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MODELLING THE ROLE OF CHANCE IN MATING DYNAMICS

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PREFACE

This undergraduate honors thesis examines the role of chance in mating dynamics, focusing on the popular measures of I_s and OSR and whether or not they are accurate measures of sexual selection. The first chapter is an overview of sexual selection and how biologists typically measure it, and the second chapter describes the modelling scenarios we created to assess the interaction of I_s and OSR with both chance and parental investment. Our results show that I_s and OSR have indeed been used incorrectly, and that we should shift our focus to trait-based methods when measuring sexual selection.

CHAPTER 1: AN OVERVIEW OF SEXUAL SELECTION

When it comes to evolutionary theory, sexual selection (i.e., covariation between a trait and mating success; Darwin, 1859) plays a critical role in explaining biological diversity and is important for the understanding of behavior, reproduction, genetics, and many other facets of biology. Sexual selection is one of two general forms of selection that often acts on individuals of a population, the other being natural selection (reviewed in Arnold, 1985). While natural selection describes the effects of the environment on the relationship between traits and overall reproductive success, sexual selection occurs when members of one sex with varying trait values compete for access to limited opposite-sex mates, leaving the other sex free to choose whoever they find most attractive and/or creating a situation in which members of one sex compete directly for access to mates (Darwin, 1859). In other words, natural selection occurs when some traits increase overall reproductive success (i.e., the total number of surviving offspring produced), while sexual selection occurs when some traits increase mating success (i.e., the total number of mates or successful mating events acquired), which may or may not lead to an increase in overall reproductive success (Darwin, 1859). Understanding both natural and sexual selection is key to understanding why certain traits persist in populations. In Chapter 1 of my thesis, I focus on reviewing our classic and current understanding of factors that influence sexual selection.

The operation of sexual selection is more complex than previously thought.

There are many different perspectives on sexual selection and how it should be measured. Bateman is one of the most influential sexual selection researchers. In his seminal paper that examined mating dynamics in *Drosophila melanogaster*, he focused on the variance in mating success as the key determinant of sexual selection, and he argued that: 1) sexual selection will be relatively strong in males because an increase in male mating success will typically lead to a relatively large increase in overall male reproductive success, and 2) sexual selection will typically be absent or relatively weak in females because an increase in female mating success often has no effect on overall female reproductive success (i.e., females tend not to be mate limited; Bateman, 1948). Bateman (1948) also held that the greater the variance in mating success within a population, the greater the opportunity for sexual selection. For many years, this conclusion was accepted by biologists, along with the idea that the sex with the greater variance in mating success is generally the sex experiencing sexual selection. This idea has been considered useful because it has allowed for biologists to very easily measure sexual selection, as the variance in reproductive success is generally easy to distinguish in males, whereas it is much more difficult to quantify the actual strength of selection acting on traits (discussed in Shuster & Wade, 2003).

Though a pioneer in the study of sexual selection, biologists have discovered various problems with Bateman's work over time, including concerns about the generalizability of his work and accuracy of his conclusions (see, e.g., Gowaty & Hubbell, 2005). Bateman (1948) focused on males as the major targets of sexual selection, believing females experience no reproductive challenges other than to be fertile and choose mates wisely; however, we now know that females can be mate limited in some systems (Jones & Avise, 2001; Jones *et al.*, 2000; Vincent *et al.*, 1992; Wacker & Amundsen, 2014). He also focused on polygynous species, in which males could mate repeatedly while the females could only mate once, which potentially limits the implications of his work, as females of many species can mate more than once. In general, Bateman's belief that females will always have lower variance in reproductive success than males no longer holds, as we now have greater understanding of the wide variety of mating systems and the unique behaviors that result from different mating dynamics (Tang-Martinez & Ryder, 2005). In addition, Snyder & Gowaty (2007) reexamined Bateman's initial data, finding that his results do not definitively conclude that male variance in mating success always exceeds that of females, even in the case of a polygynous mating system. Snyder & Gowaty (2007) found a variation in mean reproductive success for females that was almost equivalent to males, meaning that female reproductive success should have just as much variation as that of males, and that females could experience sexual selection just like their male counterparts. Ultimately, reevaluation of Bateman's data has shown that it is important to identify what characteristics are leading to high mating success in order to accurately evaluate sexual selection (Sutherland, 1985). Variation in mating success, in other words, does not necessarily mean that sexual selection has occurred (Sutherland, 1985).

Studies are also beginning to demonstrate evidence of sexual selection even when the variation in mating success is low or when variation in mating success does not have any effect on the variance in overall fitness (Fitzpatrick, 2014). The focus in modern studies of sexual selection is slowly shifting to include consideration of the variation in mate quality rather than only the variation in mating success (Fitzpatrick, 2014). Indeed, focusing strictly on the variance in mating success means that we are ignoring the effects of the variance in mate quality and how it affects the selection on traits (Fitzpatrick, 2014). In summary, understanding the link between variance in mating success and variance in reproductive success for males and females can provide some insight into which sex sexual selection is likely to act on (Bateman, 1948); however, we now know that mating dynamics are complex, and given this, understanding mating dynamics requires that we consider the relative importance of a range of various factors on both mating and reproductive success.

In addition to focusing on the link between mating and reproductive success, recent work has suggested a need to consider ecological dynamics and the mating behavior of all individuals in a population (e.g., Klug *et al.*, 2010a). For example, competition for resources and unsuccessful (i.e., unmated) males are often ignored when studying sexual selection, even though these factors can affect mating dynamics and the strength and sexual selection (Klug *et al.*, 2010b). For example, in many cases, individuals must compete for resources such as food or nests before they can directly compete for mates. This resource competition can ultimately influence which individuals acquire a mate, and in some cases, individuals who are unsuccessful at resource competition will be unable to acquire any mates. How such resource competition influences sexual selection is largely unknown (Klug *et al*., 2010a). In general, though, it is critical for studies of sexual selection to examine how traits influence both resource competition and direct mate competition, and ultimately, it will be key to examine how such traits influence both mating and overall reproductive success.

Given all these new findings, many biologists have begun to focus more on trait values instead of focusing exclusively on variation in mating success when studying sexual selection, and there are now attempts to create a quantitative measure of mate quality that can be used to compare individuals within a population (Irschick *et al.*, 2007). This is because mating performance can be traced back to variations in body structures and other physical features, which can be traced back to traits, which can be used to track the overall evolutionary history of the species (Irschick *et al.*, 2007). It is important to point out that this is not a means to an end: traits never reach an optimum point, but are essentially expressions of trait "trends" among the choosy sex that can be ever changing (Arnold, 1985). This means that sexual selection does not always lead to maximum fitness, but instead can create trade-offs in which traits can be both harmful to the individual in relation to energy investment and/or decreased survival but helpful during courtship (such as bright coloration, loud songs, etc.). Often, it can be difficult to identify which traits in a species are being selected for, and sexual selection can affect each sex differently--strong selection on one trait in males can lead to a stabilization in the traits of females, which can cause sexual conflict (Wilkinson *et al.*, 2015). Despite such complexities in identifying sexual selection on traits, selection ultimately acts on specific traits, requiring us to focus on those traits if we are to truly understand sexual selection (Jennions *et al.*, 2012).

In general, and despite many decades of work on sexual selection, we still know relatively little about the general factors that affect mating dynamics and selection within and across populations and species. For instance, while we know that males with extreme features generally achieve greater mating and reproductive success in many species, we often don't exactly know why (Irschick *et al.*, 2007). Likewise, as mentioned before, in many cases we know relatively little about how resource competition can influence mating, and we often don't know which specific traits are under sexual selection in a given population. In addition, there is a lot of work to be done on how to accurately measure sexual selection in mating systems that are less common in the animal world, and we need to develop precise ways to quantify the multiple facets involved in sexual selection.

In the following section, I review the measures that are typically used to quantify or approximate the strength of sexual selection in natural systems. In particular, the strength of sexual selection is generally thought to be driven by the ratio of males to females ready to mate in a given time at a given location, which is known as the operational sex ratio (OSR), and OSR is often used as a proxy for the strength of sexual selection (Emlen & Oring, 1977). In addition, the strength of sexual selection is often thought to be correlated with opportunity for sexual selection, I_s, which is a measure of the maximum possible sexual selection that can act in a population on a given trait (Wade & Shuster, 2003). Our experiment (described in detail below) tests if these are accurate measures of sexual selection, or if there are problems that make them inadvisable for use.

I review these two proxies of sexual selection strength in detail below.

Selection differential does measure the strength of sexual selection.

The selection differential, which quantifies the relationship between a trait value and mating success, is a direct measure of the strength of sexual selection. Assuming heritability of relevant trait(s), the selection differential is also directly proportional to the phenotypic shifts induced by selection. The selection differential is measured as the difference in the trait mean before and after sexual selection or the mean trait value of those breeding minus the average of the full population (Arnold, 1985; Jones, 2009). It is important to note that selection and response to selection are not the same (Jones, 2009). Selection is the correlation between certain trait values and the chances of survival and reproduction, and so can be measured in a theoretical manner even when there is no response to it, or in other words, even when a sexually advantageous trait is not chosen over a less popular trait. Because of this, we can use the selection differential as a measure of the strength of sexual selection regardless of what ends up being inherited in mating events (Jones, 2009). Fitze & Le Galliard (2008) have observed that OSR and the intensity of sexual selection relate in a manner that is opposite of what has so often been predicted by classic sexual selection theory, and in many cases, the OSR does not increase as the selection differential increases. The issues with assuming that OSR will correlate with the strength of sexual selection are discussed below.

OSR is not an accurate measure of sexual selection.

There are three major aspects of a population that determine the OSR: the potential reproductive rates of each sex, their distribution in time and space, and the adult sex ratio (the ratio of adult males to adult females) (Emlen & Oring, 1977; Clutton-Brock, 1992). Various studies in the past have suggested that a more biased OSR means a greater potential for sexual selection in the mate-limited sex (Emlen & Oring, 1977; Wacker *et al.*, 2013). In light of Bateman (1948), it is also often expected that the variation in reproductive success will be greater in populations with extremely biased OSRs, because only the very best members will be able to reproduce and the rest will be left unmated (Moura & Peixoto, 2013). OSR has been challenged as an accurate measure of sexual selection, however (Andrade & Kasumovic, 2005). This is because OSR and I_s are often only accurate predictors of sexual selection when mate monopolization is extreme and one or a very few individuals monopolize all mates within a population (Klug *et al.*, 2010a). The number of females per male can be low even in large sample sizes that seem comprehensive--i.e., mate monopolization will not always be high--and as such, OSR is only expected to accurately quantify the strength of sexual selection under a limited set of conditions (Jennions *et al.*, 2012). In addition, chance plays more of a role when there are fewer mates available, and this is most evident when the OSR is male-biased, even when the selection differential (the measure of actual strength of sexual selection) stays the same (Jennions *et al.*, 2012). Monopolization of mates is expected to increase with OSR, but few consider that additional male competitors could actually make monopolization of females more difficult (Klug *et al.*, 2010a). If the competition becomes more intense as the OSR becomes increasingly biased, that makes monopolization increasingly hazardous, meaning that there may come a point at which male competition actually decreases due to extreme costs (Moura & Peixoto, 2013).

Extremely male-biased OSRs have indeed been shown to increase the cost for males in Adler & Bonduriansky's (2011) study on dung flies (*Sepsis cynipsea*). When males were placed in the same container, their lifespan decreased as the proportion of males per container increased due to extremely heated competition for mates (Adler & Bonduriansky, 2011). The increase in the proportion of males had no negative consequences on the females, however, even though one might expect that increased competition would result in increased harassment and mate protection (Adler & Bonduriansky, 2011).

OSR is also affected by how much time individuals spend in the mating pool, meaning that biologists must be able to tell when individuals are prepared to mate in order to measure it correctly, otherwise the OSR is merely a measure of the adult sex ratio, which does not account for which individuals are actually in the mating pool (Monteiro *et al.*, 2013). Determining who is ready to mate is not easy, though, especially when it comes to females. Females do not often have the same obvious mating displays that males do, which forces observers to simply assume that all mature females are reproductively active (Monteiro *et al.*, 2013). OSR is further affected by mating systems, the costs of mating, timeout and time in (which will be explained in a later section of this chapter), courtship, and the number of encounters, a very long list of nuances that could alter its accuracy as a proxy for the strength of sexual selection (discussed in Fitze & Le Galliard, 2008). However, it is important to note that OSR could potentially be a better measure of sexual selection for some mating systems than others, making it important to study OSR across a multitude of species to verify its accuracy in different types of situations (Hayes *et al.*, 2016). For instance, in Hayes *et al.* 's (2016) study on fiddler crabs (*Uca mjoebergi*), the strength of sexual selection did not correlate well with OSR, and was not stronger when the OSR was male-biased as many would predict, suggesting that in this system, OSR is not an accurate measure of the strength of sexual selection (Hayes *et al.*, 2016). Indeed, according to predictions of OSR studies (Emlen & Oring, 1977), one would have expected the females to always choose the male with the largest claw, but as the OSR became more male-biased, they were in fact less likely to choose males with the largest claws, reducing the strength of sexual selection on that trait (Hayes *et al.*, 2016). Females chose the males with the largest claws more when the male bias was very small or nonexistent (Hayes *et al.*, 2016). This study highlights the fact that OSR is not always a reliable measure of the strength of sexual selection. However, more work is needed to fully understand when OSR is most likely to accurately predict the strength of sexual selection (discussed in more detail in Chapter 2 below).

I_s is not an accurate measure of sexual selection either.

OSR interplays with the opportunity for sexual selection, I_s, a unitless measure that represents the maximum strength of sexual selection (Arnold & Wade, 1984). I_s is equal to the variance in fitness (i.e., mating success, in this case) of individuals divided by the square of the average fitness of the population, a measure that is applied across species (Moura & Peixoto, 2013). The opportunity for sexual selection is equal to the maximum possible strength of sexual selection that could be acting on any given trait in a population, and it is commonly assumed that the strength of sexual selection on a sex is expected to increase as the opportunity for sexual selection increases (reviewed in Klug *et al.*, 2010a). In other words, I_s is often assumed to correlate with and reflect the actual strength of sexual selection acting on traits in a population, and it is regularly used as a measure of the strength of sexual selection in empirical studies (reviewed in Klug *et al.*, 2010a) There are problems with this belief, however. A recent study demonstrated that the actual strength of sexual selection on a trait will only ever equal I_s when females are ridiculously choosy, or when there is ruthless male competition for mates such that one or a very few males in a population monopolize all female mates and many males remain unmated (Klug *et al*., 2010a). Because of this, I_s only functions as a reliable measure of the strength of sexual selection when the strength of sexual selection is very strong; if sexual selection is weak or absent, the maximum sexual selection will never be realized and using I_s as a measure of sexual selection will incorrectly suggest that selection is strong when it is in fact not (Klug *et al*., 2010a).

