals would have and the ratio between the quantity of descendants nearby individuals produce with the resources and the quantity of descendants that would have been produced by the forfeiting individuals tends to increase with each generation due to multiple reasons examined in section 2. If assortment is sufficiently positive, more copies of the allele are produced over the ensuing generations than if the resources had not been forfeited, as the allele is selected by "jumping on the bandwagon" of these fit lineages that use the resources.

Two ways to bandwagon are introduced: resonation and reservation. In resonation, the bandwagoning allele accomplishes the two steps of bandwagoning—1) evaluating its holder's lineage fitness outlook and 2) inducing a holder with a low (i.e., poor) outlook to relinquish resources—sequentially. The necessity for reservation occurs because a lineage's fitness outlook can depend upon aspects of quality which are difficult to evaluate during a generation in which many individuals are able to avoid death or serious harm. In reservation, a bandwagoning allele solves this problem of evaluating quality by inducing its holder to reserve from (i.e., withhold) some of its ability to survive against one or more natural enemies, particularly predators or parasites: An individual that can remain healthy in spite of reserving from its ability to survive predators or parasites is likely to have genes that enable its descendants to survive when the predator or parasite threat is more severe; however, if the individual perishes or becomes sick as a result of reservation, its lineage fitness outlook is determined to be low and the relinquishment of resources occurs with this same perishing or sickness. That is, the individual's perishing or sickness due to reservation serves simultaneously: 1) to identify that individual as having a low lineage fitness outlook and 2) as the source of relinquishing the individual's resources on the basis of this low lineage fitness outlook.

Genetic bandwagoning constitutes a novel mechanism for the evolution of cooperation. Numerous paradoxes can be explained by the actions of bandwagoning alleles that use a combination of resonation and reservation, including the phenotypic cooccurrences of robust defenses against parasites and depressive symptoms; phenotypic cooccurrences of robust defenses against parasites and photosynthetic costs; phenotypic cooccurrences of susceptibility to parasites and androgenic benefits; the maintenance of honest signals when there are opportunities to cheat; the forfeiture of reproductive opportunities by functionally capable individuals; and the differential nurturing of offspring.

Keywords:

handicap principle; honest signaling; cooperation; depression; social contraception

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 to anyone but are instead 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 should commit suicide. That is, they have argued that there can be natural selection for alleles that, under these circumstances, induce their holder to commit suicide, thereby relinquishing the holder's resources to nearby individuals (e.g., Dawkins, 1976; Refardt et al., 2013). Such scenarios are typically viewed in terms of Hamilton's (1964) rule, which holds that there can be natural selection for a social act if $C < rB$, where C is the cost to the actor; B is the benefit to recipients of the act; and r is the relatedness between the actor and the recipients. The cost of suicide is the reproduction that is foregone by the actor committing it. Since a moribund actor has low reproductive outlook, its cost of suicide is low compared to the benefit nearby individuals would receive from utilizing the actor's resources. The moribund actor can expect considerably lower fitness than potential recipients would from the same resources. Consequently, there can be natural selection for a trait that leads an actor to commit suicide in response to the actor's moribundity, even if relatedness between the actor and those benefitting is low (Refardt et al., 2013).

In the present paper, I argue that the forfeiture of resources by a lower-quality individual to nearby individuals has been naturally selected to occur: 1) in numerous circumstances besides the moribundity of the lower-quality individual and 2) via numerous mechanisms besides suicide. Forfeiture of resources from a lower-quality individual becomes naturally selected in more circumstances than are currently appreciated because most analyses of the evolution of social behavior examine solely the costs and benefits that result from an act by the first

[1] The term "quality" is used often but inconsistently in evolutionary literature (Bergeron et al., 2011; Hill, 2011; Wilson & Nussey, 2010). An individual's "genetic quality" is sometimes distinguished from its "phenotypic quality"; when this occurs, the former typically refers to "good genes" and the latter to condition. The latter is typically interpreted to be an indication of the former and that is how the terms are used in the present paper. I assume, unless indicated otherwise, that an individual's "quality" in either sense covaries positively with the individual's outlook for lineage fitness, so that a higher-quality individual can, on average, expect to have a higher lineage fitness than a lower-quality individual.

generation following the act (Hunt et al., 2004). However, the descendants of a higher-quality individual can often be expected to produce more offspring per individual than the descendants of a lower-quality individual. (Some reasons for this expectation are explored in section 2.) If this expectation holds, then forfeiture of resources by a lower-quality individual to higher-quality individuals is more likely to satisfy Hamilton's (1964) rule if the costs and benefits are projected longer-term than if they are only calculated for a single generation. This point is developed below.

Consider that a focus individual can expect to produce a quantity of A offspring but that, alternatively, it can forfeit its resources to individuals that can expect to produce a total quantity of B offspring with the same resources and that the relatedness between the focus individual and the individuals that would benefit is r. According to Hamilton's (1964) rule, the focus individual should forfeit its resources if[2]:

$$A < rB \tag{1}$$

Inequality (2) offers Hamilton's rule for the same scenario as inequality (1) but when looking two generations ahead instead of one, where S represents the quantity of offspring that each of the focus individual's offspring can be expected to produce, on average; V represents the quantity of offspring that each of the utilizing individuals' offspring can be expected to produce, on average; and the other variables are the same as in inequality (1):

$$AS < rBV \tag{2}$$

Inequality (2) demonstrates that as the focus individual looks ahead two generations, the cost of forfeiting the resources would be the grandoffspring it could obtain by using the resources (which is the product of A times S) and the benefit would be the grandoffspring the utilizing individuals could obtain with the same resources (which is the product of B times V). According to inequality (1), the focus individual that evaluates the costs and benefits solely one generation ahead would only forfeit resources if $A < rB$; however, according to inequality (2), if the same individual looks ahead two generations and anticipates that $S < V$, then it might forfeit resources even if $A \geq rB$. Similarly, if the same individual looks three generations ahead, it becomes still more likely to forfeit resources than

[2] In a sexual population, there is a 50% likelihood that the focus individual shares an allele with its own offspring and there is the same 50% likelihood that the benefiting individuals share an allele with their own offspring; therefore, these effects cancel out.

if it looks two generations ahead, if it expects that its grandoffspring would produce fewer offspring per individual than the grandoffspring of the individuals that would utilize the resources. And generally, if a focus individual looks $t+1$ generations ahead, it becomes more likely to forfeit resources than if it had looked t generations ahead, as long as it expects its descendants to produce fewer offspring per individual in generation t than the descendants of the utilizing individuals produce in generation t.

In the present paper, I introduce the concept of genetic "bandwagoning." A bandwagoning allele[3] remains latent when it is located within an individual with a sufficiently high lineage fitness outlook, but when it is located within an individual with a low lineage fitness outlook, it induces that individual to act in a manner that leads that individual to forfeit some or all of its resources, which are then utilized by whatever individuals are nearby. While some nearby individuals may not possess a copy of the bandwagoning allele, numerous individuals do if assortment is sufficiently positive and most nearby individuals have a higher lineage fitness outlook than that of the individual that forfeited the resources, since the forfeiture was contingent upon a low lineage fitness outlook. If the outlooks for lineage fitness of these individuals that use the resources are high enough compared to the lineage fitness outlook of the forfeiting individual and if assortment is sufficiently high, more copies of the allele can be expected to be produced over the ensuing generations if the resources are forfeited than if the resources are not forfeited. The allele can be said to "jump on the bandwagon" of lineages that have a higher fitness outlook. If a person "jumps on the bandwagon" of some entity (e.g., person, group, cause), it means that person has only decided to support that entity because it has become successful, with the expectation of sharing in the entity's future success. A "bandwagoning allele" fits this description. Regardless of whether or not the allele is located within an individual that has a high lineage fitness outlook, it is acting to increase the likelihood that resources to which its holder has access are utilized

[3] Two clarifications about the usage of the term "bandwagoning allele" in the present paper: The singular "bandwagoning allele" 1) is used to represent any heritable element(s) (e.g., gene, epigenetic mark) responsible for bandwagoning within a single individual and 2) may represent a multiplicity of heritable elements within that individual. The term "bandwagoning allele" is used to represent the totality of bandwagoning elements operating within a single individual and "bandwagoning alleles" is used to represent the totality of bandwagoning elements operating on a scale larger than the individual.

by individuals with a high lineage fitness outlook: If it is located within an individual with a high lineage fitness outlook, it is latent so that the individual can use its resources and if it is located within an individual with a low lineage fitness outlook, it induces forfeiture of resources so that they can be utilized by nearby individuals that have a higher lineage fitness outlook. Some of these forfeited resources are used by individuals that have a high lineage fitness outlook and a copy of the bandwagoning allele and the copies of the bandwagoning allele increase in quantity by being part of these lineages that have high fitness.

1.1) The concept of genetic bandwagoning illuminated via analogy

Consider an analogy to finance. A low-quality individual that is induced by a bandwagoning allele to forfeit resources to higher-quality individuals to which it is related by *r* is analogous to a person who forgoes investing his or her own capital in order to have it allocated by an investing manager who can earn a higher rate of return on the capital but who also keeps all but a fraction, *r*, of the final sum. In this analogy, the rates of return represent, respectively, the quantity of offspring the low-quality individual's lineage could produce per individual per generation and the quantity of offspring the higher-quality individuals' lineages could, on average, produce per individual per generation. The greater the difference in return rate, or in offspring produced per individual per generation, and the longer this difference persists, the lower the *r* that is acceptable. The obvious difference between these two cases is that in genetic bandwagoning, resources are forfeited to whatever individuals happen to be nearby, whereas in investing, people are typically aware of the specific quantities of capital they are directing to particular managers. However, in each case, the individual that gives up the assets (e.g., resources, capital) sacrifices some part of the ultimate proceeds. In exchange for investing capital, managers typically would keep some fraction of the final sum, leaving the person with the rest, which is analogous to how the descendants produced via forfeited resources would not all possess the bandwagoning allele, as some of the forfeited resources would be spent by individuals that do not share the bandwagoning allele. In both cases, the greater capabilities of those spending the assets would, over time, make up for that fraction of the proceeds.

Another analogy may also be illuminating. Maynard Smith (1978) wrote that the natural selection of alleles that increase mutation or recombination rates is best understood in terms of the hitchhiking effect, wherein an allele is selected not for its influence upon an individual's phenotype, but because it is located next to alleles that favorably influence an individual's phenotype. In Maynard Smith's thinking, a gene increasing the mutation rate

would exert mostly unfavorable effects upon the individuals in which it is located, but it would be selected if the descendants of an individual that is favorably affected were to gain in quantity over the ensuing generations until they more than make up for all of the individuals that were unfavorably affected. The mutator gene would be carried to higher frequency by the descendants of the favorably-affected lineage, having "hitched a ride" with them (Maynard Smith, 1978, pg. 113). A bandwagoning allele must also make up for a fitness loss it imposes upon some of its holders. For the bandwagoning allele, this loss is incurred by the holders that forfeit resources, some of which wind up being utilized by individuals that do not hold a copy of the bandwagoning allele. Like a hitchhiking allele, a bandwagoning allele makes up for that loss by "hitching a ride"—not with individual mutations but with an entire genotype as it gains frequency over the ensuing generations. An allele that jumps on the bandwagon of a genotype in the manner introduced in the present paper would likely continue to be associated with a fitter genotype, even if the genotype were subjected to recombination and sex, since, after recombination and sex, it would still be located with approximately half of the alleles to which its fitness advantage was attributable and since the half with which it would be newly located would likely also offer a fitness advantage, given sexual selection upon both males and females (Amundsen & Forsgren, 2001; Clutton-Brock et al., 2006; Edward & Chapman, 2011, 2012, 2013) and positive assortment by quality (Bos et al., 2009; Dakin & Montgomerie, 2014; Holveck et al., 2011; Holveck & Riebel, 2010; Schultzhaus et al., 2017; Veen & Otto, 2015).

1.2) Outline of the remainder of the paper

Section 2 examines three factors—differential allocation, heritability of quality and fitness, and stochastic dominance—that can often lead the lineage of a higher-quality individual to grow faster than that of a lower-quality individual, which increases the likelihood of natural selection for genetic bandwagoning because a forfeiture of resources from a lower-quality individual to higher-quality individuals is more likely to satisfy Hamilton's rule if the ratio of a higher-quality individual's number of descendants can be expected to grow compared to a lower-quality individual's number of descendants. Section 3 introduces two ways in which bandwagoning can occur: resonation and reservation. In particular, a model combining resonation and reservation is introduced verbally in section 3.2.5 and algebraically in section 3.3. Section 4 offers guidelines for applying this model that combines resonation and reservation to empirical phenomena and section 5 examines six empirical paradoxes that can be explained by this

model. The concluding section 6 includes interpretations of genetic bandwagoning as a mechanism for the evolution of cooperation and as a phenomenon that exerts significant evolutionary influence.

2) Why the ratio of a higher-quality individual's number of descendants to a lower-quality individual's number of descendants would grow over time

2.1) Differential allocation

Mothers commonly invest more resources in offspring that they produce with fitter and/or higher-quality fathers (Burley, 1986; Harris & Uller, 2009; Ratikainen & Kokko, 2010; Sheldon, 2000; Stiver & Alonzo, 2009). This has been reported to include investment in larger and more eggs, larger clutches, more androgens, and greater parental care (Stiver & Alonzo, 2009). Fathers have also been found to invest more in offspring produced with higher-quality mothers (Ratikainen & Kokko, 2010; Stiver & Alonzo, 2009). By investing more in offspring from higher-quality mates, parents invest more in offspring that figure to "generate higher returns on investment" than others (Harris & Uller, 2009; Sheldon, 2000).

