Vinicius Montagner

Interação entre seleção sexual pré- e pós-copulatória e sua influência sobre a evolução de táticas alternativas de acasalamento

Interaction between pre- and post-copulatory sexual selection and its influence on the evolution of alternative reproductive tactics

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de título de Mestre em Ecologia, na área de Ecologia: Ecossistemas Terrestres e Aquáticos.

Orientador: Danilo Germano Muniz da Silva

Programa de Pós-Graduação em Ecologia, Universidade de São Paulo, Brasil

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Nome: MONTAGNER, Vinicius

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Dr. Danilo Germano Muniz da Silva

(Orientador)

For such a model there is no need to ask the question "Is the model true?". If "truth" is to be the "whole truth" the answer must be "No". The only question of interest is "Is the model illuminating and useful?"

George E. P. Box

On "Robustness in the Strategy of Scientific Model Building", 1979

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Resumo

As táticas alternativas de acasalamento (TAAs) nos machos geralmente são condicionais (fenotipicamente plásticas): machos em boas condições corporais tornam-se guardiões agressivos, enquanto aqueles em más condições corporais tornam-se furtivos não-agressivos. Cada macho possui um *switchpoint* genético que determina a condição corporal acima da qual um indivíduo se desenvolve como guardião. A seleção sexual pré e pós-copulatória opera de maneira diferente em cada tática de acasalamento e, portanto, influencia a evolução do *switchpoint*. Além disso, pode haver uma correlação entre a promiscuidade dos machos e a das fêmeas com as quais copulam (isto é, 'correlação de promiscuidade'), criando uma interação entre os processos pré e pós-copulatório. Utilizamos modelos baseados em indivíduo para investigar como a interação entre a seleção sexual pré e pós-copulatória influencia a evolução das TAAs condicionais. Os resultados de nossas simulações mostram que a variação do *switchpoint* é mantida consistentemente alta ao longo das gerações, o que não é esperado em cenários com forte seleção sexual. Fornecemos previsões adicionais para o modelo *environmental threshold*, e nossas previsões podem ser testadas experimentalmente ou em um contexto comparativo para espécies com TAAs condicionais. A correlação de promiscuidade influencia a oportunidade de seleção sexual e intensidade de competição espermática enfrentada pelos guardiões, mas teve pouca influência na própria evolução do *switchpoint*.

Palavras-chave: modelo individual, dimorfismo intrassexual, sistemas de acasalamento, modelagem, correlação de promiscuidade, competição espermática.

Abstract

Male alternative reproductive tactics (ARTs) are usually conditional (phenotypically plastic): males in good body condition become aggressive guards, while those in poor body condition become non-aggressive sneakers. Each male carries a genetic switchpoint that determines the body condition above which an individual develops into a guard. Pre- and post-copulatory sexual selection operates differently on each mating tactic and thus influences switchpoint evolution. Additionally, there can be a correlation between the promiscuity of males and that of the females with which they copulate (i.e., 'promiscuity correlation'), creating an interaction between pre- and post-copulatory processes. We used individual-based models to investigate how the interaction between pre- and post-copulatory sexual selection influences the evolution of conditional ARTs. The results of our simulations show that switchpoint variation is kept consistently high through generations, which is not expected in scenarios with strong sexual selection. We provide additional predictions for the *environmental threshold model,* and our predictions can be tested experimentally or in a comparative context for species with conditional ARTs. The promiscuity correlation influences the opportunity for sexual selection and sperm competition intensity faced by guards, but it had little influence on switchpoint evolution itself.

Keywords: individual-based model, intrasexual dimorphism, mating systems, modeling, promiscuity correlation, sperm competition.

CONTENT

1. INTRODUCTION

Alternative Reproductive Tactics (ARTs) occur when, within a population, individuals from the same sex have two or more strategies for obtaining copulations (Gross, 1996). ARTs are more common among males and occur in a varied number of invertebrates and vertebrates species (see examples in Oliveira et al., 2008). Commonly, males can adopt one of two strategies: (1) guards, which aggressively monopolize access to individual females, harems, or reproductive territories; and (2) sneakers, which invade territories or harems and copulate furtively with the females (e.g., insects: Buzatto et al., 2014; fish: Taborsky, 2008; amphibians: Zamudio & Chan, 2008). Given the stark differences between guards and sneakers in their mating tactics, males from each tactic are under different sexual selection pressures, in both the pre and post-copulatory sexual selection episodes (Eberhard, 2009; Birkhead & Pizzari, 2002). Pre-copulatory sexual selection favors the capacity of copulating with many females, while post-copulatory sexual selection favors the capacity to fertilize many eggs, once the male was able to copulate (Eberhard, 2009; Birkhead & Pizzari, 2002).

In the pre-copulatory sexual selection episode, guards engage in contests for territories or females with other guards, while sneaker males only need to locate females and approach them (Parker, 1998). That is, guards engane in contest competition amongst themselves, while sneakers engage in scramble competition (*sensu* Andersson 1994). Additionally, females may prefer to copulate with guards than sneakers, indirectly increasing sexual selection among males via female preference (Alonzo, 2008). After copulation, guards only face sperm competition if his territory or harem is invaded by sneakers. Sneakers, however, almost always face sperm competition, since their mating tactic consists in searching females paired with guards (Parker, 1990). Thus, both the risk and the intensity of sperm competition are usually higher for sneakers than for guards (e.g., Simmons, 2001). So, the evolution of male ARTs should be influenced by what happens both before and after the copulation, but what happens when these episodes of selection are not

so separate? What if there is a correlation between sexual selection operating pre and post-copula?

Pre and post-copulatory sexual selection can be correlated when there is a *promiscuity correlation:* a correlation between a male's mating success (promiscuity) and the promiscuity of the females with which he mates (Mcdonald & Pizzari, 2016). Both positive and negative values of promiscuity correlation have been observed in natural populations (examples in McDonald & Pizzari, 2018). And the presence of such correlation is expected to influence the intensity of sexual selection (McDonald & Pizzari 2018). In a population with alternative mating tactics, positive promiscuity correlation means that highly successful (promiscuous) guards (i.e., those who have large harems) mate with highly promiscuous females (i.e., females that mate with various sneakers). The consequence of this positive correlation is that the most successful guards face stronger competition in the post-copulatory episode, which can decrease the benefit of being highly successful in the pre-copulatory selection episode. On the other hand, a negative promiscuity correlation value means that highly successful guards mate with females of low promiscuity (that mate with few or no sneakers). In this scenario, guards who are the most successful in the pre-copulatory episode will face weaker competition in the post-copulatory episode, and thus these males are doubly favored. Therefore, a negative promiscuity correlation is expected to increase variation in reproductive success among guards, which should intensify sexual selection in guards (Mcdonald & Pizzari, 2016), and perhaps create more opportunities for sneakers (Shuster & Wade, 2003). However, it is not clear how the promiscuity correlation could influence the reproductive success of sneakers, and thus it is difficult to predict how promiscuity correlation should influence the evolution of alternative mating tactics of males.

The adoption of the guard or sneaker tactic is frequently phenotypically plastic, *i.e.*, it is determined by a conditional strategy (Gross, 1996). The main model used to explain the evolution and maintenance of alternative mating tactics is the Environmental Threshold Model (ET model), a quantitative genetics model elaborated by Hazel et al. (1990). The ET model postulates that an individual's

mating tactic is determined by an interaction between an environmental cue and an internal (genetically heritable) switchpoint. The switchpoint, determines the point of the environmental cue above which an individual male becomes a guard, rather than a sneaker. The internal switchpoint is expected to vary within populations, so that even if exposed to equal environmental conditions, different individuals can express different tactics (Fig 1a). The environmental cue is usually an individual's body condition, the amount of accumulated energy reserves, so that males in better body condition at reproductive maturation become guards, while individuals in poor body condition become sneakers (Gross, 1996). From the population's perspective, the switchpoint and environmental cue distributions determine the proportion of each tactic in the population and the relationship between the environmental cue and the mating tactics (Fig. 1b). The ET model predicts the switchpoint to be under stabilizing selection, so that over time, understable environmental conditions, switchpoint variation will decrease and its mean will stabilize at an optimum value (causing most individuals to assume the best reproductive tactic given its environmental cue, Tomkins & Hazel, 2007).
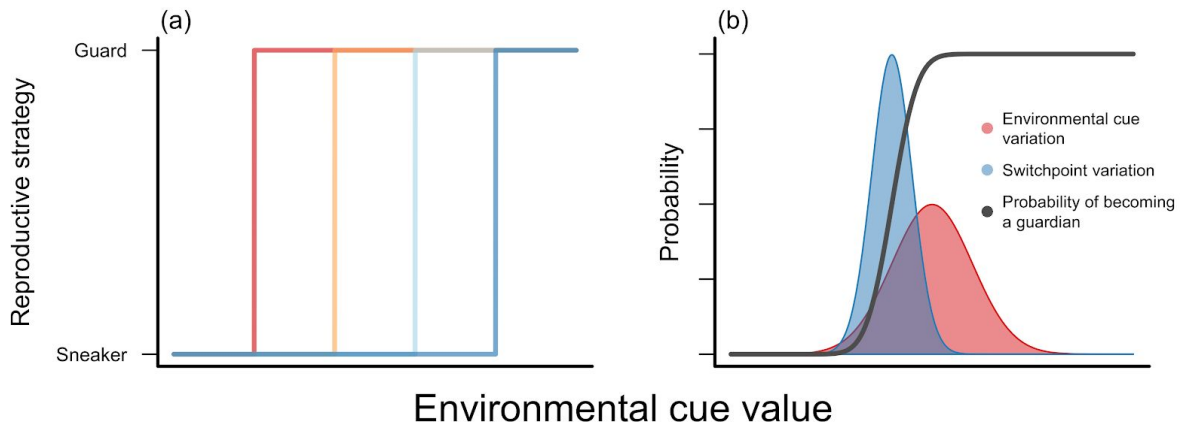
Figure 1. Graphical explanation of the Environmental Threshold (ET) model. In **(a)** we present the perspective of individuals: each line (and each color) represents the reaction norm of an individual male, which adopts the guard reproductive strategy if it is exposed to an environmental cue higher than its internal switchpoint. In **(b)** we present a population perspective, the shaded area in red represents the distribution of the environmental cue, while the shaded area in blue represents the distribution of switchpoint values. In this particular population, the switchpoint has a lower mean and less variation than the environmental cue. The thick black line represents the probability that an individual exposed to a given environmental cue value becomes a guard in this population. Notice that individuals exposed to very low environmental cue values are never guards: no individual in this population has such a low switchpoint value. Individuals exposed to environmental cue values close to the mean switchpoint have a moderate probability of becoming guards; while individuals exposed to very high values of the environmental cue always become guards: no individual in this population has such a high switchpoint.