When I_s fails to correlate with the actual strength of sexual selection on phenotypic traits, chance is more likely to be determining the outcome of mating dynamics (Jennions *et al.,* 2012). In other words, when the variance in mating success is high--which is the case when I_s is relatively large--but the strength of sexual selection on traits is relatively small, this suggests that the relationship between trait values and mating success is weak, which would be expected to occur when chance events are determining mating success (Jennions *et al.,* 2012). Recent theoretical work has demonstrated that there is an increase in stochastic events at increasingly biased OSRs (Jennions *et al.,* 2012; Wacker *et al.,* 2013). The fact that the importance of chance covaries with OSR (Jennions *et al.,* 2012) further suggests that I_s is unlikely to be a reliable proxy for sexual selection. I_s is also too often used across a wide variety of mating systems, even though the very first sexual selection equation involving I_s

implicated that I_s reflected the potential intensity of sexual selection on males alone and is only applicable to polygynous mating systems (Jones, 2009).

Density could also covary with I_s and OSR.

Population density can also affect whether I_s and OSR are likely to be accurate proxies of sexual selection strength. A higher population density could lead to more contact between individuals and therefore higher mortality, resulting in a much different strength of sexual selection (i.e., selection differential) than if the population density were smaller (Hayes *et al.*, 2016). A crowded environment means more waste and more infection transference, as well as increased competition for both mates and resources, and therefore a higher mortality (Adler & Bonduriansky, 2011). The I_s was not affected by male density in Wacker *et al.*'s (2013) study, but perhaps a change in both male and female density could have an effect on mating dynamics and sexual selection. In general, more work is needed to fully understand how population density affects mating dynamics and sexual selection.

Should we dismiss I_s and OSR?

Despite the limitations of I_s and OSR, there remains debate over whether they should be used in studies of sexual selection. Krakauer *et al.* (2011) in particular praises I_s as being able to reflect mate choice, socialization, mate monopolization, and other factors within its parameters, and claims it is a standardized mean of the reproductive fitness of populations. As mentioned previously, though, the first use of I_s was in an equation designed for polygynous systems, not a variety of systems, and as such, it is unclear whether it captures the variables Krakauer *et al.* (2011) claim in other systems.

Krakauer *et al.* (2011) also point out that I_s may not measure selection on specific traits, but that most who examine sexual selection are looking at the total potential for selection, which I_s measures well. One cannot ignore the fact, however, that the total potential selection is due to these specific traits and that selection acts on traits (Jennions *et al.*, 2012), and so they cannot be ignored, just as one cannot assume 2+2=5 and expect to get the correct answer out of a very complex mathematical calculation. If we are to measure sexual selection accurately, we must have a measure that can correctly portray the small details as well as the big picture. Yes, traits that are being selected can be very hard to identify, but we must make the attempt if we are to truly understand the evolution of traits in a broad range of species. Krakauer *et al.* (2011) also suggests that tests showing the inaccuracies of I_s and OSR have values for these measures that are often extreme and do not occur in the natural world. However, assuming extreme monopolization involved in male-biased OSR and I_s is also an extreme situation that does not happen in the natural world. In summary, previous work suggests that OSR and I_s might not be appropriate or accurate proxies of the strength of sexual selection, but the debate over their usefulness continues, and their usefulness will require further study.

Sex roles impact timeout and ultimately change the OSR.

There is still much to be learned about how to accurately measure sexual selection, and further research is needed to identify additional factors that influence mating dynamics. In addition to the factors discussed above, sex roles and parental investment are also expected to influence mating and sexual selection. As mentioned previously, there are many species in which males seem to invest little in offspring, making the females choosy and the males competitive (De Jong *et al.*, 2009) and indeed, such a mating pattern is considered to be the most common. Mating competition arises when there is a limited availability of the opposite sex that restricts the production of offspring (De Jong *et al.*, 2009). There are deviances from these conventional sex roles, however. In many species it has been shown that males prefer virgin females or females with certain features, which generates competition among females to attract mates (Andrade & Kasumovic, 2005). When females are the more competitive sex, the sex role is considered to be reversed. Classical selection theory focuses on the variation in mating success, as explained earlier, in which females show a much lower variation in mating success than males, making it seem as if sexual selection on females is nonexistent (Fitzpatrick, 2014). Competition among females for high quality males could serve as a force of selection, though, and more research should focus on sex-role reversed systems in order to better understand how sexual selection operates on females (Fitzpatrick, 2014).

Some biologists attribute sex roles to anisogamy, supposing that it will cause many males to compete for few females (Kokko *et al.*, 2006). Trivers (1972) argues that the body’s initial investment in gametes leads to future investment behavior, and specifically he suggests that because eggs take more energy to produce, females will be predisposed to continue that investment in their offspring, whereas cheap production of sperm will have males investing relatively little in offspring (Tang-Martinez & Ryder, 2005). Trivers' (1972) assumption that a female continues to invest more in offspring because she has already invested more to produce gametes exhibits the Concorde fallacy--past investment does not predict future investment--and so recently, researchers have thus argued that Trivers' (1972) original arguments are flawed (Kokko & Jennions, 2003;

Kokko & Jennions, 2008). Acceptance of Trivers' ideas leads biologists to ignore for many decades a whole host of other elements that could be involved in sexual selection. For instance, we have not often bothered to look at other ways that males invest in offspring, such as in territory and resource acquisition, mate defense, and the often hazardous competition for females (Tang-Martinez & Ryder, 2005; Kokko & Wong, 2007). We have also ignored the possibility that there could be an element of mate choice on the male's part (Tang-Martinez & Ryder, 2005), and more research on male mate choice is warranted. Some have argued that the lower potential reproductive rate of females limits their future reproduction and therefore makes them less likely to abandon care of their offspring (Clutton-Brock & Parker, 1992). Clutton-Brock & Parker (1992) argued that the potential reproductive rates of each sex is determined more by the time and energy available for mating rather than the cost involved in making gametes. This idea and the focus on potential reproductive rate--which is often quantified empirically as the maximum reproductive rate of a given sex--does not consider, however, that an individual's reproductive rate depends on the availability of mates (Kokko & Jennions, 2008). Indeed, mate availability will affect the realized reproductive rate, and as such, we must understand how a range of factors influence mating dynamics and reproductive rate to fully understand the operation of mating and sexual selection (e.g., Kokko & Jennions, 2008).

Some have hypothesized that there is a relationship between OSR and sex roles, and some believe that varying OSRs--particularly highly female-biased OSRs--can cause sex role reversal (Kokko & Jennions, 2008). For instance, there could be instances in which extreme costs of competition for a mate could decrease the number of available males and cause a sex role reversal in which females compete for mates (Andrade & Kasumovic, 2005). Others have hypothesized that when the OSR is male-biased, males will compete more intensely for mates (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992). When it is female-biased, it is believed that the females will be the more competitive members (Clutton-Brock, 2009). Kokko & Jennions (2008) argue that OSR preserves sex roles in that with male-biased OSRs, the opportunity cost for mating is reduced, meaning that males are selected to provide more care than females. When the OSR is female-biased, the reverse happens (Kokko & Jennions, 2008). In Bateman's (1948) experiments, however, there was no evidence that certain males were more competitive and mated with a disproportionate number of females as a result of being less invested in offspring (Sutherland, 1985). In Andrade & Kasumovic's (2005) study on redback spiders, *Latrodectus hasselti*, a switch in the OSR bias did not lead to sex role reversal. In Head *et al.*'s (2007) study on guppies, *Poecilia reticulata*, females were more highly pursued at male-biased OSRs, but this did not affect the sexual selection that resulted. Jirotkul's (1999) study on the same guppies did not show a role reversal either. Individual males simply mated less and females mated more at male-biased OSRs. The conclusion to be drawn is that OSR should not be considered a sole indicator of which sex will be more competitive, as there are simply too many factors at play (Clutton-Brock, 2009).

OSR does, however, affect more subtle behaviors associated with sex roles in ways that go beyond strict sex role reversal. OSR is often biased toward the sex that mates faster (Clutton-Brock, 2009). This is also the sex that typically has the higher mortality rates due to the costs of acquiring mates (Clutton-Brock, 2009). In Monteiro *et* *al.* ’s (2013) work on pipefish, *Nerophis lumbriciformis*, OSR was shown to correlate with the level of parental investment and the costs of reproduction (Monteiro *et al.*, 2013), and these features were never previously related to OSR. OSR can indeed be affected by the parental care each parent supplies (Kokko & Jennions, 2008). The sex that exhibits parental care less may be selected to give more care (Kokko & Jennions, 2008). Parental investment leads to a skew in the number of females to males, which then can also affect OSR and in some cases predict sexual selection (Kokko & Jennions, 2008)

In studies of the relationship between OSR and sex roles, competition for mates is generally believed to be greater when the OSR is more biased (Hayes *et al.*, 2016). It is important to note that greater competition does not necessarily lead to greater sexual selection, though. Sexual selection is the response to competition, not the competition itself (Hayes *et al.*, 2016). In many situations, an individual may be better off to aim for other valuable traits if the competition to obtain a particular trait is leading to costly competition (Kokko & Jennions, 2008; Hayes *et al.*, 2016). This means that as the OSR becomes more male-biased, the variation in mating success may sometimes decrease (Hayes *et al.*, 2016).

Some other authors have raised other concerns about the relationship between OSR and sex roles (e.g. Schärer *et al.*, 2012). For instance, if competition for mates depends on OSR, it would not be any more likely for either sex to have either sex role, and yet we see a clear tendency across species for female choice and male competition (Schärer *et al.*, 2012). The question becomes whether or not increased competition leads to higher likelihood of sexual selection. If this is the case, then OSR is a good predictor of sexual selection, but if not, other options should be considered (Kokko *et al.*, 2012). In a female-biased OSR it may seem that the males would become the choosy members, but they may still compete for females if breeding is costlier for the females. This is why cost for each sex should be seriously considered in studies of mating dynamics and sexual selection (Kokko & Monaghan, 2001; Kokko *et al.*, 2006). There are costs to reproduction that can be both immediate or gradual, whether it be death upon copulation/delivery or wearing on the body from many matings over time (Adler & Bonduriansky, 2011). In insects, for example, it has been shown that increased mating can be costly for females, causing damage through the copulation itself or harassment from the male (Adler & Bonduriansky, 2011). There are other nuances as well, just as the fact that it has so often been considered that the males that harass females the most are the most successful, while some studies have shown that the weaker males are the more persistent (Hall *et al.*, 2008).

This brings us back to the idea of parental investment and timeout from the mating pool. Over the course of a lifetime, individuals have a certain amount of time dedicated to mating, which affects the number of possible mate encounters they have (Gowaty & Hubbell, 2005). The more mate encounters, the more opportunities to mate (Gowaty & Hubbell, 2005). Courtship takes up a portion of this time, in which the individual is focusing on one mate and losing its opportunity to mate with others (Gowaty & Hubbell, 2005). The individual's survival probability must be added to this time, as this also predicts future mating success (Gowaty & Hubbell, 2005). Variance in mating success is reduced as males spend more time in each copulation, so if there are two males and two females, and one male is genetically superior but spends a long time mating with one female, the other female will already be mated before he can move on to her

(Sutherland, 1985). With all of this in mind, it is also critical to consider the proportion of time that individuals spend in the mating pool (i.e., in a time in state) versus the time that they spend out of the mating pool (i.e., in a timeout state).

Our experiment puts these ideas to the test.

While early and classic work on sexual selection and mating dynamics focused on how OSR and I_s can both affect and function as accurate measures of sexual selection, it is now clear that a range of other factors can influence mating; in some cases, OSR and I_s are unlikely to be the primary drivers or most accurate measures of sexual selection. In addition to the range of factors discussed above, mating dynamics will sometimes be determined by chance events. Surprisingly, biologists have rarely considered the role that chance will play in determining the outcome of mating dynamics. Our theoretical experiment (described in Chapter 2) aims to examine the role that chance can play in mating dynamics by assessing the relationship between OSR, $I_{s,}$ and the strength of sexual selection on traits (i.e., selection differentials) across biological scenarios of interest (described in Chapter 2). This study will allow us to 1) evaluate the validity of OSR and I_s as measures of sexual selection and 2) identify the scenarios when chance is most likely to be driving mating dynamics, which is expected to occur when there is high opportunity for sexual selection but little to no selection on traits.

In the next chapter, our theoretical experiment and methods will be described, and the results will be discussed in relation to the background material given in Chapter 1. We will specifically hone in on the possible role of chance in creating discrepancies in OSR and I_s and will explore how chance could be playing out in the natural world in relation to mating.

CHAPTER 2: MODELLING THE ROLE OF CHANCE IN SEXUAL SELECTION

When it comes to mating dynamics, the impact of chance cannot be overemphasized. Stochastic events play a major role in determining who mates during a given breeding attempt, even in very large populations with members that differ in traits that determine their likelihood of mating (Jennions *et al.,* 2012). Despite decades of intense research on sexual selection and mating dynamics, scientists often fail to take the role of chance into account when studying sexual selection. We instead implicitly or explicitly ignore the role of chance in determining patterns of mating and more often rely on proxies of sexual selection such as the operational sex ratio (i.e. the ratio of males to females that are prepared to mate at a given time and place, OSR; Emlen & Oring, 1977; see also Chapter 1) and I_s (i.e. a standardized measure of variation in mating success; Wade & Shuster, 2003) when attempting to quantify, predict, and/or explain patterns of sexual selection. Our continuing use of metrics such as OSR and I_s and our failure to consider the role of chance in determining mating success is potentially leading to conclusions about sexual selection that are skewed, and calls for a means of more accurately quantifying and studying sexual selection with the role of chance included (Klug *et al.,* 2010a). In particular, it will be critical to quantify the role chance plays in influencing mating dynamics and examine whether the impact of chance on sexual selection covaries with measures such as OSR and I_s. Indeed, if chance tends to be relatively more important under some conditions (e.g., when OSR is biased or unbiased), then this would suggest that chance covaries with factors that are expected to influence OSR, and this in turn would suggest that chance can influence our general understanding of sexual selection and mating dynamics.