A narrower set of analyses has reported what seems to be a reverse pattern, by which parents allocate more resources to offspring with non-preferred parents (Gowaty et al., 2007; Ratikainen & Kokko, 2010; Stiver & Alonzo, 2009). Findings fitting this pattern have usually been explained by invoking the reproductive compensation hypothesis (Gowaty, 2003; Gowaty, 2008; Gowaty et al., 2007), which is intended to explain parental allocation under the exclusive set of circumstances in which preference for progenitors is self-referential (Gowaty, 2008). However, an analysis by Harris & Uller (2009) concluded that greater investment in offspring with higher-quality mates can be expected to occur much more often than the reverse. Consequently, a lower-quality individual can often anticipate that its offspring are likely to receive less resources from a parent that mates with multiple individuals, which reduces the lower-quality individual's lineage fitness outlook compared to that of higher-quality individuals.

2.2) Heritability of quality and fitness

2.2.1) Genic capture explains the lek paradox

If higher-quality and fitter individuals are more likely than other individuals to produce higher-quality and fitter descendants, there is more likely to be natural selection for a bandwagoning allele that induces lower-quality individuals to forfeit resources. Historically, theory has predicted the heritability of fitness to be minimally low—that is, that variation in fitness between individuals would 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 & 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 & 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 & Ryan, 1991; Rowe & Houle, 1996). This apparent contradiction between theory and empirical observations is known as the lek paradox (Borgia, 1979; Kirkpatrick & Ryan, 1991; Kotiaho et al., 2001; Taylor & Williams, 1982).

A well-received resolution to the lek paradox has emerged over the past two decades. It holds that: 1) An individual's condition is influenced by alleles at many different loci—enough loci to allow a quantity of mutations from one generation to the next that maintains substantial levels of additive genetic variance for condition (Pomiankowski & Moller, 1995; Rowe & Houle, 1996) and 2) An individual's condition is a determinant of that individual's ability to exhibit displays for mates (e.g., ornaments, dances, songs); therefore, 3) These mate-attracting displays "capture" the individual's condition, so that a variance in display characteristics owes to a variance in alleles that contribute to 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).

2.2.2) Values of fitness heritability tend to underestimate the likelihood of natural selection for bandwagoning

The heritability of fitness has been reported to be significant but low—approximately 10% (reviewed in Burt, 1995 and in Merila & Sheldon, 2000). However, natural selection for genetic bandwagoning may be more likely than values of fitness heritability would suggest. Heritability of fitness is often calculated as a parent-

offspring regression: the covariance between parent fitness and offspring fitness divided by the variance of parent fitness. Multiple factors can exert an influence that leads the offspring of high-quality individuals to be fitter than their parents and/or the offspring of low-quality individuals to be less fit than their parents, which can lead covariance between parent fitness and offspring fitness (and, therefore, heritability of fitness) to be lower than otherwise, while also making natural selection for genetic bandwagoning more likely since these factors contribute to greater lineage fitness advantages for fitter individuals. These factors include differential allocation, which is reviewed above in section 2.1. Additionally, sexual selection can have the effect of reducing reproduction (in some cases to nil) by lower-quality individuals that would otherwise have the capacity to reproduce, since, in sexual selection, females exercise their choice to mate with higher-quality individuals. The occurrence of either sexual selection or genetic bandwagoning makes the other more likely to occur: If a female is likely to refuse to mate with a low-quality individual, a bandwagoning allele is more likely to be selected to induce forfeiture of resources by that low-quality individual prior to reproductive age, since it is less likely to reproduce anyway; likewise, a female is more likely to refuse to mate with a low-quality individual if it is likely that bandwagoning alleles located within that individual's offspring will induce them to forfeit their resources. These lower-quality individuals that do not reproduce because of sexual selection or genetic bandwagoning are not included as parents in parent-offspring regression calculations for heritability of fitness since they produce no offspring; however, they are included in these calculations as offspring and it is likely that the reductions in their fitness that result from sexual selection and genetic bandwagoning lead their fitness to be more dissimilar to that of their parents, which leads the covariance between parent fitness and offspring fitness (and, therefore, heritability of fitness) to be lower than otherwise. In accordance with this notion, sexual selection and genetic bandwagoning exert a greater influence upon the fitness of lower-quality individuals than upon the condition of lower-quality individuals, which may explain why heritability values for condition are often substantially higher than heritability values for fitness (Birkhead et al., 2006; Kotiaho et al., 2001; Parker & Garant, 2004), even though the heritability of fitness is believed to occur through the "capture" of heritable condition (Pomiankowski & Moller, 1995; Rowe & Houle, 1996). In sum, differential allocation and sexual selection can increase the likelihood of natural selection for genetic bandwagoning, yet differential allocation and sexual selection, as well as genetic bandwagoning, can reduce heritability values for fitness and differential allocation and genetic bandwagoning can reduce heritability values for condition;

consequently, reported values of heritability for fitness and condition can underestimate the likelihood that there is natural selection for genetic bandwagoning.

2.3) An increasing difference between two lineages' expected quantities of descendants

In section 2.2, it was noted that heritability values for both quality and fitness are often significantly positive. When the heritability of fitness is positive, the expected quantity of descendants of a fitter individual's lineage, ceteris paribus, increases from generation to generation in comparison to the expected quantity of descendants of a less fit individual's lineage. This is explained as follows. Suppose that one individual produces s offspring and another individual produces r offspring, with $s > r$, and suppose that the fitter individual's higher fitness is, at least, partly due to its "good genes." This means that the fitter individual passes at least part of its fitness advantage to its offspring. Suppose that this heritable fitness advantage is such that the offspring of the fit individual are expected to have a mean fitness of a and the offspring of the less fit individual are expected to have a mean fitness of b, with $a > b$. Due to germ-line mutation and recombination, different offspring from the same parents inherit different mutations and genetic combinations, some of which have a positive effect upon fitness and some of which have a negative effect. Consequently, there is variation in the fitnesses of the offspring of either individual about these mean offspring fitness values of, respectively, a and b and this variation is heritable, since it is due to mutations and genetic combinations. (There may also be environmental sources of variation in fitness, but the point here is that the variation is, at least, partly heritable and the following algebra concerns this heritable variation.) The heritable variation in the fitnesses of the fitter individual's offspring can be modeled as s random choices from a distribution that has a mean of a and the heritable variation in the fitnesses of the less fit individual's offspring can be modeled as r random choices from a distribution that has a mean of b. Since the fitter individual produces more offspring, $s > r$, and since the mean fitness of the fitter individual's offspring exceeds the mean fitness of the less fit individual's offspring, $a > b$. 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 i^{th} 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 i^{th} 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 less fit individual, there is an offspring produced by the fitter individual that has an expected fitness that is higher by more than a-b. Since these distributions represent the heritable variation of fitness, this higher fitness expectation is due to heritable factors and the heritable fitness advantage that is passed by the fitter individual's offspring to the fitter individual's grandoffspring exceeds a-b, which is the heritable fitness advantage that is passed by the fitter individual to its offspring. This serves to illustrate that if the heritability of fitness 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.

3) Two ways of bandwagoning: Resonation and Reservation

Section 3 introduces two ways in which bandwagoning occurs: resonation and reservation. In addition, section 3 offers detail about how resonation and reservation accomplish the two steps of bandwagoning: 1) evaluating the holder's lineage fitness outlook and 2) inducing a holder with a low lineage fitness outlook to forfeit resources. Section 3 builds up to a particular combination of resonation and reservation which is presented and explained verbally in section 3.25 and modeled algebraically in section 3.3.

3.1) Resonation

In resonation, the two aspects of bandwagoning are accomplished sequentially: A bandwagoning allele 1) evaluates its holder's lineage fitness outlook and 2) if this outlook is low relative to that of other individuals, it induces its holder to forfeit resources. The term "resonation" is chosen to represent this way of bandwagoning because it describes how the bandwagoning allele responds to an evaluation of its holder's lineage fitness outlook with a direct influence upon the holder's lineage fitness outlook that resonates with the evaluation: An already-low lineage fitness outlook is the catalyst for the bandwagoning allele to directly make that lineage fitness outlook even lower.

3.1.1) How a bandwagoning allele can evaluate its holder's lineage fitness outlook

Through various types of interactions with others, individuals receive information about their quality relative to conspecifics. A bandwagoning allele within an individual would evaluate the lineage fitness outlook of

its holder by using information from these interactions directly or by using its holder's hormonal responses to these interactions. Examples follow.

Parents evaluate the fitness outlooks of their offspring in order to determine how to allocate resources to their offspring in a manner that maximizes their "return on investment" (Harris & Uller, 2009; Sheldon, 2000). Consequently, the amount of resources and nurturing that an individual receives from its parents are indicators of that individual's lineage fitness outlook compared to its siblings. Likewise, both the "good genes" (Andersson, 1982; Byers & Waits, 2006; Iwasa & Pomiankowski, 1994; Moller & Alatalo, 1999) and "sexy son" (Fisher, 1930; Weatherhead & Robertson, 1981) hypotheses of sexual selection assume that individuals evaluate the fitness outlooks of potential mates in order to determine whether the production of offspring with them would constitute a good investment (Kokko et al., 2002). Therefore, the amount of positive attention an individual receives from potential mates constitutes an indicator regarding how that individual's lineage fitness outlook compares to that of conspecifics. Still another potential indicator of an individual's lineage fitness outlook involves direct competition, such as a competitive bout. Performance in competitive bouts determines dominance, which is often heritable (Boag & Alway, 1981; Dewsbury, 1990; Moore, 1990) and covaries with reproductive success (Andersson, 1994). Dominance is also often reflective of other aspects of a lineage fitness outlook (e.g., immunocompetence: reviewed in Georgiev et al., 2015), which supports the notion that a lineage fitness outlook determines dominance through an influence upon performance in competitive bouts. Additionally, individuals can directly compare the resources (e.g., territory) they have managed to obtain with those of other individuals. Individuals can also compare their quality to others via the exchange of honest signals (Andersson, 1994)—for example, honest signals of levels of stress incurred in development—which serves as another means of evaluating their lineage fitness outlook.

Many of the interactions mentioned above engender hormonal reactions that a bandwagoning allele can potentially use in order to evaluate the lineage fitness outlook of its holder. For example, in many species, individuals increase testosterone production in response to indications that they compare favorably to conspecifics, whether this is indicated by interactions with parents (Gil et al., 1999; Stiver & Alonzo, 2009), potential mates (Archer, 2006; Gleason et al., 2009; Oliveira, 2004), or rivals (Archer, 2006; Gleason et al., 2009; Mazur & Lamb, 1980; McCaul et al., 1992; Oliveira, 2004), which suggests a bandwagoning allele may be able to use the quantity and/or timing of testosterone production as a cue in evaluating its holder's lineage fitness outlook.

3.1.2) How a bandwagoning allele can induce its holder to forfeit resources

If a bandwagoning allele evaluates its holder to have a low lineage fitness outlook, it then induces its holder to forfeit resources. This can involve the suicide of the individual, which would result in a complete relinquishment of the resources to which the individual has access and would have access in the future. However, even if an individual's lineage fitness outlook is low compared to others, there is the possibility that it can change as a result of, for example, the deaths of other individuals or a change in its environment. If an individual's lineage fitness outlook is more likely to change, a bandwagoning allele is more likely to induce its holder to forfeit resources in a manner that allows the holder to stay alive and/or allows the holder's offspring (if any) to stay alive while still releasing some resources to nearby individuals that might have a more favorable lineage fitness outlook. One way of accomplishing this is to impose upon each holder, irrespective of that holder's quality, an honest signal of that holder's quality. The benefit from an honest signal of quality is correlated with the signaler's quality, so that honest signalers of high quality are favorably influenced by the signal, but honest signals can cost low-quality signalers food, territory, or mates. The food, territory, and mates are then utilized by nearby individuals. Thus, the imposition of an honest signal of a holder's quality, irrespective of that holder's quality, is a way of inducing a forfeiture of resources from lower-quality individuals while sparing higher-quality individuals, but also allowing lower-quality individuals to remain alive in case any of their fitness outlooks change. Additionally, the inducement of depression, self-handicapping, or a physical ailment upon a lower-quality individual can lead that individual to forfeit resources it might otherwise utilize, but also leave the individual alive. Other ways in which an individual with a low lineage fitness outlook can be induced to forfeit resources but remain alive include a cessation of the functioning of the reproductive apparatus, a reduced interest in pursuing mates, and a diminishment in sexually-selected characteristics. This point of allowing an individual with a low lineage fitness outlook to remain alive in case this outlook changes also goes for that individual's lineage. Therefore, there may be natural selection for a bandwagoning allele that allows an individual with a low lineage fitness outlook to produce some quantity of offspring that is lower than the maximum quantity of offspring or grandoffspring that it could expect to support. This would allow the individual's lineage to remain alive for another generation or two in case the lineage's fitness outlook changes, yet it would also free up resources to be used by lineages with a higher fitness outlook. Bandwagoning of this form might involve, for example, inducing an impairment in sperm competition or a diminished allocation of food or nurturing to extant offspring.

