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RELIABLE SIGNALS AND THE SEXUAL SELECTION: AGENT-BASED SIMULATION OF THE HANDICAP PRINCIPLE

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ABSTRACT

This paper describes an agent-based simulation extension of Grafen's model of the handicap principle. This signaling game explains how evolution leads to reliable signaling between animals in situation when individuals have a motivation to deceive each other, e.g. when their traits are not observable. The standard theory implies that the cost of a signal, which is relatively higher for the inferior individuals, ensures its reliability. The aim of our model is to investigate the possible evolutionary stable equilibria existing in this communication system. We performed analysis of the proposed model using simulation. The obtained results show that there exist equilibria in which cheating is an evolutionary stable strategy and identify conditions needed for such a situation. Additionally we observe that the taste of females becomes homogeneous in time, which is in line with the runaway process concept proposed by Fisher.

1 INTRODUCTION

The development of the secondary, exaggerated sexual ornaments is a main topic of a long raging debate. The theory of sexual selection, which emphasized the role of traits such as the tail plumes of the peacocks, the antlers of antelopes or deer, the rich ornamentation of many other animal species was originated by Darwin (1874), who described it as an cumulative effect of females preference for certain male types. He suggested that the disadvantage to male survival induced by these characters, are compensated for by more or better females preferring that individual to other males. This idea was improved and expanded by Fisher (1915) and Fisher (1930), who suggested a correlation between the traits preferred by females and the quality of the male. He supposes that males traits could have evolved in the following manner: a mutant female started selecting a mate according to some extravagant and wasteful trait rather than mating at random. At the beginning, only the strongest males can develop this feature and survive with it. So the preference of female could be an advantage to her progeny and it would spread in the population. When more females have started to select males by looking at their extravagant traits, males have raised these features. This evolutionary response started a process, named a "runaway process", resulting in males developing their traits as long as they could. Once all males invested in the wasteful, extravagant trait, it is no longer correlated to quality. O'Donald's model (O'Donald 1962; O'Donald 1972) in a manner consistent with Fisher's proposition showed that an attribute of a male is attractive to a female because it helps her to choose the better partner. Another finding by O'Donald was that a small increase in the male trait results in a small loss of viability but a large gain in mating advantage in the sexual selection process.

A fundamental question was what mechanism ensures the correlation between the observable trait and the unobservable quality of male and why the signals are reliable and resistant to cheating. The answer to this question and the next step in the evolution of the theory of sexual selection was a concept of a

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handicap principle, proposed by Zahavi (1975) and Zahavi (1977). His solution was based on signal costs, the stronger males are able to create a bigger signal and "waste" more of the unobservable quality by trading it off for a signal than weaker ones. The size of a handicap indicates an innate, unobservable quality of a male.

Zahavi's theory was widely discussed and very often rejected as "intuitive only" and unprovable (Zahavi 2003), see also: Maynard Smith (1976), Pomiankowski (1987), Kirkpatrick (1982) and Davis and O'Donald (1976); until Alan Grafen justified the handicap principle mathematically, showing the model based on this concept (Grafen 1990b; Grafen 1990a). He proved that when males during the mating have a motivation to bluff females, the marginal cost of advertising, which is increasing in quality and relatively lower for better males, ensures the credibility of the signal. The gains from cheating are lower than the cost of increasing the advertising level, so there is no incentive to raise it above the level, which correspond to the male's quality. And when the signal is reliable and reveals the real, unobservable quality of potential partners, females will use it as the best method to assess male innate quality. This means that the pair of strategies: *(i)* males are honest and their advertising level reveals their true quality, *(ii)* females used it to determine the true quality of male, will be equilibrium and evolutionary stable strategies. But even today, the handicap principle is an object of many controversies and one of the most widely disputed theories in evolutionary biology, see: Hurd (1997), Számadó (1999), Számadó (2011), Lachmann, Számadó, and Bergstrom (2001), Maynard Smith and Harper (2003) and Getty (2006).