OSR in particular is considered a primary factor that determines the strength of sexual selection in a population, and many researchers have argued that it can be used as a proxy for the strength of sexual selection (reviewed in Klug *et al.*, 2010a; Chapter 1). The strength of sexual selection is expected to increase as the OSR becomes more male or more female biased, and some have hypothesized that mate monopolization will increase at more biased OSRs, leading to strong sexual selection on traits of the more common sex (Emlen & Oring, 1977; reviewed in Chapter 1). Unfortunately, the logic behind the idea that monopolization of mates by the more prevalent sex will increase as OSR increases is not rooted in any general principles, and there is evidence that suggests mate monopolization will not necessarily increase as OSR becomes more biased (Klug *et al.*, 2010a). Indeed, increased OSR can make mate monopolization more difficult because there are so many members of the same sex to compete with, and as such it becomes equally plausible that mate monopolization will become more difficult as OSR increases and that sexual selection will be relatively weak at biased OSRs (Klug *et al.*, 2010a; discussed in Chapter 1). It is also very problematic to assume a relationship between OSR and sexual selection without knowing the traits that can lead to monopolization, as traits are ultimately the target of selection (Klug *et al.*, 2010a). OSR, in other words, does not necessarily predict whether sexual selection occurs or how the strength of sexual selection varies across different scenarios.

I_s is a standardized measure of mating success that quantifies the maximum potential strength of sexual selection that can occur given the mating dynamics of a group of individuals, and as with OSR, the strength of sexual selection is expected to increase as I_s increases (Wade & Shuster, 2003; discussed in Chapter 1). This hypothesis is based on the idea that the greater variance of fitness in a population, the stronger the impact of sexual selection (Wade & Shuster, 2003; reviewed in Klug *et al.,* 2010a). This argument assumes that the opportunity for sexual selection is equivalent to the realized strength of selection (i.e., it assumes that all variation in fitness is due to traits), even though large variation in mating success does not necessarily mean that some individuals are mating more than others because of their traits (Klug *et al.,* 2010a). I_s is not linked to traits--rather, it is simply a measure of variation in mating success that quantifies the maximum possible strength of sexual selection in a given situation--and sexual selection by definition occurs when certain traits allow some individuals to acquire more mates than other individuals who lack those preferred traits (discussed in Klug *et al.,* 2010a; Chapter 1). Recent theoretical work has found that I_s also does not consistently predict or correlate with the actual strength of sexual selection across OSRs (Klug *et al.,* 2010a), which contrasts with the prediction that I_s and the realized strength of sexual selection on traits will increase as monopolization increases (Wade & Shuster, 2003). The prediction that I_s and the strength of sexual selection will increase as this monopolization increases is based on the assumption that sexual selection is the only cause of unequal mating success, which is unlikely to be consistently true, particularly when chance events affect mating success (Klug *et al.,* 2010a). Indeed, I_s will only consistently and reliably predict the strength of sexual selection when the monopolization of mates is high at all OSR values (Klug *et al.,* 2010a). In other words, I_s only reflects the maximum sexual selection in a population, not its actual sexual selection, and it is only expected to accurately reflect the strength of sexual selection if sexual selection is very strong (Klug *et al.,* 2010a;

Chapter 1).

Using I_s as a measure or predictor of sexual selection fails to account for the many random events that could determine mating patterns, and instead only looks at the deterministic processes that affect mating success (Jennions *et al.*, 2012). For example, even the simple fact that mating success must be an integer (it is impossible to have a fraction of a mate) creates stochasticity in mating success, and such stochasticity should be accounted for in our understanding of sexual selection and mating dynamics (Jennions *et al.*, 2012). In light of these recent realizations, chance has been seen as an increasingly important factor to consider when studying patterns of mating dynamics and sexual selection. Chance dynamics in mating can play a major role in creating variation when partners are scarce, while at the same time controlling the breeding of large populations (Jennions *et al.*, 2012). In part, this is because even when there are many partners to choose from, an individual can only mate with so many of them (Jennions *et al.*, 2012). This means that not every individual will get to mate even if they have an advantageous trait, and that some individuals with less preferred traits may get to mate repeatedly. It is very important, then, to quantify many aspects of mating dynamics, including selection on traits of interest, intra-sexual variation in mating success, and the random events that might also affect mating success.

In order to enhance our understanding of how chance can influence mating dynamics, we conducted a theoretical study to examine the role of chance in affecting mating dynamics across a range of biologically realistic scenarios. We focused on how chance might vary across OSRs; specifically, we quantified the relationship between the strength of sexual selection on a hypothetical trait and I_s across OSRs for the cases in which 1) mating success is entirely deterministic (i.e., it is entirely determined by trait value, and mating success is not restricted to an integer), and, 2) mating success is affected by the fact that mating success is an integer, which introduces a fundamental element of chance to our calculations. We hypothesized that as I_s increases, the strength of sexual selection (i.e., the selection differential; see Chapter 1 for discussion of selection differentials) will increase initially in both scenarios, but then begin to plateau as chance begins to play more of a role especially in our scenario that restricts mating success to integer values. We also suspect that when mating success is forced to be an integer (Fig. 1) (i.e., when we account for a very basic source of stochasticity), the relationship between I_s and the selection differential may have little correlation. As OSR increases and population density increases, we also expect to find high evidence of the strong influence of chance and a lack of correlation between OSR and I_s.

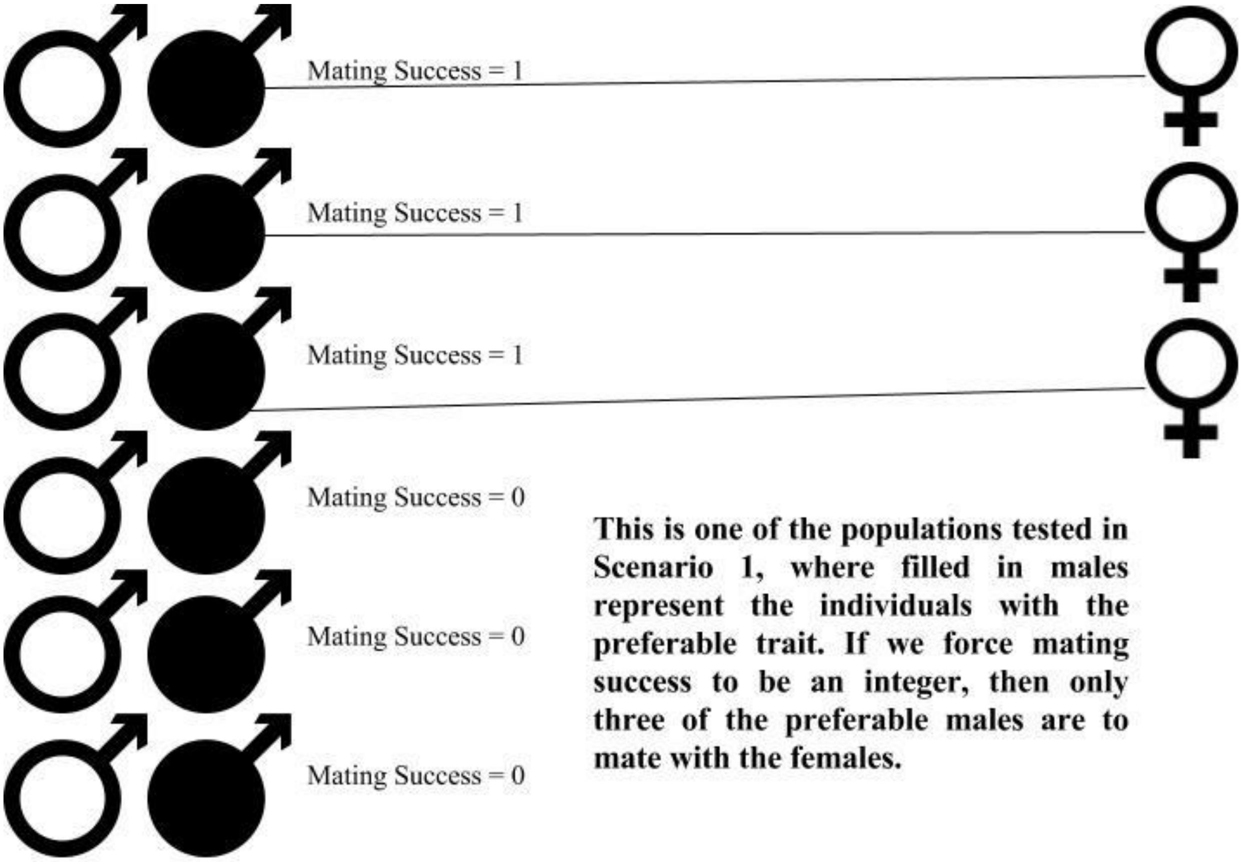

Figure 1: An example of Scenario 1 Dynamics in which we assume stochasticity due to mate number being an integer.

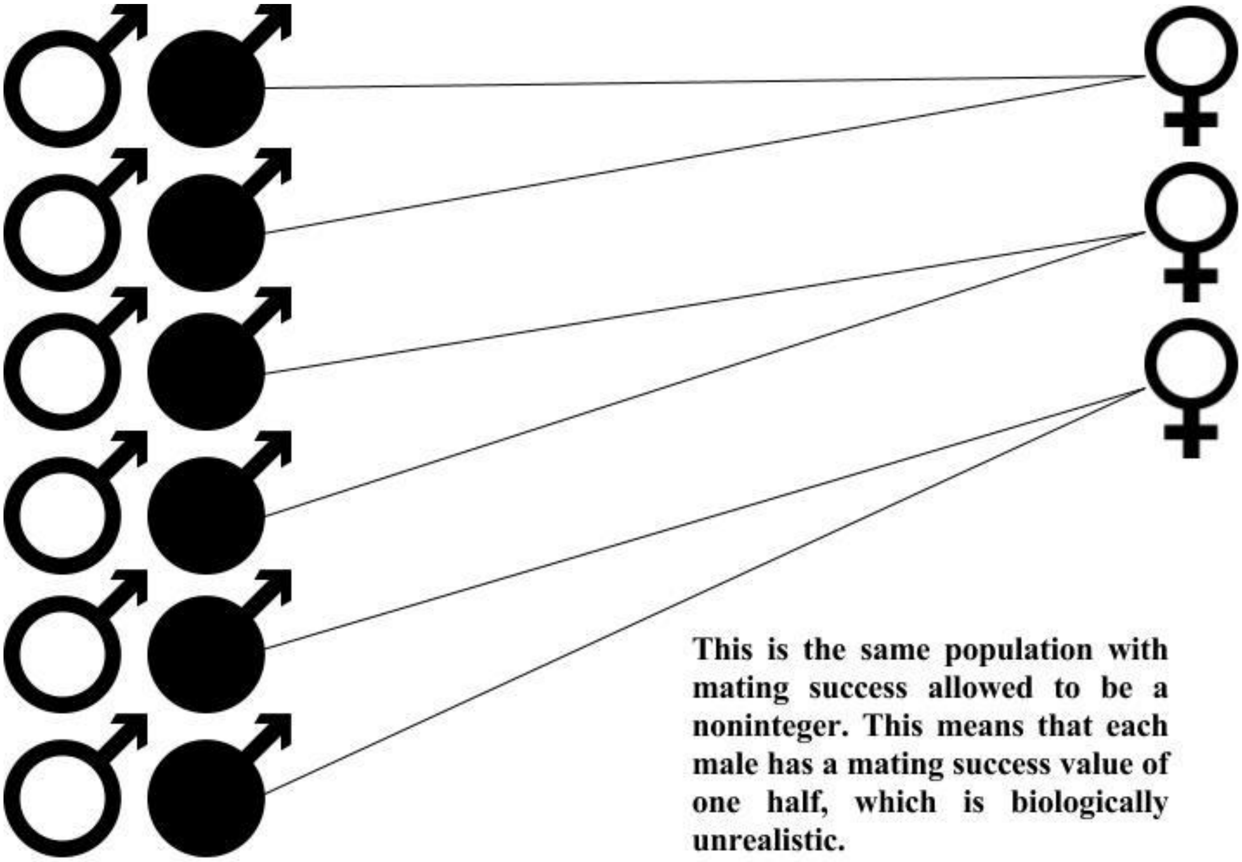

Figure 2: An example of Scenario 1 Dynamics in which we do not assume stochasticity due to mate number being an integer.

Methods

We created seven simple, but biologically realistic, scenarios to examine the relationship between I_s and OSR assuming that 1) mating success is unaffected by chance (i.e., mating success is directly related to trait value and not forced to be an integer (Fig. 2) and 2) mating success is stochastic because mating success must be an integer (Fig. 2). In the first three scenarios we assume that all females mate at once and are then permanently removed from the mating pool, while in the last four scenarios we allow females to leave and return at various rates.

For simplicity, we assume that sexual selection acts only on males, and we assume that males either have a preferred trait that makes a female likely to choose them or they lack such a trait and are not preferred as mates by females. Each scenario consisted of twelve populations with varying numbers of males and females, as well as specific ratios of males with the preferred trait (i.e., the trait that is being sexually selected for), with male trait values designated as 1 for the preferred trait or 0 for the non-preferred trait.

To illustrate that chance can be important even in relatively simple scenarios, we assumed the classic scenario in which females are choosy and males are non-discriminate (i.e., they mate with any female available and sexual selection is not acting on females). We also assumed that the males with the preferred trait are the only members to receive mates (i.e., females never mate with males who lack the preferred trait in our scenarios). We recorded the number of mates that each preferred male obtained, and then calculated the variation of male mating success, the opportunity for sexual selection, I_s, and the selection differential, s, which is a measure of the strength of sexual selection on the male trait (Table 1). We did all calculations 1) forcing the mating success values to be integers (because one male cannot mate with 2.5 females; see e.g., Fig. 1), which allows chance to influence mating success, and 2) allowing the mating success values to be non-integers (see e.g., Fig. 2), which is biologically unrealistic but is what would have to occur if chance has no effect on mating success. We did this in order to see if limiting mating success to integer values, which introduces some stochasticity into our calculations, would affect the relationship between s and I_s across OSRs. Because our scenarios and calculations were relatively simple, all calculations were performed in Microsoft Excel (Appendix). All calculations were performed using the standard equations outlined in Table 1 (Arnold & Wade, 1984; Shuster & Wade, 2003), and specifically, for each scenario we quantified: 1) the OSR; 2) variation in male mating success, and, 3) the coefficient of variation in male mating success, which then allowed us to calculate 4) the opportunity for sexual selection on males, and, 5) the strength of sexual selection on the simulated male trait in our population (Table 1).

Table 1. Equations Used: The following equations were used in all analyses to calculate the Operational Sex Ratio, the Opportunity for Sexual Selection, and the Selection Differential.