3.2) Reservation

3.2.1) The problem: Difficulty encountered in evaluating a holder's lineage fitness outlook

In preceding sections, it has been explained that a bandwagoning allele evaluates the lineage fitness outlook of the individual in which it is located and induces that individual to forfeit resources if that outlook is low. In resonation, a bandwagoning allele accomplishes the two steps of bandwagoning—evaluation and forfeiture—sequentially. However, there are heritable abilities that are relevant to an individual's lineage fitness outlook but that are sometimes difficult to measure even for the individual itself (or for a bandwagoning allele within the individual), which poses a challenge for the bandwagoning allele in its attempt to accomplish the first step of bandwagoning—that of evaluating its holder's lineage fitness outlook. The dilemma is clarified with the following discussion.

As a population coevolves with its natural enemies (e.g., predators, parasites, prey), there may be wide intergenerational variance in the quantity of individuals in the population that are able to survive and reproduce. In some generations, many individuals may be able to survive and reproduce. In other generations, a dearth of available prey or a proliferation of well-adapted predators or parasites may mean that only a few individuals survive to reproductive age. Individuals have a more favorable lineage fitness outlook if they have genes that can allow survival when prey are not plentiful and/or when there is a prevalence of well-adapted predators or parasites, though it can be difficult to determine which individuals have these "good genes" during a generation in which conditions are unchallenging and numerous individuals can survive to reproductive age.

In particular, it can be difficult to determine which of numerous living individuals are better at surviving predators and/or parasites, since it is frequently the case that an individual has either perished or has survived without injury from predators or parasites. This binary manner of classifying an individual's success at surviving predators and/or parasites differs from that of acquiring prey and/or territory, which is more given to representation with a continuum, since an individual that occasionally fails at either prey or territory acquisition is more likely to remain alive than an individual that fails against predators or parasites. As the life-dinner principle goes, a predator that is unsuccessful loses its dinner, while a prey that is unsuccessful loses its life. In other words, an individual is more likely to be able to determine, with honest signaling, whether the quantity of meals it has missed is more or less than that of another individual than whether the quantity of predator encounters it has failed is more or less than

that of the other individual, since it is more likely that both individuals have survived all predator encounters without injury than it is that both have never missed a meal.

Even if two individuals can survive to reproductive age in unchallenging conditions, one individual's descendants may be less likely than the other individual's descendants to survive to reproductive age. One reason this may occur is that the former individual's survival is more attributable to luck. Perhaps that individual would have been captured by numerous predators that, instead, pursued other prey or would have been killed by several parasite strains but was, instead, exposed to weaker ones, while the latter individual has genes and/or epigenetic marks that allow it the speed, strength, mimicry or camouflage (or other factors) to survive many of the natural enemies to which the former individual would have succumbed. Another possible reason is that, even if the two individuals are exposed to largely the same natural enemies, the former individual may be able to survive by a lesser margin than the latter individual. That is, some natural enemies may be nearly fast enough, strong enough, or otherwise well-adapted enough to successfully predate or parasitize the former individual, but not so nearly the latter individual because of genes and/or epigenetic marks held by the latter individual. Even though both individuals may be able to survive to reproductive age, descendants of the predators and parasites that are better-adapted than their predecessors are more likely to kill descendants of the former individual than those of the latter individual. Thus, two reasons have been identified for why one individual may be able survive to reproductive age as well as another individual, even though its descendants are less likely to survive and reproduce than descendants of the other: 1) the former individual's luck of exposure to less well-adapted natural enemies and 2) the former individual's lower margin of survival against the natural enemies that both faced. Hamilton's rule might be satisfied by a forfeiture of resources from the former individual to the latter individual due to the higher lineage fitness outlook of the latter individual, except that neither individual knows which has "better" genes for surviving the natural enemies that afflict the population because both individuals are able to survive to reproductive age.

3.2.2) A solution to the problem of evaluating a holder's lineage fitness outlook: Reservation

A bandwagoning allele can solve this dilemma of evaluating its holder's lineage fitness outlook by inducing its holder to act in a manner that detracts from its ability to survive predators and/or parasites. That is, the bandwagoning allele can reserve (i.e., withhold) some of its holder's capacity to survive one or more of these natural enemies. In section 3.2.1, it was argued that one surviving individual's descendants are less likely to survive to

reproductive age than those of another surviving individual if: 1) the former individual's survival was attributable to a lack of exposure to more well-adapted predators or parasites in the population that would have killed it but the latter individual's survival was less attributable to luck and could have survived more of the natural enemies that would have killed the former individual or 2) there were natural enemies that were nearly well-adapted enough to have killed the former individual but the latter individual was able to survive more securely. The reservation induced by a bandwagoning allele can serve to reduce the likelihood of both of these two causes of the survival of a less well-adapted individual. That is, a bandwagoning allele can reduce the likelihood of the first cause by increasing its holder's exposure to natural enemies, which diminishes the likelihood that there are well-adapted natural enemies to which the individual is not exposed. For example, it can induce its holder to position itself in close proximity to predators, to make conspicuous displays or loud calls, or to eschew certain forms of mimicry or camouflage, all of which would increase its holder's exposure to natural enemies. Furthermore, a bandwagoning allele can reduce the likelihood of the second cause by inhibiting its holder's ability to survive the natural enemies to which the holder is exposed, which leads to the perishing of individuals that, without reservation, would be able to survive by a low margin. For example, it can induce its holder to do such things as exhibit weighty ornaments or produce lower quantities of antibodies than otherwise, which would impair its holder's ability to survive the natural enemies to which it is exposed.

If a holder can survive in spite of this reservation, it is more assured of being able to produce descendants that will be able to survive to reproductive age during conditions that are more severe. Alternatively, a holder may perish or become sick as a result of this reservation, in which case it would forfeit some or all of its resources to nearby individuals. That is, if a holder perishes or becomes sick as a result of reservation, the two steps of bandwagoning are accomplished simultaneously: The identification of the holder's poor lineage fitness outlook and the forfeiture of that holder's resources both occur with the holder's perishing or sickness.

A reader may wonder about the purpose of inducing an individual to perish in order to forfeit resources to individuals with "better genes" when that individual's descendants would forfeit their resources to the descendants with "better genes" when they perish: If the resources are going to the descendants with "better genes" anyway, what's the purpose of inducing reservation in order to forfeit the resources a generation or two beforehand? The answer is that there is no guarantee that an individual with "better genes" will produce any surviving descendants, as

some of the population's predators or parasites could evolve to be so well-adapted that the entire population is killed prior to reproductive age. However, the more descendants that are produced by individuals with "better genes," the more likely it is that at least one will be able to survive to reproductive age. Likewise, the more descendants produced by "better genes" individuals that hold the bandwagoning allele, the more likely the bandwagoning allele gains fixation by being located within an individual capable of surviving a very well-adapted natural enemy population.

Natural selection would act on multiple aspects of this reservation, including the natural enemies against which the reservation occurs and the degree to which it occurs. A bandwagoning allele should not be expected to evolve to induce reservation of its ability against all of its holder's natural enemies. If there are seldom generations in which a particular natural enemy population evolves in such a manner that it kills most of a population's individuals, it is unlikely that a bandwagoning allele in that population would evolve to induce its holders to reserve from its ability against that natural enemy population, since lineages of holders that survive the reservation are unlikely to have a fitness advantage in ensuing generations.

3.2.3) The possibility of adjusting the degree of reservation to the severity of the threat

A bandwagoning allele 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 against better-adapted natural enemies. Alternatively, a bandwagoning allele that induces too much reservation runs the risk of inducing the death of every holder of a bandwagoning allele in the population, as even the individuals with the "better genes" against the natural enemies would not be able to survive the reservation, whereupon there would be no individuals with a bandwagoning allele left to utilize resources forfeited by the perished individuals. However, what constitutes an appropriate degree of reservation suitable for the satisfaction of Hamilton's rule may vary from generation to generation. As noted in section 3.2.1, 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. During some generations, many individuals may be able to survive to reproductive age. During other generations, there may be only a few individuals that can survive, owing to the proliferation of well-adapted predator or parasite individuals. 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." If few individuals remain alive, it is less likely that the average individual that would utilize the forfeited resources is substantially more capable at evading the natural enemies than the forfeiting individual would be. Consequently, it is less likely that Hamilton's rule would be satisfied by the forfeiture. Natural selection would, therefore, act upon a bandwagoning allele to vary the degree of reservation it induces during a generation or a point in a generation, such that it would reserve more if many individuals have been able to survive and it would reserve less if many individuals have perished during the generation or if numerous individuals have rapidly perished within a short time period.

A problem with this manner of calibrating the degree of reservation to the threat presented by a natural enemy is that the threat presented by predators or parasites can escalate with little warning. A predator or parasite population can evolve during what constitutes a generation for, respectively, a prey population or a host population. Indeed, a parasite epidemic is often apparent only in retrospect. Therefore, a bandwagoning allele 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 rapidly intensifies. If this were to occur, there would be no bandwagoning allele holders left to utilize the resources forfeited by the perished individuals. Therefore, it is likely that there would be natural selection for a bandwagoning allele that hedges against the possibility that conditions rapidly deteriorate by varying the timing and degree of the reservation it induces its holders to undertake.

3.2.4) Varying the timing and degree of reservation

A bandwagoning allele that hedges in this manner may vary the timing and degree of the reservation it induces depending upon certain characteristics of its holder, such as, for example, whether the holder is male or female or whether the holder is a first-born or later-born individual. A hedge based upon the timing of reservation may involve a bandwagoning allele that induces holders with one characteristic to reserve during a particular span in its life history and holders with another characteristic to reserve during another span in its life history. A hedge based upon the degree of reservation may involve a bandwagoning allele that induces holders with one characteristic to reserve more over the totality of its life than holders with another characteristic. In a model offered introduced in section 3.2.5, a bandwagoning allele varies the degree of reservation based upon indications about the holder's quality.

3.2.5) Hedging the degree of reservation based upon a tentative evaluation of a holder's lineage fitness outlook

Prior sections have included discussion of the premise that at any particular time during a generation, an individual (and a bandwagoning allele within the individual) has partial but incomplete information about that individual's lineage fitness outlook. It was explained in section 3.2.1 that an individual (and a bandwagoning allele within the individual) is more likely to know how its ability to procure food or territory compares with that of other individuals than how its ability to survive predators or parasites compares with that of other individuals. Reservation has been presented as a way that can be used by a bandwagoning allele to identify its holder's abilities in areas that are difficult to evaluate when conditions are unchallenging (e.g., its holder's ability to survive against predators or parasites) in order to garner greater certainty about the holder's lineage fitness outlook. Discussion in section 3.2.4 focused upon the role of varying the timing and degree of reservation based on the holder's particular characteristics. The present section 3.2.5 considers a bandwagoning allele that varies the degree of reservation it induces depending upon the information about the holder's lineage fitness outlook that it has already received. Specifically, holders that have received information indicative of a favorable lineage fitness outlook are induced to reserve more over the course of their lives and individuals that have received information indicative of a less favorable lineage fitness outlook are induced to reserve less over the course of their lives. This information regarding the holder's lineage fitness outlook can come in the forms reviewed in section 3.1.1. That is, individuals that have, for example, been preferred more by parents and mates, acquired more food and territory, and performed better in competitive bouts are induced to reserve more against a natural enemy. In accordance with the discussion in section 3.2.1, it is less likely that individuals would receive information about their ability to survive against parasites or predators; however, any individuals that are sickened by parasites or wounded by predators but remain alive are induced to reserve less against a natural enemy. Natural selection would act upon a bandwagoning allele to vary reservation in this manner for the following reasons.

If the information available suggests that a holder's lineage fitness outlook is high—that is, if a holder fares well in comparison to other individuals in, for example, food, territory, and mate acquisition—a bandwagoning allele would induce its holder to reserve against one or more natural enemies in order to determine whether the holder has high ability against these natural enemies, in addition to the other abilities that have led to the favorable

outlook; if so, its outlook can be evaluated to be high with greater certainty. However, the more poorly a holder compares to other individuals in food, territory, and mate acquisition, the more likely it is that Hamilton's rule would be satisfied by the holder's forfeiture of resources if the bandwagoning allele's information about its holder's lineage fitness outlook were more complete—if, for example, the holder's abilities against predators and parasites were known in comparison to other individuals. This is because the lower a holder's abilities to acquire food, territory, and mates compared to others, the more likely it is that there are numerous individuals that have both better abilities to acquire food, territory, and mates and better abilities against predators and parasites and, therefore, the more likely it is that Hamilton's rule would be satisfied if the holder were to forfeit its resources because there would be enough individuals utilizing the resources that have a more favorable lineage fitness outlook and a copy of the bandwagoning allele. In fact, if the tentative evaluation is that the individual's lineage fitness outlook is very low, the best chance that Hamilton's rule would not be satisfied by a total forfeiture of that individual's reproduction is likely to be if severe conditions suddenly ensue, characterized by a newly well-adapted natural enemy population, such that many individuals that formerly had a more favorable lineage fitness outlook and were induced to engage in reservation were to perish due to the reservation. However, if the holder with a low lineage fitness outlook were to have reserved as much as other individuals and these severe conditions were to have occurred, the holder would have likely been among the perished due to its reservation. In other words, a holder with a very low lineage fitness outlook will probably satisfy Hamilton's rule by forfeiting resources even if they can survive in spite of reservation, unless conditions are severe enough to kill most (or all) reserving individuals, but if they were to reserve, they would also probably perish. That is, reservation is probably pointless for individuals with a very low lineage fitness outlook, but if they do not undertake reservation, they have a chance of surviving the severe conditions that would warrant their reproduction (that is, conditions that would mean their forfeitures would not satisfy Hamilton's rule). Therefore, the lower a holder's lineage fitness outlook, the less the bandwagoning allele induces that holder to reserve. Instead, the bandwagoning allele induces a holder with a low lineage fitness outlook to forfeit some resources but also allows the holder to remain alive in case the holder's lineage fitness outlook changes. This is in accordance with the observation in section 3.1.2: If an individual's lineage fitness outlook is more likely to change, there is more likely to be natural selection for a bandwagoning allele that induces its holder to forfeit resources in a manner that allows the holder to stay alive and/or allows the holder's offspring (if any) to stay alive while still releasing some resources to nearby individuals that might have a more favorable lineage fitness outlook.