The previous simulations of the handicap principle (Bell 1978; Ticona and Penna 2003) showed that under specific conditions handicap principle can be an evolutionary stable strategy. Another significant question is how the handicap impacts on overall fitness and welfare of the population. In this text we develop an agent-based simulation and try to answer to this question. To examine the evolutionary stability of the equilibrium and conditions that guarantee it, we introduce a new type of males – dishonest ones, which are bluffing and which signal exceed the value corresponding to their true quality. Another extension of the model is an implementation of more sophisticated assessment for the males' unobservable quality. Females assess not only the strength of the males signal, but also their other traits that are correlated with the quality. Moreover, tastes of females vary; it allows us to investigate the role of females preferences (especially the preference for the handicapped signal) in their reproductive success. The proposed model allows us to: *(i)* examine the impact of different exogenous conditions on the equilibrium, *(ii)* contribute to the research on the sexual selection field by providing another example of the animal communication model and by studying the relationships between different theories of the sexual selection.

The rest of the paper is organized as follows. The description of the model used for the simulation is presented in Section 2. In Section 3 we describe simulation setup and demonstrate the results. The results are discussed in Section 4. Section 5 concludes.

2 MODEL DESCRIPTION

In this section we characterize agents, their behavior and strategies; we also describe implemented sexual selection mechanism and the prevailing conditions in environment. The specification replicates model of the handicap principle proposed by Grafen (1990a) with extensions allowing for different males strategies. We also introduce female preferences for different male traits, which allows us to analyze the influence of the female choice on her reproductive success.

Consider an area on which there are N agents, divided into three groups: females, honest males and dishonest males. Females believe that all males are honest and their advertising level determines their true quality, honest males signal reveals their true quality and dishonest males are cheating and their advertising level is raised above the level representing their true quality.

At the beginning of the simulation the population of agents is generated are initially placed into random locations of the area represented by a $k \times k$ square grid. After placing all the agents in the grid, each cell is either occupied by only one agent or is empty. Each agent is described by a quality q, which is an uniform random number between 0.2 and 1.0 and by viability $v(q)$, the function of q, which is representing the strength of each individual and its probability of surviving. Every time step each agent moves to a random vacant part of the area and gets older. When agent's age is higher than a maximum possible age, agent dies. At each time step every female is looking for a best partner and when she finds one, they reproduce and one new agent is created. Localization of female determine her potential partners set; she can only choose one of males in her nearest environment. This constraint represents real life situations; female's choice is limited to the group of males encountered during the mating. There is no adolescence; every new individual in the population is already adult. The population size $N(t)$ is growing, and when it reaches $N_{\max}$, the maximum population size the environment can support, for each individual a random number between 0.0 and 1.0 is generated and compared with its viability; if it is higher than viability, the individual dies independently of its age.

2.1 Males Characteristic and Behavior

Honest and dishonest males are described by their advertising function $A(q)$ and perceived quality function $P(q)$. Both advertising and perceived quality functions used in this simulation came from an example presented in Grafen (1990a). The advertising function measures the strength of a male's signal and is equal to:

$$A(q) = \delta \left[a_0 - r \ln \left(\frac{\ln(q)}{\ln(q_{\min})} \right) \right],$$

where $\delta \geq 1$ is the rate of the males' dishonesty, a_0 is the lowest possible signal level and is equal to 1, which means that a male with advertising level a_0 does not send any signal and does not bear any costs, $q_{\min} = 0.2$ is the lowest level of quality in the population and $r > 0$ is a measure of overall strength of the signal. For example, when r is close to 0 the signal is very weak and males do not advertise themselves, they are cryptic and look similar to the females. When r raises males starts to be more conspicuous and vary from females. The value of r can be also interpreted as a measure of the strength of the effect of female choice on male fitness (Grafen 1990a). Higher value of r means that females are preferring males with a stronger signal.

A major difference between honest and dishonest males lies in their δ value. It measures how much stronger the signal of a male is in comparison with the situation when his advertising level represent his true quality. It means that for the honest ones δ is always equal to 1, because their strategy always reveals their innate, true quality. Dishonest males increase their signal above the level corresponding to their true quality and their $\delta > 1$. For example, when $\delta = 1.5$, dishonest males advertise 1.5 times stronger than honest males with the same quality. We assume that dishonest males do not vary in their strategies and that for all of them the level of dishonesty is the same.