Measure	Equation	Variables
Operational sex ratio (OSR)	# of males/# of females	This specifically represents males and females *ready to mate*, not just the ratio of adult males to females.
Variation in Male Mating Success (VMS)	$\sum(K_i^2 \times M_i)/\sum(M_i) - [\sum(K_i \times M_i)/\sum(M_i)]^2$	K_i: the mating success of each male M_i:the value of each male (always 1)
Coefficient of Variation	stdev(K_i)/avg(K_i)	Stdev: standard deviation K_i: the mating success of each male Avg: average
Opportunity for sexual selection (I_s)	VMS/avg(K_i)	VMS: variation in male mating success (equation above) Avg: average K_i: the mating success of each male

Selection differential (s)	covar(K_i,M_i)	Covar: covariance K_i: the mating success of each male M_i:the value of each male (always 1)

After the calculations were complete, we compared the opportunity for sexual selection with the selection differential across OSRs for each scenario. According to classical sexual selection predictions (Emlen and Oring, 1977; Arnold & Wade, 1984; Wade & Shuster, 2003), the opportunity for sexual selection is expected to correlate strongly with the strength of sexual selection, and both are expected to increase as OSR increases (i.e., becomes more biased). If we observed such a correlation, then chance was not involved in determining mating success and does not covary with OSR, as a strong positive correlation between OSR, I_s and s would suggest that the opportunity for and actual strength of sexual selection are consistent across scenarios. In contrast, if s began to plateau as I_s continued to increase, or is in some other way not correlated consistently with I_s, this would suggest that the maximum potential for sexual selection is not being realized across scenarios, and that instead chance is affecting mating dynamics under some conditions. We created line graphs of the results to visualize the relevant relationships.

The seven scenarios performed are described below.

- *Scenario 1, Varying Female Numbers Leads to Variation in OSR:* In this scenario there were twelve populations which all had twelve males each. Each population had varying levels of females, so that six of the populations had male-biased OSRs of varying intensity and six had female-biased OSRs of varying intensity. The ratio of males with the preferred trait was kept at one half, so six males in all twelve populations had the preferred trait and were able to obtain mates. All members mated at once.

- *Scenario 2, Change in OSR with a Constant Population Size Leads to Variation in I_s:* In this scenario there were twelve populations of 70 individuals each. I adjusted the ratio of males to females in each population so that so that there were six populations with male-biased OSRs of varying intensity and six populations with female-biased OSRs of varying intensity. In all twelve populations one-third of males had the preferred trait and so were able to obtain mates. All members mated at once.
- *Scenario 3, Change in the Number of Males with the Preferred Trait Leads to Variation in I_s:* In this scenario there were twelve populations with 12 males and twelve females each. In the first population I had only one male with the preferred trait, and then with each population I steadily increased the number of males with the preferred trait by 1 until all twelve males had the preferred trait, so that with each population an increasing number of males were able to mate.
- *Scenario 4, Timeout Scenarios Lead to Significant Differences Between Integer and Noninteger Calculations:* In this scenario there was one population of 50 males and 50 females. 25 of the males had the preferred trait, and I assumed that once a female mated she was permanently out of the mating pool. I set a constant mating rate, so with each round of mating 20% of the reproductively available females mated and were removed from the mating pool. I did this for 12 rounds.
- *Scenario 5, An Increasing Mating Rate Promotes a Stable I_s:* In this scenario there was one population of 50 males and 50 females. 25 of the males had the

preferred trait, and I assumed that once a female mated she was permanently out of the mating pool. I set a steadily increasing mating rate, starting with 2% of the available females mating and increasing the number of females mating by 2% each round. I did this for 12 rounds.

- *Scenario 6, A Decreasing Mating Rate Promotes a Stable I_s*: In this scenario there was one population of 50 males and 50 females. 25 of the males had the preferred trait, and I assumed that once a female mated she was permanently out of the mating pool. I set a steadily decreased mating rate, starting with 24% of the available females mating and decreasing the number of females mating by 2% each round. I did this for 12 rounds.
- *Scenario 7, Returning Females Promote a Stable I_s*: In this scenario there was one population of 50 males and 50 females. 25 of the males had the preferred trait. In each round of mating 20% of the available females mated and were removed in the mating pool, while at the same time 10% of those that were already in timeout came back into the mating pool. I did this for 12 rounds.

Results

Scenario 1, Varying Female Numbers Leads to Variation in OSR:

In the first scenario, calculating I_s and s with non-integer mating success values resulted in a progression predicted by classical models for all OSRs considered (Fig. 3). As the opportunity for sexual selection increased, the strength of sexual selection also increased, suggesting that the maximum strength of sexual selection was realized across all scenarios. When mating success values were forced to be integers (i.e., when we accounted for chance), however, the results were quite unexpected given classic sexual selection theory. In cases where there were not enough females for every favorable male to be able to mate, the selection differential wildly fluctuated as I_s increased for some OSR scenarios. This suggests that in some cases chance will affect mating success simply because there are not enough females to mate with all males with the preferred trait.

As the OSR increased in the first scenario, I_s initially plummeted at the same rapid rate for both integer and noninteger calculations (Fig. 4). This goes directly against the conventional belief that I_s increases with increasing OSR, and in fact suggests the opposite, that the opportunity for sexual selection will decrease as males increasingly outnumber females. As OSR continued to increase, I_s values began to plateau, with a slight upward trend in integer calculations and a slight downward trend in noninteger calculations. This suggests that there comes a point at which there are so many males that chance begins to play a much greater role, causing the I_s to stabilize. All of this could be due to increasing male competition for mates, leading to less monopolization and a more equal likelihood for all members of a group of preferred males to receive mates. The rapid decrease in I_s could also correlate with the lower and fluctuating s values, representing the cases in which there were not enough females for each favorable male to be able to mate.

In both integer and noninteger calculations, as OSR increased, s rapidly decreased and then plateaued (Fig. 5). This suggests that the actual sexual selection taking place also decreases as the ratio of males to females decreases, and that chance plays an increasing role with an increasing number of males.

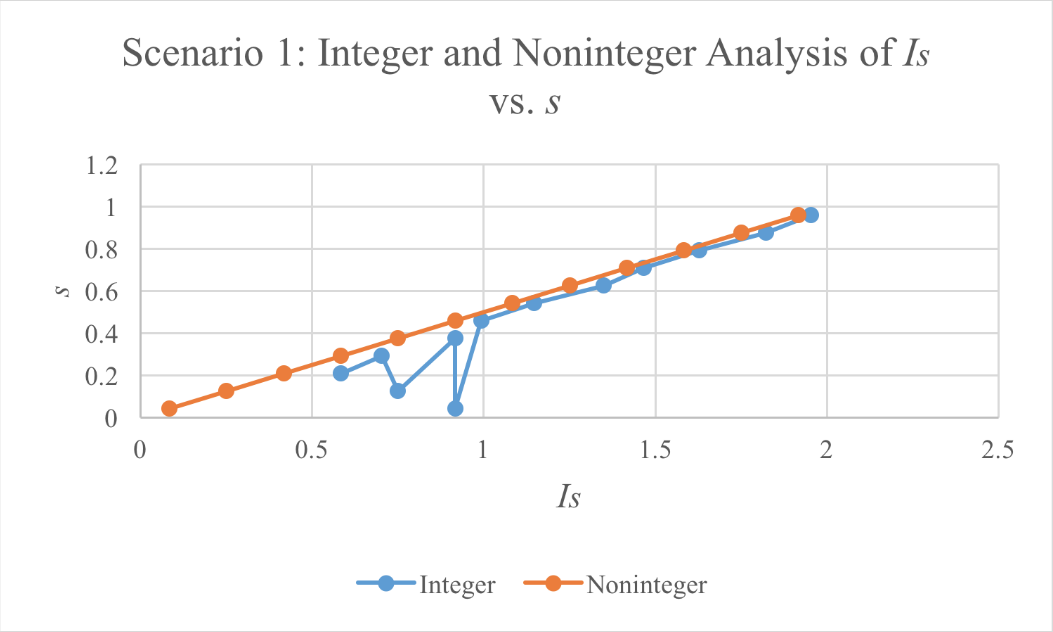

Figure 3. Scenario 1 Results: A comparison of the I_s *and s values found in Scenario 1, both with forced integer and noninteger calculations.*

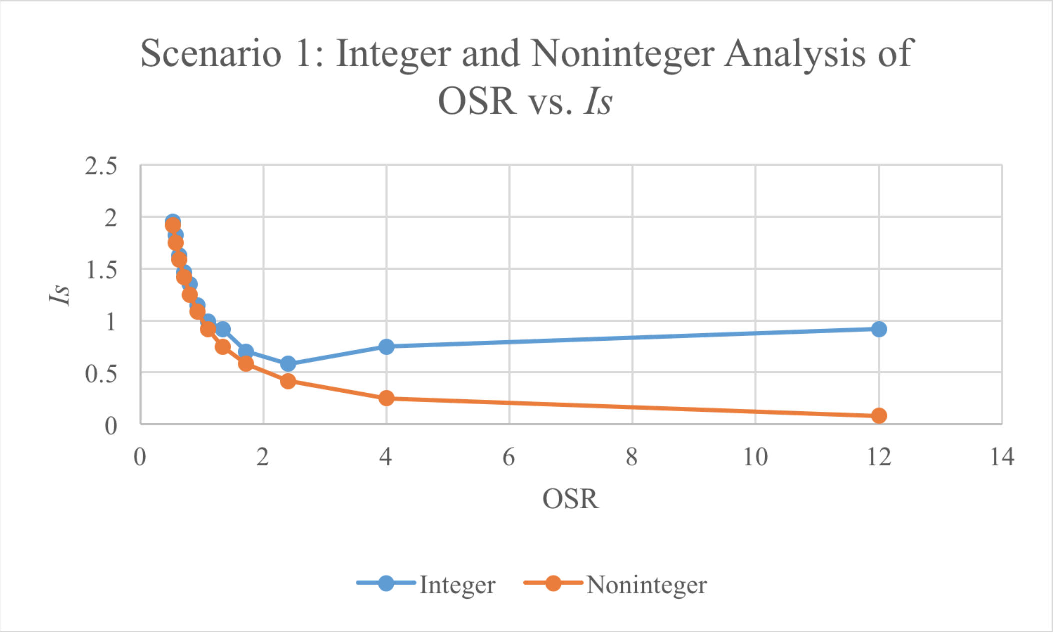

Figure 4. A comparison of the OSR and I_s *values found in Scenario 1, with both forced integer and noninteger calculations.*

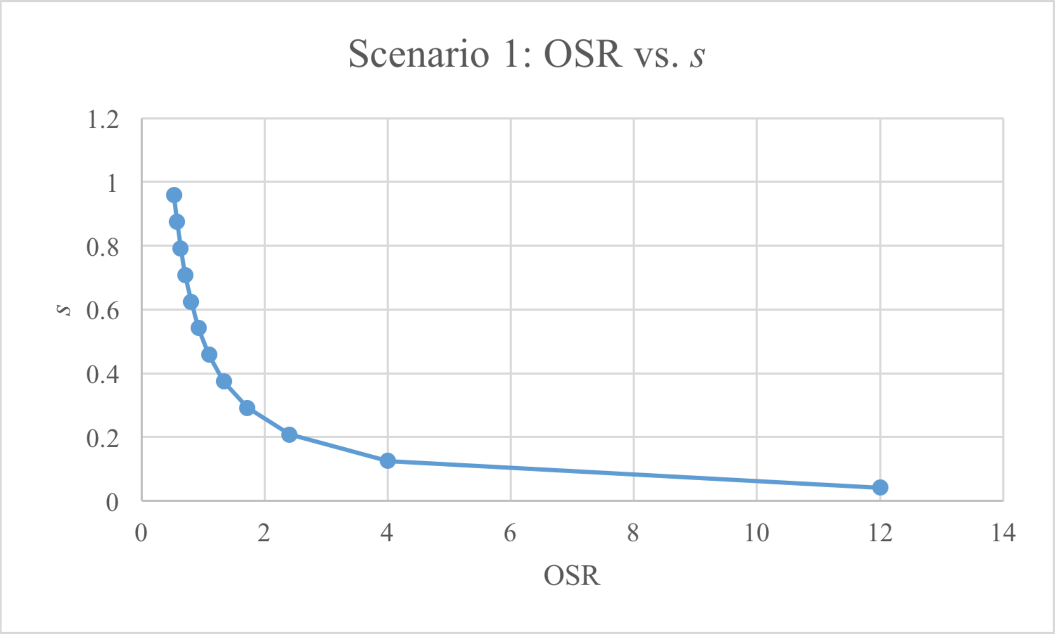

Figure 5. Scenario 1 Results: A comparison of the s and OSR values found in Scenario 1. In this case the selection differential and OSR for both integer and noninteger calculations were the same.

Scenario 2, Change in OSR with a Constant Population Size Leads to a Change in I_s*:*

In the second scenario, calculating I_s and s with both non-integer and integer mating success values resulted in a progression predicted by classical models for all OSRs considered (Fig. 6). In the second scenario, all preferred males were able to mate, versus Scenario 1 in which there were some cases where there were simply too few females for all males with the preferred trait to be able to mate. This scenario shows that in order for non-integer calculations to be accurate, all preferred males must be able to acquire mates. Otherwise chance plays a role in determining which preferred males will be successful. Forcing mating success values to be integers could have also led to differences because of the fact that the population density was kept the same, instead of having various population sizes as in Scenario 1.

Scenario 2 was similar to Scenario 1 in that I_s rapidly decreased as the OSR increased with both integer and noninteger calculations (Fig. 7). This reinforces our hypothesis that the opportunity for sexual selection will not increase as the number of males in the mating pool increases. This also shows that whether or not a population has a constant or fluctuating density has little effect on the opportunity for sexual selection - regardless, the I_s will increase as OSR increases.

In both integer and noninteger calculations, as OSR increased, *s* rapidly decreased and then leveled out at 0 (Fig. 8). These results suggest that at a certain point, there can be so many males that sexual selection is not possible. Male competition for mates and the fact that females have so many options can cause chance to be the sole component in determining mating success.