The ET model has been highly successful in explaining the occurrence of ARTs in a wide variety of species, and one of its key predictions is that there can be among-population variation in mean switchpoint values. Yet, there are few specific predictions about what should influence a population's mean switchpoint as well as its within-population variation. Additionally, the ET model does not incorporate the possibility of correlation between pre and post-copulatory sexual selection, in other words, it assumes a promiscuity correlation of zero. Here, our general objective is to fill these gaps. We conducted a theoretical investigation of how pre- and post-copulatory sexual selection, as well the interaction between these two processes, influence the evolution of conditional alternative male mating tactics. Thus, we built upon the classic Environmental Threshold model ("ET model", Hazel et al., 1990, 2004; Tomkins & Hazel, 2007) to investigate how promiscuity correlation influences the mean and variation of the internal switchpoint in populations in which males can be guards or sneakers.. To do so, we used an individual-based model (IBM) approach. These computational models allow the simulation of populations

formed by explicitly separate individuals, which may vary among themselves and interact with each other and their environment. Thereby, IBMs are a powerful tool for theory development in behavioral and evolutionary ecology because they allow theoretical models to incorporate complex individual behaviors, variability among individuals, and eco-evolutionary feedback (DeAngelis & Mooij, 2005; Grimm & Railsback, 2005).
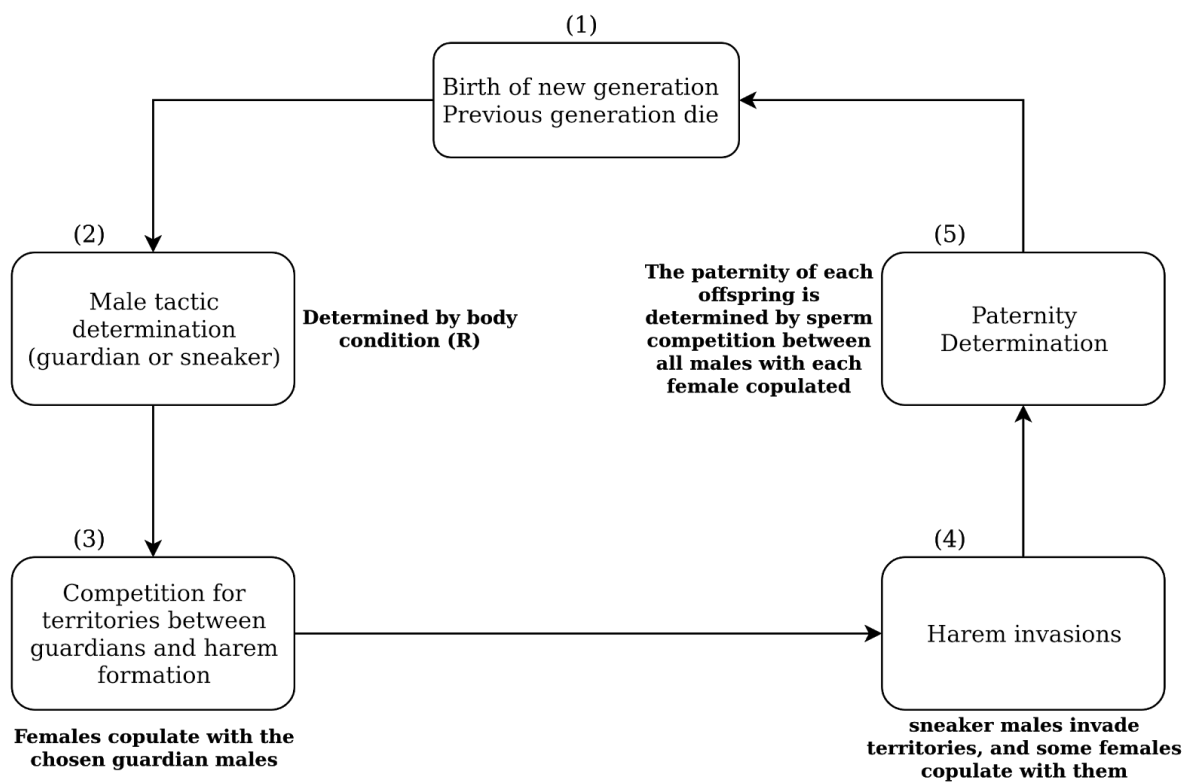
2. METHODS

2.1 Model overview

Our model simulates a sexual population with a mating system of defense polygyny with alternative mating tactics: males can be either guards or sneakers. Moreover, our model is based upon the Environmental Threshold model of alternative mating tactics, so that the tactic (or morph) adopted by each male within the simulation is determined by an interaction between genetic and environmental factors (i.e., internal switchpoint and body condition, see details below). Guards engage in contests for the ownership of a resource that allows them to have access to females. We will refer to this resource as territory, but the model is applicable to any species in which contest success grants a male more copulations. Guards without territories do not have access to females. Sneakers do not engage in contests, instead they invade territories to mate furtively with the females, and thus are always engaged in sperm competition.

The life cycle within the model can be summarized as follows (Fig. 1): (1) *birth*: individuals of the new generation are born and all adults from the previous generation die; (2) *male tactic determination*: males reach sexual maturity and their mating tactic is determined by an interaction between switchpoint and body condition; (3) *competition for territories and harem formation*: guards compete for territories, and females choose in which territory they will settle and copulate with the owner guard. Competition for territories and female attraction are influenced by guards' body condition; (4) *harem invasions*: sneaker invade territories, and some females copulate with them; (5) *paternity determination*: the paternity of each offspring is determined by sperm competition between all males with which each female copulated. Each simulation represents 400 generations of a population with 2000 individuals, with a 1:1 sex ratio, and discrete generations.

We explored the parameter space using the Latin hypercube sampling technique, which is a highly efficient method of exploring the parameter space of a model, and is especially recommended for models with many parameters (McKay et al*.,* 1979; Chalom & Prado, 2012, details below).

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                                    (1)
                        ┌─────────────────────────┐
                        │  Birth of new generation │
                        │  Previous generation die │
                        └─────────────────────────┘
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Figure 2 - Life cycle within the model of alternative mating tactics evolution. After individuals are born, the mating tactic of each male is determined by an interaction between its genes (Y) and its environment (R). Then, guards compete for females and, afterwards, sneakers invade the guards' harems to mate furtively. Finally, after sperm competition, the paternity of the offspring is determined. After the birth of the new generation, all adult individuals die.

2.2 Male tactic determination

Males are characterized by two traits: a heritable switchpoint x and a non-heritable value of body condition R (after the word *Resource*). These two traits interact to determine the male's mating tactic (or morph). The body condition R represents the amount of resources an individual was able to accumulate before sexual maturation and, for simplicity, we assume it to be totally non-heritable. Thus, the value of R of each individual male encapsulates all ecological factors that could influence the his development and energy accumulation. The switchpoint Y determines the value of body condition R above which an individual will develop into a guard. The value of Y varies among individuals within the simulated populations and, since it is heritable, it can evolve. Thus, a male mating tactic is determined by an interaction between a genetic factor (the switchpoint Y) and an environmental factor (the body condition R).

In the first generation of each replicate simulation, each individual receives a random switchpoint value taken from a normal distribution with mean 5 and standard deviation 1. In the following generations, each individual inherits its switchpoint from its parents (details below). Similarly, at each generation, each male receives a random value of body condition R from a normal distribution with mean 5 and standard deviation R_{SD}. When a male reaches sexual maturity, if his R value is above its Y value, he becomes a guard, otherwise, he becomes a sneaker.