The perceived quality function $P(q)$ is a function of females strategy and is used to assess the true quality of males. It is equal to:

$$P(q) = q_{\min}^{\exp[-(A(q)-a_0)/r]},$$

Note that for honest males it reveals their innate, unobservable quality $P(q) = q$. And when the level of dishonesty δ, will be higher than 1, which means that a male is dishonest, the perceived quality of male will be higher than its true quality:

$$P(q) > q.$$

The viability $v(q)$ of males is equal to $v(q) = q^a$. In the model presented in this paper cost of the signal is represented only by increasing probability of death. A growth of $A(q)$ results in a loss of viability and decreasing likelihood of surviving, for higher $A(q)$ this cost is greater and when $A(q) = a_0 = 1$ cost of the signal is equal to 0. Furthermore, because the function of viability takes the form described above, its value will be lower for dishonest males than for honest ones. A male's viability decreases in its dishonesty:

$$q^a > q^{\delta a}.$$

2.2 Females Characteristic and Behavior

Each female is described by her viability $v(q)$, which is equal to her quality:

$$v(q) = q,$$

and by α (a uniform random number between 0 and 1), which is a variable showing the preferences for the males signal. Higher value of α means that its role in an assessment of a male's quality is greater. If the signal is the best way to determine the true quality of male, a stronger preference for the signal (higher α) should increase reproductive success of females (Grafen 1990a).

Every time step each female is looking for a best candidate to her offspring father. Females do not bear any costs of reproduction; they also do not look back; in the decision making process they consider only the present situation and their previous decisions have no influence on their choice. Every female is searching for a male with the highest real, unobservable quality. To assess candidates in her nearest environment she uses a simple rule:

$$\text{Assessment} = \alpha P(q) + (1 - \alpha) \times \text{male\_age}.$$

The age of a potential partner also can be considered as a function of q. Only a strong individual, with a high quality can survive a long periods of time without being harmed by predators, illnesses and other external threats. Thus, the distribution of male quality changes with age and the mean quality of the older males will be higher than younger ones. It means that a female who mates with older males may have fitter offspring (Brooks and Kemp 2001; Proulx, Day, and Rowe 2002). When one of the candidates is selected, one new agent is created. Quality of a newborn individual is a geometric mean of its parents qualities:

$$q = \sqrt{q_{\text{mother}} * q_{\text{father}}}.$$

The level of a male's signal does not have influence on the quality of his offspring; we consider the situation when only the male bears the cost of his signal, for further explanation see Grafen (1990a). With a probability 0.5 new agent will be a female, with a value of α inherited from her mother. In opposite case, it will be a male, who will inherit his strategy (being honest or dishonest) from his father. Algorithm 1 describes details of the implementation.

The simulation was implemented as a Python 3.5.1 script. We use Anaconda3 distribution, with SimPy 3.0.8 framework. Access to the source code is provided by authors upon an e-mail request.

3 SIMULATION RESULTS

In this section we first we describe the setup of the simulation experiment and then we present the results.

3.1 Experiment Setup

The parameter range for the simulation is given in Table 1. The values of parameters: location dimensions, maximum age, number of females, number of honest males, number of dishonest males, $N_{\max}$ are constant for all simulations. These parameters describe only the technical conditions of the simulation and do not affect the results and equilibrium. We set range of the parameter r to [0.0; 4.0] to ensure existence of equilibrium. The strength of the signal must be positive real number; r cannot be lower than 0; $r < 0$ means that increasing signal implies lower costs for all males, so in the equilibrium, signal raised to the infinite level would be the best strategy for all males. The upper bound was arbitrary chosen; a value higher than 4 will result in extinction of the population, because the cost of the signal will be too high to bear for any male. The range for the parameter level of dishonesty is a value in the interval [1.0; 5.0]. When δ is lower than 1, dishonest males will advertise below the honest males level, so there will be no incentive to be dishonest (even if it will increase the likelihood of surviving), because dishonesty will decrease a chance to find a partner. When it is higher than 5, the cost of being dishonest will be too high to bear.

