

# **The Tragedy of the Lek:**

a game-theoretic approach to understanding  
courtship disruption in male sage-grouse

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A Senior Thesis in partial fulfillment of the requirements for the  
Yale College Bachelor of Science in Ecology and Evolutionary Biology

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## ABSTRACT

Until the 1980s, the role of fighting between males of lek-mating bird species was largely assumed to be for establishing dominance hierarchies or territories. The presumption that female choice is determined exclusively by the outcome of these fights has since been challenged by the hypothesis that the role of fighting between males is actually to interfere with female choice by interrupting rivals' courtship displays and even copulations. We develop a game-theoretic model to test the mathematical logic of this hypothesis and to refine the way it accounts for the costs and benefits of courtship disruption. This model provides support for the role of fighting as courtship disruption in lek mating systems and serves as a mathematical proof-of-concept for a novel understanding of its benefits — Unattractive males can benefit from conflict with their more successful neighbors merely by preventing them from courting females and enjoying a small share of their redistributed would-be mates.

## BACKGROUND

The phrase “intrasexual selection” generally calls to mind violent clashes between male elephant seals or bighorn rams battling to the death for access to female mates. In these systems, access to females, and thus reproduction, correlates strictly with social hierarchy determined by fighting ability (Le Boeuf 1974; Hogg 1984). This type of male-male competition is fairly well understood: if the value of the resource at stake – in this case the opportunity to pass on one's genes to the next generation – outweighs the risk of injury or death, males will choose to fight (Maynard Smith 1974; Enquist & Leimar 1990). However, in other systems, male-male competition can take on a different, more complicated form. In species with lek mating systems, including many birds, several

individuals of one sex (almost always males and referred to hereafter as such) aggregate in a well-defined location and perform courtship displays. Meanwhile, females come and go for the purpose of choosing a suitable mate (Emlen & Oring 1977). Thus, males still compete for access to a limited number of females, but unlike head bashing or death matches, this type of spatial-temporal aggregation requires some degree of tolerance between the competing males. However, it isn't all cooperation all the time either. In many lek mating systems, including the Greater Sage-grouse (*Centrocercus urophasianus*), fights between lekking males are common (Wiley 1973). In this paper, we describe a game-theoretic approach to modeling the costs and the potential benefits of male-male fighting in lek-mating birds, using sage-grouse as a case study. By shedding light on the dynamics of conflict in these systems, we hope to achieve a better understanding of the evolution of the lek.

Sage-grouse practice an extreme form of polygyny in which it is typical for only a small handful of males to mate over the course of the entire three-month mating season, and among these males, reproductive success is heavily skewed (Scott 1942; Hartzler 1972; Wiley 1973). During the breeding season, males spend all morning and evening on the lek continuously performing an elaborate display, known as "strutting", for the purpose of attracting females (Scott 1942). This display includes both a visual and an acoustic component. The strut consists of repeatedly inflating and then rapidly deflating a large esophageal pouch, which only males have, making their conspicuous white chest bob up and down, producing a series of swishes, pops, and low frequency whistles (Wiley 1973; Gibson & Bradbury 1985). Meanwhile, females visit the lek in groups to evaluate the males' performances. If and when they find a suitable mate, females assume a crouched posture in front of the chosen male in order to solicit a copulation with him (Wiley 1973).

Males strut more or less constantly, pausing only occasionally to fight with one another. Broadly, there are two distinct types of male-male conflicts. Wing-smacking fights are conflicts in which males vigorously beat one another with their wings. In spite of the apparent intensity of wing smacking, serious injuries are very rare (Wiley 1973). Wing-smacking fights typically last only a few seconds at a time, although they are often resumed after a brief pause (Klempay, unpubl. obs.). The second type of conflict consists of two males assuming an aggressive, anti-parallel posture. The opponents advance, retreat, and switch places tensely, vying for better position. These face-offs, sometimes referred to as “squaring off” or “facing-past encounters”, can last anywhere from a few seconds to several minutes punctuated by bouts of wing smacking (Scott 1942; Wiley 1973; Pellis *et al.* 2013). Face-offs are quite common, sometimes occupying a significant proportion of an individual male’s time on the lek, even more than strutting in a few cases (Wiley 1973). Thus, while fights between male sage-grouse are subdued in comparison with bighorn rams or elephant seals, there is a cost to conflict: time. Male sage-grouse cannot engage in both strutting and a face-off at the same time, so in addition to facing a small risk of injury, they forgo a substantial part of their limited time on the lek by fighting. The same general logic of animal conflicts applies just as well to sage-grouse as to bighorn rams and elephant seals. In order for it to be an evolutionarily viable behavior, the benefits of fighting must outweigh its costs. Therefore, the benefits of agonistic behavior in male sage-grouse require further explanation.

Hypotheses for the benefits of fighting in sage-grouse courtship behavior fall into two distinct categories. The first adheres to a more traditional view of intrasexual selection in which fighting is understood primarily as a means of giving females information on the quality of their potential mates. One such hypothesis suggests that males fight for social dominance like elephant seal males or bighorn rams (Le Boeuf 1974; Hogg 1984). The

males would establish a hierarchy among themselves, and females would then consistently and uniformly choose to mate with males at the top of this hierarchy. Another hypothesis in this category is that males fight for territory within the lek. It is important to note that males of lek-mating species contribute absolutely no resources other than genetic material to reproduction. Therefore, territory quality does not depend on the presence of defensible resources (Bradbury 1981; Foster 1983). Rather, the literature supporting the territoriality view describes the sage-grouse lek as being spatially structured around a “center of mating”, the area of the lek receiving the most visits from females. Territory quality depends on proximity to this center of mating. Thus, fighting is a contest for territory close to the center of mating, and the males with the best territory would enjoy the greatest reproductive success (Wiley 1973). Evidently, this theory can easily go hand-in-hand with the social-dominance framework; the alpha males would claim the largest, central territory, and the subordinate males would then claim peripheral territories in accordance with their social order.

The second category of hypotheses favors female choice rather than male-male competition as the primary source of skew in males’ mating success. According to this view, females choose mates based on their attractiveness by evaluating the quality of their display (Gibson & Bradbury 1985). Thus, the most attractive male is not necessarily the most successful fighter. Fighting is instead hypothesized to be an attempt by males to interfere with female mate choice (Foster 1983; Trail 1985). The most obvious way to accomplish this is by interrupting other males’ copulations. In this way, females are directly prevented from mating with the male of their choice. This behavior is commonly observed in sage-grouse as well as other lek-mating birds (Wiley 1973; Bradbury & Gibson 1983; Foster 1983; Trail 1985). The effectiveness of this strategy is not entirely known as some data indicate that many interrupted copulations still result in successful

fertilizations (Hartzler 1972; Lill 1976; Gibson & Bradbury 1985), and other reports suggest that females regularly return to the same male after a copulation attempt is interrupted (Bradbury & Gibson 1983). Nevertheless, male sage-grouse persist in interrupting one another's copulations, suggesting that doing so is a viable reproductive strategy (Foster 1983).