2.3 Competition for territories and harem formation

Guards compete for territory ownership, and the guards' body condition R determines both its probability of owning a territory and his attractiveness to females. Each simulation has a limited number of territories T, so that if a population has more guards than territories, some guards will not own a territory (and thus will be excluded from the mating pool). Since guards vary in attractiveness, the number of females per harem may also vary. We do not explicitly simulate one-on-one male contests, rather, we consider that males with higher body condition (R) values possess higher Resource Holding Potential (RHP, Parker, 1974) and thus a higher probability of owning a territory. To produce this effect, in each generation, for each territory, we draw a guard randomly to be its owner, but the probability of being drawn is proportional to his R value. Each guard can be draw only once (sampling without replacement). The probability of a guard i being drawn as owner of a territory j is given by:

$$P_{ij} = \frac{R_i^{S_G}}{\sum_{k=1}^{G} R_k^{S_G}} \qquad \text{(equation 1)}$$

where R_i represents the body condition of guard i, G represents the total number of guards in the population, and S_G is a parameter that determines the intensity of pre-copulatory sexual selection among guards. The higher the parameter S_G value, the more important is the guard's body condition during competition for territories

(Fig. 2a). When S_G equals zero, the probability of owning a harem is independent of a guard's body condition.

After territory ownership is determined, females are distributed among guards that own a territory. To do this, for each female, a guard that owns a territory is drawn randomly to be her mate, and the female joins his harem. Again, the probability of a guard being drawn is proportional to his R value. Each guard can be draw more than once (sampling with reposition). Thus, the probability of drawing a guard i for a female j is determined by the following equation:

$$P_{ij} = \frac{R_i^{S_G}}{\sum_{k=1}^{G} R_k^{S_G}} \quad \textbf{(equation 2)}$$

The parameters of the harem formation equation have the same meaning as the territory ownership equation (equation 1). So, when $S_G > 0$, guards with high body condition have a greater probability of acquiring a territory and of attracting more females, causing S_G to have a double effect in guards reproductive success. This simulates scenarios where the strongest guards (with higher RHP) are more attractive to females and/or can secure higher quality territories, which are more attractive for females (i.e., indirect mate choice *sensu* Wiley & Poston, 1996).

2.4 Harem invasion

After harem formation, the sneakers try to perform sneak copulations. This is a process with two steps: (1) finding a female and (2) attempting to copulate with her. In the first step, the sneaker finds a female randomly in the population: all females are equally likely to be found by a sneaker at this step. The sneaker's body condition determines the number of copulation attempts N_S, he can perform, as in the following equation:

$$N_S = C \cdot \left[1 + S_S \cdot \left(\frac{R_j - R_{mean}}{R_{mean}} \right) \right]$$ **(equation 3)**

In this equation, *C* is the number of copulation attempts that a sneaker has when his body condition (R_j) is equal to the population mean body condition (R_{mean}), and S_S is a parameter that determines the intensity of pre-copulatory sexual selection among sneakers (i.e., males' ability to find receptive females). High *C* values mean that the population has sneakers with a high average copulation number, which leads to increased sperm competition for the guards. The higher the S_S value, more important body condition is in determining the sneakers' ability to find females (Fig 2b). Thus, high S_S values increase the variation in the number of copulation attempts among sneakers (Fig. 2b). When S_S equals zero the sneaker's body condition does not affect the number of copulation attempts, and all sneakers have the same number of copulation attempts.

The next step in the sneaker copulation process is to determine if the attempt is successful. The probability of success is determined by the number of females in the harem where the sneaker is attempting a copulation. The probability Q_{ij} that a sneaker *i* will successfully copulate with a female *j* is given by the equation:

$$Q_{ij} = \frac{1}{1 + exp\left(-p \cdot s(H_j) \right)}$$ **(equation 4)**

where H_j is the number of females in female's *j* harem (i.e., harem size), and the parameter *p* determines the population promiscuity correlation. When *p* = 0, the promiscuity correlation is zero, so that the sneakers probability of success is independent of harem size. Thus, from the perspective of guards, *p* = 0 means that the intensity of sperm competition they face is independent of harem size. When *p* is negative, sneakers are more likely to copulate with females in small harems, so guards with high mating success face less intense sperm competition (negative

promiscuity correlation). Finally, when *p* is positive, the probability of sneaker success is higher when the female is in a large harem, so guards with high mating success face more intense sperm competition (positive promiscuity correlation, Fig. 2c). The function *s(H$_i$)* is a transformation in which *H* values are ranked and then standardized to mean zero and standard deviation one. This transformation is just a way to ensure that mean sneaker success is independent of the parameter *p* (see Supplemental Material for details). Indeed, across all simulations, we kept mean sneaker success at 50%, and modulated the intensity of sperm competition by varying the *C* parameter.

2.5 Sperm competition and paternity determination

After all copulations occur, there is fertilization of the females' eggs and offspring paternity determination. Population size and sex ratio are maintained fixed through generations, so at each new generation 1,000 males and 1,000 females are born. For each next generation offspring born, a female is picked randomly from the current population to be its mother. This is equivalent to each female generating a high number of offspring, but only 1,000 males and 1,000 females surviving to reproduce in the next generation. If the female picked as mother has only copulated with the guard from her harem, then the guard is the father of the offspring. If the female also copulated with sneakers, there is sperm competition. Each additional sneaker copulation with the female increases the sperm competition intensity, reducing the guard's chance of siring the offspring (paternity probability decreases with sperm competition). The paternity probabilities of the guard (P_G) and each of the sneakers (P_S) who copulate with the female are:

$$P_G = \frac{L}{L + N_{sneakers}} \quad \textbf{(equation 5)}$$

$$P_S = \frac{1}{L + N_{sneakers}} \quad \textbf{(equation 6)}$$

where $N_{sneakers}$ is the number of sneakers that mated with that female and L represents the advantage that the guard has in sperm competition. Thus, when $L = 1$, there is no advantage in sperm competition between morphs, and fertilization is a fair raffle. However, then L is different from one, the fertilization process is a loaded raffle. When L is less than 1, guards have a disadvantage in sperm competition against sneakers, and when L is greater than 1, guards have an advantage — higher values of L increase this advantage (Fig. 2d). We explored scenarios where sneakers have advantage against guards (Fig. 2d, curve 0.5), but in most scenarios, guards will have advantage against sneakers, because it seems to be the most likely scenario under natural conditions (Simmons, 2001).
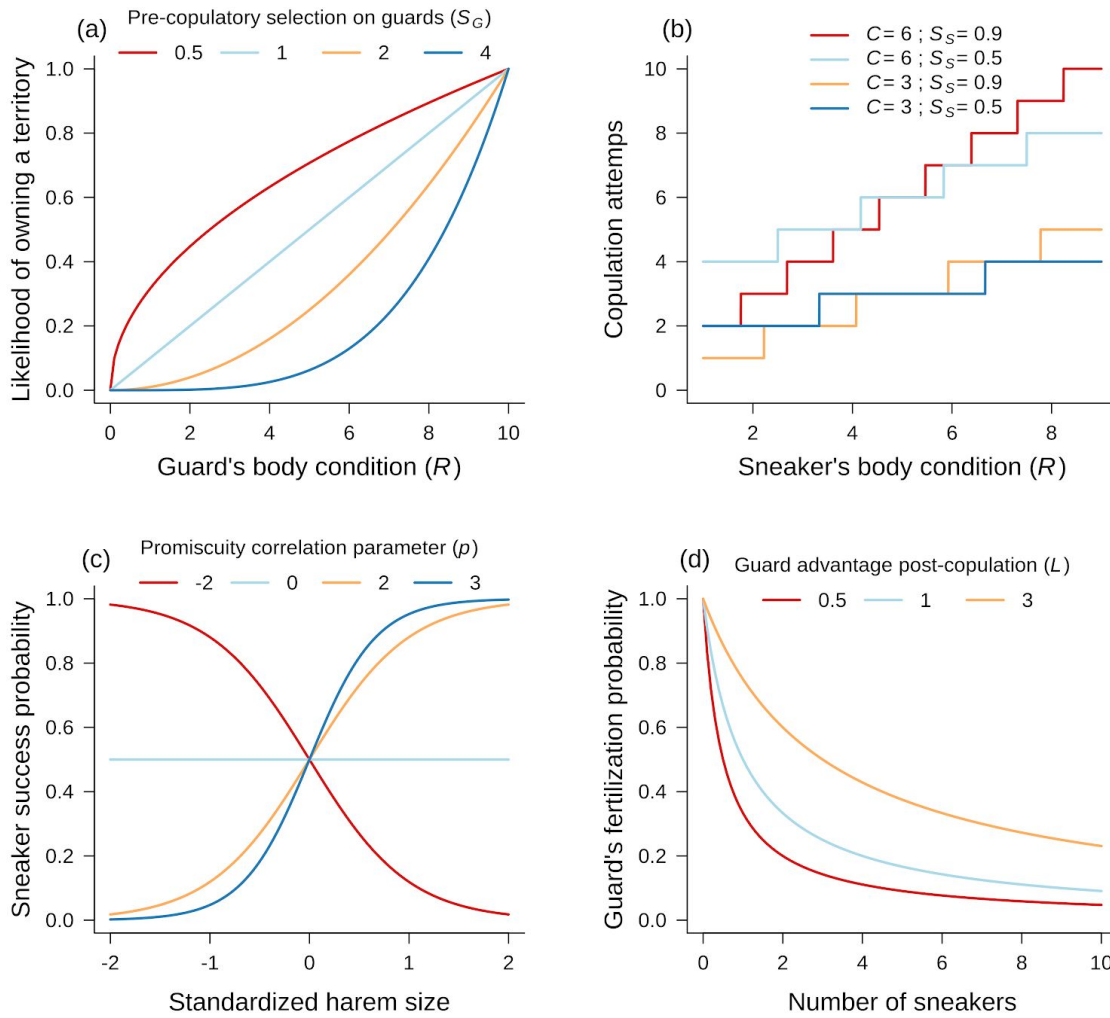
Figure 3 - Values of the parameters we used in different steps of the life cycle in our IBM. *(a) Likelihood of a guard owning a territory/attracting females*: the competition intensity among guards (S_G) determines how important is the guard's body condition (R) in increasing his likelihood of owning a territory, and, after that, of attracting females. *(b) Sneaker's copulation attempts*: the number of copulation attempts by a sneaker is determined by the interaction between two parameters: C, the number of attempts of an individual with body condition equal to the population average, and S_S, the intensity of pre-copulatory sexual selection on sneakers. **(c)** *Probability of sneaker copulation success:* the promiscuity correlation parameter determines the relationship between harem size and the probability of success in a sneaker copulation attempt. Positive values of promiscuity correlation lead to a greater success when sneakers try to copulate with females from large harems, and lower success in small harems. The opposite pattern occurs when the promiscuity correlation is negative. **(d)** *Guard's fertilization probability*: a guard's fertilization probability decreases as the number of competing sneakers increases, and this effect is modulated by the parameter L, which determines the advantage of guards in the sperm competition process (when $L = 1$, fertilization is a fair raffle, whereas then $L > 1$, it is a loaded raffle in favor of the owner guard).