Algorithm 1 Find best partner and reproduce.

$potential\_partners = \{\}$
for all *agent* in nearest environment **do**
  if *agent* is not *female* **then**
    add *agent* to *potential_partners*
  end if
end for
$best\_Assessment = 0$
for *i* in *potential_partners* **do**
  $assessment = \alpha * P(q_i) + (1-\alpha) * \frac{i\_age}{max\_age}$
  if $assessment > best\_Assessment$ **then**
    $best\_Assessment = assessment$
    $father = i$
  end if
end for
if $random\_number < 0.5$ **then**
  new_agent is *female*
  $new\_agent\ q = \sqrt{q_{\text{mother}} * q_{\text{father}}}$
  $new\_agent\ \alpha = \alpha_{\text{mother}}$
else if *father* is *honest* **then**
  new_agent is *honest*
  $new\_agent\ q = \sqrt{q_{\text{mother}} * q_{\text{father}}}$
  $new\_agent\ A(q) = a_0 - r * \ln\left(\frac{\ln(q)}{\ln(q_{\min})}\right)$
  $new\_agent\ P(q) = q_{\min}^{\exp[-(A(q)-a_0)/r]}$
else
  new_agent is *dishonest*
  $new\_agent\ q = \sqrt{q_{\text{mother}} * q_{\text{father}}}$
  $new\_agent\ A(q) = \delta * \left[a_0 - r * \ln\left(\frac{\ln(q)}{\ln(q_{\min})}\right)\right]$
  $new\_agent\ P(q) = q_{\min}^{\exp[-(A(q)-a_0)/r]}$
end if

Table 1: Simulation parameter value range.

parameter	description	values
location dimensions k	dimensions of the area	51
number of females	initial quantity of females	50
number of honest males	initial quantity of honest males	25
number of dishonest males	initial quantity of dishonest males	25
$N_{\max}$	carrying capacity of the environment	500
r	overall strength of the signal	[0.0,4.0]
δ	level of dishonesty	[1.0,5.0]
max age	maximum life span	20

3.2 Results

In total 20908 simulation runs were performed. In every run new value of δ was randomly generated from [1.0; 5.0] range and r was generated from [0.0; 4.0] range. Every run was stopped after 5000 iterations or when the α value for all females becomes a constant, homogeneous number. In our analysis we used linear regression metamodeling approach to ensure simple interpretation of the results. To verify the results we have checked them also by visual plots and generalized additive models and they confirmed them. It allows us to obtain a satisfactory fit to the data and helps us to better understand the relationships between the dependent variables and predictors. The regression results for the average α value are presented in Table 2. *avg_alpha* denotes the mean value of α in the population; r and level of dishonesty are coded as r and *dishonesty*. Table 3 shows the results for the regression of the average value of quality in the population. The predictor variables are again δ and r and they are denoted in the same way as for average value of α; The mean quality is coded as *avg_quality*. The results for the structure of population, percentage of males in overall population are presented in Table 4. The structure of the population is denoted as *male_pct*, predictors are the same as in previous cases. All regressions are computed for the variables in the final iteration, when the equilibrium is reached.

Figure 1 shows the conditional density of dishonest males in the overall males population. For small levels of dishonesty δ (lower than 1.2) the change of the equilibrium can be observed. Dishonesty becomes a new evolutionary stable strategy. This is at odds with the theoretical model presented by Grafen (1990a) and shows that even under his very strong assumptions, which are very often criticized (Getty 2006), we can observe a situation when the costs, relatively higher for worse males, do not guarantee a reliability of the signal. In this situation, for small δ, benefits from cheating surpass the costs of advertising above the true quality level. This solution follows the intuition of Dawkins and Krebs (1978). According to their theory, cheating is widespread among animals and they communicate in order to manipulate and deceive each other. The stability of this communication system is guaranteed by a low level of cheating – checking the honesty of the signaler will be costlier for the receiver than believing in the information. In terms of this model: changing the method of assessing males quality will be costlier for females than allowing males to cheat on some significantly low level.