However, fighting among males on the lek is not limited to occasional bouts of smacking when a copulation is about to take place. Males regularly engage in both face-offs and wing smacking throughout the day (Wiley 1973), and when a conflict arises, neither male can resume strutting until it is concluded (Klempay, unpubl. obs.). This behavior suggests an attempt by the initiators of such conflicts to interfere with female mate choice by interrupting their neighbor's display. In this way, females are prevented from assessing the attractiveness of a potential mate, and the initiator has an opportunity to receive a share of the females' redirected mate choice (Foster 1983; Trail 1985). We hypothesize that fighting is potentially a viable strategy not only for dominant, alpha males, but also for subordinate or less attractive males who hope to improve their reproductive success by thwarting their neighbors' attempts to attract and mate with females.

Before claiming a favorite hypothesis, it should be noted that none of these explanations for the role of fighting between males of lek-mating birds are mutually exclusive. Indeed, both types of agonistic strategies, dominance/territoriality and courtship-interruption, are almost certain to occur in some amount in male sage-grouse. On one hand, males are regularly observed interrupting their neighbors' copulations (Wiley 1973), which strongly supports the courtship-disruption hypothesis. On the other hand, males are also frequently observed fighting even when no females are present on the lek (Klempay, unpubl. obs.). This evidence excludes the possibility that courtship disruption accounts for all instances of agonistic behavior, suggesting instead that dominance, territoriality, or yet another

mechanism contributes to a more nuanced explanation of the function of fighting between males of lek-mating birds. However, in this paper, we will focus primarily on courtship disruption, since this aspect of lek mating systems is currently less well understood than its counterparts, which favor a more traditional, male-centered view of intrasexual selection.

The courtship-disruption hypothesis for the role of fighting in lek-mating birds has been proposed on several occasions in the scientific literature on lek mating (Bradbury & Gibson 1983; Foster 1983; Trail 1985). However, in this study we take several novel approaches to modeling this type of agonistic behavior. First, we make no assumption that courtship disruption directly increases the aggressor's probability of mating with the interrupted female. It is currently contested whether courtship disruption generally confers reproductive benefits directly to the aggressor in this way, or whether he merely benefits indirectly from the redistribution of her mate choice across all males on the lek (Foster 1983; Trail 1985). Our model provides mathematical support for the hypothesis that the latter, secondary benefits alone are sufficient to outweigh the costs of courtship disruption, making it an evolutionarily viable strategy.

Moreover, we disambiguate between interrupting a competitor's copulation and merely interrupting his display. The former imposes an extreme cost on the interrupted male for a relatively small price to the aggressor (Foster 1983). The latter on the other hand seems to impose similar costs on both belligerents; both the aggressor and his opponent are unable to display for the duration of the fight (Klempay, unpubl. obs.). But while its benefits are less intuitive, this strategy is worthy of attention in its own right. We propose with this model that variation in attractiveness between males causes asymmetry in the cost of conflict. Thus, courtship disruption does not primarily benefit attractive males. They should maximize the amount of time spent displaying in order to attract more

mates. Rather, the relatively unattractive males who cannot hope to outstrut their rivals have the most to gain from conflict. In this paper, we develop a game-theoretic model to test the plausibility of the hypothesis that unattractive males can benefit from conflict with their more successful neighbors merely by preventing them from courting females and enjoying a small share of their redistributed would-be mates.

## MODELS AND RESULTS

### I. Assumptions and Variables

While the Greater Sage-grouse is used here as a relevant case study, the purpose of this model is to explore more generally the dynamics of male-male conflict in birds with lek mating systems. Therefore, in order not to confine the implications of this study to a single species, we are intentionally parsimonious with the assumptions of this model. These assumptions can be categorized into critical and logistical assumptions. The critical assumptions create a logical and mathematical framework for testing our verbal hypothesis. These must be biologically realistic for the model to have any real-world significance. Logistical assumptions are necessary to make a complex biological system more tractable. They should not qualitatively alter or negate the behaviors predicted by the critical assumptions (Servedio *et al.* 2014).

The critical assumptions of this model are as follows: (1) Males can choose either to display or to fight with another male. Thus, their total time on the lek is divided entirely between time spent displaying,  $t$ , and time spent fighting,  $u$ . (2) In the absence of competitors, mating success increases with time spent displaying. (3) Males can force one another to fight. In real lekking systems males may be able to extricate themselves from a conflict. However, for tractability, in this model we will assume that males cannot “refuse” to fight. (4) There is variation in the attractiveness,  $a$ , of males, and the



attractiveness of each male is known by all male competitors. In this model, we assume that a male's attractiveness corresponds to the quality of his display. (5) The population of available females,  $f$ , is finite, and females can only mate once. Males on the other hand can mate with multiple females. (6) The optimal courtship strategy for each male is the strategy that maximizes his mating success relative to the other males in the population. The relevant variables are summarized in Table 1.

The logistical assumptions of this model are as follows: (7) Males fight in pairs. (8) Mating, displaying, and fighting all occur in discrete time periods, all at once (i.e. males cannot change their strategies over the course of a single unit of time).

Table 1. Summary of variables for two-player game.

Variable	Symbol	Range	Notes
Attractiveness	$a, b$	$0 < a \leq 1$	$a$ : Male 1 :: $b$ : Male 2
Time fighting	$u$	$0 \leq u \leq 1$	$u = \max\{u_1^*, u_2^*\}$
Time displaying	$t$	$0 \leq t \leq 1$	$t + u = 1$
Number of females	$f$	$0 < f < \infty$	
Absolute reproductive success	$R_i$	$0 \leq R_i \leq f$	
Relative reproductive success	$r_i$	$0 \leq r_i \leq 1$	$r_i = \frac{R_i}{\sum_n R_n}$

These rules allow us to develop a quantitative framework for assessing the costs and benefits of agonistic strategies. As stated above in Assumption 5, we model the dynamics of fighting versus displaying as a competition between individual males for female mates. Therefore, we begin by writing an equation for males' mating success as a function of their behavior. This equation will depend on the number of males present on the lek, so we first take the simplest case of a single male displaying in the absence of competitors.

$$R = atf$$

Though simple, this formula qualitatively reflects the observed relationships between attractiveness, courtship behavior, and mating success in many lekking systems including

that of sage-grouse. Independent of the effect of competitors, it is expected that reproductive success increases with attractiveness, time spent displaying, and the number of available females (Bradbury & Gibson 1983; Gibson & Bradbury 1985; Fiske *et al.* 1998). However, when a second male is introduced, the number available females is directly reduced by the competitor's mating success since females can only mate once. This relationship gives the following system of equations:

$$\begin{aligned} R_1 &= at_1(f - R_2) & \Rightarrow & R_1 = \frac{at_1f(1-bt_2)}{1-abt_1t_2} \\ R_2 &= bt_2(f - R_1) & \Rightarrow & R_2 = \frac{bt_2f(1-at_1)}{1-abt_1t_2} \end{aligned}$$