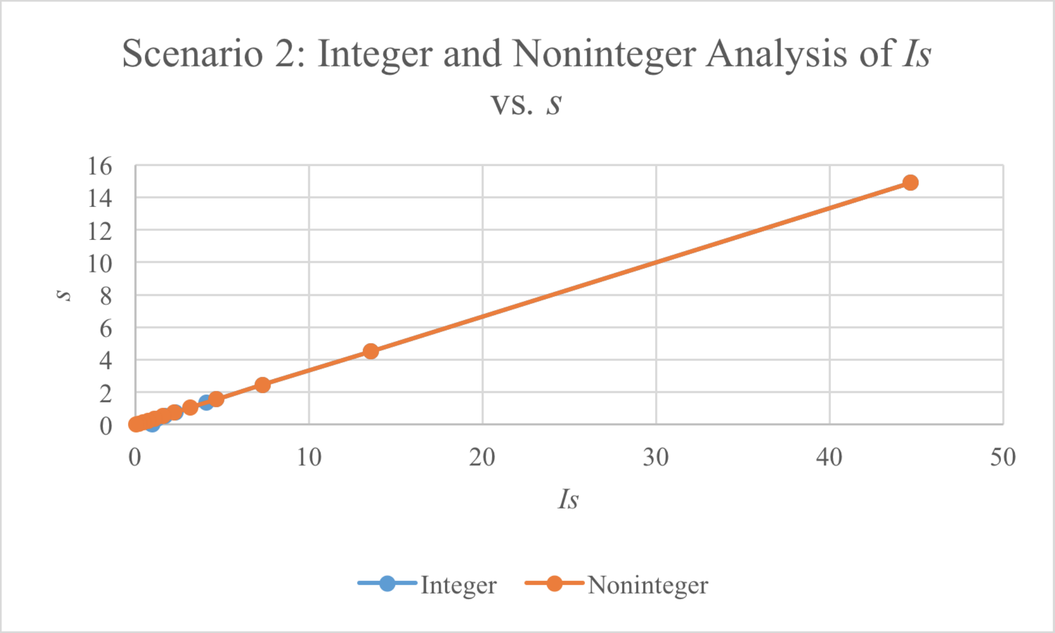

Figure 6. Scenario 2 Results: A comparison of the I_s *and s values found in Scenario 2, both with forced integer and noninteger calculations.*

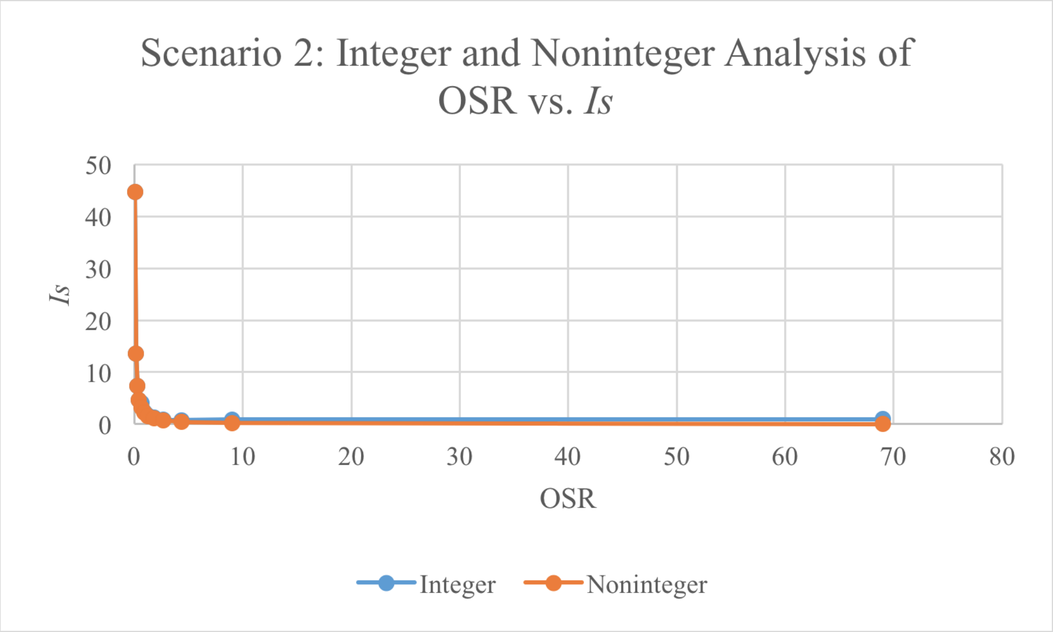

Figure 7. Scenario 2 Results: A comparison of the I_s *and OSR values found in Scenario 2, both with forced integer and noninteger calculations.*

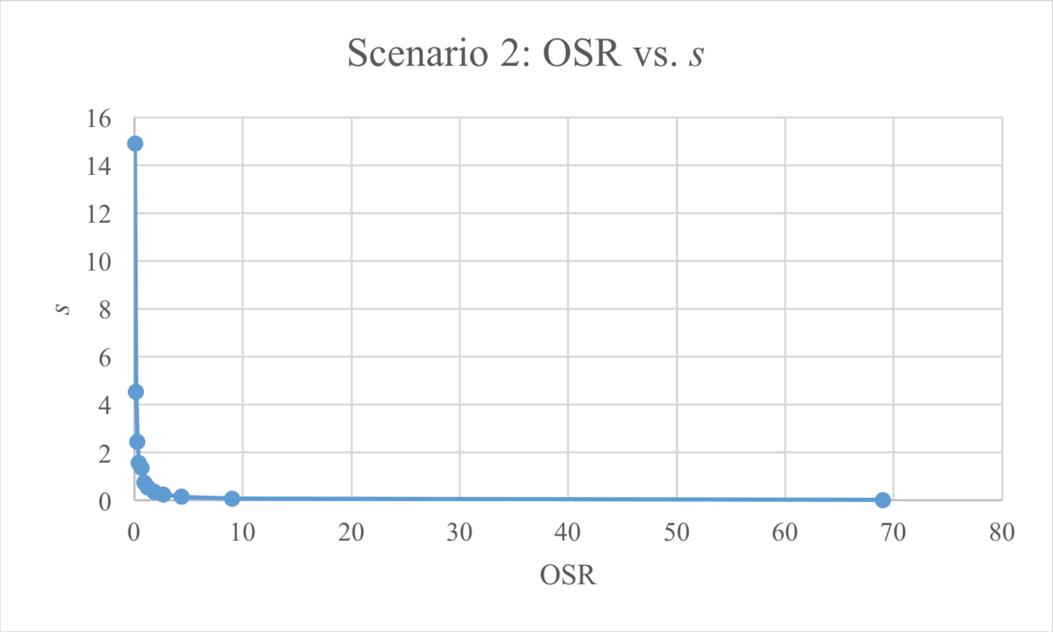

Figure 8. Scenario 2 Results: A comparison of the OSR and s values found in Scenario 2. In this case the selection differential and OSR for both integer and noninteger calculations were the same.

Scenario 3, Change in the Number of Males with the Preferred Trait Leads to Variation in I_s*:*

In the third scenario, *s* increased as I_s increased as predicted in classical models of sexual selection (Fig.9). When the population density and OSR were kept the same and only the number of males with the preferred trait was changed, however, the way in which the selection differential increased was different than in scenarios 1 and 2. Instead of a linear increase, the values of *s* eventually plateaued after reaching a certain value for I_s. This means that as the opportunity for sexual selection increases, the actual sexual selection taking place does increase for a time. There comes a point, however, at which the opportunity for sexual selection becomes more and more irrelevant and chance begins to play more of a role, leading to the plateau in the line graph. Since OSR remained constant this scenario, we did not compare it with I_s or *s* for in this scenario.

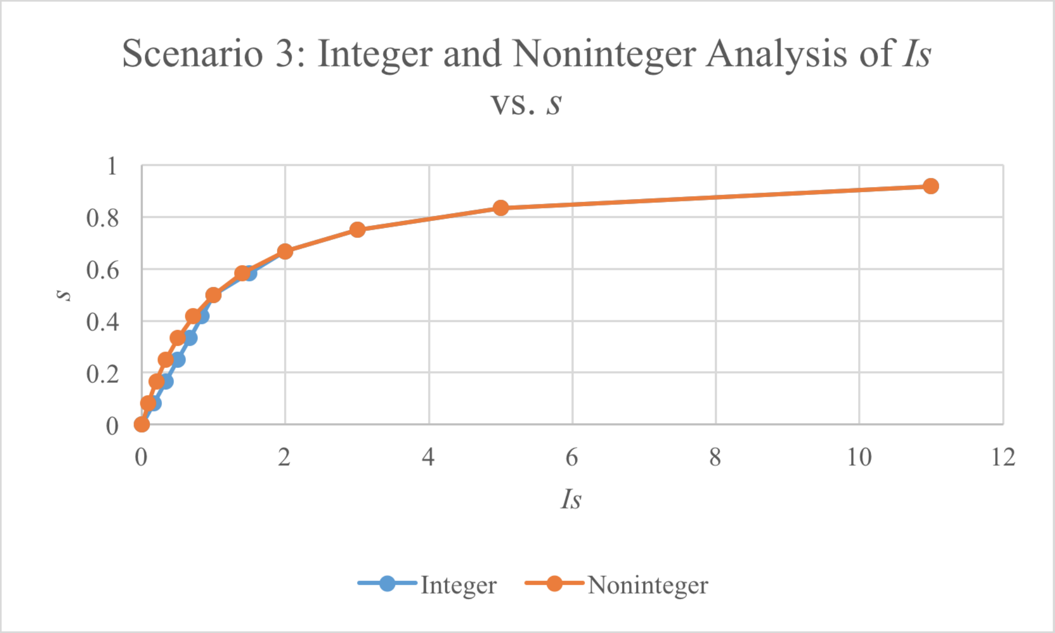

Figure 9. Scenario 3 Results: A comparison of the I_s *and s values found in Scenario 3,*

both with forced integer and noninteger calculations.

Scenario 4, Timeout Scenarios Lead to Significant Differences Between Integer and Noninteger Calculations:

In this scenario, using integer and noninteger mating success values led to radically different results: when integer values were used, the selection differential decreased with I_s, whereas with noninteger values s increased (Fig. 10). At its height, integer calculations also had I_s values four times higher than those of noninteger calculations. This is because when noninteger calculations were used, there was never a case in which any of the preferred males received one full female--all mating success values for the 25 preferable males were decimal values far below 1, which caused the variation in mating success to be much lower, and therefore the I_s to be much lower. This follows Bateman's (1948) idea that the lower the variation in mating success, the lower the level of sexual selection.

Integer and noninteger calculations both generally exhibit little change in I_s as OSR increases (Fig. 11). Integer calculations have an initial slight increase and noninteger values have an initial slight decrease, and the large difference in I_s values for integer and noninteger values is still visible. Even though s values were quite opposite as I_s increased, they were relatively similar as OSR increased for both integer and noninteger calculations. As OSR increased, s values decreased and the plateaued (Fig. 12).

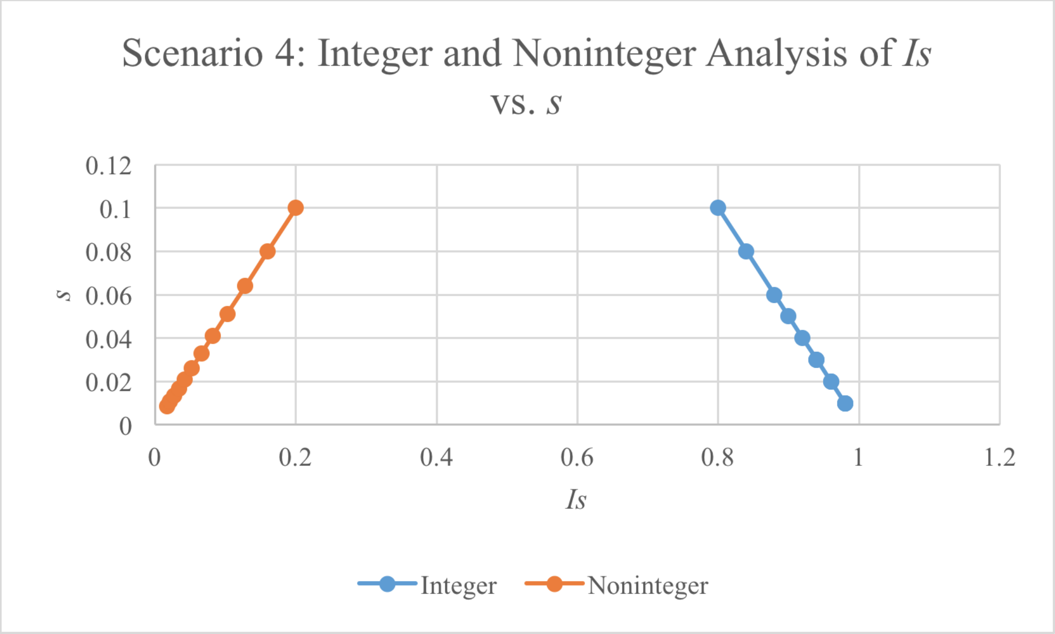

Figure 10. Scenario 4 Results: A comparison of the I_s and s values found in Scenario 4, both with forced integer and noninteger calculations.

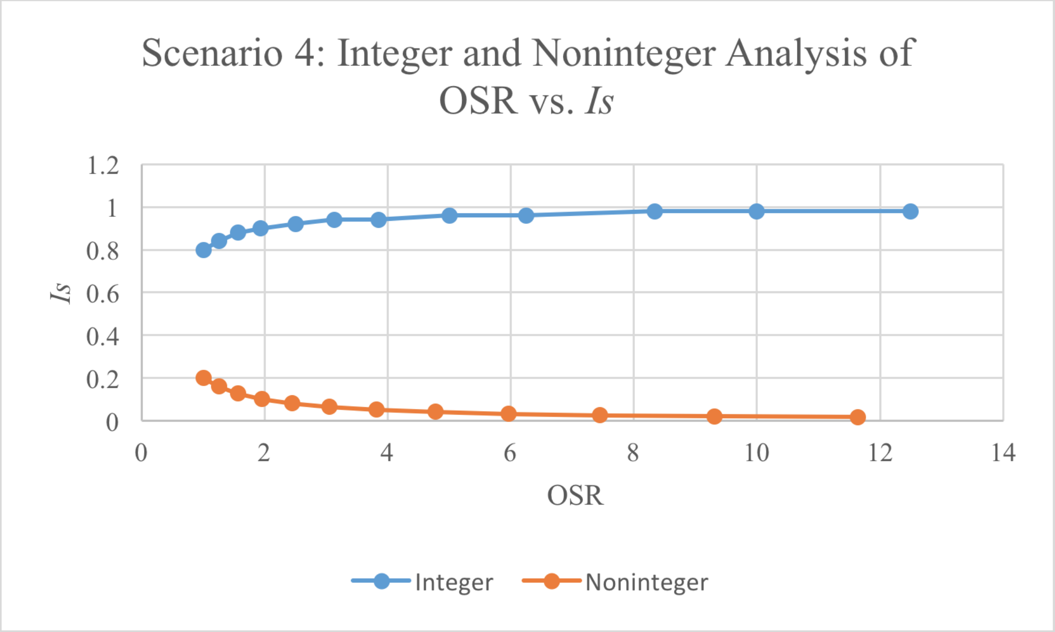

Figure 11. Scenario 4 Results: A comparison of the I_s and OSR values found in Scenario 4, both with forced integer and noninteger calculations.