Finally, the next generation of individuals is born, and all the individuals of the current generation die (Fig. 2). As the switchpoint value is inherited, the switchpoint of a new individual *i*, born from parents *j* and *k* is determined as:

$$Y_i = \frac{(Y_j + Y_k)}{2} + \varepsilon$$

(equation 7)

in which ε is the segregation variance, which is sampled from a normal distribution with mean 0 and standard deviation 1. This is a simplified way to model the inheritance and evolution of continuous traits that are influenced by a large number of small effect loci with additive effects (Barton et al. 2017).

2.6 Parameter space exploration and analyses

In order to generate predictions from the model, we explored the parameter space using the method of Latin Hypercube Sampling (LHS, McKay et al., 1979; Chalom & Prado, 2012), which generates a sample of parameter values from a multidimensional distribution once a range of values is determined for each parameter of interest (Table 1). The simplest example of an LHS is a Latin square, in which there are only two dimensions (parameters) to sample (Fig. 4). In this squared plane, each point represents a unique combination of parameter values. After a range is set for each parameter, the square is divided in rows and columns, from which samples can be taken (Fig. 4). The method of sampling can be called Latin if, and only if, there is exactly one sample in each row and each column (Chalom & Prado, 2012). The Latin hypercube extends this Latin square concept for an arbitrary number of dimensions and allows each input parameter to have all portions of the distribution value represented, ensuring a fully stratified representation for each parameter (McKay et al., 1979). Each parameter has to be divided by the number of samples chosen *a priori* and has to be linked to a distribution probability. We established the distribution of all parameters as uniform (minimum and maximum values are in Table 1) and took 3,000 samples from the hypercube, so that we ran 3,000 replicate simulations, each with a unique combination of parameter values. In this way, we could efficiently explore a wide range of parameter space.

Figure 4 - A Latin square, the two-dimensional version of a Latin hypercube with two hypothetical parameters (A and B). Each "X" represents a combination of parameter values sampled from this parameter space. Note that each row and each column is only sampled once.

After running all simulations, we quantified the influence of the model parameters on the model output variables using partial rank correlation coefficients (PRCC). The PRCC is a robust form of measuring the intensity of monotonic relationships between continuous variables that does not make *a priori* assumptions about data distribution (Marino et al., 2008). Also, the PRCC is easily interpretable, since it is a standardized measure of effect size that varies between -1 and 1. The PRCC is recommended for use in theoretical models, especially when Latin hypercube sampling is used (Marino et al., 2008, Chalom & Padro, 2012). Therefore, for all output (response) variables of the model, we calculated PRCC scores for all the following model parameters: p, S_G, T, S_S, L, C, and R_{SD} (Table 1). We performed this analysis using the package *sensitivity* (loss et al., 2019) in the software R (R Core Team, 2019).

Table 1 - Description of the symbols and the respective parameters space values used in the simulations.

Parameter name	Description	Parameter space values
Sex ratio	Population proportion between males and females	1:1
N	Population size	2000
p	Promiscuity correlation value	-3 to 3
S_G	Intensity of pre-copulatory sexual selection on guards	0 to 5
T	Number of territories for which guards compete for	100 to 800
S_S	Intensity of pre-copulatory sexual selection on sneakers	0 to 1
L	Advantage the owner guard has over sneakers in determining paternity	⅕ to 5
C	Number of copulation attempts that a sneaker presents when his body condition is equal to the population average body condition	0.5 to 8
R_{SD}	Standard deviation of male body condition	0.25 to 3
$\overline{R}$	Mean male body condition	5
Y_{SD}	Initial standard deviation of the switchpoint	1
$\overline{Y}$	Initial mean switchpoint	5

2.7 Response variables

We measured all output variables described below at the end of the 400th generation of each simulated population. In preliminary tests, the model's output variables were already stable after 300 generations, therefore measurements taken after 400 generations properly describe the population patterns after evolutionary stabilization (see Supplemental Material, Figure S6).

2.7.1 Switchpoint evolution

We measured the proportion of sneakers, the mean switchpoint value, and switchpoint variation (standard deviation) of all simulated populations. These three variables were used to verify how the evolution of the switchpoint occurred in the simulations.

2.7.2 Measurements of sexual selection and sperm competition intensity

We used three main measures of sexual selection: (1) the potential for sexual selection I_S; (2) the mean sperm competition intensity on guards (mean *SCI*); and (3) the promiscuity correlation (*SCIC*) of guards, which is a measure of the correlation between pre- and post-copulatory sexual selection events (it is an operational measure of promiscuity correlation).

The potential for sexual selection, I_S, is a measure of variation in the male reproductive success (Wade, 1979; Shuster & Wade, 2003), which is calculated as:

$$I_s = \frac{\sum_{j=1}^{N}(w_j - w')^2}{N} \cdot \frac{1}{(w')^2}$$ **(equation 8)**

In this formula, *N* is the number of males included in the calculation (in this case, all males in the population), w_j represents the reproductive success of each male *j*, and *w'* represents the mean male reproductive success. High values of I_S represent high variation in male reproductive success, so that a few males are highly successful while many males are not successful in acquiring fertilizations. Thus, in our simulations, we consider that high I_S values characterize populations with stronger sexual selection. In our simulations, the expected value for I_S under no sexual

selection (random distribution of reproductive success) is 0.5 (see Supplemental Material for details).

The sperm competition intensity, *SCI,* is a metric that is calculated from the point of view of a single male, and it represents the inverse of the expected paternity share of that male with the females with which he mated (Mcdonald & Pizzari, 2016). For instance, a *SCI* of 1 represents no sperm competition, since the expected paternity is 100% (the inverse of 1 is 1). In turn, a *SCI* of 5 represents intense sperm competition, since the male is expected to sire only 20% (1/5) of the offspring from the females with which he copulated. Thus, to characterize the overall sperm competition intensity on guards, we calculated the mean *SCI* of all guards in each simulated population. The sperm competition intensity faced by guard *j*, *SCI_j*, is calculated as:

$$SCI_j = \left(\sum_{i=1}^{n_j} \frac{1}{m_i} \right)^{-1}$$
(equation 9)

In this formula, n_j is the number of females with which guard *j* has mated (his promiscuity), while m_i is the number of matings by each female *i* (their promiscuity). Finally, we measured the Sperm Competition Intensity Correlation (*SCIC*, Mcdonald & Pizzari, 2016) among the guards of the population. The *SCIC* is calculated as the Pearson correlation coefficient between the mating success and the *SCI* of the guards.

As additional measures of sexual selection, we measured the variation in guards reproductive success using the standard deviation in the offspring number among guards. We also recorded the standard deviation in the reproductive success of guards that owned a territory. Finally, we measured the proportion of guards that owned territory but did not get females in their harem, and the proportion of guards that owned territory but did not sire offspring. These measures were taken because selection can only occur if there is variation in reproductive success within a population (Wade, 1979), and because, particularly for sexual selection among males, a large proportion of this variation is generated by the presence of males with

no reproductive success (Shuster & Wade, 2003). Therefore, these additional measures allow us to understand in greater detail how sexual selection affects guards at each stage of the reproductive process.

3. RESULTS

3.1 Switchpoint evolution and sneaker proportion

The mean switchpoint ranged from -2.58 to 9.30 (mean$\pm$SD = 3.17$\pm$2.19), which resulted in a variation in the proportion of sneakers in the simulated populations from 0 to 0.94 (mean$\pm$SD = 0.27$\pm$0.25). The parameters that most influenced the mean switchpoint were the pre-copulatory selection on guards (S_G), number of copulation attempts by the sneakers (C), post-copulatory advantage of the guards (L), and standard deviation of body condition (R_{SD}). The mean switchpoint was strongly positively correlated with S_G, C, and R_{SD} (all PRCC > 0.68), and it was negatively correlated with L (PRCC = -0.72). Consequently, these parameters were also those that most influenced the proportion of sneakers. The proportion of sneakers was strongly positively correlated with S_G, C, and R_{SD} (all PRCC > 0.7), and it was negatively correlated with L (PRCC = -0.712). The PRCC values for the effect of all input parameters on all output variables are presented in Table 2.