Another interesting simulation result is unification of females preferences. In every single simulation the average value of α becomes a constant number, the same for all females (see Fig. 2 for an example of a single run of the simulation). This result is in accordance with the Fisherian runaway hypothesis (Fisher 1930). The preferences of the female who achieved the greatest reproductive success spread in the population and become a standard of males assessment for all females. However, the preferences themselves have no influence on the female reproductive success; greater value of α does not help to find better, stronger partner. Even when r rises, it has no impact on the females success and well-being. The relationship between r and average α is very weak (see Table 2). This outcome of the simulation follows the results obtained by Kirkpatrick (1982), who suggests that males traits do not have any correlation with their quality and there is a multiple possible evolutionary equilibria. He shows that any kind of males characteristics could be chosen as the preferred one by females and not necessarily one which represents a disadvantage or cost to males. We can assume that rather the females preferences have an influence on males strategy than the preferences for some traits increase the likelihood of the reproductive success of females. It explains why sexual dimorphism of some species is stronger than that of other species and why even closely related species can differ in their plumage (Owens and Hartley 1998).

Quite interesting is also how the growing strength of the signal influences the average quality of the population (see Table 3). Even if theoretically only males pay cost of the advertising it has a negative effect on the overall fitness. Both, stronger signal and higher level of dishonesty reduce the average quality. So the populations, in which the extravagant traits, conspicuous plumage, etc. are developed, are on average weaker than those in which males are more cryptic and similar to the females. It also means that the cost of the signal is not only associated with males: females also bear the cost of males advertising, because

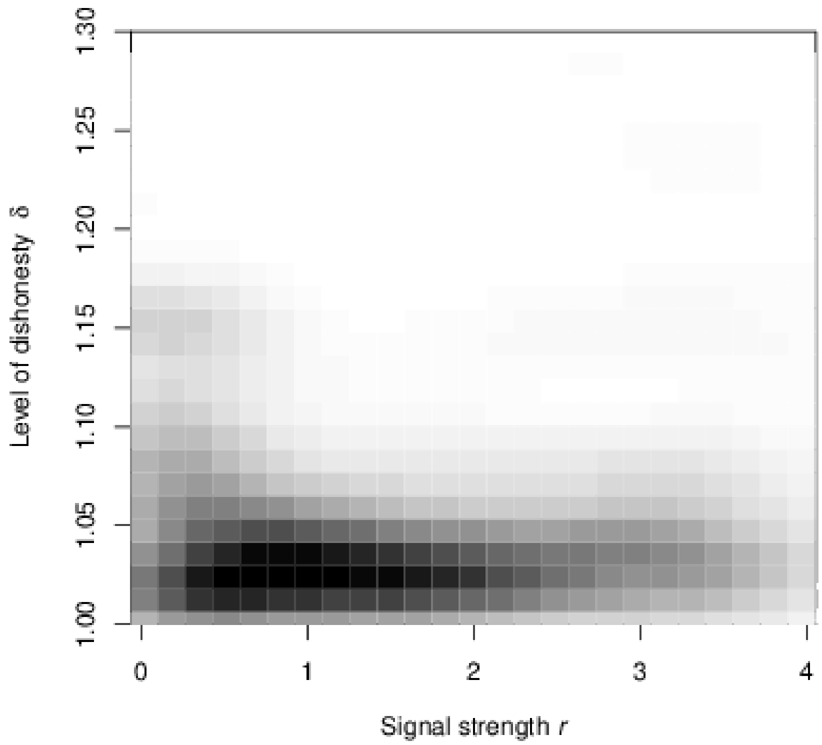

Figure 1: Conditional density of dishonest males in the population. The darker the plot the higher the probability of dishonest equilibrium.