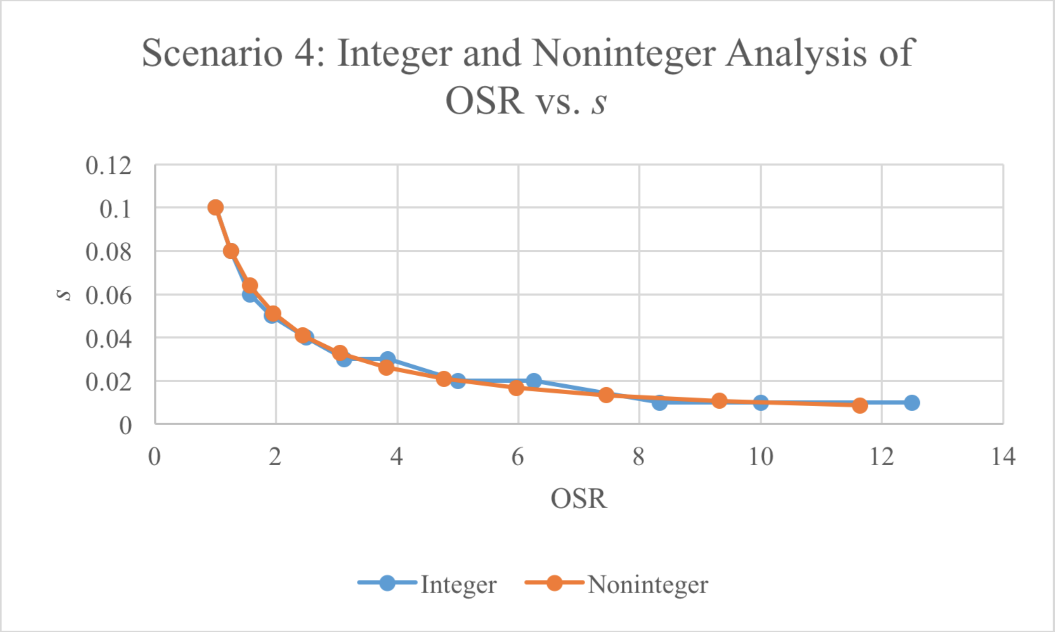

Figure 12. Scenario 4 Results: A comparison of the OSR and s values found in Scenario 4 with both forced integer and noninteger calculations.

Scenario 5, A Decreasing Mating Rate Promotes a Stable I_s*:*

The fifth scenario gave very similar results to Scenario 4. In noninteger calculations, *s* increased as I_s increased. In integer calculations, I_s values were again four times higher and *s* decreased as I_s increased (Fig. 13). Once again, this is because of the fact that when mating success values were designated as nonintegers, no male received one full female to mate with, and so the ultimate values of I_s were very low.

The comparison of OSR vs. I_s also gave similar results, with I_s remaining largely constant as OSR increased (Fig. 14). Interestingly, though, *s* experienced an initial increase as OSR increased, unlike in Scenario 4. This shows that the rate of mating does, in fact, have an effect on sexual selection--the initial rapid increase in *s* values as OSR increases shows that a steadily increasing mating rate does lead to increases sexual selection (Fig. 15). There comes a point, however, as seen in Fig. 15, at which either the high OSR or the very high percentage of females mating causes chance to play more of a role. It could be possible that this rise in sexual selection can be attributed to the increased involvement of females. While the same percentage of males mated in each round, the percentage of females participating in each round increased, and so could have led to the increase in sexual selection. This would mean that, contrary to Bateman's (1948) beliefs, females do have a measureable impact on the variance in mating success. The variation in mating success for the noninteger calculations is really low, but the selection differential shows a large increase, and this reinforces Fitzpatrick's (2014) belief that variance in mating success and sexual selection cannot always be correlated.

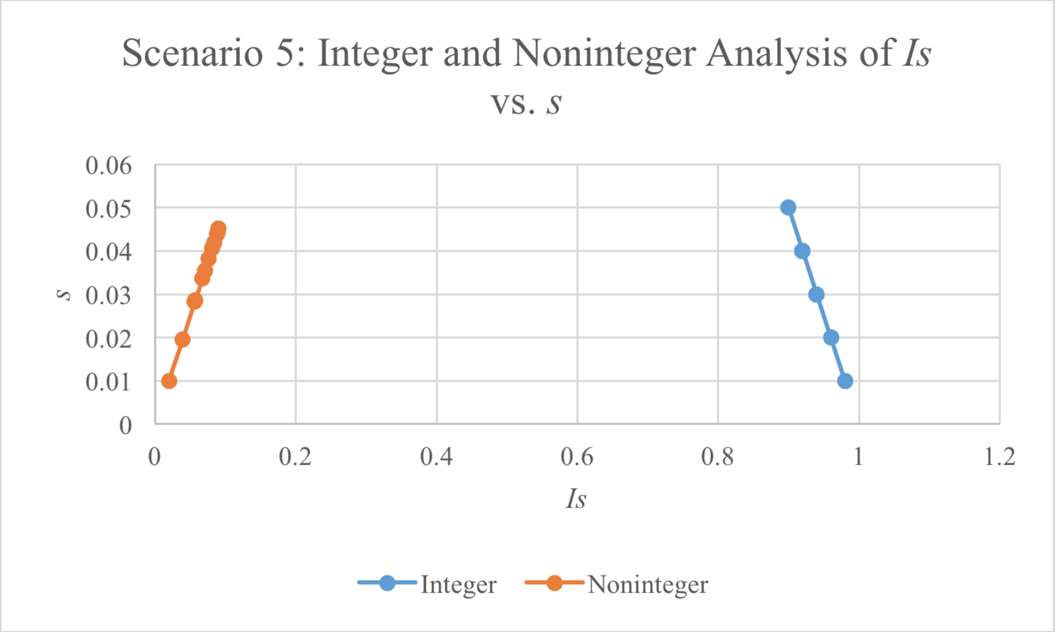

Figure 13. Scenario 5 Results: A comparison of the I_s and s values found in Scenario 5, both with forced integer and noninteger calculations.

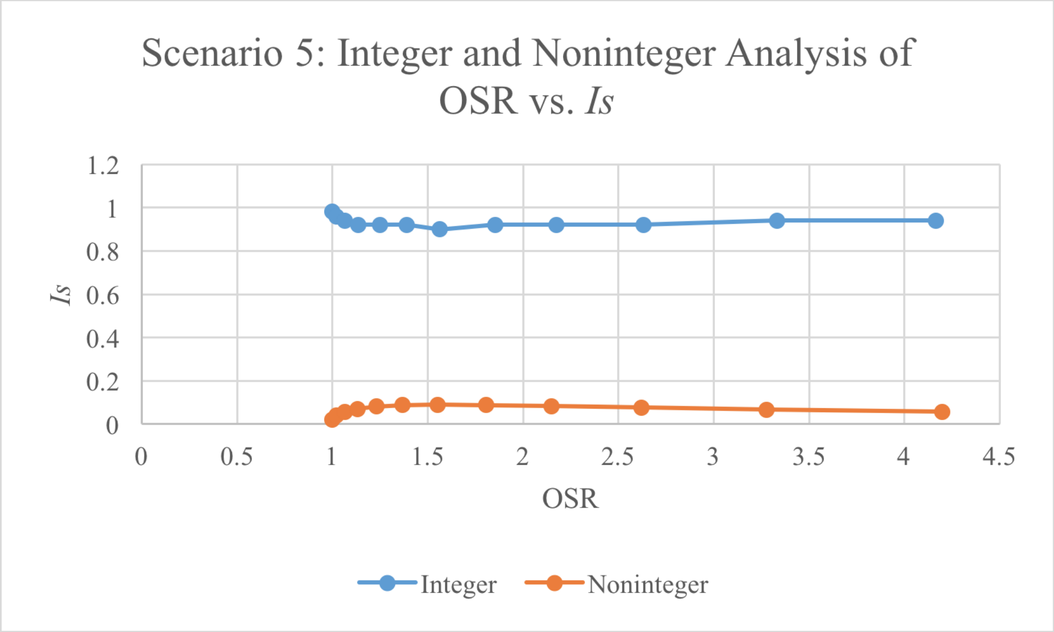

Figure 14. Scenario 5 Results: A comparison of the I_s and OSR values found in Scenario 5, both with forced integer and noninteger calculations.

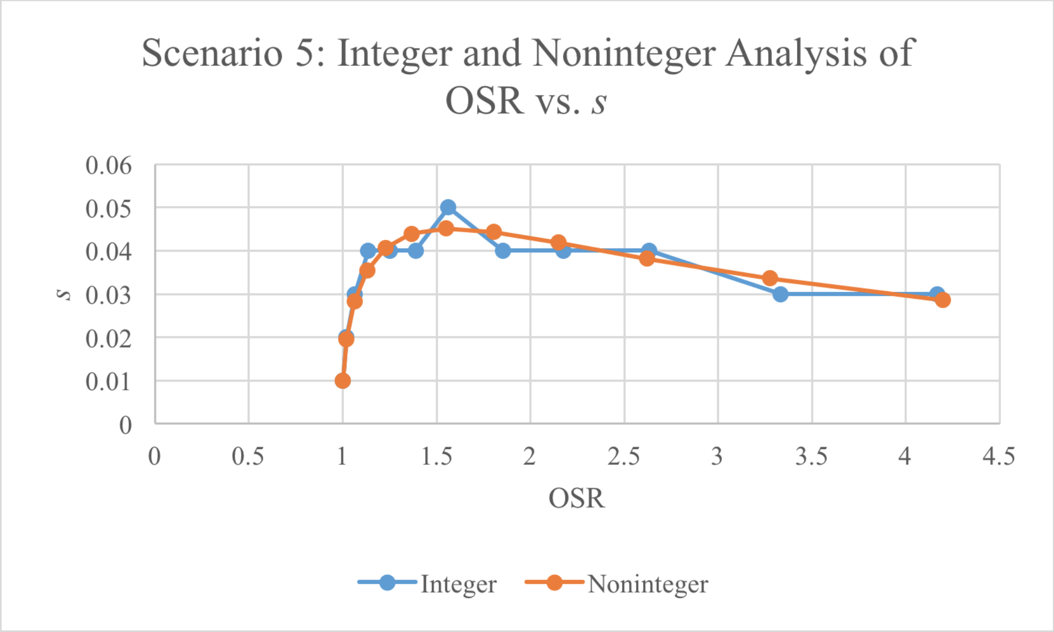

Figure 15. Scenario 5 Results: A comparison of the OSR and s values found in Scenario 5 with both forced integer and noninteger calculations.

Scenario 6, An Increasing Mating Rate Promotes a Stable I_S*:*

Scenario 6 gave results almost indistinguishable from those of Scenario 4 (Fig. 16-18). Since the results are so similar, this suggests that a decreasing mating rate leads to about the same results as a constant mating rate, and therefore, a decreasing mating rate has little to no effect on sexual selection.

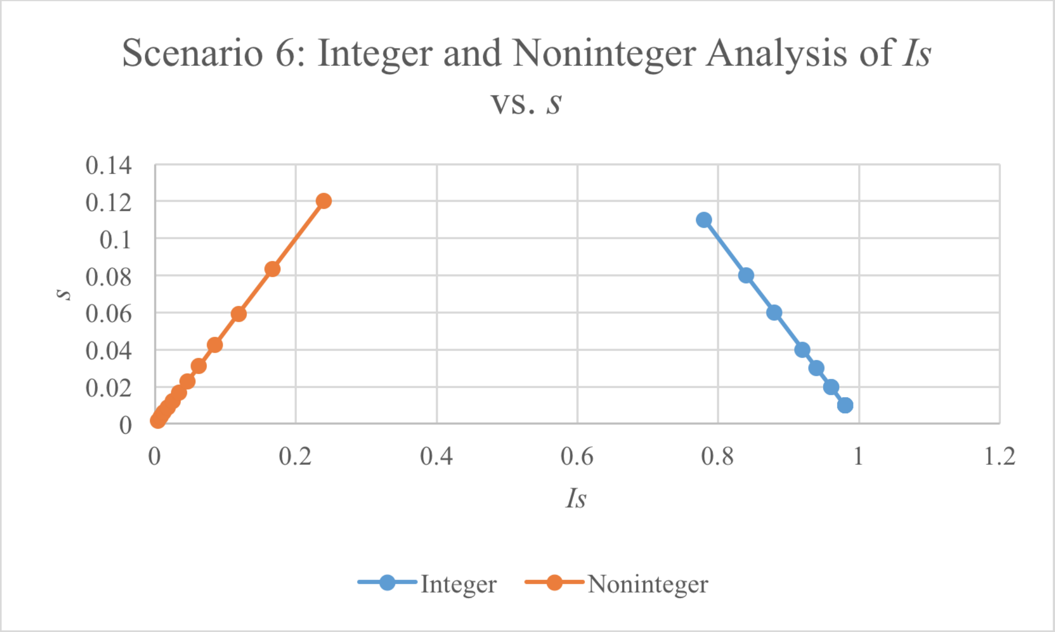

Figure 16. Scenario 6 Results: A comparison of the I_s *and s values found in Scenario 6, both with forced integer and noninteger calculations.*

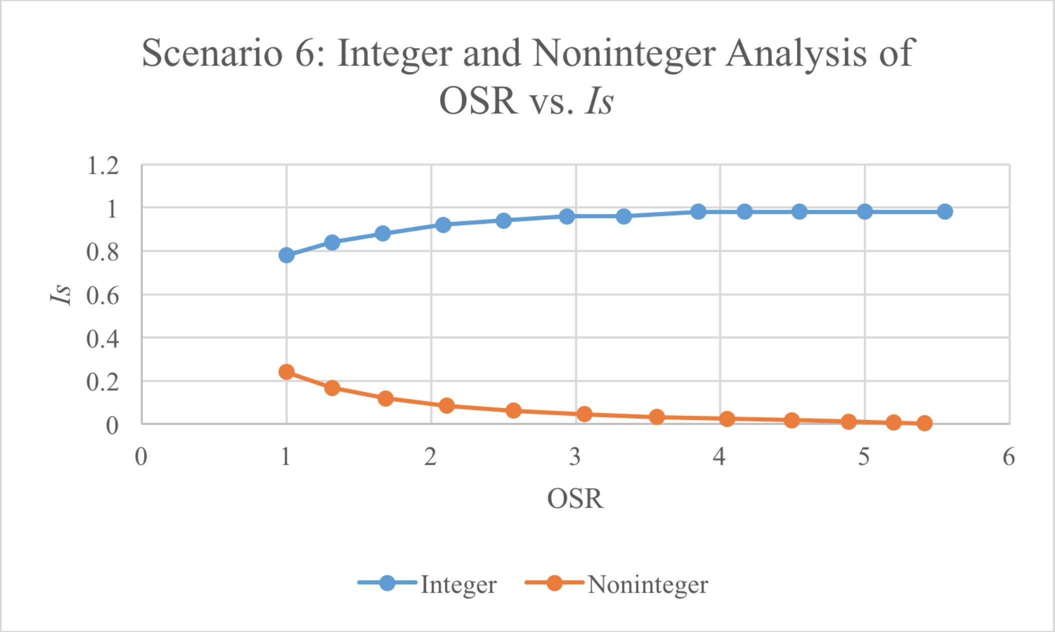

Figure 17. Scenario 6 Results: A comparison of the I_s *and OSR values found in Scenario 6, both with forced integer and noninteger calculations.*