Table 2 - Summary of the quantitative analysis of the effect of input parameters on the output variables of the model of alternative mating tactics evolution. The effect size of each input parameter was quantified as the Partial Rank Correlation Coefficients (PRCC). The symbols are: p is the promiscuity correlation; S_G is the pre-copulatory selection on guards; T is the number of territories available for guards; S_S is the intensity of pre-copulatory sexual selection on sneakers; L is post-copulatory advantage of the guards; C is the number of copulation attempts by the sneakers; and R_{SD} is standard deviation of body condition.

	p	S_G	T	S_S	L	C	R_{SD}
Sneaker proportion	-0.122	0.703	-0.262	-0.079	-0.712	0.730	0.757
Mean switchpoint	-0.121	0.736	-0.280	-0.085	-0.718	0.746	0.683
Variation switchpoint	0.010	-0.192	0.046	0.010	0.056	-0.104	-0.081
Mean *SCI*	-0.501	0.622	-0.112	-0.208	-0.619	0.832	0.636
SCIC	0.858	-0.017	-0.030	0.010	0.063	-0.120	-0.037
I_S	-0.386	0.478	-0.802	0.072	0.432	-0.479	0.238
Additional measures of sexual selection							
Guard's reproductive variation	-0.394	0.568	-0.794	0.08	0.246	-0.265	0.449
Guard's with *T* reproductive variation	-0.408	0.52	-0.814	0.079	0.339	-0.382	0.322
Guards with *T* but without females	0.068	0.521	0.889	-0.033	0.204	-0.092	0.286
Guard with *T* but without offspring	-0.257	0.554	0.895	-0.074	-0.314	0.282	0.375

3.2 Switchpoint variation

There was little among-population variation in switchpoint variation (mean $\pm$ SD = 1.40 $\pm$ 0.04, Fig. 4a). In all simulations, there was an increase in the switchpoint standard deviation (SD) during the first generations, followed by stabilization (with slight but continuous oscillation) until the last generation (Fig. 5b). None of the input parameters had a strong effect on the switchpoint SD (most absolute PRCC values were below 0.1, Table 2, Figs. 5c-d). The input parameter with the strongest effect was the pre-copulatory selection on guards, S_G, which was negatively correlated with switchpoint SD (Fig. 5d, PRCC = -0.192).
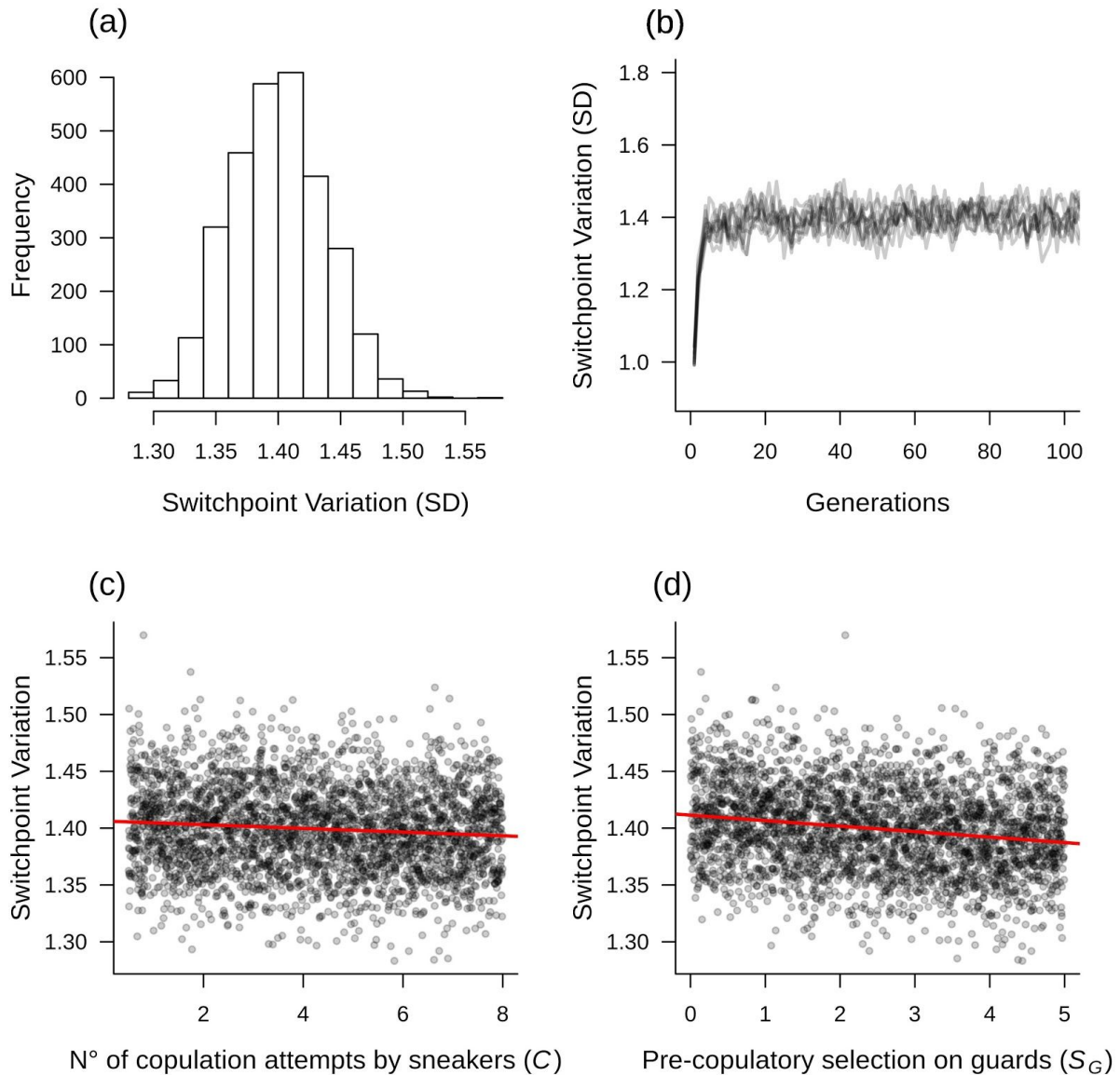
Figure 5 - Intra-populational switchpoint variation in the model of alternative mating tactics evolution. **(a)** Histogram of switchpoint variance values of all simulations in the 400th generation. **(b)** Switchpoint variation over 100 generations from 10 replicate simulations chosen randomly. All simulations present the same patterns of increased variation, followed by continuous oscillation. We show a reduced number of simulations and generations for better visualization. **(c-d)** Relationship between intra-populational switchpoint variation and the two input variables more strongly correlated with it: **(c)** the number of copulation attempts by the sneakers, C, and **(d)** the pre-copulatory selection on guards, S_G (see effect sizes in Table 2).

3.3 Main measurements of sexual selection

The opportunity for sexual selection, I_S, ranged from 0.9 to 19.8 (mean $\pm$ SD = 3.7 $\pm$ 2.1), so that it was usually higher than the expected in the absence of sexual selection (I_S = 0.5, see Supplementary Material). The parameters that most

influenced the I_S were the number of territories (T), number of copulation attempts by the sneakers (C), post-copulatory advantage of the guards (L), promiscuity correlation value (p), and pre-copulatory selection on guards (S_G). The I_S is positively correlated with L and S_G, and it is negatively correlated with T, C, and p. The parameter T has the greater PRCC value (PRCC = -0.80), while the PRCC of the other parameters ranged from -0.47 to 0.47 (Table 2).

The mean sperm competition intensity (SCI) ranged from 1 to 5.03 (mean$\pm$SD = 1.54$\pm$0.72). The parameters that most influenced the mean SCI were the number of copulation attempts by the sneakers (C), post-copulatory advantage of the guards (L), standard deviation of body condition (R_{SD}), pre-copulatory selection on guards (S_G), and promiscuity correlation value (p). The mean SCI was positively correlated with C, S_G, and R_{SD} and negatively correlated with L and p. Finally, the sperm competition intensity correlation ($SCIC$) ranged from -0.86 to 0.92 (mean$\pm$SD = 0.02 $\pm$0.42), and was most influenced by the promiscuity correlation parameter p. This finding is a demonstration that the model was effective in simulating scenarios in which there is a correlation between mating success and intensity of sperm competition faced by guards (Fig. 7f). The other parameter that most influenced the $SCIC$ was the number of copulation attempts by the sneakers (C). The $SCIC$ had a positive correlation with p (PRCC = 0.85) and a negative correlation with C (PRCC = -0.120).

3.4 Additional measures of sexual selection

The reproductive success variation (SD) among guardians ranged from 1.67 to 23.39 (mean$\pm$SD = 4.16$\pm$1.58). It was mainly affected by the number of territories T, pre-copulatory selection on guards S_G, body condition standard deviation R_{SD}, and the promiscuity correlation parameter p. T and p had a negative effect on the variation of guard reproductive success, while S_G and R_{SD} have a positive effect. The proportion of guards with territory but without females ranged from 0 to 0.54 (mean$\pm$ SD = 0.12$\pm$0.11), and was positively influenced by the number of territories T, pre-copulatory selection on guards S_G, and body condition standard deviation R_{SD}.