In sum, for a bandwagoning allele located within a holder that has had interactions that suggest a high lineage fitness outlook, the holder reserves and, if it survives, it reproduces; however, for a bandwagoning allele located within a holder that has had interactions that suggest a low lineage fitness outlook, it does not induce the holder to reserve as much and instead induces the holder to forfeit some resources but allows the holder to remain alive in case its lineage fitness outlook changes. Figure 1 is a flowchart of the actions that a bandwagoning allele would take if it were to engage in bandwagoning of the form introduced in the present section 3.2.5.

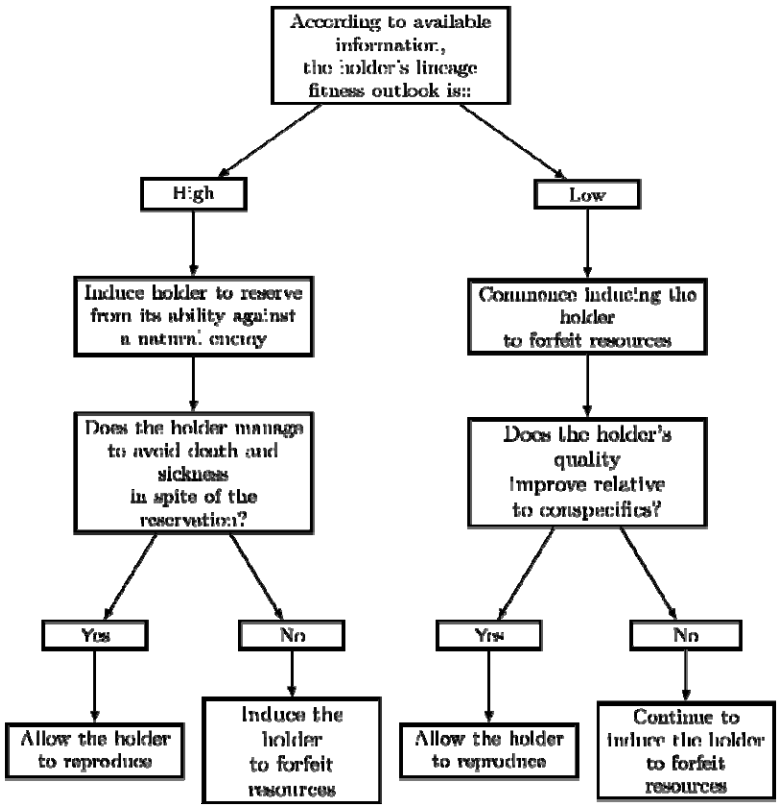

Figure 1. Flowchart that represents how a bandwagoning allele acts according to the model introduced in section 3.

A bandwagoning allele that acts in this manner can be said to combine resonation and reservation: If its holder is suggested to have a high lineage fitness outlook by the information that has already accrued to the allele, the allele induces reservation; if its holder is suggested to have a low lineage fitness outlook by the information that has already accrued to the allele, the allele induces its holder to refrain from reproduction. In the interest of offering

further clarity, a bandwagoning allele that combines resonation and reservation in this manner introduced in the present section is algebraically modeled in section 3.3, which serves to illustrate why a bandwagoning allele that combines resonation and reservation in this manner would be selected in favor of a bandwagoning allele that solely practices resonation.

3.3) Model

The model in this section serves to demonstrate why there would be natural selection for one type of bandwagoning allele, one which does both resonation and reservation in the manner described in section 3.2.5, at the expense of another type of bandwagoning allele, one which only does resonation. Therefore, in this model, there are two bandwagoning alleles in the host population: an *R_R* allele which does both resonation and reservation in the manner described in section 3.2.5 and an *R* allele which does only resonation.

Each individual in the host population is closer than any other individual to one unit of resources. This resource unit is intended to represent food, territory, or mates that an individual could use in order to produce offspring or, alternatively, that an individual could forfeit, in which case it is used for reproduction by other individuals. If the individual forfeits its unit, it is divided for reproduction by other individuals according to the assortment of the population. In modeling the assortment of a population, it is common to suppose, without specifying how the assortment arises in three-dimensional space, that an individual interacts with a same-type individual with probability r and with a random member of the population (including same-type individuals) with probability 1-r (Allen & Nowak, 2015; Cooney et al., 2016; Grafen, 1979; Okasha & Marens, 2016; Van Cleve & Akcay, 2014). Analogously, it is supposed in the present model that if an individual does not use its resource unit, an r fraction of that unit is used by individuals with the same allele and a 1-r fraction is divided evenly among the entire population (including individuals with the same allele).

Individuals in the host population differ in two dimensions of heritable ability: A_R ability, which refers to an individual's ability to resist parasites, and A_O ability, which refers to an individual's ability in all other aspects (e.g., obtaining food, territory, and mates and avoiding predators). Each individual in the population has either high or low A_R ability and high or low A_O ability. An allele within a host individual knows whether the host individual has high or low A_O ability but does not know whether the host has high or low A_R ability unless, or until, the host does reservation. An individual with high A_R ability survives in spite of reservation, but an individual with low A_R ability

cannot; consequently, reservation can be used to identify individuals with high A_R ability because an individual that survives in spite of reservation is guaranteed to have high A_R ability.

Additionally, the parasite threat in the population during generation t is either T_M or T_S. A T_M threat means that half of the individuals in the population have high A_R ability and half have low A_R ability, while a T_S threat means that there are no individuals in the population with high A_R ability. Since a holder with high A_R ability can survive in spite of reservation but a holder with low A_R ability cannot, this means that if the threat is T_M, half of the holders that reserve can survive in spite of reservation, but if the threat is T_S, no holders can survive reservation. This feature of a T_S threat will help illustrate the reason a bandwagoning allele varies the degree of reservation it induces.

Suppose that if an individual reproduces in generation *t*, the quantity of descendants of the same type that it can expect to have by some future generation $t+x$ (where $x > 1$) for every unit of resources it uses to reproduce in generation t varies according to the individual's heritable ability, as described in Table 1. It is assumed that both high A_O ability and high A_R ability lead to greater quantities of descendants by a future generation $t+x$ than, respectively, low A_O ability and low A_R ability; therefore, $C > D > F$ and $C > E > F$.

Heritable ability	Descendants by generation $t+x$ per unit used in generation t
High A_O ability and high A_R ability:	C
High A_O ability and low A_R ability:	D
Low A_O ability and high A_R ability:	E
Low A_O ability and low A_R ability:	F

Table 1. The descendants by generation t+x that individuals with each combination of ability can expect per unit of resources used in generation t.

The difference between the two types of bandwagoning alleles in the host population is that an *R* allele induces resonation only: If a holder of an *R* allele has high A_O ability, it reproduces; if it has low A_O ability, it does

not reproduce. An *R_R* allele induces both resonation and reservation: If a holder of an *R_R* allele has high A_O ability, it reserves and only if it survives in spite of reservation does it reproduce; if a holder has low A_O ability, it does not reserve and it does not reproduce unless some of the individuals with high A_O ability have perished.

At generation *t*, there are 4*A* holders of the *R_R* allele and 4*B* holders of the *R* allele. Half of the holders of each allele have high A_O quality and half have low A_O quality. With probability *G*, the parasite threat in generation *t* is T_M and with probability 1-*G*, the parasite threat in generation *t* is T_S. If the threat is T_M, half of each allele's holders of both high A_O ability and low A_O ability have high A_R ability and half have low A_R ability. If the threat is T_S, there are no holders of either allele with high A_R ability, as all holders of each allele have low A_R ability.

3.3.1) The quantities of descendants expected by generation *t*+*x* if the threat in generation *t* is T_M

When the threat is T_M, there are *A R_R* holders and *B R* holders each with: 1) high A_O ability and high A_R ability; 2) high A_O ability and low A_R ability; 3) low A_O ability and high A_R ability; and 4) low A_O ability and low A_R ability. When the threat is T_M, the only *R_R* holders to reproduce are those with high A_O ability and high A_R ability. This is because when the threat is T_M, the *A R_R* holders with high A_O ability but low A_R ability perish due to reservation and all 2*A R_R* holders with low A_O ability refrain from reproducing due to resonation. Since three-fourths of the 4*A R_R* holders do not use their resource units for reproduction, the total resource units forfeited by *R_R* holders is 3*A*. By contrast, *R* holders reproduce if they have high A_O ability, whether they have high or low A_R ability. The one-half of the 4*B R* holders with low A_O ability forfeit their resources due to resonation, so the total resource units forfeited by *R* holders is 2*B*.

Consequently, if the threat during generation *t* is T_M, *R_R* holders can expect a quantity of descendants by generation *t*+*x* that is given by (3), which is calculated as the quantity of descendants the reproducing *R_R* holders can expect per resource unit times the resource units they use. When the threat is T_M, the only *R_R* holders to reproduce are those with high A_O ability and high A_R ability. According to Table 1, these holders can expect *C* descendants per resource unit. The resource units they use are their own resource units, *A*; plus *r* times the resource units forfeited by other *R_R* holders, 3*A*; plus (1-*r*) times the total resource units forfeited by both *R_R* and *R* holders, 3*A*+2*B*, times the proportion of reproducing individuals that are *R_R* holders, *A*/(*A*+2*B*).

$$C[A+r3A+(1-r)(3A+2B)A/(A+2B)] \qquad (3)$$

If the threat during generation t is T_M, R holders can expect a quantity of descendants by generation $t+x$ that is given by (4). The reproducing R holders with high A_O ability and high A_R ability can expect C descendants per resource unit and the reproducing R holders with high A_O ability and low A_R ability can expect D descendants per resource unit. The resource units available for R holders are their own resource units, $2B$; plus r times the resource units forfeited by other R holders, $2B$; plus $(1-r)$ times the total resource units forfeited by both R_R and R holders, $3A+2B$, times the proportion of reproducing individuals that are R holders, $2B/(A+2B)$. Since the quantity of R holders with high A_O ability and high A_R ability is equal to the quantity of R holders with high A_O ability and high A_R ability, half of the resource units available for R holders are multiplied by C and half are multiplied by D.

$$(C+D)[B+rB+(1-r)(3A+2B)B/(A+2B)] \quad (4)$$

3.3.2) The quantities of descendants expected by generation $t+x$ if the threat in generation t is T_S

If the threat is T_S, there are no holders of either allele that have high A_R ability (that is, there are no holders of either allele that have the ability to survive reservation). Instead, there are $2A$ R_R holders and $2B$ R holders that have high A_O ability and low A_R ability and $2A$ R_R holders and $2B$ R holders that have low A_O ability and low A_R ability.

The R_R holders with high A_O ability and low A_R ability perish due to reservation. For the R_R allele, the perishing of individuals with high A_O ability is the criterion for allowing reproduction by holders with low A_O ability. If the threat is T_S, all of the R_R holders with high A_O ability perish; consequently, R_R holders with low A_O ability reproduce. Since one-half of the $4A$ R_R holders forfeit their resource units, the total resource units forfeited by R_R holders is $2A$. Alternatively, R holders reproduce if they have high A_O ability and there is no reproduction by R holders with low A_O ability. The one-half of the $4B$ R holders with low A_O ability forfeit their resources due to resonation, so the total resource units forfeited by R holders is $2B$.