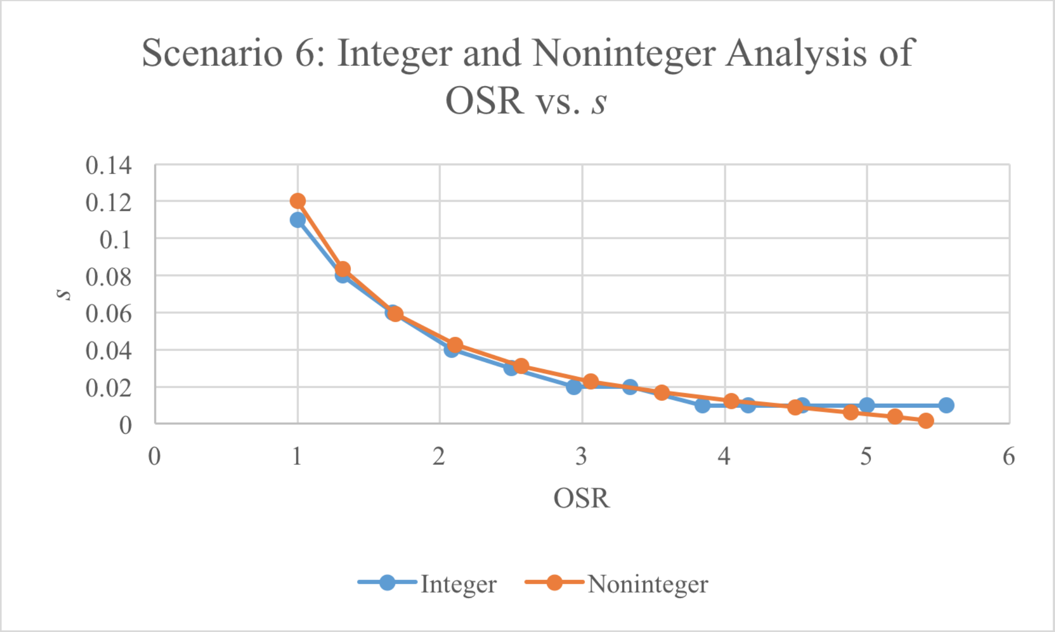

Figure 18. Scenario 6 Results: A comparison of the OSR and s values found in Scenario 5 with both forced integer and noninteger calculations.

Scenario 7, Returning Females Promote a Stable I_s:

This scenario also has results that are almost identical to scenarios 4 and 6. Noninteger and integer calculations give radically different results, with a stable I_s and a decreasing *s* with increasing OSR (Fig. 19-21). In each round of this scenario, 20% of females in the mating pool mated while 10% of females that had been in timeout returned to the mating pool. It makes sense, then, that this scenario would be similar to the scenario with a decreasing mating rate, since this scenario, albeit slightly more complicated, still has a constantly decreasing mating rate.

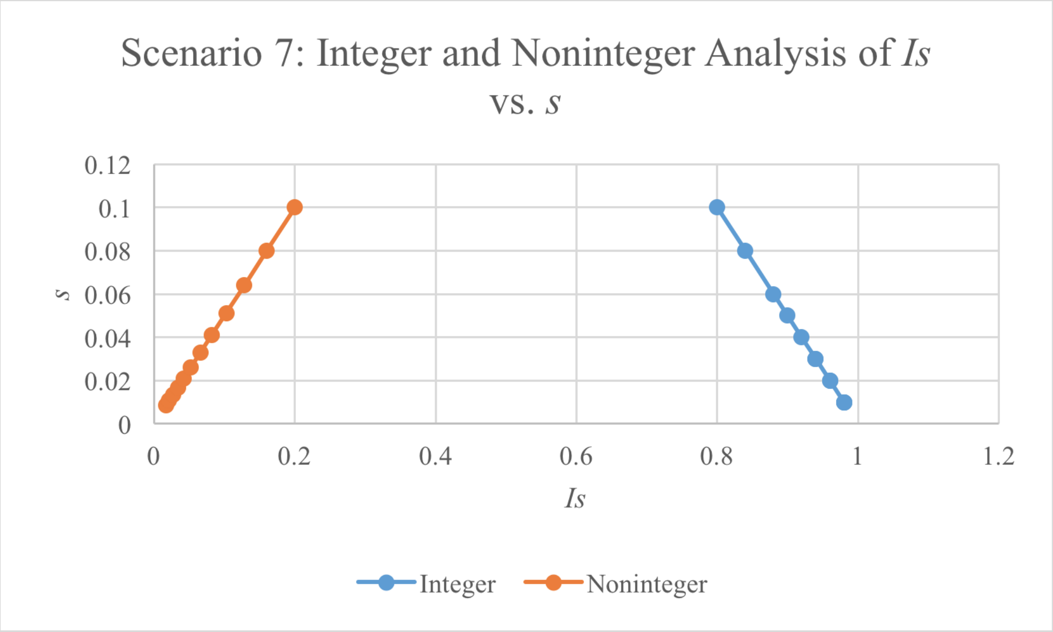

Figure 19. Scenario 7 Results: A comparison of the I_s and s values found in Scenario 7, both with forced integer and noninteger calculations.

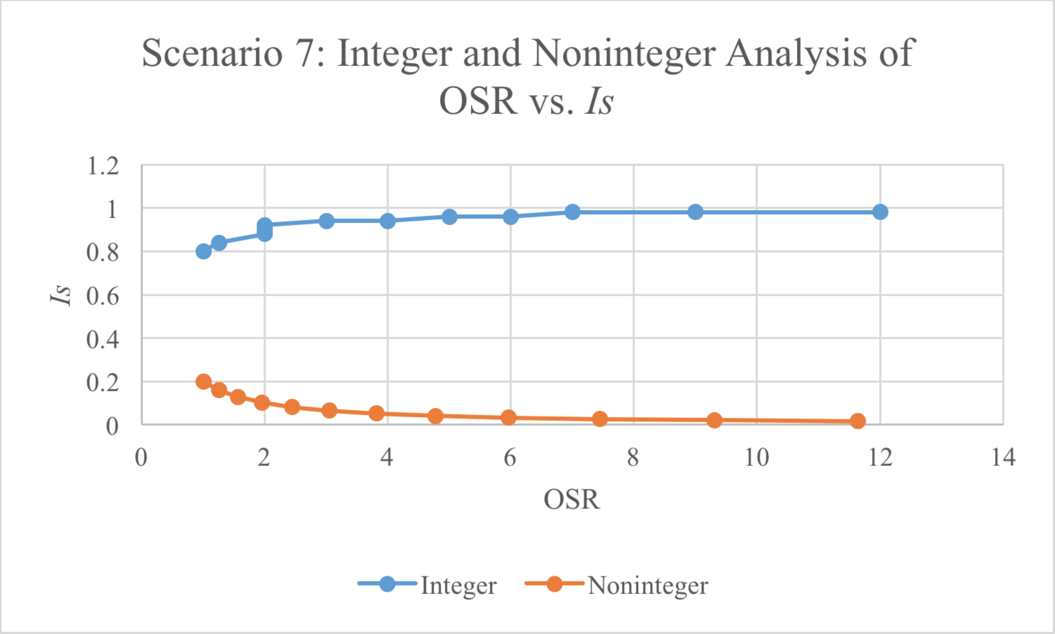

Figure 20. Scenario 7 Results: A comparison of the I_s *and OSR values found in Scenario 7, both with forced integer and noninteger calculations.*

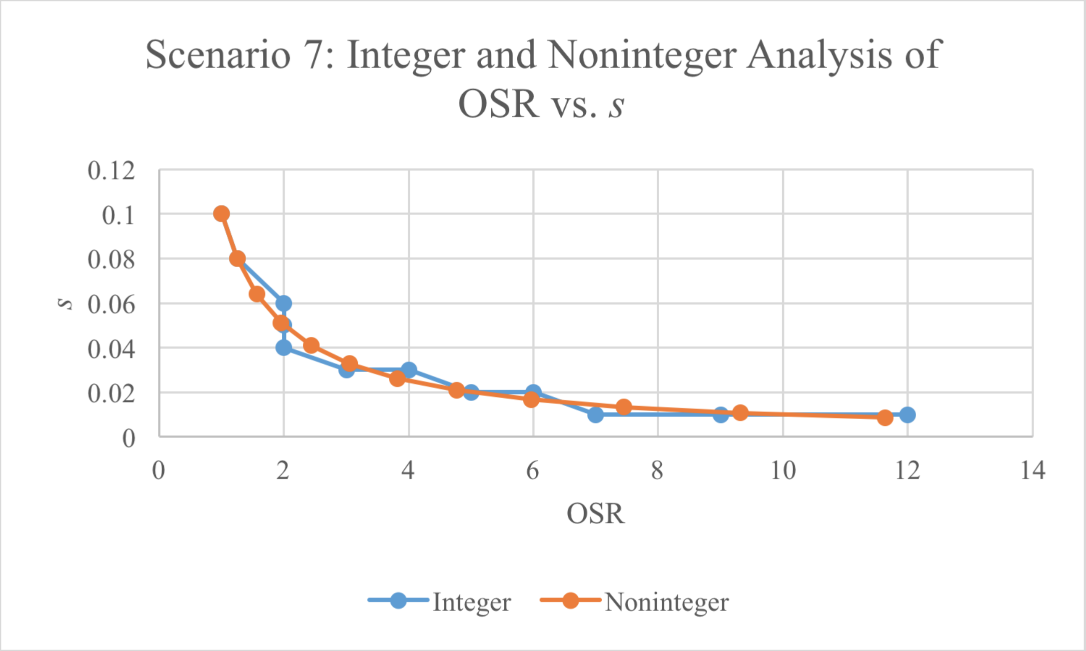

Figure 21. Scenario 7 Results: A comparison of the OSR and s values found in Scenario 7 with both forced integer and noninteger calculations.

Discussion

The scenarios created and explored in this thesis suggest that chance can play a role in determining mating success, and that I_s and OSR do not consistently correlate well with sexual selection strength. These results are consistent with our hypothesis. It has long been assumed that I_s increases with an increasing male-biased population, but our simple models have shown that the opposite occurs in some cases (Wade & Shuster, 2003; Chapter 1). In many cases, as the OSR increases, the opportunity for sexual selection tends to not only decrease, but to decrease precipitously, which could be due to the increased male competition, and risk associated with that competition, as described in Chapter 1. In our timeout scenarios, the opportunity for sexual selection did not increase with increasing OSR either, but rather remained relatively stable. The fact that no increase in I_s was seen at all, even in scenarios as simple as these, shows that our long held belief that the opportunity for sexual selection increases with male bias is unfounded and incorrect.

When it comes to the behavior of I_s, Fig. 6 of Scenario 2 shows the only instance in which our data agreed with classical sexual selection theory (Bateman, 1948; Chapter 1), because the graph shows actual sexual selection increasing in conjunction with I_s. In Scenario 3, the relationship between I_s and s was what we hypothesized: the actual sexual selection may have increased initially, but chance gradually began to take over and values gradually began to plateau. This suggests that I_s and s will not always be correlated and that there will be some OSRs for which chance is more important than others (Klug *et al.*, 2010a; Chapter 1). Since chance covaries with OSR, this suggests that OSR cannot be assumed to be a reliable proxy for the strength of sexual selection.

In Scenario 1, we were surprised to find that when there were not enough females for each male to mate, that there was no parallel between selection differential and the opportunity for sexual selection. This is a finding that has not been reported before, but our simple test showed that when there are not enough females for every preferable male, I_s is an extremely unreliable predictor for sexual selection. With the exception of Scenario 5, every single scenario also showed that the selection differential decreases with OSR. In other words, the actual sexual selection taking place and the change in phenotypic traits of a population is expected to decrease as the population gets more male-biased (Klug *et al.,* 2010a; Chapter 1).

Our comparison of integer versus noninteger calculations also proved insightful. The timeout scenarios were the most telling, revealing that integer and noninteger calculations can have notably different results, which means that researchers should seriously consider what specific proxies of sexual selection are quantifying when measuring sexual selection. Integer and noninteger calculations not only led to differences in whether or not s was increasing or decreasing with I_s, but also resulted in radically different I_s values. Scenarios 1 and 2 may have shown a relationship between s and I_s that lines up with classical sexual selection theory, but the timeout scenarios we performed are examples of what generally more often happens in the natural world, and so should be considered with more weight. It was also surprising to find that our hypothesis was often correct regardless of whether or not calculations involved integer or noninteger values of mating success. I_s often decreased with increasing OSR regardless of whether or not integers or noninteger values were used.

These results were found via incredibly simple means, which reaffirms our need to reconsider the dedication that so many researchers so often have to I_s and OSR (e.g., Shuster & Wade, 2003). There were many possibilities that were not included in these scenarios, and additional scenarios might further highlight the role of chance in mating dynamics. For example, we only considered polygynous species, even though there are a plethora of species in which the females are sexually selected for, and in which males enter and leave the mating pool (Hayes *et al.*, 2016; Jones, 2009; Tang-Martinez & Ryder, 2005; Chapter 1). We also had no means to consider male mate competition or mutual mate choice--if we had, the number of males in the mating pool could have been fluctuating just as much as the number of females due to the costs of pursuit. We also did not measure the variance of mating success in females, which, in the case of the timeout scenarios, could have revealed mutual sexual selection taking place even in our very simple scenarios. There is much to still be discovered about sexual selection, and our findings show that if we are to grow in our understanding of the birds and the bees, we must reconsider how we measure it.

APPENDIX

Here is the raw data for the scenarios performed and described in Chapter 2. All scenarios were performed on Excel.