Similarly, the proportion of guards with territory but without offspring ranged from 0 to 0.57 (mean $\pm$ SD = 0.16 $\pm$ 0.13), and was positively influenced by the number of territories T, pre-copulatory selection on guards S_G, and body condition standard deviation R_{SD}.
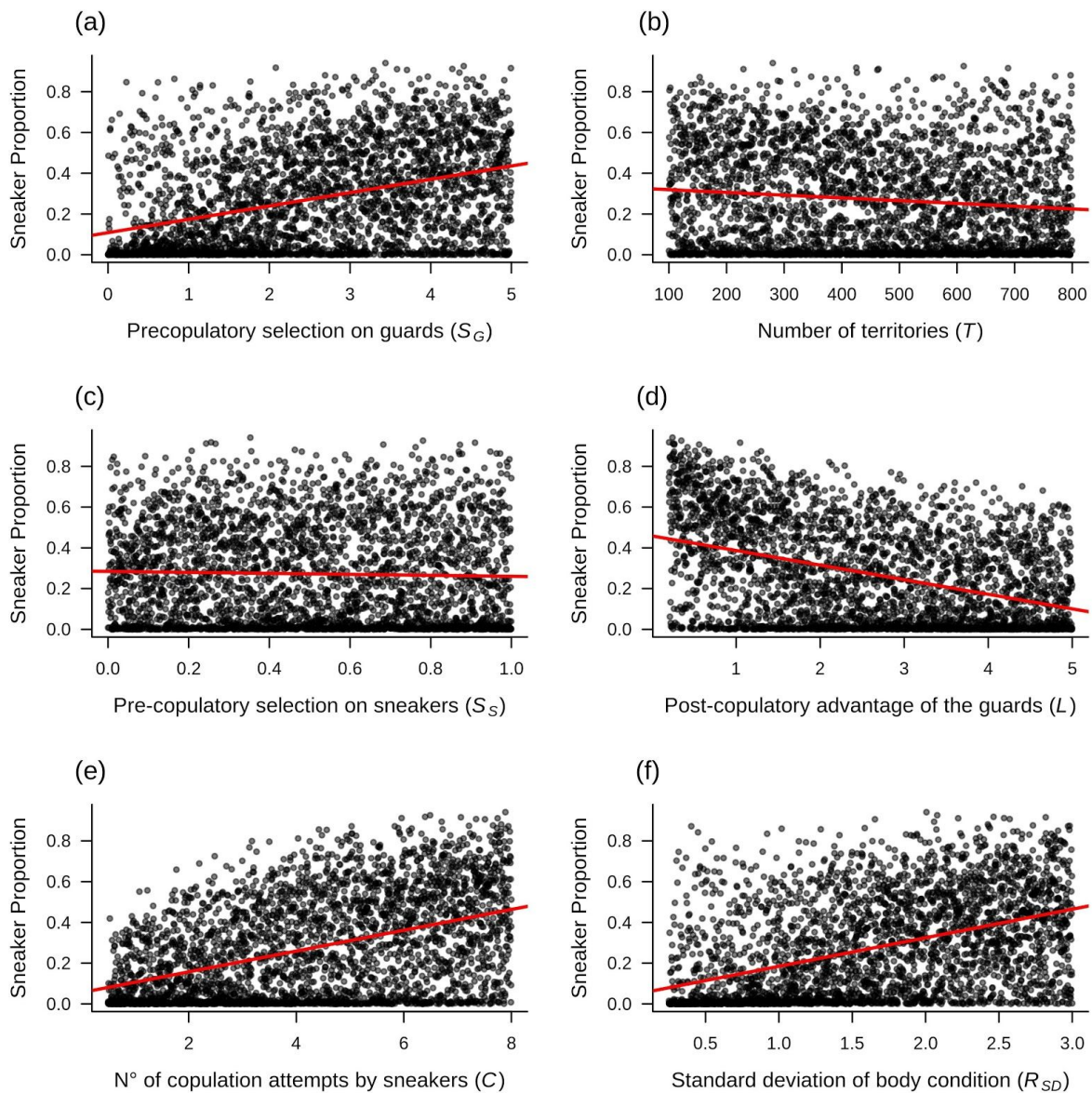

Figure 6 - Sneaker proportion and its correlation with the input parameters in the model of alternative mating tactics evolution. Each point represents the last generation from one replicate simulation (from a total of 3,000 simulations). The three parameters with the strongest positive influence on sneaker proportion are: **(a)** pre-copulatory selection on guards, S_G, **(f)** number of copulation attempts by sneakers, C, and **(g)** standard deviation body condition, R_{SD}. The **(e)** post-copulatory advantage of the

guards, *L*, had a negative influence in sneaker proportion. Red trend lines were generated by simple linear regression. See effect size values in Table 2.
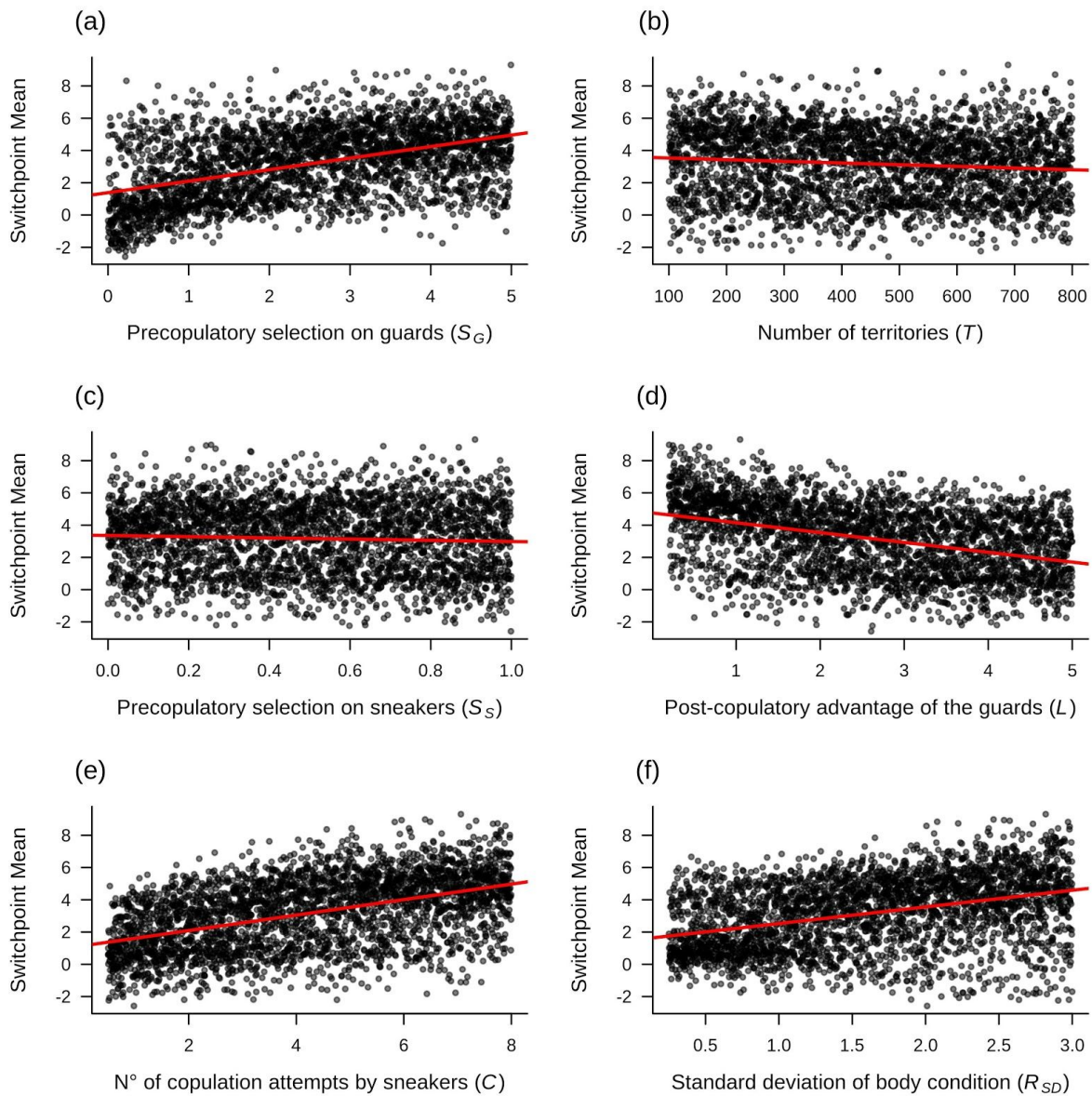
Figure 7 - Mean switchpoint and its correlation with the input parameters in the model of alternative mating tactics evolution. Each point represents the last generation from one replicate simulation (from a total of 3,000 simulations). The three parameters with the strongest positive influence were: **(a)** pre-copulatory selection on guards, S_G, **(f)** number of copulation attempts by the sneakers, *C*, and **(g)** body condition standard deviation, R_{SD}. The **(e)** post-copulatory advantage of the guards, *L*, had a negative influence in sneaker proportion. Red trend lines were generated by simple linear regression. See effect size values in Table 2.
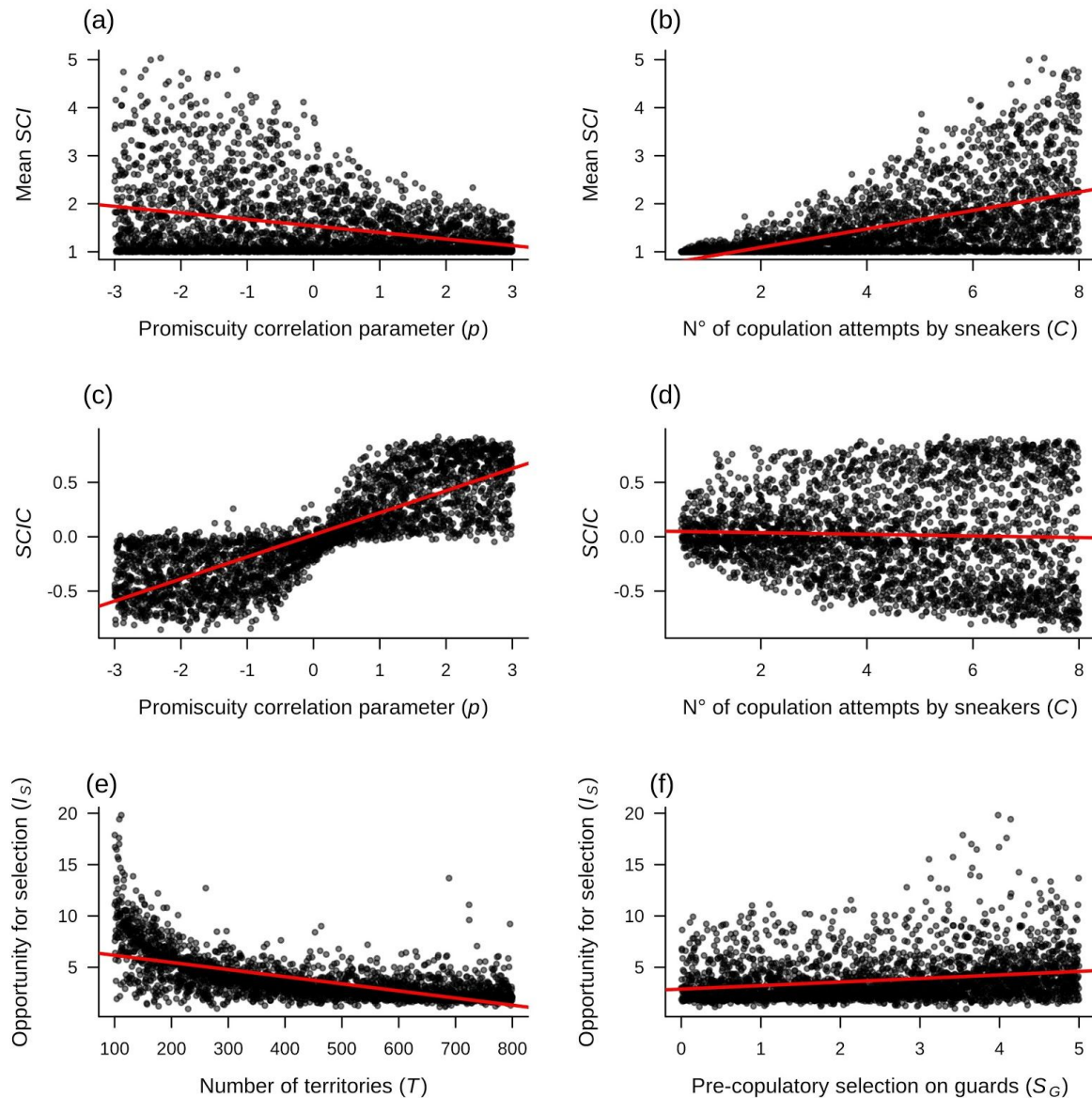
Figure 8 - Main measurements of sexual selection and their strongest relationships with input parameters of the model of alternative mating tactics evolution. **(a-b)** Mean sperm competition intensity *SCI* was negatively correlated with the promiscuity correlation parameter *p* and positively correlated with number of copulation attempts by the sneakers, *C*. **(c-d)** Sperm Competition Intensity Correlation (*SCIC*) was positively correlated with the promiscuity correlation parameter *p* and its variation increased in simulations with high number of copulation attempts by the sneakers, *C*. **(e-f)** The opportunity for sexual selection I_S was negatively correlated with the number of territories number, *T*, and positively correlated with pre-copulatory selection on guards, S_G. Red trend lines were generated by simple linear regression. See effect size values in Table 2.