If the threat during generation t is T_S, R_R holders can expect a quantity of descendants by generation $t+x$ that is given by (5). Since the reproducing R_R holders have low A_O ability and low A_R ability, they can expect F descendants per resource unit. The resource units they use are their own resource units, $2A$; plus r times the resource units forfeited by other R_R holders, $2A$; plus $(1-r)$ times the total resource units forfeited by both R_R and R holders, $2A+2B$, times the proportion of reproducing individuals that are R_R holders, $2A/(2A+2B)$.

$$F[2A+r2A+(1-r)(2A+2B)2A/(2A+2B)] \quad (5)$$

If the threat during generation t is T_S, R holders can expect a quantity of descendants by generation $t+x$ that is given by (6). Since the reproducing R holders have high A_O ability and low A_R ability, they can expect D descendants per resource unit. The resource units they use are their own resource units, $2B$; plus, r times the resource units forfeited by other R holders, $2B$; plus $(1-r)$ times the total resource units forfeited by both R_R and R holders, $2A+2B$, times the proportion of reproducing individuals that are R holders, $2B/(2A+2B)$.

$$D[2B+r2B+(1-r)(2A+2B)2B/(2A+2B)] \quad (6)$$

3.3.3) The quantities of descendants expected by generation *t+x*

The expected quantity of descendants for R_R holders by generation $t+x$ (7) is the expected quantity of descendants for R_R holders by generation $t+x$ if the threat in generation t is T_M, which is given by (3), times the probability that the threat is T_M, G, plus the expected quantity of descendants for R_R holders by generation $t+x$ if the threat in generation t is T_S, which is given by (5), times the probability that the threat is T_S, $(1-G)$.

$$GC[A+r3A+(1-r)(3A+2B)A/(A+2B)]+(1-G)F[2A+r2A+(1-r)(2A+2B)2A/(2A+2B)] \quad (7)$$

The expected quantity of descendants for R holders by generation $t+x$ (8) is the expected quantity of descendants for R holders by generation $t+x$ if the threat in generation t is T_M, which is given by (4), times the probability that the threat is T_M, G, plus the expected quantity of descendants for R holders by generation $t+x$ if the threat in generation t is T_S, which is given by (6), times the probability that the threat is T_S, $(1-G)$.

$$G(C+D)[B+rB+(1-r)(3A+2B)B/(A+2B)]+(1-G)D[2B+r2B+(1-r)(2A+2B)2B/(2A+2B)] \quad (8)$$

The ratio of (7) to (8) represents the ratio of the expected quantity of descendants for R_R holders by generation $t+x$ to the expected quantity of descendants for R holders by generation $t+x$. The R_R allele gains in frequency between generation t and generation $t+x$ if the ratio of (7) to (8) exceeds the ratio of the quantity of R_R holders at generation t to the quantity of R holders at generation t. The quantity of R_R holders at generation t is $4A$ and the quantity of R holders at generation t is $4B$, so the ratio of the quantity of R_R holders at generation t to the quantity of R holders at generation t is A:B. This ratio of A:B is equivalent to each of: a) the ratio of the first term inside the brackets in the first half of (7) to its counterpart of (8); b) the ratio of the third term inside the brackets in

the first half of (7) to its counterpart of (8); and c) the ratio of the entire value inside the brackets in the second half of (7) to its counterpart of (8). Since $D > 0$, this means that the ratio of GC times the first term inside the brackets in the first half of (7) to $G(C+D)$ times its counterpart of (8) is exceeded by A:B. Additionally, this means that the ratio of GC times the third term inside the brackets in the first half of (7) to $G(C+D)$ times its counterpart of (8) is exceeded by A:B. Additionally, since $D > F$, the ratio of $(1-G)F$ times the entire value inside the brackets in the second half of (7) to $(1-G)D$ times its counterpart of (8) is exceeded by A:B. That is, each of these terms in (7), in comparison to their counterparts in (8), would, on their own, contribute to a loss of frequency for the *R_R* allele between generation t and generation $t+x$. The only way the *R_R* allele can gain frequency between generation t and generation $t+x$ is if this loss is made up by the difference between GC times the second term inside the brackets in the first half of (7), $r3A$, minus $G(C+D)$ times the second term inside the brackets in the first half of (8), rB. In other words, what is responsible for any expected increase in frequency for the *R_R* allele between generation t and generation $t+x$ is that *R_R* holders in the aggregate forfeit a higher percentage of the resources to which they are close ($3A$ by *R_R* holders versus $2B$ by R holders) and, of these resources, $r3A$ are used by *R_R* holders with high A_O ability and high A_R ability, whereas only rB are used by *R* holders with high A_O ability and high A_R ability (since rB are also used by *R* holders with high A_O ability and low A_R ability); consequently, the fraction of resources close to *R_R* holders that are used by *R_R* holders with high A_O ability and high A_R ability is triple the fraction of resources close to *R* holders that are used by *R* holders with high A_O ability and high A_R ability.

The second halves of (7) and (8) give the likelihood that the parasite threat during generation t is T_S times the expected quantities of descendants by generation $t+x$ of, respectively, *R_R* holders and *R* holders if the parasite threat during generation t is T_S. Since the ratio of the second half of (7) to its counterpart of (8) is exceeded by A:B, a higher likelihood that the parasite threat during generation t is T_S means a lower frequency of the *R_R* allele at generation $t+x$. This makes sense: When reservation occurs during a generation in which there is a threat that is sufficiently considerable that no individual in the population is able to survive in spite of reservation, it has a negative effect upon the frequency of the bandwagoning allele that practices it because there are no holders of the allele left to utilize the resources forfeited by the perished individuals.

This model makes the simplifying assumptions that an individual either reproduces to capacity or completely forfeits reproduction and that an individual can delay reproduction (that is, an individual with high A_O

ability can delay reproduction until it has survived reservation and an individual with low A_O ability can delay reproduction until it determines whether individuals with high A_R ability have survived reservation or perished because of it) and still reproduce to full capacity. In a more realistic scenario, an individual that delays reproduction may forego reproductive opportunities and may, therefore, reproduce less than it could have, once the bandwagoning allele that it holds has determined that it should reproduce.

3.4) Parallels between the model and established theory

A model for the natural selection of a bandwagoning allele that practices both resonation and reservation is represented verbally in section 3.2.5 and algebraically in section 3.3. For the purposes of conferring both clarity and credibility to this model, it is worthwhile to note parallels between it and both the handicap principle (Getty, 2006; Grafen, 1990; Szamado, 2011; Zahavi, 1975) and bet-hedging theory (Gillespie, 1973, 1974; Schreiber, 2015; Seger & Brockmann, 1987; Slatkin, 1974; Starrfelt & Kokko, 2012).

Zahavi (1975) introduced the handicap principle to explain exhibitions that apparently impair their exhibitor, such as loud songs, conspicuous displays, and colorful plumage. Zahavi argued that individuals engage in these costly exhibitions (i.e., handicaps) in order to demonstrate their superior genes to potential mates. He reasoned that individuals with superior genes tend to be in better condition than others and are, therefore, capable of surviving a larger handicap; consequently, individuals that maintain a larger handicap do so to demonstrate their superior genes. While Zahavi's original examples focused on individuals that impair their ability to evade predators for the purpose of signaling their quality to potential mates, the handicap principle has since been developed further (Getty, 2006; Grafen, 1990; Szamado, 2011) and has been applied across the animal and plant kingdoms to explain ostensibly avoidable costs incurred by individuals that impair their abilities against parasites, prey, and conspecifics (Folstad & Karter, 1992; Johnstone, 1995; Zahavi & Zahavi, 1997). Later applications of the handicap principle have involved the demonstration of ability that may or may not owe to "good genes," which is a departure from Zahavi's original formulation that emphasized heritable ability, though it is a general feature of the handicap principle that costs are incurred by an individual in order to demonstrate that individual's ability.

The model of bandwagoning described in sections 3.2.5 and 3.3 shares numerous properties with the handicap principle. Both bandwagoning theory and Zahavi's original formulation of the handicap principle maintain that natural selection has promoted alleles that help identify whether their holder has "good genes" by burdening that

holder. Both maintain that this identification of good genes occurs through the satisfaction of a criterion of differential costliness: The burden is prohibitively costly for individuals without good genes and not as costly (and possibly not at all costly) for individuals with superior genes. Both maintain that this burden is incurred conditionally and is, therefore, not necessarily incurred by the parent to the same extent that it is incurred by the offspring. Specifically, both predict that the extent of the burden incurred varies in this respect: Individuals that are better at procuring food, territory, mates, and other areas incur a greater burden. However, the two models make this prediction for different reasons. The handicap principle holds that individuals that are better in these areas are of higher quality and can, therefore, afford to incur a greater burden**.** Bandwagoning theory holds that individuals that are inferior in these areas would, even if all of their abilities were fully known, likely have a lower lineage fitness outlook, and would, therefore, be rendered by bandwagoning alleles to forfeit resources through resonation unless the natural enemy threat is severe enough that numerous individuals with a higher lineage fitness outlook perish, but they would only survive a severe natural enemy threat if they were to not undertake the degree of reservation undertaken by individuals with a higher lineage fitness outlook.

A major difference between the handicap principle and bandwagoning theory is that the handicap principle holds that an individual incurs the burden in order to demonstrate (i.e., signal) the individual's good genes to others (particularly mates), while bandwagoning theory holds that the individual incurs the burden in order to identify whether the individual has good genes for the bandwagoning allele that induces the burden. Consequently, bandwagoning theory is better at accounting for situations in which it does not appear that an honest signal could be enforced because of the opportunity for selfish dishonesty. In particular, this includes situations in which the intended recipient of the signal cannot directly perceive the mechanism that makes the signal costly to individuals with inferior genes. For example, Folstad & Karter (1992) argued that testosterone 1) reduces immunocompetence and 2) contributes to the development of ornaments and display behaviors; therefore, individuals can demonstrate good genes for resisting parasites by increasing testosterone production and, therefore, signaling to potential mates via their ornaments and display behaviors that they can resist parasites in spite of the associated immunity deficits. However, since potential mates that view these signals cannot verify, via direct observation, the antibody production within the body of the individual that exhibits these signals, there may have been mutations over evolutionary time scales that would have allowed an individual to maintain immunity while also producing attractive ornaments and displays. If there is evidence of the potential for these mutations, their absence in natural populations is not

explained by the handicap principle, but it is explained by bandwagoning theory. Bandwagoning theory would hold that the production of these ornaments and display behaviors does, indeed, constitute an honest signal of both the individual's quality (as indicated by information available to the bandwagoning allele about the abilities that have been identified) and the immunity burden incurred by the individual, but that this honesty is enforced by a bandwagoning allele which is practicing resonation by inducing low-quality holders to signal suboptimally and is practicing reservation by inducing high-quality holders to incur a burden versus parasites. Bandwagoning theory would, therefore, hold that there was natural selection for a bandwagoning allele (or alleles) responsible for this dual effect of testosterone. (This concept is visited further in section 5.)

Additionally, there are signals that: 1) are communicated honestly between individuals with conflicting interests but 2) do not appear to involve any burden associated with communicating a more favorable signal. In order to account for the honesty with which such signals are communicated, scholars have advanced the index hypothesis, which states that a signal reporting a characteristic of an individual's condition is reliable if the signal is tied (i.e., indexed) to the characteristic in such a manner that a dishonest signal cannot be made (Maynard Smith & Harper, 1995). Biernaskie et al. (2014) argued that the honesty with which index signals are communicated also owes to the criterion for the preservation of signal honesty on which the handicap principle is based: Dishonest signals would be too costly to fake. It follows that if there is any evidence that a signal that is communicated honestly with no cost could have evolved to have been communicated dishonestly with no additional cost, it is not well explained by the handicap principle, but it is attributable to bandwagoning in the form of resonation: Honest signals of quality are less favorably transmitted by individuals of lower quality, so that by signaling honestly, lower-quality individuals wind up foregoing food, mates, and territory compared to higher-quality individuals that signal honestly.

The handicap principle relies upon (and bandwagoning theory allows) the assumption that it is possible, at times, for individuals to identify, prior to incurring a burden upon their ability to resist a natural enemy, that their ability to resist the natural enemy is better or worse than that of another individual. For bandwagoning theory, this can occur if: 1) one individual or the other has become sick or wounded by the particular natural enemy and 2) this sickness or wounding is visible or is signaled honestly. (Signaling honesty may, in fact, be imposed by a bandwagoning allele and this notion is discussed further in section 5.4.) Both the handicap principle and

bandwagoning theory hold that an individual that identifies that its ability to resist a natural enemy is worse than that of another individual would, ceteris paribus, incur a more modest burden upon its ability to resist that natural enemy than that other individual. However, bandwagoning theory can better explain situations in which an individual incurs more of a burden to its ability to resist a natural enemy than another individual even when it appears that it could not have determined that its ability to resist the natural enemy is better than that of the other individual. For example, the handicap principle and the model of bandwagoning offered in sections 3.25 and 3.3 both predict that an individual that compares favorably to others in obtaining food and territory would incur a greater burden upon its ability to resist parasites. If there is evidence that indicates that individuals that are better at obtaining food and territory cannot expect to be better at resisting parasites, the greater burdens against parasites that they incur is not well explained by the handicap principle and is, instead, better explained by bandwagoning theory.

A recent result (Schreiber, 2015) that has developed out of bet-hedging literature[4] holds that long-term natural selection favors a genotype with, ceteris paribus, 1) a higher expected number of offspring produced by individuals with the genotype across space and time; 2) a lower net variance of offspring produced by individuals with the genotype across space and time; and 3) a lower correlation of offspring produced between two randomly selected individuals with the genotype from the same generation. The bandwagoning model presented in sections 3.25 and 3.3 has features that satisfy each of these three properties. By engaging in resonation in order to ensure that lower-quality holders forfeit resources, a bandwagoning allele yields resources to lineages that have, ceteris paribus, a higher expected number of offspring (property 1 above), some of which would hold copies of the bandwagoning allele. A lineage that is not capable of surviving a severe environment has, ceteris paribus, a higher net variance in offspring produced than a lineage that can survive in a severe environment; therefore, by engaging in reservation in order to ensure that holders forfeit resources if they do not have a genotype that enables survival in a severe environment, a bandwagoning allele yields resources to lineages that have, ceteris paribus, a lower net variance in offspring produced (property 2 above), some of which would hold copies of the bandwagoning allele. Likewise, by not inducing as much reservation in some holders as in others for the purpose of ensuring that some holders stay alive if conditions are severe, a bandwagoning allele lowers the correlation in offspring number between two holders of the allele during the same generation (property 3 above).