Similarly, when a third male is introduced to the lek, we can express the mating success of individual males with the following system of equations:

$$\begin{aligned} R_1 &= at_1(f - R_2 - R_3) & \Rightarrow & R_1 = \frac{at_1f(1-bt_2)(1-ct_3)}{1-abt_1t_2-act_1t_3-bct_2t_3+2abct_1t_2t_3} \\ R_2 &= bt_2(f - R_1 - R_3) & \Rightarrow & R_2 = \frac{bt_2f(1-at_1)(1-ct_3)}{1-abt_1t_2-act_1t_3-bct_2t_3+2abct_1t_2t_3} \\ R_3 &= ct_3(f - R_1 - R_2) & \Rightarrow & R_3 = \frac{ct_3f(1-at_1)(1-bt_2)}{1-abt_1t_2-act_1t_3-bct_2t_3+2abct_1t_2t_3} \end{aligned}$$

These equations give the mating success for an individual male, which we assume is proportional to his *absolute* reproductive success. However, evolutionary game theory models like ours typically measure fitness in terms of the *relative* reproductive success of individuals (Orr 2007). Unlike absolute reproductive success, the latter is a useful proxy for an individual's contribution to the genetic composition of the next generation. Therefore, we use the relative reproductive success of different phenotypes in order to study their evolution. At every stage of the development of this model, the equation for relative reproductive success,  $r$ , is absolute reproductive success,  $R$ , divided by the total reproductive success of the lek.

$$r_i = \frac{R_i}{\sum_n R_n}$$

Thus, the equation for the relative reproductive success of Male  $i$  in a lek with two males is  $r_i = \frac{\alpha_i t_i (1 - \alpha_j t_j)}{at_1 + bt_2 - 2at_1 bt_2}$ . Note that the total number of available females,  $f$ , has been divided

out of the equation. In a three-male lek,  $r_i = \frac{\alpha_i t_i (1 - \alpha_j t_j)(1 - \alpha_k t_k)}{at_1 + bt_2 + ct_3 - 2(at_1 bt_2 + at_1 ct_3 + bt_2 ct_3) + 3abct_1 t_2 t_3}$ ,

and so on. In this way, we can continue increasing the number of males on the lek such

that the general formula for a lek with  $n$  males is  $r_i = \frac{\alpha_i t_i \prod_{j \neq i} (1 - \alpha_j t_j)}{-\sum_{k=1}^n (k \sum \mathbb{P}_k \{-at_1, -bt_2, \dots, -\alpha_n t_n\})}$  where

$\mathbb{P}_k S$  denotes the set of all the products of  $\binom{S}{k}$ . For all versions of this model, when  $t_i = 0$

for all  $i$ , the relative reproductive success of Male  $i$  is defined as  $\lim_{(t_1, t_2, t_3) \rightarrow (0,0,0)} r_i(t_1, t_2, t_3)$ .

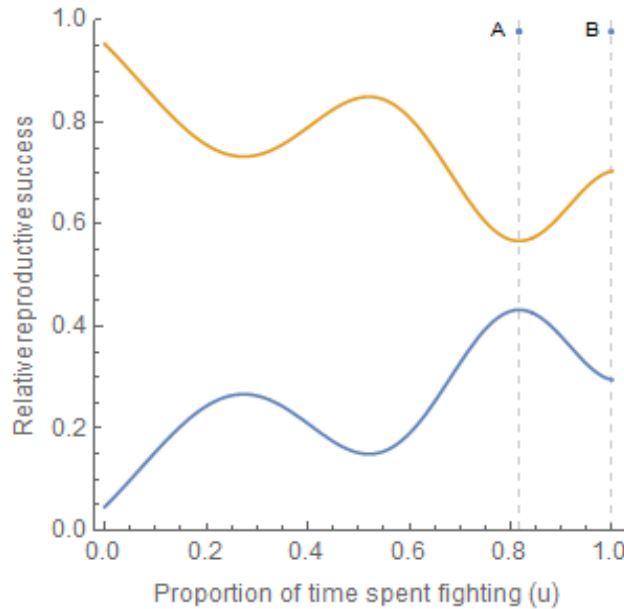
Thus,  $r_i(0,0,0) = \frac{\alpha_i}{\sum_n \alpha_n}$ .

## II. Two-Player Game

We begin with the simplified case in which only two males compete for the available females. To begin with, we define the possible strategies for each male. Both males propose a proportion of time between 0 and 1 to spend fighting with the other male, which we will call  $u_i^*$ . Since neither male can refuse to fight, the realized proportion of time spent fighting for each male,  $u_i$ , is the maximum of  $u_1^*$  and  $u_2^*$ . Thus, the realized proportion of time spent displaying for each male,  $t_i$ , is equal to  $1 - \max\{u_1^*, u_2^*\}$ . Note that when there are two players, the proportion of time both males spend displaying must be equal ( $t_1 = t_2$ ) as must their time spent fighting ( $u_1 = u_2$ ). These proportions of the total time will be referred to hereafter as  $t$  and  $u$  respectively.

The next step in developing a game-theoretic model is to define the payoffs for each player as a function of their strategies. In evolutionary models, the payoffs are the players' relative fitness. Since  $r_i = \frac{R_i}{\sum_n R_n}$  regardless of the specific equations,  $\sum_i r_i = 1$ . In other

words, relative mating success is a constant-sum game. So in a two-player game where  $r_i$  is a function of  $u$ , any change in the proportion of time spent fighting will penalize one male and reward the other by the same amount. Thus, one male or the other can always improve his relative reproductive success by fighting more, even if that corresponds to a decrease in his absolute reproductive success – just as long as it penalizes the other male more than himself. In short, either Male 1 or Male 2 always benefits from an increase in  $u$ . And since males can force one another to fight, this property of the two-player game will always lead to constant fighting, regardless of the attractiveness of the players or the details of their payoff functions (Figure 1). Therefore, the assumptions of this model alone are sufficient to show that the two-player game has a stable equilibrium when one male or the other has the strategy  $u_i^* = 1$ , and the realized proportions of time spent displaying and fighting are  $t = 0$  and  $u = 1$  respectively.



*Figure 1.* Arbitrary payoff functions for a constant-sum two-player game. The optimal strategy for the blue player is  $u_b^* = A$ , so he will force the yellow player to fight. But while still suboptimal,  $u = B$  is an improvement over  $u = A$  for the yellow player. He will therefore adopt the strategy  $u_y^* = B$ , driving the system to constant fighting.

There is, however, one exception when  $r_i$  is independent of  $u$ . For instance, when both males are equally attractive, the proportion of time spent displaying and fighting has no effect on the players' payoffs. If  $a = b$ , then  $r_1 = \frac{at(1-at)}{2at-2a^2t^2} = \frac{1}{2}$  and  $r_2 = \frac{1}{2}$ . In this case, all strategies are equivalent to one another, and so there is no stable equilibrium at  $u = 1$  or anywhere else. However, the particular case where  $a = b$  violates our assumption that there is variation in the attractiveness of males. As long as  $a \neq b$ , the two-player game has a stable equilibrium when  $t = 0$  and  $u = 1$ .