4. DISCUSSION

We used individual-based models to investigate the influence of pre- and post-copulatory sexual selection, as well the interaction between these two processes, on the total sexual selection and the evolution of conditional alternative male mating tactics. In our simulations, positive values of promiscuity correlation p weakened total sexual selection and decreased the proportion of sneakers in the populations. There was high among-population variation in the proportion of sneakers and also in the mean switchpoint value. The proportion of sneakers was mostly influenced by the intensity of pre-copulatory sexual selection on guards (S_G), the number of copulation attempts by the sneakers (C), the post-copulatory advantage of guards (L), and the within-population variation in body condition R_{SD}. Switchpoint variance varied little among populations, and none of the input parameters had a strong effect on its value. Taken together, our results provide new and detailed predictions for different populations and/or species about the evolution of alternative mating tactics under the Environmental Threshold model.

4.1 Switchpoint evolution and sneaker proportion

The initial condition of our simulations was of a mean switchpoint value equal to the mean body condition of the population, so that, initially, the populations were composed of roughly equal numbers of sneakers and guards. In most simulations, the mean switchpoint quickly decreased during the first generations, which led to a reduction on the proportion of sneakers to a mean of 0.27. Here, there are factors that reduce the population switchpoint over the generations: 1) reduction happens when individuals with low switchpoint values attain higher fitness; and 2) when individuals lose fitness by "choosing" the less advantageous tactic given its body condition. First, on average, guards have lower switchpoint values than sneakers. This is because individuals with low switchpoint values have sufficient body condition to become guardians more often (see Supplemental Material, Figure S7). Thus, when guards have greater fitness than sneakers, the average switchpoint decreases. And that is exactly what happens in our simulations. Under most parameter values (and probably in most wild populations), guards need a relatively high body condition

to secure a territory. However, once a harem is secured, guards attain higher mean fitness than sneakers, being a sneaker frequently a classic "best of a bad job strategy" (Dawkins, 1980). Second, the switchpoint reduction happens when many males "make bad decisions" during their development. Knowing that guards have a greater fitness than sneakers, if an individual with a body condition high enough to become a successful guard becomes a sneaker, he is making the wrong decision: he is producing less offspring than an individual with the same body condition, but a switchpoint value low enough to become a guard. So, by penalizing "bad decisions", selection acts on mean switchpoint until most males are making the best developmental decision by adopting the mating tactic that brings the highest fitness given its body condition.

The proportion of sneakers in the population was influenced by all three parameters that determine the strength of pre-copulatory sexual selection. Sneaker proportion increased with pre-copulatory selection on guards (S_G), and decreased with both the number of territories *(T)* and pre-copulatory selection on sneakers (S_S). Indeed, pre-copulatory selection on guards was the parameter with the strongest effect on the proportion of sneakers. The mechanism behind this pattern is that increasing pre-copulatory selection on guards increases the concentration of females on harems of guards with high body condition, making guards with low body condition more likely to remain unmated. In this way, many guards with low body condition achieve no reproductive success, generating selective pressure for individuals with low body condition to assume a sneaker tactic (increasing the mean switchpoint). This effect can be seen in the positive effect of S_G on the proportion of guards with territory but without offspring (Table 2). Thus, when competition among guardians in fierce (high S_G), the mean switchpoint tends to stabilize at higher values, since it only pays to become a guard for males with relatively high body condition.

The number of territories (*T*) had less than half the effect of S_G on sneaker proportion (PRCC = -0.262), while pre-copulatory selection on sneakers (S_S) had a still weaker effect (PRCC = -0.079). Regarding the weak effect of *T* in the proportion of sneakers, first it is important to remember that sneakers do not compete for territories to obtain copulas, as occurs with guards. Therefore, it is natural to imagine

that the number of territories would have a weaker effect on the success of sneakers. Still, any effect of T on sneaker proportion is probably mediated by its effect on the guards. More territories mean more opportunities for being a guard and owning a harem, so that it makes sense to find less sneakers when territories are more abundant. The S_S parameter represents the effect of body condition on the number of sneaker copulation attempts (invasions), so that higher the values of S_S increase the variation in the number of copulation attempts among sneakers. However, increasing variation in the mating success among sneakers had a weak effect on maintenance of the sneaker tactic. This may happen because sneaking is already the "best of a bad job", thus even though higher values of S_S decrease the fitness of low-body condition sneakers, there is no other mating tactic for males in such a bad condition to adopt.

It is important to note that the effects of T and S_S may be smaller than the effect of pre-copulatory selection on guards (S_G), because S_G influences both territory acquisition and female attraction by guards. So that S_G has "double effect" on the guards' reproductive success. However, this "double effect" may occur in nature, as it is likely that the males more likely to secure territories are also the ones that accumulate more females. This may happen both because females may perform mate choice based on traits related to Resource Holding Power (RHP, Berglund et al., 1996), and because high-RHP males may secure high-quality resources and thus become more attractive to females (indirect mate choice *sensu,* Wiley & Poston, 1996). While the proportion of sneakers was only mildly affected by T, the number of territories strongly influences the concentration of mating success among guards. So much so that the parameter T had the strongest effect on the value of the potential for sexual selection I_S (Fig. 7e, Table 2), a strong effect of territory availability on the intensity of sexual selection is indeed a classic prediction from mating systems theory (Emlen & Oring, 1977). In summary, the parameters that strengthen the pre-copulatory competition among guards, increasing the variation in fitness among guards, increase the proportion of sneakers. This was a prediction of Shuster & Wade (2003) in the context of genetically fixed alternative reproductive strategies, which here we show that is also valid for the condition dependent mating tactics.