[4] While Schreiber's (2015) result is developed out of bet-hedging literature, a bandwagoning allele that acts according to the model in sections 3.25 and 3.3 is not necessarily bet-hedging because these acts do not necessarily result in a reduction of arithmetic mean fitness for the holders of the allele.

4) Guidelines for applying bandwagoning theory to empirical phenomena

In theory, it is possible that in populations of some species, there is natural selection for a bandwagoning allele to induce resonation but not reservation. This is more likely if the bandwagoning allele is selected in a population that tends not to be subjected to substantial intergenerational variance of the quantity of individuals that survive to reproductive age as a result of, in particular, predators or parasites. And just as it is theoretically possible for there to be natural selection for a bandwagoning allele that does not induce reservation at all or induces reservation from ability against one natural enemy, it is also theoretically possible for there to be natural selection for a bandwagoning allele that induces reservation against multiple natural enemies in separate ways. However, the model in sections 3.25 and 3.3 was offered due to its ability to account uniquely for numerous paradoxical empirical phenomena (examples of which are offered in sections 5.1-5.6). The fundamental elements of this model are a response by a bandwagoning allele to an indication that its holder has a high lineage fitness outlook with reservation—a burden imposed to its holder's ability to survive a natural enemy—and a response by a bandwagoning allele to an indication that its holder has a low lineage fitness outlook with resonation---a cost imposed against its holder's ability to utilize resources. It was explained in section 3 that as a result of the possibility that individuals with a high lineage fitness outlook would perish, individuals with a low lineage fitness outlook may engage in some forfeitures of resources, but are less likely to completely forfeit all of the resources to which they currently have access and all of the resources to which they will have access in the future. In lieu of an absolute forfeiture of resources, partial forfeitures can occur numerous times through an individual's life, in response to indications that the individual's lineage fitness outlook is low (but potentially subject to change). Additionally, given the present paper's emphasis upon analyses longer than a single generation, it should be noted that there may be a partial forfeiture not just by an individual but also by that individual's lineage. This would involve an individual with a low lineage fitness outlook that, for example, produces some non-zero quantity of offspring but does not produce as many offspring as it could or does not nurture its offspring as much as it could. As the severity presented by the natural enemy increases, it becomes increasingly likely that an individual previously judged to have a low lineage fitness outlook no longer has a low lineage fitness outlook because individuals previously judged to have a higher lineage fitness outlook have perished; therefore, as the severity presented by the natural enemy increases, the degree to which an individual previously judged to have a low lineage fitness outlook utilizes its resources can also be expected to increase.

What follows in section 5 is an analysis of six paradoxical phenomena. It is argued in section 5 that these phenomena represent: 1) an individual's response to indications that its lineage fitness outlook is low by restricting its ability to utilize resources (which would suggest resonation) and with an increase in ability against a natural enemy (which would be suggestive of a relaxation of reservation) and 2) an individual's response to indications of a high lineage fitness outlook with a reversal of a restriction against resource utilization (which would suggest a relaxation of resonation) or with a decrease in ability against a natural enemy (which would be suggestive of reservation). Additionally, it is argued that there would have been mutations over evolutionary time scales that would have allowed an individual to be spared of the costs associated with the restriction and/or the burden that would not exceed the costs of the restriction and/or burden. Their absence is indicative of natural selection for a coupling of the restriction in an individual's ability to use resources and that individual's ability against the natural enemy, such that individuals tentatively evaluated to have a low lineage fitness outlook restrict their ability to use resources but can resist fully against the natural enemy and individuals tentatively evaluated to have a high lineage fitness outlook do not restrict their ability to use resources but cannot resist fully against the natural enemy. In this paper, the term "bandwagoning allele" represents whatever heritable elements are responsible for this pattern and these elements may involve genes or epigenetic marks that control some genes involved in resource utilization and natural enemy resistance, but may also involve mutations to some of these genes that are involved in resource utilization and natural enemy resistance. There is natural selection for the "bandwagoning allele" if there is natural selection for whatever heritable elements are responsible for this pattern. Table 2 lists, for each of the six phenomena examined in section 5, the restriction incurred by individuals with a low lineage fitness outlook in utilizing resources and the burden incurred by individuals with a high lineage fitness outlook in resisting a natural enemy.

Section	Restriction to resource utilization	Burden against natural enemy
5.1	Costs of depression.	Susceptibility to parasites.
5.2	Photosynthetic cost.	Susceptibility to parasites.
5.3	Diminished sexually-selected characteristics.	Susceptibility to parasites.

5.4	Less advantageous signaling.	Susceptibility to parasites.
5.5	Reproductive inhibition.	Susceptibility to parasites.
5.6	Costs from diminished nurturing.	Susceptibility to parasites.

Table 2.

Additionally, there is a focus in section 5 upon burdens incurred against parasites as examples of reservation; however, this should not be interpreted to necessarily mean that reservation occurs more commonly against parasites than predators. Burdens incurred that make survival against predators more difficult, such as behaviors, ornaments or displays, are highly visible to conspecifics; therefore, these burdens are accounted for by well-established theory, such as the handicap principle discussed above. They are also accounted for by bandwagoning theory, but it is typically not necessary to invoke bandwagoning theory in order to explain burdens incurred against predators. The focus in the section below upon burdens that make survival against parasites more difficult occurs because these burdens are not accounted for well by the handicap principle, since they involve burdens to immunity that are not directly observable by conspecifics. Some scholars claim that signals relied upon by conspecifics are indexed to these burdens, but without an ability to directly observe these burdens, there is also the potential for the evolution of a dishonest signal. If there is an opportunity for a dishonest signal to evolve that would allow individuals to signal that they are bearing the burdens without actually incurring them, then the handicap principle does not account for these burdens that are incurred, but bandwagoning theory might. Therefore, there is an emphasis in the sections below upon burdens incurred that make survival against parasites more difficult.

5) Empirical applications

5.1) The coupling of robustness against parasites and depressive symptoms

Depression is a response to chronic and uncontrollable stress that is characterized by sadness, self-loathing, and anhedonia; impaired cognition, concentration, and memory; changes in psychomotor, sleeping, and eating patterns; and diminished fertility and libido (Anders et al., 2013; Austin et al., 2001; Sun et al., 2013). Among humans, depression is both prevalent and costly: It increases the mortality rate for all major disease-related causes of death (Mykletun et al., 2007) and is a significant risk factor for suicide (Hagen, 2003), which claims

approximately one million people worldwide each year (Hawton & van Heeringen, 2009). Individuals in many species are susceptible to learned helplessness (Seligman, 1976), which is provoked by stress, is characterized by many of the symptoms associated with depression (e.g., anhedonia, psychomotor retardation, reduced self-care, and diminished appetite and libido), and has been induced, via application of uncontrollable stress, in many species, including insects, cats, dogs, rats, birds, fish, and primates (Franklin et al., 2012; Sapolsky, 1998; Weiss, J. et al., 1982). Though there are obstacles in determining the intent, some models of learned helplessness have included suicide and self-mutilation (Crawley et al., 1985; Preti, 2011; Sapolsky, 1998; Seligman, 1976). These depressive symptoms are considered maladaptive and are reversed in animals by the same therapies that are used to treat depression in humans (Russo et al., 2012; Weiss, J. et al., 1982).

Some scholars have argued that there was natural selection for depression (e.g., Andrews & Thomson, 2009; Raison & Miller, 2013; Watson & Andrews, 2002), citing the commonness of depressive responses among humans of all ages—including ages at which natural selection is strong (Medawar, 1952)—and the prevalence of depression risk alleles (Anders et al., 2013; Raison & Miller, 2013). Many evolutionary explanations for depression have been offered, yet none have been embraced by a scholarly consensus (Hagen, 2003; Kinney & Tanaka, 2009; Nettle, 2004; Raison & Miller, 2013; Varga, 2012). Of particular relevance to genetic bandwagoning theory, a recent set of hypotheses have been advanced, holding that depression was selected in conjunction with the prevention of infection by parasites and pathogens (Anders et al., 2013; Kinney & Tanaka, 2009; Raison & Miller, 2013). These scholars have pointed to evidence for a mutually causal relationship between immune activation and depression, noting that immune activation leads to depression, whereas depressive symptoms are associated with greater resistance against infections. According to these hypotheses, the depressive mood is adaptive for fighting infection since it encourages energy preservation and it also leads to solitude, which protects the afflicted individual from further exposure to infection and also protects kin from exposure to the afflicted individual. Under these views, the immunity activation and depression that occur in response to a wide range of stressors (including psychosocial stressors) are adaptive, since over evolutionary time scales, most stressors related to hunting, escaping predators, or fighting conspecifics in dominance hierarchies, and infection risk was increased by wounds associated with these activities. These hypotheses account well for the immune activation among depressives, but do not account as well for the self-loathing and its associated costs. Depression is a response to a wide variety of stress sources and while some causes of depression might have 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 depressive mood 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). Indeed, depression is caused by numerous non-infectious diseases, even if the individual is unaware that he or she is diseased (Dowlati et al., 2010; Irving & Lloyd-Williams, 2010; Parker & Brotchie, 2017; Pryce & Fontana, 2017; Yirmiya et al., 1999). Additionally, depression is a costly way of exerting a preference for solitude and it would seem that mutations could have occurred over evolutionary time scales that would have instilled in a sick individual a preference for solitude without requiring that individual to incur the costs of self-loathing, given that some well-adjusted individuals exhibit a preference for solitude (Berger, 1995).

The self-loathing and immunity activation features of depression are well-explained by genetic bandwagoning theory. Since chronic stress is an indication of lower quality and a lower lineage fitness outlook[5], the reproductive costs incurred by the chronically stressed (e.g., diminished fertility and libido; suicide) are re-interpreted as resonation by individuals with a lower lineage fitness outlook, which allows their resources to be utilized by nearby individuals. The augmented defenses versus parasites that have been associated with depression are also re-interpreted: Individuals of higher quality that do not undertake these defenses are engaging in reservation against these natural enemies.

Genetic bandwagoning theory also accounts better for 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 (Brilman & Ormel, 2001; Ghaziuddin et al., 1990; Kendler et al., 2000; Solomon et al., 2000). Evolutionary explanations that maintain that depression is a response to infection risk fare poorly in explaining the increasing intensification of depressive symptoms, since a history of chronic stress that has not yet resulted in an infection would be suggestive of a reduced marginal risk of infection from further incidents of stress. However, in the context of genetic bandwagoning theory, a history of chronic stress is more suggestive than a single stress bout that the stress-afflicted individual's lower quality is irreparable; therefore, a

[5] Some stressors, such as stressors relating to physical exercise, are not indicative of lower quality or a lower lineage fitness outlook, but these stressors also do not typically contribute to the likelihood of depression (Schuch et al., 2016).

bandwagoning allele is more likely to induce its holder to completely forfeit its resources if the holder has been subjected to a history of chronic stress.

5.2) The coupling of robustness against parasites and photosynthetic costs

Plants of many species respond to a wide variety of stressors by increasing anthocyanin production, which makes their leaves redder. Examples of sources of stress that lead to an increase in anthocyanin production include strong light, UV-B radiation, temperature extremes, drought, nutrient deficiencies, bacterial and fungal infections, wounding, herbivory, herbicides, and various pollutants (Gould et al., 2009). This production of anthocyanins imposes a photosynthetic cost, as anthocyanins absorb visible light without being photosynthetic (Gould et al., 2009; Karageorgou et al., 2008; Manetas, 2006).

The reddening of plant leaves[6] is biochemically well-explained but is an evolutionary paradox that has, over the past century, invited many hypotheses, none of which are thought to adequately explain the variation in spatial and temporal patterns of anthocyanin production (Cooney et al., 2012; Gould et al., 2009; Kovinich et al., 2014; Manetas, 2006; Menzies et al., 2016). Of interest to genetic bandwagoning theory, anthocyanins are produced in a common biosynthetic pathway with defensive compounds against parasites (e.g., phenols, tannins: Schaefer & Rolshausen, 2006), so that when plants produce anthocyanins, they also augment their defenses versus parasites. Therefore, when plants that are subjected to stress produce anthocyanins, they incur a photosynthetic cost, but also enhance their defenses against parasites. One reason for the paradox is that the tradeoff between photosynthesis and defense against parasites does not appear to have been imposed by physical constraints. These plants evidently could have evolved to produce anthocyanins and defense compounds against parasites in separate pathways without making additional energy expenditures or incurring other costs. This would have allowed a plant to experience the parasite defense without the photosynthetic cost from the anthocyanins. The absence of plants with this ability (or the pervasiveness of plants without it) is well-explained by genetic bandwagoning theory: Plants that are afflicted by a stress source, ceteris paribus, have a lineage fitness outlook that is lower than plants that are able to resist the same source without becoming stressed. By producing anthocyanins, plants with a lower lineage fitness outlook incur a photosynthetic cost, which is consistent with resonation, but they also enhance their defenses against parasites. The individuals that do not produce additional anthocyanins (that is, individuals with a higher lineage

[6] Plants produce anthocyanins in other contexts besides stress response that likely are unrelated to genetic bandwagoning theory.

fitness outlook) do not enhance their defenses against parasites and are, in fact, engaging in reservation by underperforming their maximum resistance against parasites. The interpretation in terms of genetic bandwagoning theory is that, over evolutionary time scales, many plants could defend against parasites without incurring a photosynthetic cost, which allowed individuals with a high lineage fitness outlook to defend to greater capacity against parasites and which allowed individuals with a low lineage fitness outlook to avoid a photosynthetic cost. However, their absence today, and the common coupling of anthocyanin production and production of defense compounds, is evidence of natural selection for genetic bandwagoning alleles that have imposed this tradeoff between photosynthesis and defense against parasites.