While this solution for the two-player version of our model is fairly simple, it is far from trivial. It demonstrates that (a) spending time fighting with a more attractive neighbor can at least sometimes be a viable strategy for unattractive males, and it predicts that (b) as long as there is variation in attractiveness and males can force one another to fight, intrasexual selection pressure will inevitably push two-male leks to constant fighting. We will now consider a three-player version of the same game with the expectation that the introduction of a third male will dissuade the other two from fighting all the time. Unlike in the two-player game, now when two males fight, they give the third male the opportunity to display unmolested. This may be sufficient to prevent either belligerent from improving his relative fitness by fighting more and thereby avoid this “tragedy of the lek”.

### III. Three-Player Game

The three-player version of this model differs from the simpler two-player model in several important ways. Males still divide their time between fighting and displaying, but now they may fight with either or both of their neighbors. Thus, instead of only one interaction between males,  $u$ , there are now three: the proportion of the total time Male 1 spends fighting with Male 2 ( $u$ ), Male 1 with Male 3 ( $v$ ), and Male 2 with Male 3 ( $w$ ). In the

same way, each male's strategy now consists of two proposals for the proportion of time to spend fighting, one for each interaction he is a part of (Figure 2). The sum of these values must be between 0 and 1. As before, the realized proportion of the total time spent fighting in a particular interaction is the maximum of the two implicated males' proposals. Thus,  $u = \max\{u_1^*, u_2^*\}$ ,  $v = \max\{v_1^*, v_3^*\}$ , and  $w = \max\{w_2^*, w_3^*\}$ . While it is given by the constraints of the model that no male can propose to fight more than one hundred percent of the time ( $u_1^* + v_1^* \leq 1$ ,  $u_2^* + w_2^* \leq 1$ , and  $v_3^* + w_3^* \leq 1$ ), it is possible for the sum of the proposals of a male's neighbors to exceed 1. In this case, the realized time spent displaying by that male is 0. For instance, if  $u_2^* + v_3^* > 1$ , then  $t_1 = 0$  and not  $1 - u_2^* - v_3^*$ . Thus,  $t_1 = \max\{0, 1 - u - v\}$ ,  $t_2 = \max\{0, 1 - u - w\}$ , and  $t_3 = \max\{0, 1 - v - w\}$ .

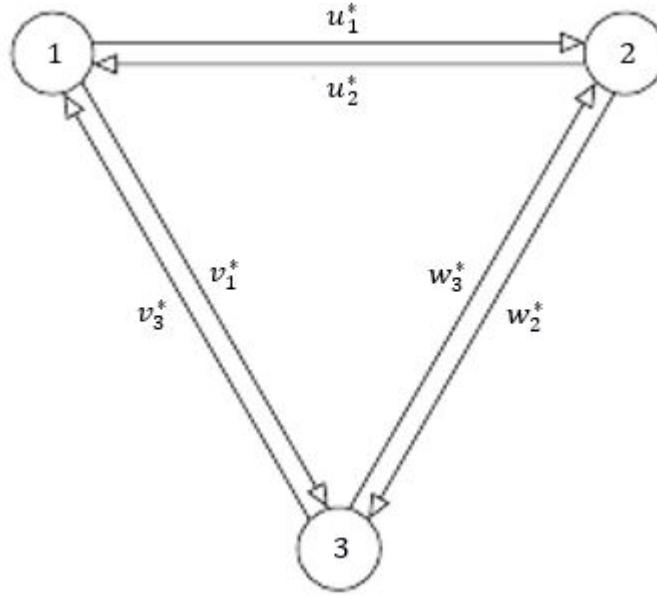


Figure 2. Diagram of males' strategies and interactions between males in a three-player game.

As in the two-player game, the payoff function for each player is his relative mating success,  $r_i$ . Each player's payoff therefore depends on  $u$ ,  $v$ , and  $w$ , but his strategy can only modify two of the three interactions. The optimal strategy for each player (his best response) can then be found by maximizing his  $r_i$  with respect to the two interactions he is implicated in. Each male's best response depends not only on the attractiveness of his neighbors and his own, but also on the third fighting interaction in which he is not implicated. For example, the best response for Male 1,  $(u_1, v_1)$ , is a function of  $a$ ,  $b$ ,  $c$ , and  $w$ . The best responses for Male 2 and Male 3 depend in turn on  $v$  and  $u$  respectively. This feedback between best-response functions offers the possibility to use best-response dynamics to solve the model for a Nash equilibrium if one exists (Box 1; Kleinberg & Tardos 2006).

**Box 1. Background and definitions of best-response dynamics.**

BEST RESPONSE is the strategy,  $\sigma_i$ , which maximizes a player's payoff given the other players' strategies,  $\sigma_{-i}$ , denoted  $B_i(\sigma_{-i})$ . Formally, if the expected payoff to player  $i$  is  $E(\sigma_i, \sigma_{-i})$ , then  $E(B_i, \sigma_{-i}) \geq E(\sigma'_i, \sigma_{-i})$  for all  $\sigma'_i$ .

NASH EQUILIBRIUM is a set of strategies, strategy profile, for which no player can improve their payoff by modifying their strategy. In other words, each player's strategy is the best response to all of the other players' strategies;  $B_i(\sigma_{-i}) = \sigma_i$  for all  $i$  (Nash 1950).

BEST-RESPONSE DYNAMICS is a process by which Nash equilibria can be found if one exists. We begin with an arbitrary starting position  $\sigma$  and an arbitrarily chosen player  $i$ . If any unilateral deviation from  $\sigma_i$ , say  $\sigma'_i$ , is beneficial to player  $i$ 's payoff, then we move to the new position  $(\sigma'_i, \sigma_{-i})$ . Such a deviation will always be possible unless  $\sigma_i = B_i(\sigma_{-i})$ . This process is repeated with a new arbitrarily chosen player each time. The process will only terminate if  $\sigma_i = B_i(B_{-i}(\sigma))$ , that is, if  $\sigma$  is a Nash equilibrium. If no Nash equilibrium exists, the best-response dynamics will never terminate. For example, player 1 improves  $\sigma_1$  at the expense of player 2, who in turn improves  $\sigma_2$  at the expense of player 1, and so on. These cyclical dynamics will continue in a loop forever (Kleinberg & Tardos 2006).