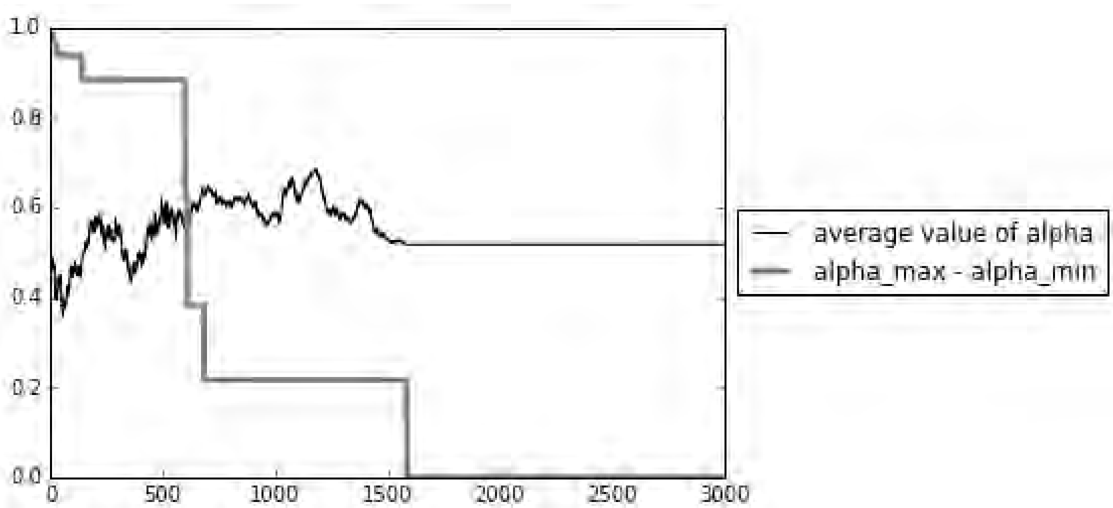

Figure 2: Changes of the value of α during one example simulation (parameters: $\delta = 2$ and $r = 1$).

Table 2: Linear regression of the avg_alpha

	Estimate	Std.Err	t-value	Pr(> $\|t\|$)
(Intercept)	0.529691	0.006530	81.111	0.00000
r	-0.005189	0.001726	-3.006	0.00265
dishonesty	-0.003563	0.001723	-2.067	0.03870
	RSE: 0.2883 on 20905 DF			

Table 3: Linear regression of the avg_quality

	Estimate	Std.Err	t-value	Pr(> $\|t\|$)
(Intercept)	0.7274825	0.0009378	775.70	0.00000
r	-0.0192355	0.0002479	-77.60	0.00000
dishonesty	-0.0046369	0.0002475	-18.73	0.00000
	RSE: 0.0414 on 20905 DF			

Table 4: Linear regression of the male_pct

	Estimate	Std.Err	t-value	Pr(> $\|t\|$)
(Intercept)	0.3502922	0.0016669	210.149	0.00000
r	-0.0719145	0.0004406	-163.238	0.00000
dishonesty	0.0005252	0.0004399	1.194	0.23300
	RSE: 0.07358 on 20905 DF			

the quality and viability of their offspring will be weaker than if the species does not show handicapped signals.

The last obtained results, presented in Table 4, follows the intuition of Grafen (1990a). According to his paper if r is high only the very best males gain many mates, when r is low the average number of mates are much more proportional. He describes r as an effect of the females choice on males fitness (because their fitness depends more on the number of their offspring than on their probability of surviving) and in some way, as a factor of the polygamy in the population. As we can see from the Table 4 polygamy is not only an effect of females' preferences but also a result of natural selection – only few males can survive when the extravagant traits are strongly developed in the population, because the costs of them are so high and many males cannot bear it and die.

4 DISCUSSION

Obtained results show that even under very strong assumptions there exist some equilibria in which the cost of the signal do not guarantee its reliability. In some cases, when the signal is unreliable, but only slightly higher than its credible counterpart, it is better to bluff, because the growth of the costs of the signal is lower than gains from cheating. It will still be a stable communication system; the cost of changing the method of assessment will be higher than cost of males dishonesty; for females it is better to turn a blind eye to males cheating. The agent-based model also shows that the correlation between females reproductive success and preferences for the signal is very weak, so we cannot state that the wasteful and extravagant traits are the best method of assessment of males true, unobservable quality. There exists an infinite number of equilibria, in which the role of the advertising can vary and it strength is a result of some random events. The best description of this process is the Fisherian runaway. It shows the great strength of the concept proposed by Fisher, even after a century of the development of evolutionary biology. After the introduction of many others, more sophisticated theories his idea still can be used to explain some mechanisms lying behind the sexual selection. Moreover, results of this simulation somehow explain why animal species are so strongly differentiated in their mating habits and courtship displays.