5.3) The coupling of susceptibility against parasites and androgenic benefits

Individuals of lower quality tend to utilize androgens (e.g., testosterone) less than individuals of higher quality (Folstad & Karter, 1992; Johnstone, 1995; Muehlenbein & Bribiescas, 2005). Since androgens are utilized in strength, aggression, and mate-attracting ornaments, the lesser utilization of androgens by lower-quality individuals leads them to be disadvantaged in competition for food, territory, and mates (Folstad & Karter, 1992; Gil, 2008; Groothuis et al., 2005). An explanation commonly offered for the lesser utilization of androgens by lower-quality individuals is that the utilization of androgens steers energetic resources into reproduction and away from immunity, which those with weaker immunity cannot afford (Folstad & Karter, 1992; Groothuis et al., 2005; Habig & Archie, 2015; Muehlenbein & Bribiescas, 2005). This explanation typically invokes the handicap principle. The point raised in section 3.4 is pertinent: The handicap principle relies upon an assumption that an individual can determine prior to incurring a burden (i.e., a handicap) that the individual has superior capability for overcoming the burden in comparison to other individuals. Individuals that perform better in competitive bouts or at attracting mates raise androgen levels (Archer, 2006; Oliveira, 2004), even though it is questionable that individuals can know they are more capable of resisting parasites than others on the basis of their ability to fight conspecifics or attract mates.

Moreover, there is evidence that a tradeoff between androgens and immunity is not imposed by energy constraints. 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 & 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, 2006). Consequently, Habig & 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 the hypothesized energetic tradeoff between androgen-mediated growth and immunity.

Bandwagoning theory offers the explanation that by utilizing androgens in lesser quantity, lower-quality individuals that have a lower lineage fitness outlook are engaging in resonation via the forfeiture of resources that occurs by possessing lower strength, aggression, and mate-attracting ornaments, and that by utilizing androgens in greater quantity, higher-quality individuals that have a better lineage fitness outlook are engaging in reservation via the lesser ability to resist parasites. The evidence that there could have been mutations over evolutionary time scales that would have allowed an individual the strength, aggression, and ornaments associated with androgens without incurring a cost against parasites and the absence of these mutations, or the prevalence of androgens exerting this dual effect, is evidence of natural selection for bandwagoning alleles that mediate this dual effect.

5.4) The maintenance of honest signaling when a selfishly dishonest signal would be uncostly

It was argued in section 3.4 that the handicap principle would not account well for evidence that an uncostly signal is communicated honestly despite opportunities to communicate it dishonestly. Additionally, it was argued in section 3.1.2 that honest signaling is well explained by bandwagoning in the form of resonation: If individuals signal honesty, irrespective of quality, lower-quality individuals are disadvantaged because they signal less favorably; consequently, mating opportunities and other resources that are determined by signaling are more likely to be obtained by higher-quality individuals than if honest signaling were not to occur. Honest signaling is, therefore, a means by which a lower-quality individual relinquishes resources to higher-quality individuals.

The index hypothesis has been advanced to account for the honesty of some uncostly signals (Husak & Swallow, 2011). However, there is evidence that signals that were thought to be indices are not true indices because they are subject to selection (Emlen et al., 2012; Simons et al., 2015). Thus, there is the paradoxical occurrence of honest but apparently uncostly signals.

For example, carotenoid ornaments reliably reflect quality, even though carotenoids are evidently not limiting **(**Hill, 2006, 2014; McGraw & Blount, 2009; Simons et al., 2014) and there are mutations that would allow an individual to cheat with a dishonest signal that would cost the cheater less than the cost imposed by honesty (Simons et al., 2015). Additionally, zebra finches use song as an honest signal of quality, even though it is metabolically cheap (Ritschard et al., 2010; Zollinger et al., 2011); stressed birds incur song deficits even after a song allotment that is adequate for exact copying in other birds (Brumm et al., 2009); and some nutritionally stressed populations of wild zebra finches have more complex songs than populations with greater food availability (Zann & Cash, 2008), which indicates that zebra finches could have evolved the ability to learn complex song despite undergoing nutritional stress.

There is a role for testosterone in mediating the honesty of these signals: In many species, an individual's testosterone levels are reduced by stressors that are suggestive of that individual's lower quality and lower lineage fitness outlook, such as nutritional, developmental, and psychological stressors (Dong et al., 2004; Lynn et al., 2015; Nelson et al., 1989). Chronic stress is more likely than acute stress to lead to a decrease in testosterone production (Chichinadze & Chichinadze, 2008), which is consistent with the notion that an individual's testosterone levels correlate with its lineage fitness outlook, since a chronic stressor is a more reliable indicator than an acute stressor that the stressed individual's lineage fitness outlook is low. Additionally, there is evidence that the expression of carotenoid ornaments is dependent upon testosterone and that testosterone mediates the relationship between individual quality and carotenoid ornament color by being produced more in higher-quality individuals and engendering more prominent carotenoid ornament production (McGraw & Blount, 2009; Weaver et al., 2017).

There is also evidence that the structure of zebra finch song, which is important in attracting mates (Woodgate et al., 2012), is an indicator of the testosterone levels that zebra finch has experienced in its history (Fedurek et al., 2016; Ritschard et al., 2011) and, therefore, is an indicator of the degree to which that zebra finch's lineage fitness outlook. In addition to augmenting signals, testosterone leads to greater susceptibility to parasites,

which was discussed in section 5.3, and there is evidence that this also occurs in songbirds, including zebra finches (Alonso-Alvarez et al., 2007). In sum, testosterone is ramped up within individuals with a higher lineage fitness outlook, which leads these individuals to signal favorably to mates and conspecifics but to be more susceptible to parasites, while individuals with a lower lineage fitness outlook signal unfavorably but are less susceptible to parasites. In accordance with the above discussion, there are likely mutations that would have occurred over evolutionary time scales that would have allowed an individual to signal favorably and to resist parasites without additional susceptibility. This could have involved, for example, a way to signal favorably, irrespective of testosterone levels, or it could have involved a way of increasing testosterone without incurring the susceptibility to parasites. That these mutations are not prevalent is an indication of natural selection for genetic bandwagoning alleles that lead individuals with a low lineage fitness outlook to engage in resonation by signaling unfavorably and that lead individuals with a high lineage fitness outlook to engage in reservation by becoming more susceptible to parasites.

5.5) The forfeiture of reproduction by lower-quality individuals

In many species, subordinate individuals cooperatively care for the offspring of dominant individuals without having their own offspring, which is considered a paradox (Clutton-Brock et al., 2010; Johnstone, 2000; Saltzman et al., 2009). In some species, a group's subordinates are completely bereft of reproductive ability; however, their fertility and libido quickly return if the dominant group members depart the group (Sapolsky, 2001). The states of dominance and subordinance are commonly attributed to differential quality: Dominance consistently reflects certain aspects of quality, especially immunocompetence (Cavigelli & Chaudhry, 2012; Georgiev et al., 2015). Subordinates' reproductive inhibition (which has been called "socially induced suppression," "physiological suppression," and "social contraception") 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 (Harrison et al., 2013; Saltzman et al., 2009).

Despite well-established theory regarding how individuals in a group should be expected to divide reproduction (Vehrencamp, 1983), multiple large reviews have determined that theory is not matched well by experimental and observation results (Field, J. et al., 1998; Nonacs & Hager, 2011). Recently, a comprehensive review by Nonacs & Hager (2011) found that there is little evidence that the behavior of members in cooperatively

breeding groups is governed by an evaluation of patterns of relatedness or competitive ability in order to set reproductive skew. The review's authors wrote (pg. 295) that "some individuals appear to behave suboptimally and lose fitness by either joining disadvantageous groups or not leaving them."

Genetic bandwagoning theory offers the explanation that the forfeiture of reproduction by lower-quality individuals looks maladaptive when analyzed after one generation, but that an analysis over a longer time period would demonstrate its adaptiveness. Indeed, Nonacs & Hager (2011) noted that high heritability is suggested in species in which reproductive skew is unresponsive to internal group characteristics such as relatedness, which indicates an emphasis upon a longer-term analysis.

The reproductive inhibition of subordinates coincides with dominants' greater susceptibility to parasites, which was discussed in section 5.3. The reproductive inhibition by subordinates is an example of a forfeiture of resources by individuals with a lower lineage fitness outlook and the greater susceptibility to parasites by dominants is an example of a reservation of ability against a natural enemy by individuals with a higher lineage fitness outlook. A recurring point of emphasis in section 5 is that both phenomena are considered paradoxes, but are well-explained by bandwagoning theory: The reproductive inhibition of subordinates is an example of resonation and the greater susceptibility to parasites by dominants is an example of reservation.

5.6) Nurturing deficits toward lower-quality offspring

In numerous rodents and primates, higher levels of maternal nurturing (e.g., licking and grooming) lead to more growth (Denenberg & Karas, 1959; Field, T., 1998; Field, T. et al., 1986; Schanberg, 1995), greater cognitive function and memory (Field, T., 1998; Korosi & Baram, 2009; Zhang & Meaney, 2010), higher alertness (Field, T., 1998; Field, T. et al., 1986), greater behavioral maturity (Field, T. et al., 1986), and lower mortality risk (Denenberg & Karas, 1959; Field, T. et al., 1986), while lower levels of maternal nurturing lead to depression (Franklin et al., 2010; Franklin et al., 2011; Weiss, I. et al., 2011), anxiety (reviewed in Korosi & 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; Heiming et al., 2011; Mansuy et al., 2013; Zhang & Meaney, 2010). 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 (Drury et al., 2016; Mansuy et al., 2013; Meaney, 2001; Zhang & Meaney, 2010).

The prevalent 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; Drury et al., 2016; Pittet et al., 2012). According to this view, the additional anxiety and increased stress response associated with diminished maternal nurturing better enables the offspring to avoid danger, especially predators. However, evidence that has accumulated against this explanation includes: 1) Offspring from the same mother (and evidently the same formative environment) are induced via maternal effects to incur costs that are determined by their father's quality, even in the absence of their father's postpartum presence (Dietz et al., 2011; Dietz & Nestler, 2012; Mashoodh et al., 2012); 2) Exposure to predator odor during gestation has been found to stimulate postpartum maternal affection (Mashoodh et al., 2009; McLeod et al., 2007)—the opposite of what would be expected if reduced nurturing were intended to increase vigilance toward predators; and 3) Offspring of preferred males, which tend to receive more nurturing, exhibit more risk-averse behavior in a predator-avoidance test (Curley et al., 2011).

Work by Sapolsky (1998) and Suomi (1997) also suggests that reduced maternal nurturing exerts a negative influence upon offspring. They independently documented what they considered inefficient stress responses in, respectively, baboons and rhesus monkeys. These animals apparently do not distinguish in their reactions to threatening and innocuous situations: Their resting glucocorticoid levels are pathologically higher than the average but their glucocorticoid response to a real stressor is smaller and slower (Sapolsky, 1998). This condition, which Sapolsky (1998) and Suomi (1997) each considered maladaptive, is both a cause and an effect of reduced maternal nurturing.

Genetic bandwagoning theory offers another evolutionary explanation for differential maternal nurturing. A chronically stressed individual has, ceteris paribus, a lower lineage fitness outlook. Therefore, a bandwagoning allele would respond to chronic stress experienced by its holder by inducing its holder to nurture its offspring less than other individuals nurture their offspring, which disadvantages its offspring and leads these offspring to use less resources for their own reproduction in comparison to the offspring of other individuals. This is a way of inducing

lineages with a lower lineage fitness outlook to use less resources while not eliminating the lineages, in case of a change to their lineage outlooks.

Moreover, there is evidence that in addition to the resonation occurring from differential nurturing, there is also reservation by nurtured individuals. In numerous species, diminished maternal nurturing is associated with increases in inflammation (Chen et al., 2011; Figueiredo et al., 2016; Gracia-Rubio et al., 2016; Miller et al., 2011), which are associated with resistance against parasites (Anders et al., 2013; Raison & Miller, 2013). Since it has not been argued that individuals incur costs from diminished nurturing in order to save energy directed into resistance against parasites, it appears that, over evolutionary time scales, the resistance against parasites could have occurred without incurring the costs from diminished nurturing. The scarcity in natural populations of this coupling in the same individual is a paradox that is explained by bandwagoning theory: Resonation is exemplified by the costs from diminished nurturing and reservation is exemplified by the greater susceptibility to parasites by nurtured individuals.