In order to find any Nash equilibria predicted by our model for a given combination of attractiveness parameters, we developed a stochastic optimization algorithm in R 3.2.3 (see Appendix; R Core Team 2015). The algorithm computationally searches the strategy space using best-response dynamics. To begin, values are assigned to parameters  $a$ ,  $b$ , and  $c$ . A starting strategy profile  $\sigma = ((u_1^*, v_1^*), (u_2^*, w_2^*), (v_3^*, w_3^*))$  is randomly selected from a uniform distribution given the constraints of the model (Figure 3). A male  $i$  is then randomly chosen to propose a new strategy,  $\sigma'_i$ . This is done by making a small deviation from the current value of one component of his strategy and fixing the other component. The size and direction of this deviation is chosen from a Normal distribution with mean 0 and standard deviation 0.01. Thus, the new strategy for Male  $i$  has one new component and one old component, chosen at random. The proposed new strategy profile,  $\sigma'$ , is  $(\sigma'_i, \sigma_{-i})$ . Male  $i$ 's new strategy is then tested against his old strategy. If  $r_i(\sigma') \geq r_i(\sigma)$ , Male  $i$  accepts  $\sigma'_i$  and  $\sigma'$  becomes the new current strategy profile. The current values of  $t_1$ ,  $t_2$ , and  $t_3$ , whether they are new or not, are then stored in a path matrix, which allows the algorithm to determine when an equilibrium is reached. The process is repeated with a new randomly chosen male each time until there is no change in the realized proportion of time spent displaying within the last one hundred steps of the path. At this point, we assume that a Nash equilibrium has been reached. If after one million steps, the path has still not converged, we assume that the best-response dynamics are cyclical and that no Nash equilibrium exists for that particular combination of attractiveness parameters. The final value reported in this case is the modes of  $t_1$ ,  $t_2$ , and  $t_3$  over the last one hundred steps of the path, which approximate the non-Nash stable equilibrium if one exists.



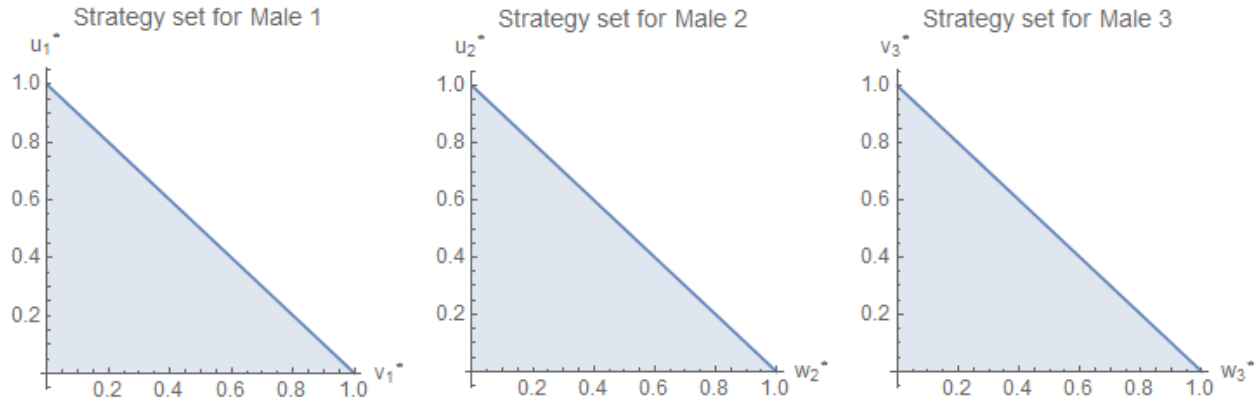


Figure 3. Strategy sets for Males 1, 2, and 3. The six-dimensional strategy space for this model is equal to the intersection of these strategy sets.

Using this method we solved for equilibria at 22,100 evenly distributed points across the parameter space,  $(a, b, c) \in (0, 1]^3$  – that is every possible combination of discrete values of  $a$ ,  $b$ , and  $c$  at intervals of 0.02 apart. Computing these equilibria using best-response dynamics was performed with the help of the High Performance Computing clusters at the Yale Center for Research Computing. In order to avoid spending computational effort on redundant permutations, we specified the rule  $a \geq b \geq c$  with the assumption that the order of the parameters doesn't matter. We will follow this rule for the remainder of the analysis unless explicitly stated otherwise.

The most striking result of these simulations is that by far the most common equilibrium is  $t_1 = t_2 = t_3 = 0$ , or constant fighting. In nearly half of the sampled parameter space (47.4%), constant fighting is a Nash equilibrium. On the other hand, for a few parameter combinations where  $a \approx b \approx c$  (24.0%), constant displaying is a Nash equilibrium; that is none of the males offer to fight ( $u_1^* = u_2^* = v_1^* = v_3^* = w_2^* = w_3^* = 0 \therefore t_1 = t_2 = t_3 = 1$ ). For the remainder of the parameter combinations, the realized proportion of time spent fighting is between 0 and 1 at equilibrium (Figure 4).

For parameter combinations where constant fighting is a Nash equilibrium,  $u_1^* + v_1^* < 1$  but  $u_2^* + v_3^* \geq 1$  at equilibrium, therefore  $t_1 = 0$ . In other words, the two less attractive males work together to prevent the most attractive male from displaying at all. At this point, Male 1's absolute mating success is 0, and the model for the remaining two males effectively becomes a two-player game. Thus, as shown in Section II, the best-response dynamics inevitably lead to constant fighting unless  $b = c$ . It should be noted that there are infinitely many strategy profiles that give values of  $u$ ,  $v$ , and  $w$  such that  $u + v \geq 1$ ,  $u + w \geq 1$ ,  $v + w \geq 1$ , and therefore  $t_1 = t_2 = t_3 = 0$ . The payoffs to each of the three players are the same for all of these strategy profiles. All that is required for a Nash equilibrium is that no player can strictly improve his payoff by changing his strategy. Therefore, for the parameter combinations where the best-response dynamics lead to constant fighting, each of these strategy profiles is an equivalent Nash equilibrium.

Constant-fighting equilibria occur generally when the variation in attractiveness among males on the lek is large. In particular, the attractiveness of Male 1 must be such that both subordinate males always benefit from increasing the proportion of time spent fighting with him. Otherwise put, any amount of displaying by Male 1 is so costly to Male 2 and Male 3 that both are willing to accept the smaller, but significant, cost of forgoing approximately half of their display time in order to prevent Male 1 from mating. Once Male 1 is excluded from mating, the relative attractiveness of Male 2 to Male 3 is irrelevant, as shown in Section II; the system will inevitably fall into the “tragedy of the lek”. Thus, in order for constant fighting to be a Nash equilibrium, it is necessary and sufficient that  $a$  be greater than some threshold, which is a function of  $b$  and  $c$ .