Sexual selection is a very sophisticated phenomenon, it cannot be explained by only one theory; it is rather a result of various independently working processes. For different animal species the intensity of these mechanisms may be different, so every case, every communication system should be investigated separately, because only then the most appropriate answers can be found.

However, this agent-based model has limitations; generalized conclusions should be drawn carefully. There is no genetics; the process of inheriting the traits from the parents is very simplified. We also assume that all random variables are uniformly distributed. It is a strong assumption; the actual distribution of the traits in the existing animal populations may be different. The mechanism of assessment of males is another thing that can be changed. We use only two traits: the signal and the age of male, which can be change to any other male's characteristic correlated with quality, but not directly revealing it, like for example, number of offspring. Of course, this mechanism can be more sophisticated, it can use more than two variables, assessment function can take different form etc. Also introducing costs of having offspring or more complex reproduction strategy can change the behavior of females and the results of the model. For example, when females are maximizing the overall quality of their progeny, which means that they will rather choose to have less but stronger offspring, they will be much pickier and it will probably change the model's output. Another simplification of model is assumption that all males use the same strategy. When r and δ will be random variables the equilibrium will change (Johnstone and Grafen 1993), but it will allow us to analyze the influence of females preferences on males strategy.

Even if the handicap principle is still very controversial and a widely disputed theory for biologist it gains some popularity in social sciences, mainly because of it economic heritage (Hammerstein and Hagen 2002), (Getty 2006). The handicap principle is often used to describe some unusual or irrational human behavior, for example, see Bliege Bird, Smith, and Bird (2001), Bliege Bird and Smith (2005), Hawkes and Bliege Bird (2002). Particular applications are Veblen's concept of conspicuous consumption (Bliege Bird, Smith, and Bird 2001), the evolution of music and other arts (Miller 2000), human mating mechanism (Griskevicius et al. 2007), customers behavior (Griskevicius, Tybur, and Van den Bergh 2010) or the participation of young men in risky and violent competitive interactions (Wilson and Daly 1985). However, several doubts on its correctness and usefulness arouse concerns about the possibility of implementation of this theory into different fields. Handicap principle can be considered as a very strong and great looking metaphor of the information exchange systems. But maybe alternative signaling models and theories are better explanation of biological, social and economic phenomena (for example, see Zollman (2013), Scott-Phillips (2008)).

5 CONCLUDING REMARKS

We presented an agent-based model based on the ESS model of handicap principle. It extends the standard model proposed by Grafen (1990a) by introduction of second strategy for males – being dishonest and by implementing a more complex assessment of males' quality, based not only on the strength of the produced signal, but also on his other traits that are correlated with the quality.

We showed that stronger advertising reduces the overall welfare of the population. The cost of the signal concerns not only males, but also females. Increasing the signal decreases the viability of male, which reduces the quality of his offspring.

We discovered that the female preferences for male traits have no influence on her reproductive success, even if the advertising level shows the true, unobservable quality of the male. It shows that there are multiple possible evolutionary equilibria in which the role of the males signal can vary. This model's outcome follows the results obtained by Kirkpatrick (1982). However, after many generations, taste of the female who achieve the greatest reproductive success spread in the population and the preferences become homogeneous. It can be explained by the Fisherian runaway process (Fisher 1930).

Most importantly we found out that in some specific situations the cost of the signal and conditions proposed by Grafen do not guarantee the stability of the equilibrium. When the level of cheating is very low, it is better to be dishonest, because the gains from bluffing exceed the additional costs of increasing the signal above the level corresponding to the true quality. In this situation Dawkins and Krebs (1978) hypothesis is a better explanation why the communication system is stable – for females the cost of changing the assessment method would be higher than losses from the males unreliable advertising.

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