Scenario 1 Data Table:

SCENARIO 1				
INTEGER ANALYSIS				
OSR	Males	Females	Is	s
12	12	1	0.9166666667	0.04166666667
4	12	3	0.75	0.125
2.4	12	5	0.5833333333	0.2083333333
1.714285714	12	7	0.7023809524	0.2916666667
1.333333333	12	9	0.9166666667	0.375
1.090909091	12	11	0.9924242424	0.4583333333
0.9230769231	12	13	1.147435897	0.5416666667
0.8	12	15	1.35	0.625
0.7058823529	12	17	1.465686275	0.7083333333
0.6315789474	12	19	1.627192982	0.7916666667
0.5714285714	12	21	1.821428571	0.875
0.5217391304	12	23	1.952898551	0.9583333333
NONINTEGER ANALYSIS				
OSR	Males	Females	Is	s
12	12	1	0.08333333333	0.04166666667
4	12	3	0.25	0.125
2.4	12	5	0.4166666667	0.2083333333
1.714285714	12	7	0.5833333333	0.2916666667
1.333333333	12	9	0.75	0.375
1.090909091	12	11	0.9166666667	0.4583333333
0.9230769231	12	13	1.083333333	0.5416666667
0.8	12	15	1.25	0.625
0.7058823529	12	17	1.416666667	0.7083333333
0.6315789474	12	19	1.583333333	0.7916666667
0.5714285714	12	21	1.75	0.875
0.5217391304	12	23	1.916666667	0.9583333333

Scenario 2 Data Table:

<table>
<tr><th colspan="5">SCENARIO 2</th></tr>
<tr><td colspan="5">INTEGER ANALYSIS</td></tr>
<tr><td>OSR</td><td>Males</td><td>Females</td><td>Is</td><td>s</td></tr>
<tr><td>0.044776119</td><td>3</td><td>67</td><td>44.66666667</td><td>14.88888889</td></tr>
<tr><td>0.147540984</td><td>9</td><td>61</td><td>13.56648452</td><td>4.518518519</td></tr>
<tr><td>0.272727273</td><td>15</td><td>55</td><td>7.333333333</td><td>2.444444444</td></tr>
<tr><td>0.428571429</td><td>21</td><td>49</td><td>4.666666667</td><td>1.555555556</td></tr>
<tr><td>0.627906977</td><td>27</td><td>43</td><td>4.09023569</td><td>1.358024691</td></tr>
<tr><td>0.891891892</td><td>33</td><td>37</td><td>2.311220311</td><td>0.747474748</td></tr>
<tr><td>1.258064516</td><td>39</td><td>31</td><td>1.688999173</td><td>0.52991453</td></tr>
<tr><td>1.8</td><td>45</td><td>25</td><td>1.244444444</td><td>0.37037037</td></tr>
<tr><td>2.684210526</td><td>51</td><td>19</td><td>0.837977296</td><td>0.248366013</td></tr>
<tr><td>4.384615385</td><td>57</td><td>13</td><td>0.771929825</td><td>0.152046784</td></tr>
<tr><td>9</td><td>63</td><td>7</td><td>0.888888889</td><td>0.074074074</td></tr>
<tr><td>69</td><td>69</td><td>1</td><td>0.985507246</td><td>0.009661836</td></tr>
<tr><td colspan="5">NONINTEGER ANALYSIS</td></tr>
<tr><td>OSR</td><td>Males</td><td>Females</td><td>Is</td><td>s</td></tr>
<tr><td>0.044776119</td><td>3</td><td>67</td><td>44.66666667</td><td>14.88888889</td></tr>
<tr><td>0.147540984</td><td>9</td><td>61</td><td>13.55555556</td><td>4.518518519</td></tr>
<tr><td>0.272727273</td><td>15</td><td>55</td><td>7.333333333</td><td>2.444444444</td></tr>
<tr><td>0.428571429</td><td>21</td><td>49</td><td>4.666666667</td><td>1.555555556</td></tr>
<tr><td>0.627906977</td><td>27</td><td>43</td><td>3.185185185</td><td>1.061728395</td></tr>
<tr><td>0.891891892</td><td>33</td><td>37</td><td>2.242424242</td><td>0.747474748</td></tr>
<tr><td>1.258064516</td><td>39</td><td>31</td><td>1.58974359</td><td>0.52991453</td></tr>
<tr><td>1.8</td><td>45</td><td>25</td><td>1.111111111</td><td>0.37037037</td></tr>
<tr><td>2.684210526</td><td>51</td><td>19</td><td>0.745098039</td><td>0.248366013</td></tr>
<tr><td>4.384615385</td><td>57</td><td>13</td><td>0.456140351</td><td>0.152046784</td></tr>
<tr><td>9</td><td>63</td><td>7</td><td>0.222222222</td><td>0.074074074</td></tr>
<tr><td>69</td><td>69</td><td>1</td><td>0.028985507</td><td>0.009661836</td></tr>
</table>

Scenario 3 Data Table:

SCENARIO 3				
INTEGER ANALYSIS				
OSR	Males	Females	Is	s
1	12	12	11	0.916666667
1	12	12	5	0.833333333
1	12	12	3	0.75
1	12	12	2	0.666666667
1	12	12	1.5	0.583333333
1	12	12	1	0.5
1	12	12	0.833333333	0.416666667
1	12	12	0.666666667	0.333333333
1	12	12	0.5	0.25
1	12	12	0.333333333	0.166666667
1	12	12	0.166666667	0.083333333
1	12	12	0	0
NONINTEGER ANALYSIS				
OSR	Males	Females	Is	s
1	12	12	11	0.916666667
1	12	12	5	0.833333333
1	12	12	3	0.75
1	12	12	2	0.666666667
1	12	12	1.4	0.583333333
1	12	12	1	0.5
1	12	12	0.714285714	0.416666667
1	12	12	0.5	0.333333333
1	12	12	0.333333333	0.25
1	12	12	0.2	0.166666667
1	12	12	0.090909091	0.083333333
1	12	12	0	0

Scenario 4 Data Table:

SCENARIO 4					
NONINTEGER ANALYSIS					
OSR	Males	Females	Females That Mate	Is	s
1	50	50	10	0.2	0.1
1.25	50	40	8	0.16	0.08
1.5625	50	32	6.4	0.128	0.064
1.953125	50	25.6	5.12	0.1024	0.0512
2.44140625	50	20.48	4.096	0.08192	0.04096
3.051757813	50	16.384	3.2768	0.065536	0.032768
3.814697266	50	13.1072	2.62144	0.0524288	0.0262144
4.768371582	50	10.48576	2.097152	0.04194304	0.02097152
5.960464478	50	8.388608	1.6777216	0.033554432	0.016777216
7.450580597	50	6.7108864	1.34217728	0.026843546	0.013421773
9.313225746	50	5.36870912	1.073741824	0.021474836	0.010737418
11.64153218	50	4.294967296	0.858993459	0.017179869	0.008589935
INTEGER ANALYSIS					
OSR	Males	Females	Females That Mate	Is	s
1	50	50	10	0.8	0.1
1.25	50	40	8	0.84	0.08
1.5625	50	32	6	0.88	0.06
1.923076923	50	26	5	0.9	0.05
2.5	50	20	4	0.92	0.04
3.125	50	16	3	0.94	0.03
3.846153846	50	13	3	0.94	0.03
5	50	10	2	0.96	0.02
6.25	50	8	2	0.96	0.02
8.333333333	50	6	1	0.98	0.01
10	50	5	1	0.98	0.01
12.5	50	4	1	0.98	0.01

Scenario 5 Data Table:

<table>
<tr><th colspan="6">SCENARIO 5</th></tr>
<tr><td colspan="6">NONINTEGER ANALYSIS</td></tr>
<tr><td>OSR</td><td>Males</td><td>Females</td><td>Females That Mate</td><td>Is</td><td>s</td></tr>
<tr><td>1</td><td>50</td><td>50</td><td>1</td><td>0.02</td><td>0.01</td></tr>
<tr><td>1.020408163</td><td>50</td><td>49</td><td>1.96</td><td>0.0392</td><td>0.0196</td></tr>
<tr><td>1.06292517</td><td>50</td><td>47.04</td><td>2.8224</td><td>0.056448</td><td>0.028224</td></tr>
<tr><td>1.130771458</td><td>50</td><td>44.2176</td><td>3.537408</td><td>0.07074816</td><td>0.03537408</td></tr>
<tr><td>1.22909941</td><td>50</td><td>40.680192</td><td>4.0680192</td><td>0.081360384</td><td>0.040680192</td></tr>
<tr><td>1.365666011</td><td>50</td><td>36.6121728</td><td>4.393460736</td><td>0.087869215</td><td>0.043934607</td></tr>
<tr><td>1.551893195</td><td>50</td><td>32.21871206</td><td>4.510619689</td><td>0.090212394</td><td>0.045106197</td></tr>
<tr><td>1.804526971</td><td>50</td><td>27.70809238</td><td>4.43329478</td><td>0.088665896</td><td>0.044332948</td></tr>
<tr><td>2.148246394</td><td>50</td><td>23.2747976</td><td>4.189463567</td><td>0.083789271</td><td>0.041894636</td></tr>
<tr><td>2.619812675</td><td>50</td><td>19.08533403</td><td>3.817066806</td><td>0.076341336</td><td>0.038170668</td></tr>
<tr><td>3.274765844</td><td>50</td><td>15.26826722</td><td>3.359018789</td><td>0.067180376</td><td>0.033590188</td></tr>
<tr><td>4.198417749</td><td>50</td><td>11.90924843</td><td>2.858219624</td><td>0.057164392</td><td>0.028582196</td></tr>
<tr><td colspan="6">INTEGER ANALYSIS</td></tr>
<tr><td>OSR</td><td>Males</td><td>Females</td><td>Females That Mate</td><td>Is</td><td>s</td></tr>
<tr><td>1</td><td>50</td><td>50</td><td>1</td><td>0.98</td><td>0.01</td></tr>
<tr><td>1.020408163</td><td>50</td><td>49</td><td>2</td><td>0.96</td><td>0.02</td></tr>
<tr><td>1.063829787</td><td>50</td><td>47</td><td>3</td><td>0.94</td><td>0.03</td></tr>
<tr><td>1.136363636</td><td>50</td><td>44</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>1.25</td><td>50</td><td>40</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>1.388888889</td><td>50</td><td>36</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>1.5625</td><td>50</td><td>32</td><td>5</td><td>0.9</td><td>0.05</td></tr>
<tr><td>1.851851852</td><td>50</td><td>27</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>2.173913043</td><td>50</td><td>23</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>2.631578947</td><td>50</td><td>19</td><td>4</td><td>0.92</td><td>0.04</td></tr>
<tr><td>3.333333333</td><td>50</td><td>15</td><td>3</td><td>0.94</td><td>0.03</td></tr>
<tr><td>4.166666667</td><td>50</td><td>12</td><td>3</td><td>0.94</td><td>0.03</td></tr>
</table>

Scenario 6 Data Table:

SCENARIO 6					
NONINTEGER ANALYSIS					
OSR	Males	Females	Females That Mate	Is	s
1	50	50	12	0.24	0.12
1.315789474	50	38	8.36	0.1672	0.0836
1.686909582	50	29.64	5.928	0.11856	0.05928
2.108636977	50	23.712	4.26816	0.0853632	0.0426816
2.571508509	50	19.44384	3.1110144	0.062220288	0.031110144
3.061319653	50	16.3328256	2.286595584	0.045731912	0.022865956
3.559674015	50	14.04623002	1.685547602	0.033710952	0.016855476
4.045084108	50	12.36068241	1.236068241	0.024721365	0.012360682
4.494537898	50	11.12461417	0.889969134	0.017799383	0.008899691
4.88536728	50	10.23464504	0.614078702	0.012281574	0.006140787
5.197199235	50	9.620566337	0.384822654	0.007696453	0.003848227
5.413749203	50	9.235743683	0.184714874	0.003694297	0.001847149
INTEGER ANALYSIS					
OSR	Males	Females	Females That Mate	Is	s
1	50	50	12	0.78	0.11
1.315789474	50	38	8	0.84	0.08
1.666666667	50	30	6	0.88	0.06
2.083333333	50	24	4	0.92	0.04
2.5	50	20	3	0.94	0.03
2.941176471	50	17	2	0.96	0.02
3.333333333	50	15	2	0.96	0.02
3.846153846	50	13	1	0.98	0.01
4.166666667	50	12	1	0.98	0.01
4.545454545	50	11	1	0.98	0.01
5	50	10	1	0.98	0.01
5.555555556	50	9	1	0.98	0.01

Scenario 7 Data Tables:

SCENARIO 7								
NONINTEGER ANALYSIS								
OSR	Males	Females	Females That Leave This Round	Females That Return This Round	Total Females in Time In After This Round	Total Females in Timeout After This Round	Is	s
1	50	50	10	0	40	25	0.2	0.1
1.25	50	40	8	2.5	32	22.5	0.16	0.08
1.5625	50	32	6.4	2.25	25.6	20.25	0.128	0.064
1.953125	50	25.6	5.12	2.025	20.48	18.225	0.1024	0.0512
2.44140625	50	20.48	4.096	1.8225	16.384	16.4025	0.08192	0.04096
3.051757813	50	16.384	3.2768	1.64025	13.1072	14.76225	0.065536	0.032768
3.814697266	50	13.1072	2.62144	1.476225	10.48576	13.286025	0.0524288	0.0262144
4.768371582	50	10.48576	2.097152	1.3286025	8.388608	11.9574225	0.04194304	0.02097152
5.960464478	50	8.388608	1.6777216	1.19574225	6.7108864	10.76168025	0.033554432	0.016777216
7.450580597	50	6.7108864	1.34217728	1.076168025	5.36870912	9.685512225	0.026843546	0.013421773
9.313225746	50	5.36870912	1.073741824	0.968551223	4.294967296	8.716961003	0.021474836	0.010737418
11.64153218	50	4.294967296	0.858993459	0.8716961	3.435973837	7.845264902	0.017179869	0.008589935

SCENARIO 7								
INTEGER ANALYSIS								
OSR	Males	Females	Females That Leave This Round	Females That Return This Round	Total Females in Time In After This Round	Total Females in Timeout After This Round	Is	s
1	50	50	10	0	40	25	0.8	0.1
1.25	50	40	8	3	32	23	0.84	0.08
2	50	32	6	2	26	20		
			6	2	26	20	0.88	0.06
2	50	26	5	2	20	18	0.9	0.05
2	50	20	4	2	16	16	0.92	0.04
3	50	16	3	2	13	15	0.94	0.03
4	50	13	3	1	10	13	0.94	0.03
5	50	10	2	1	8	12	0.96	0.02
6	50	8	2	1	7	11	0.96	0.02
7	50	7	1	1	5	10	0.98	0.01
9	50	5	1	1	4	9	0.98	0.01
12	50	4	1	1	3	8	0.98	0.01

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