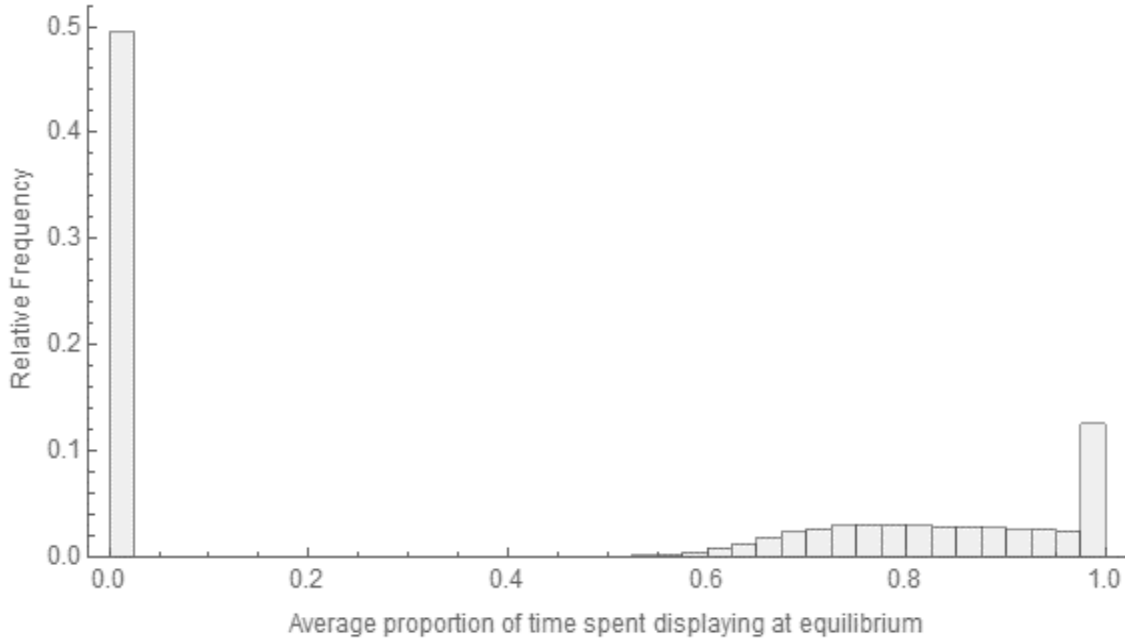


Figure 4. Histogram of  $\hat{t}_1 + \hat{t}_2 + \hat{t}_3$  at equilibrium for all 22,100 simulations.

In order to quantitatively approximate this threshold, we divided the parameter space into two disjoint categories for graphical analysis: constant-fighting equilibria ( $\hat{t}_1 + \hat{t}_2 + \hat{t}_3 = 0$ ) and all other equilibria ( $\hat{t}_1 + \hat{t}_2 + \hat{t}_3 > 0$ ). As predicted, the first condition is met in the region of the parameter space where there is significant variation in the values of  $a$ ,  $b$ , and  $c$ . The second condition is met in the other half of the parameter space, centered about the line  $a = b = c$ . A minimum convex hull for the latter set of sampled parameter values was calculated using Mathematica 11.1.0 (Wolfram 2017) in order to visually approximate the boundaries of the region in the parameter space where non-constant-fighting equilibria occur (Figure 5). The volume defined by the intersection of  $a \leq b + c$ ,  $b \leq a + c$ , and  $c \leq a + b$  closely approximates the resulting hull. Therefore, since constant-fighting and non-constant-fighting equilibria are disjoint and complimentary, the region of the parameter space with constant-fighting equilibria is approximately defined by the union of  $a > b + c$ ,  $b > a + c$ , and  $c > a + b$ .

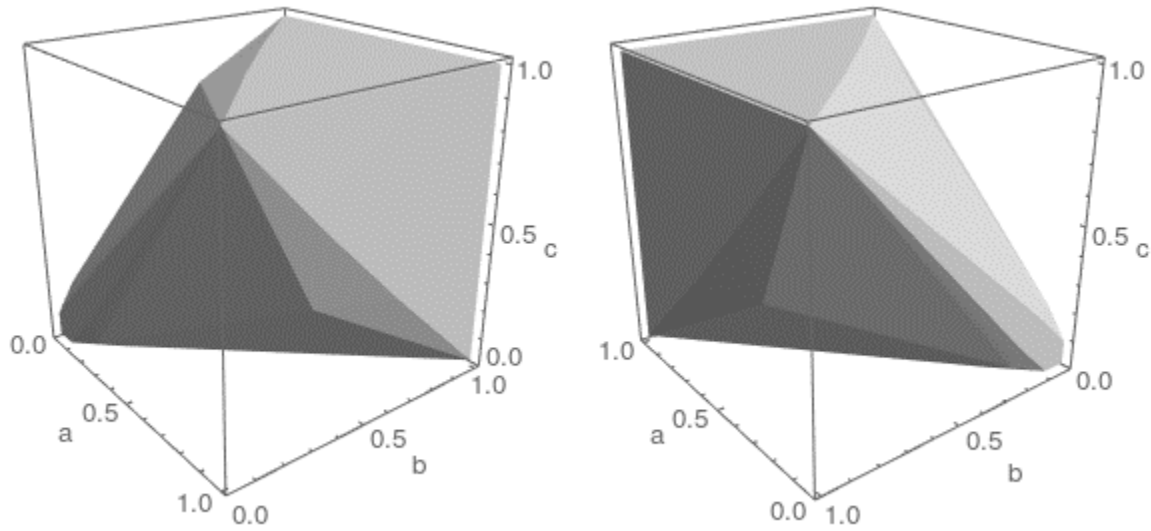


Figure 5. Minimum convex hull for all 63,839 (out of 125,000 possible) permutations of attractiveness parameter with non-constant-fighting equilibria, seen from two different angles. In order to visualize the entire, unit-cube parameter space, redundant parameter permutations were reintroduced into the dataset by extrapolating from simulated equilibria assuming that  $\hat{\sigma}(a, b, c) = \hat{\sigma}(a, c, b) = \hat{\sigma}(b, a, c) = \dots$  for all permutations of  $\{a, b, c\}$ .

We therefore conclude our analysis of the three-player model with two key generalizations for our model of lek mating systems with three reproductive males: (a) for all but a few combinations of attractiveness parameters where  $a \approx b \approx c$  some nonzero amount of fighting is an evolutionarily viable strategy for the less attractive males on the lek, and (b) when the skew in male's attractiveness is extreme ( $a > b + c$ ), competition for a limited number of mates will drive the lek to constant fighting, leaving no time for displaying (Figure 6). These results show that under biologically realistic conditions, the secondary benefits of courtship disruption (even redistribution of a rival's would-be mates across males on the lek) can outweigh the cost of fighting. They demonstrate, moreover, that the addition of a third reproductive male to the lek is not sufficient to avoid the “tragedy of the lek”.