6) Conclusions

In this paper, it is argued that there can be natural selection for an allele that induces its holder to forfeit resources if that holder's outlook for lineage fitness is sufficiently low in comparison to the individuals nearby and/or if other parameters (e.g., values for heritability and relatedness) are satisfactorily high. When this occurs sequentially—that is, when an allele responds to an indication that its holder has a low lineage fitness outlook by inducing that holder to forfeit resources—it is called resonation. However, if a holder's lineage fitness outlook depends upon heritable dimensions that are difficult to evaluate under non-severe conditions (e.g., abilities against parasites or predators), an allele induces that holder to reserve from (i.e., withhold) its ability to survive one or more natural enemies, which leads that holder to become sick or perish if its ability to survive the natural enemy against which it reserves is sufficiently low that its lineage fitness outlook is low, and this sickness or perishing by a holder with a low lineage fitness outlook leads that holder to be less capable of procuring, attracting, or utilizing resources, which constitutes a forfeiture of resources to nearby individuals. This is called reservation.

The focus in this paper is upon a model in which an allele uses a particular combination of resonation and reservation: The allele evaluates its holder's lineage fitness outlook on the basis of information it has available, such as information about the holder's ability to obtain food, territory, and mates, and whether the holder has been

sickened by parasites or wounded by predators (however, in accordance with the discussion in this paper, it is less likely that the allele has information about the holder's ability to survive against parasites or predators). The allele then induces its holder to a degree of reservation against a natural enemy that is positively correlated to that evaluation of its holder's lineage fitness outlook and a degree of resource forfeiture that is negatively correlated to that evaluation of its holder's lineage fitness outlook: The higher that holder's lineage fitness outlook is evaluated, the less the allele induces it to forfeit resources and the more the allele induces it to reserve against a natural enemy and the lower that holder's lineage fitness outlook is evaluated, the more the allele induces it to forfeit resources and the less the allele induces it to reserve against a natural enemy. Holders that are tentatively evaluated to have a high lineage fitness outlook are induced to reserve from their ability against the natural enemy in order to determine which of these holders have "good genes" for surviving the natural enemy and to induce forfeitures by individuals that do not have "good genes" for surviving the natural enemy. Holders that are tentatively evaluated to have a low lineage fitness outlook are also induced to forfeit resources, but are induced to reserve less against the natural enemy for the following reason: If the natural enemy threat is of typical severity, Hamilton's rule is likely satisfied by the forfeiture of resources by individuals that are tentatively evaluated to have a low lineage fitness outlook, even if these individuals are good at surviving natural enemies. The best chance that Hamilton's rule would not be satisfied by the forfeiture of individuals that are tentatively evaluated to have a low lineage fitness outlook is if the natural enemy threat becomes unexpectedly severe, in which case numerous individuals that had a high lineage fitness outlook would perish due to their reservation, but if individuals with a low lineage fitness outlook were to reserve as much, they, too, would perish.

The six empirical phenomena in section 5 are presented as examples of well-documented but heretofore paradoxical phenomena, which are uniquely accounted for by this model of bandwagoning. Each case involves: 1) a response to an indication that an individual's lineage fitness outlook is low with a restriction of that individual's ability to utilize resources (which indicates resonation) and an increase in the robustness of that individual's defenses against natural enemies (which indicates a relaxation of reservation) and 2) a response to an indication that an individual's lineage fitness outlook is high with a relaxation of that restriction against resource utilization (which indicates a relaxation of resonation) and a decrease in the robustness of that individual's defenses against natural enemies (which indicates reservation). In each case, it appears that mutations could have occurred over evolutionary time scales that would have allowed the individual to avoid the restriction and/or the burden against natural enemies

at a cost lower than the cost associated with the restriction and/or the burden. The paradoxical absence of such mutations is indicative of natural selection for a bandwagoning allele that would induce these responses. Each of these six cases lends: a) support for the notion that the parameters (e.g., relatedness, heritability of fitness and condition) required for the natural selection of a bandwagoning allele do tend to occur in natural populations and b) relevance to genetic bandwagoning as an evolutionary theory that can account for empirical phenomena.

Sections 5.1, 5.2 and 5.3 examine phenomena for which the restriction and the burden are reported as aspects of the same phenomena and individuals are assumed (by, at least, some scholars) to be constrained to choose one or the other. That is, individuals are assumed to have to choose, respectively, the costs of depression or susceptibility to parasites; the costs of anthocyanin production or susceptibility to parasites; and the absence of sexually-selected characteristics or susceptibility to parasites. In each case, they are assumed to be unable to have both. Sections 5.4, 5.5 and 5.6 examine phenomena for which the restriction and the burden are not reported together. That is, robustness (or the absence of susceptibility) against parasites is assumed to merely coincide with, respectively, disadvantageously honest signaling, reproductive inhibition, and diminished nurturing. These cases for which tradeoffs are not even suspected lend credibility to the argument that the phenomena that fit this pattern that is consistent with the model of genetic bandwagoning introduced in section 3 (3.25 and 3.3) are not attributable to tradeoffs imposed by physical constraints, but are rather attributable to bandwagoning alleles.

Thus, there are the following major theories presented in this paper:

1) There can be natural selection for genetic bandwagoning in the form of resonation, in which an allele evaluates its holder's lineage fitness outlook and acts, in any of a large number of ways, to induce that holder to forfeit resources if that outlook is low.

2) There can be natural selection for genetic bandwagoning in the form of reservation, in which an allele cannot normally evaluate some facets of its holder's lineage fitness outlook and, therefore, induces its holder to reserve from its ability to evade predators, resist parasites, capture prey, or otherwise survive, which allows the allele to identify its holder's lineage fitness outlook on the basis of the degree to which it can overcome this reservation and which leads a holder with an unfavorable lineage fitness outlook to forfeit resources due to death, injury, or sickness from the reservation.

3) There can be natural selection for genetic bandwagoning in the form of a combination of resonation and reservation, which is verbally outlined in section 3.2.5 and algebraically demonstrated in section 3, in which individuals that receive information that suggests they have a high lineage fitness outlook reserve from their ability to compete or survive against one or more natural enemies, while individuals that receive information that suggests they have a low lineage fitness outlook forfeit resources to nearby individuals but reserve less (if at all) from their ability against natural enemies and remain alive insofar as it is likely that their lineage fitness outlook can change.

4-9) The six empirical phenomena analyzed in sections 5.1 to 5.6 are not well-explained by contemporary evolutionary theory and are best explained as products of natural selection for genetic bandwagoning that uses the combination of resonation and reservation that is referenced in theory 3 above in this summary.

6.1) Challenging the theories presented in this paper

Successful challenges to the theories presented might involve a demonstration that, for example: a) the parameters required for the natural selection of bandwagoning do not usually occur in nature and/or b) it is not necessary for an allele within an individual to induce reservation against a natural enemy in order to evaluate that individual's ability against that natural enemy. Any argument that demonstrates that any of the six phenomena considered in section 5 does not require an explanation by bandwagoning theory would subtract some relevance from the theory and reduce support for the notion that the parameters required for the natural selection of bandwagoning tend to occur in nature.

6.2) Potential for future research

The foregoing examples do not constitute an exhaustive set of phenomena that can be accounted for by resonation and/or reservation. Productive avenues for further utilization of the concepts of resonation and reservation in evolutionary explanations may include, for example, the phenomena by which 1) stressed individuals tend to produce male offspring (Cameron, 2004), even though theory holds that less competitive individuals should generally prefer to produce female offspring (Trivers & Willard, 1973) and 2) individuals that are defeated in competitive bouts tend, ceteris paribus, to perform more poorly in subsequent bouts (Dugatkin, 1997; Hsu et al., 2006; Rutte et al., 2006).

6.2) A bandwagoning allele does not necessarily act against the interests of alleles at other loci

By inducing resonation and/or reservation, a bandwagoning allele should not necessarily be interpreted to be acting against the interests of alleles at other loci, even if it acts to induce its holder to forfeit resources. Insofar as a bandwagoning allele's frequency can be expected to increase over ensuing generations if the individual in which it is located forfeits resources to individuals with a more favorable lineage fitness outlook, the frequencies of alleles at other loci within the same individual can also be expected to increase over the ensuing generations as a result of the same forfeiture of resources—via shifting the resources to fitter lineages, some of which would hold a copy of the same alleles. That is, an effect of a bandwagoning allele upon alleles at other loci would be to induce the forfeiture resources from the holders of those alleles that have the lowest lineage fitness outlooks to the holders of those alleles that have the highest lineage fitness outlooks, allowing those alleles to, ceteris paribus, benefit from having the resources utilized by holders with the highest lineage fitness outlooks. The term "ceteris paribus" is used above because if an allele at another loci has a negative influence upon fitness, it would likely be disproportionately represented within the genotypes of the forfeiting individuals, thereby being disadvantaged by the bandwagoning allele, and if an allele at another loci has a positive influence upon fitness, it would likely be disproportionately represented within the genotypes of the utilizing individuals, thereby being benefited by the bandwagoning allele.

6.3) 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, greenbeard discrimination, group selection, limited dispersal, and spatial selection have been offered as ways in which there can be evolution of cooperation for indirect benefits (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 (and ultimately, their lineages) to turn the resources into fitness over ensuing generations. Figure 2 depicts various explanations for cooperation on a Cartesian curve whose coordinates are the combinations of the minimum values of relatedness and benefit-to-cost ratio that allow Hamilton's rule to be satisfied by cooperation.

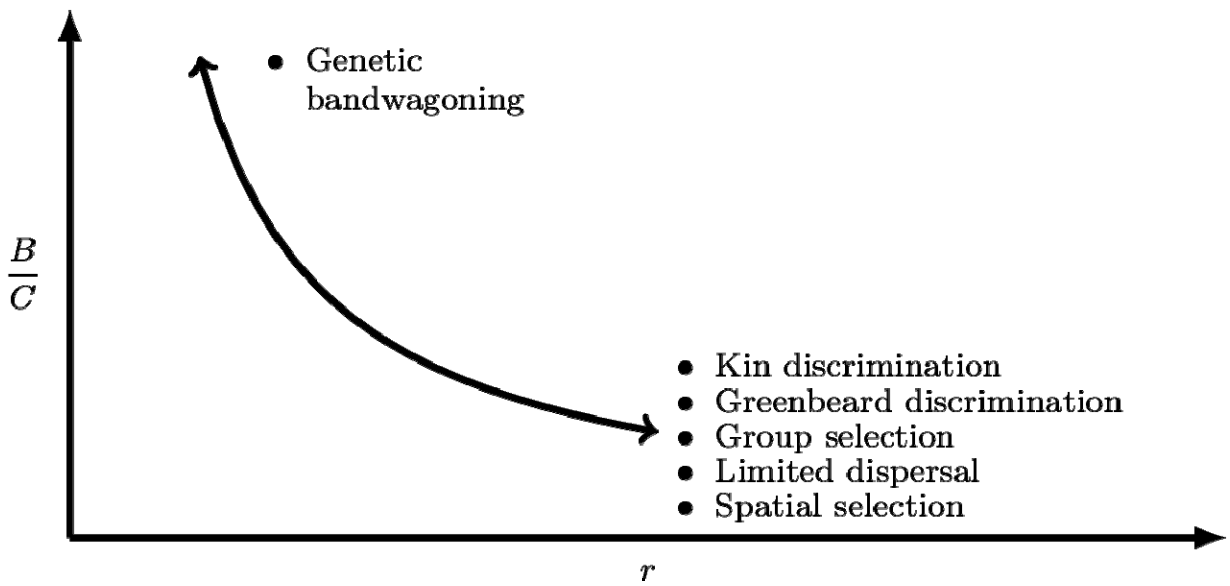

Figure 2. The minimum values for B/C for a given r value that are required for the satisfaction of Hamilton's rule. The curve represented is B/C=1/r. (Curve is not drawn to scale.)

At one end of the Cartesian curve in Figure 2 are kin discrimination, greenbeard discrimination, group selection, limited dispersal, and spatial selection, which are explanations for the evolution of cooperation due to indirect genetic benefits that are typically reliant upon high relatedness (r >> 0) and that can accommodate a low benefit-to-cost ratio (B/C ≈ 1). At the other end is genetic bandwagoning, which relies upon a high benefit-to-cost ratio (B/C >> 1) and can accommodate relatedness not much higher than 0 (r ≈ 0).

6.4) The evolutionary influences exerted by a bandwagoning allele

By inducing resonation and/or reservation, a bandwagoning allele exerts an evolutionary influence upon other genes in the population. Through both resonation and reservation, the bandwagoning allele acts to direct resources from genotypes with a long-term fitness disadvantage to genotypes with a long-term fitness advantage and the bandwagoning allele 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 allele accelerates the fixation of the genes at other loci on these genotypes that are responsible for this long-term fitness advantage.

By inducing reservation against natural enemies, a bandwagoning allele exerts 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 or parasitizing easier for, respectively, the predators or parasites against which the reservation occurs. Just as reservation is differentially costly—that is, costlier to individuals that do not have high ability against these natural enemies—to reserving individuals, reservation is also differentially beneficial to individuals in these natural enemy populations—that is, it is more beneficial to low-ability predators or parasites. Predator individuals or parasite individuals 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. Thus, a bandwagoning allele that induces reservation from ability that is used against a natural enemy population can act to attenuate the intensity of natural selection upon that natural enemy population.

In sum, a bandwagoning allele acts to increase the intensity of natural selection upon the population in which the bandwagoning allele is located. A bandwagoning allele that induces reservation from ability used against a natural enemy population can also act to attenuate the intensity of natural selection upon that natural enemy population.

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No competing interests.

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