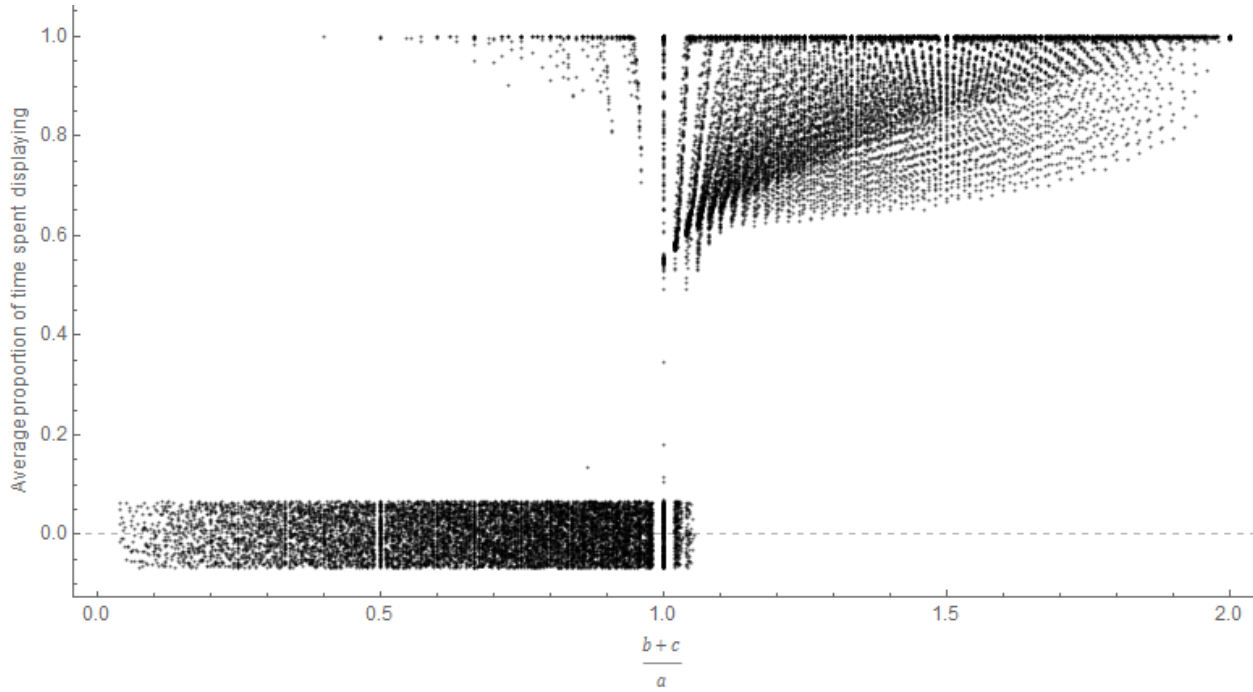


Figure 6. Scatterplot of  $\frac{t_1+t_2+t_3}{3}$  against  $\frac{b+c}{a}$  at equilibrium for all combinations of attractiveness parameters (assuming  $a \geq b \geq c$ ). Jitter was added to the  $y$ -values of points where  $t_1 + t_2 + t_3 = 0$  in order to show the frequency of such equilibria – i.e. the “tragedy of the lek”.

## DISCUSSION

Both the two-male and the three-male version of this model demonstrate that males can plausibly improve their reproductive success by interfering with their neighbor’s ability to display. This result provides theoretical support for the role of courtship disruption in explaining agonistic behaviors between males of lek-mating bird species. However, previous discussions of the evolution of male-male fighting in lek-mating birds have dismissed the role of secondary benefits of courtship disruption as insignificant and implausible. They argue that if the only benefit to the aggressor is that he prevents another male from mating, the remaining males on the lek will benefit even more since they do not incur the cost of fighting, and therefore, this is not a viable strategy for the

aggressor (Foster 1983). In a two-male lek, this hypothesis cannot be tested since the aggressor, being the only other male on the lek, receives the entirety of his rival's redistributed mating success. Thus, in order to challenge the presumption that the secondary benefits of display interruption alone cannot justify fighting, it was necessary to develop a three-male version of our model.

In this version, some amount of fighting was in many cases a viable strategy even though we made no assumption that courtship disruption increases the aggressor's probability of mating with the interrupted female. Thus, the results of this three-player game provide a mathematical proof-of-concept for our hypothesis that secondary benefits alone are in fact sufficient in many cases to justify agonistic strategies for the less attractive males in lek mating systems. We conclude, therefore, that the adoption of this strategy by less attractive males plays a significant (though currently under-studied) role in the dynamics of conflict and tolerance in leks. This conclusion from the three-player model provides additional support for the courtship-disruption hypothesis, and it presents a new mechanism for the evolutionary viability of this strategy.

Moreover, by simulating the best-response dynamics for leks with varying degrees of heterogeneity in males' attractiveness, we found that the amount of fighting between males increases with the level of skew in their attractiveness. In fact, our model predicts that when one male is sufficiently more attractive than either of his neighbors, the benefits of courtship disruption for the less attractive males will lead to constant fighting. We call this paradox the tragedy of the lek; in order to maximize their relative reproductive success, males adopt a strategy which reduces their absolute reproductive success to zero. Thus, any lek in which the variation in attractiveness exceeds a critical threshold is instantly doomed. According to this model prediction, leks with extreme skew in males' mating success, such as sage-grouse leks, should be impossible.

How then can the continued existence of such leks be explained? Two hypotheses suggested in previous literature offer plausible solutions to this paradox. They propose some direct cost, external to our model, which mitigates the benefits of agonistic strategies. In order to effectively moderate fighting, this cost must asymmetrically disadvantage the aggressor. We will discuss these hypotheses briefly and present one of our own, which does not require the addition of any new assumptions to our model.

One of the prevailing hypotheses in previous literature is that distance between males mediates the frequency of fighting. The aggressor alone incurs the cost of traveling to a neighbor's territory in order to interrupt his display; as the distance increases, so does the travel time, and thus the risk that he will forgo the opportunity to mate with a female who arrives at his territory during his absence (Foster 1983; Pruett-Jones & Pruett-Jones 1994). However, this hypothesis does little to explain the relative tolerance between males in sage-grouse leks where neighbors are only a few meters apart, and the skew in males' mating success is great (Scott 1942). Asymmetric fighting ability may also outweigh the benefits of courtship disruption if we assume that the potential aggressor, who is less attractive, is also the weaker fighter. In this case, he incurs a greater risk of injury as a result of fighting. Once again, while plausible in other lek-mating species, this explanation does not accurately reflect the nature of male-male fighting in sage-grouse, which seldom results in injury and consists primarily of apparently symmetric contests, face-offs (Wiley 1973; Klempay, unpubl. obs.).

We propose an alternate resolution to the tragedy of the lek, which requires only the existence of an outside option for females to mate. Preliminary analyses of a four-player, two-lek version of our model show that selection between leks as well as within leks (see Lill 1976, Bradbury & Gibson 1983, Foster 1983) significantly mitigates the benefit of courtship interruption. In this case, all four males compete for a limited number of

available females, but males in different leks cannot fight with one another. A simple thought experiment is sufficient to show that the tragedy of the lek is avoided in this version of the model. If either lek fights constantly (say Male 1 and Male 2  $\therefore t_1 = t_2 = 0$ ) while the other lek displays for any amount of time ( $t_3 = t_4 > 0$ ), then  $r_1 = r_2 = 0$  and  $r_3 + r_4 = 1$ . Thus, constant fighting can never be a Nash equilibrium. Therefore, for one two-male lek, the tragedy of the lek is inevitable, but for two two-male leks, the tragedy of the lek is impossible. Merely by making mate choices based on males' displays, females impose selective pressure for cooperation between males at the group level.

This result is highly significant, as it provides a mechanism for females of lek-mating bird species to exercise mate choice even as males seek to thwart their very ability to do so. While we show with the two- and three-player versions of this model that courtship disruption can be beneficial to males, it imposes obvious costs on females. Direct costs include increasing the time and energy they must expend in order to find suitable mates and successfully copulate. This may, in turn, increase females' vulnerability to predators (Hartzler 1974; Foster 1983). Importantly, in addition to these direct costs, courtship disruption imposes indirect costs on females (paid via their offspring) by limiting their sexual autonomy – their ability to mate with the male of their choice. Thus, courtship disruption, like other mechanisms of sexual coercion, effectively reduces the attractiveness of females' sons (Fisher 1930; Brennan & Prum 2012).

Our model suggests that female preference for tolerance, and even cooperation between males (see Lill 1976, McDonald 1989) is critical not only for ensuring female sexual autonomy (see Prum 2015), but also for preserving the stability of the lek and saving it from the tragedy of the lek. These results provide theoretical support for the role of both female preference and group selection in the evolution of the lek, and they emphasize the need for further theoretical and empirical research in this area.



## ACKNOWLEDGMENTS

I am extremely grateful to David Heiser and the Peabody Museum Student Summer Research Award for supporting this research. I am also thankful for the invaluable contributions of Dr. Larry Samuelson, for his patience, and for his time. This research would not have been possible without the hours of video footage of sage-grouse generously provided by Dr. Gail Patricelli's lab at the University of California, Davis. Additionally, the high-performance computing resources at the Yale Center for Computing Research were essential to this project. I would like to extend my special thanks to Dr. Richard Prum for advising me in this research and for his insights on birds in general. Above all, I am deeply grateful to Samuel Snow for his endless help and for the hours of work he put into supporting me in this endeavor.

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## APPENDIX

## R Script for optimization of player strategies

```

# three-player game
# PARAMETERS:
a <- 0.68
b <- 0.32
c <- 0.08

REPS <- 50
store.length <- 100 # number of steps that are stored at one time to check for convergence
step.sd <- 0.01

# PAYOFF FUNCTIONS:
# input: {t1,t2,t3} => output: {r1,r2,r3}
r <- function(T){
  if(T[1]+T[2]+T[3]==0) c(a/(a+b+c),b/(a+b+c),c/(a+b+c)) else {
    c(a*T[1]*(1-b*T[2])*(1-c*T[3])/
      (a*T[1]+b*T[2]+c*T[3]-2*(a*b*T[1]*T[2]+a*c*T[1]*T[3]+b*c*T[2]*T[3])+3*a*b*c*T[1]*T[2]*T[3]),
      b*T[2]*(1-a*T[1])*(1-c*T[3])/
      (a*T[1]+b*T[2]+c*T[3]-2*(a*b*T[1]*T[2]+a*c*T[1]*T[3]+b*c*T[2]*T[3])+3*a*b*c*T[1]*T[2]*T[3]),
      c*T[3]*(1-a*T[1])*(1-b*T[2])/
      (a*T[1]+b*T[2]+c*T[3]-2*(a*b*T[1]*T[2]+a*c*T[1]*T[3]+b*c*T[2]*T[3])+3*a*b*c*T[1]*T[2]*T[3]))
  }
}

# FUNCTION: calculate realized proportion of time spent displaying given strategies
# input: {u1,u2,v1,v3,w2,w3} => output: {t1,t2,t3}
display.time <- function(X){
  c(max(0,1-max(X[1],X[2])-max(X[3],X[4])),
    max(0,1-max(X[1],X[2])-max(X[5],X[6])),
    max(0,1-max(X[3],X[4])-max(X[5],X[6])))
}

# STEP FUNCTION:
# input: all current strategies => output: new strategy
step <- function(X,UVW){
  new <- rnorm(1,X[UVW],step.sd)
  if(new<0) new <- 0
  if(new>1) new <- 1
  new
}

# create blank data frame for results
results <- data.frame("a" = rep(a,REPS),"b" = rep(b,REPS),"c" = rep(c,REPS),
  "u1" = rep(NA,REPS),"u2" = rep(NA,REPS),"v1" = rep(NA,REPS),
  "v3" = rep(NA,REPS),"w2" = rep(NA,REPS),"w3" = rep(NA,REPS),
  "t1" = rep(NA,REPS),"t2" = rep(NA,REPS),"t3" = rep(NA,REPS))

# create blank matrix for path
path <- matrix(NA,store.length,3)

# START SIMULATION HERE:
for(i in 1:REPS){
  # set step counter
  STEPS <- 0

  # begin simulation with a randomly chosen set of strategies (seed)
  valid <- FALSE
  while(valid == FALSE){
    x <- runif(6)
    # verify that this is a valid seed
    valid <- x[1]+x[3]<=1 & x[2]+x[5]<=1 & x[4]+x[6]<=1
  }
  t <- display.time(x)

```

```

# store current realized display times in path matrix
path[1,] <- t

# begin optimization algorithm
converge <- FALSE
while(converge==FALSE){
  STEPS <- STEPS+1

  # select one strategy to change and make a new proposal
  uvw <- sample(1:6,1)
  valid <- FALSE
  while(valid==FALSE){
    prop <- x
    prop[uvw] <- step(x,uvw)
    # verify that this is a valid proposal
    valid <- prop[1]+prop[3]<=1 & prop[2]+prop[5]<=1 & prop[4]+prop[6]<=1
  }
  t.prop <- display.time(prop)

  # test new strategy for the relevant male and accept if r(t.prop) > r(t)
  male <- c(1,2,1,3,2,3)[uvw]
  if(r(t.prop)[male]>r(t)[male]) x <- prop; t <- t.prop

  # store current realized display times in path matrix
  # but begin overwriting after completing "store.length" steps
  path[STEPS+1-floor(STEPS/store.length)*store.length,] <- t

  # see if path has converged
  converge <- length(unique(path))==3

  if(STEPS<10000) converge <- FALSE # run optimization for at least 10,000 steps
  if(STEPS==5000000) converge <- TRUE # end optimization after 5 million steps no matter what
}

# report the final positions of all six strategies
results[i,4:9] <- x
# round realized display times to 3 sigfigs and report path modes (equilibrium values)
results[i,"t1"] <- as.numeric(names(sort(-table(round(path[,1],3))))[1])
results[i,"t2"] <- as.numeric(names(sort(-table(round(path[,2],3))))[1])
results[i,"t3"] <- as.numeric(names(sort(-table(round(path[,3],3))))[1])

results$meta_step.sd <- step.sd
results$meta_store.length <- store.length
results$meta_STEPS[i] <- STEPS
results$meta_nash[i] <- length(unique(path))==3
}

# GENERATE OUTPUT:
out <- data.frame("a" = a,"b" = b,"c" = c)
out$t1 <- median(results[, "t1"])
out$t2 <- median(results[, "t2"])
out$t3 <- median(results[, "t3"])
out$r1 <- r(out[,4:6])[1]
out$r2 <- r(out[,4:6])[2]
out$r3 <- r(out[,4:6])[3]

out$meta_REPS <- REPS
# check that results converge within 0.01
out$converge <- sum(abs(results[, "t1"]-out$t1)<0.01,
                  abs(results[, "t2"]-out$t2)<0.01,
                  abs(results[, "t3"]-out$t3)<0.01)/(3*REPS)
out <- as.matrix(out)

# verify that working directory contains a folder named "detail"
write.csv(results,paste("./detail/",paste("detail",a,b,c,sep = "-"),".csv",sep = ""))
write.table(out,"data_out.csv",append = TRUE,sep = ",",row.names = FALSE,col.names = FALSE)

```