The proportion of sneakers in the population was also strongly influenced (PRCC values above 0.7) by the two parameters that influence the post-copulatory sexual selection: it increased with the mean number of sneak copulation attempts (C) and decreased with post-copulatory advantage of guards (L). The parameter C can be seen as the potential for sneaker copulation in a given population. Thus, in scenarios with high C, sneakers copulate with more females and attain higher reproductive success. Thus, it makes sense that an increase in mating opportunities for sneakers should increase the proportion of sneakers in the population (Fig. 6d). On the other hand, high values of L decrease the probability of fertilization by sneakers (Fig. 3d), decreasing sneaker fitness by increasing paternity of offspring by guards. Also, high values of C increase the sperm competition faced by guards, and sneakers will steal paternity from guards more often, increasing the success and proportion of sneakers (Fig. 6e). Therefore, parameters that increase the opportunities of fertilizations by sneakers (high C and low L), produce an evolutionary increase in switchpoint values and a consequent increase in the proportion of sneakers in the population. Thus, laboratory and field studies investigating the factors that influence the copulation rate and fertilization success of sneakers, would assist in a better understanding of the difference in fitness and reproductive success between tactics, and consequently, variation in the proportion of sneakers among populations and species.

Most of the parameters that were explored in the model (Table 1) modulate the intensity of sexual selection processes, influencing competition for territories and/or females and the probability of fertilization once copulation occurs. However, there are two exceptions: the parameters R_{SD} and p. The body condition variation (R_{SD}), is more linked to ecological dynamics, which will dictate the variation in the environmental clue that determines the tactic assumed by the individuals of the population. While the promiscuity correlation value (p) defines the correlation between pre and post copulatory processes (or its absence) and influences the network of mating relationships among individuals. That said, the analysis of these two parameters will be presented separately in the next sessions.

4.2 Sneaker proportion and body condition variation

In our simulations, higher within-population variation in body condition (higher R_{SD} values) led to a higher proportion of sneakers in the populations. We believe this effect was caused by a combination of ecological (short-term) and evolutionary (long-term) processes. Ecologically, a higher variation in body condition increases the proportion of sneakers simply because it increases the number of individuals below any threshold value as long as the threshold is below the mean body condition of the population (see Fig. 9). Therefore, even if we kept the mean population switchpoint fixed, a higher variation in body condition would still produce a higher proportion of sneakers. Evolutionarily, higher variation in body condition generates some extremely high body conditions guards, which are highly successful and concentrate more females in their harems. Indeed, higher R_{SD} generated a higher proportion of guards with a territory but without females in their harems (PRCC = 0.287, Table 2), higher R_{SD} also generated higher variation in reproductive success among guards possessing territories (PRCC = 0.364, Table 2). Thus, increased variation in R_{SD} intensifies the competition among guards, which has the effect of increasing the mean switchpoint, further increasing the proportion of sneakers in the population. Thus, populations in environments that favor higher variation in the body condition of males should present a higher proportion of sneakers.
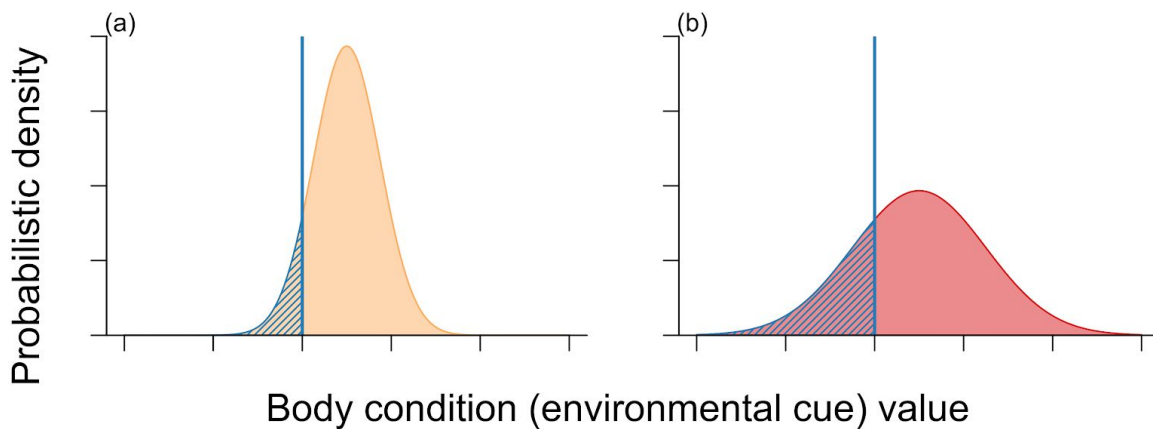
Figure 9 - The ecological (short-term) effect of body condition variation on the proportion of sneakers in the population. The two curves show the distribution of body condition values in two populations with the same mean, but the population in (a) has a lower variation than the one in (b). The thick vertical lines in both plots represent the mean switchpoint value, which is equal in both populations. The hatched areas highlight the proportion of individuals below the mean swithpoint, a larger area represents a higher proportion of sneakers. Notice that even though both populations have the same mean body condition, and the same mean switchpoint, the hatched area is larger on plot (b).

4.3 Promiscuity correlation

The promiscuity correlation parameter p had a moderate to strong effect on most measures of sexual selection, including the potential for sexual selection I_S and mean guard sperm competition intensity *SCI*. A negative promiscuity correlation increased the I_S, while a positive promiscuity correlation decreased it. This pattern is similar to what McDonald & Pizzari (2018) predicted outside the context of alternative mating tactics. Thus, our results reinforce the idea that a positive promiscuity correlation weakens sexual selection, and also extends the prediction to mating systems with conditional alternative reproductive tactics. Also, the promiscuity correlation parameter p had a negative effect on the mean sperm competition intensity faced by guards. This happened because high and positive p values concentrated sneaker invasions in a few large harems within each population. Therefore, high promiscuity correlation leaves many guards who have small harems free of sperm competition. And since most guards have small harems, a high promiscuity correlation ends up decreasing the mean sperm competition intensity faced by guards, Thus, a positive promiscuity correlation decreases the overall sexual selection on guards by concentrating sneaker invasions on large harems. As

we discussed earlier, parameters that decreased sexual selection on guards increased the proportion of sneakers, accordingly, the parameter p showed a negative correlation with sneaker proportion, even though a relatively weak one (PRCC = -0.122). Also, the value of p had essentially no correlation with switchpoint variation (PRCC = 0.01).

So far, we have discussed all factors that influenced the mean switchpoint value of the populations, and thus its proportion of sneakers. However, it is also interesting to understand what influences within-population variation in the switchpoint values. Therefore, in the next section, we discuss switchpoint variation.

4.4 Switchpoint variation

Switchpoint variation was kept consistently high through time, albeit with slight oscillations (Fig. 5b) and none of the model parameters had a strong influence on switchpoint variation. The parameter with the strongest effect was the pre-copulatory selection on guards (S_G), which had a weak negative effect on switchpoint variation (PRCC = -0.161, Table 2 and Fig. 5d). The switchpoint is expected to be under stabilizing selection in the ET model, since both too high and too low values can lead males to adopt the less profitable mating tactic (Tomkins & Hazel, 2007). Strong stabilizing selection can decrease genetic variation. But for such selection to be strong, the penalty of assuming the "wrong" tactic must be high for individuals with a switchpoint close to the mean. In other words, there should be a high difference in fitness between sneakers and guards with body condition values close to the mean switchpoint. Therefore, the maintenance of variation in the switchpoint in our simulated populations must result from weak stabilizing selection on the switchpoint, so that individuals who assume the "wrong" tactic lose little or no fitness value (as observed empirically by Tomkins, 1999 and Buzatto et al., 2011). Thus, as Tomkins (1999) suggests, natural populations may possess a *switch zone* not a point as the name *switchpoint* implies (Tomkins, 1999). A *switch zone* is a range of body condition values where males can adopt any of the two mating tactics and reach similar fitness. Still, high values of pre-copulatory sexual selection on guards (S_G) did have a small negative effect on switchpoint variation, so that increased

competitiveness among guards slightly strengthened stabilizing selection and restricted the switch zone.

5. CONCLUSION

Each simulation in our model represents a population with alternative mating tactics, each one under different environmental conditions and intensities of sexual selection. Thus, all predictions we present here are predictions about differences among populations, and should be tested by comparing multiple populations of the same species, or multiple species with similar reproductive biology. Such wide-scale tests may be challenging, but they are clearly possible. Replicate populations can be established in the laboratory, and alternative mating tactic evolution can be observed in a few generations if you choose the adequate model organism (such as mites, e.g. Buzatto & Clark, 2020). Alternatively, multiple natural populations of the same species can be compared. For instance, populations of the earwig *Labidura xanthopus* with (and without) alternative mating tactics are present throughout the west coast of South America (García-Hernández, 2015), and geographical variation in the proportion of male morphs has also been described for the European earwig *Forficula auricularia* (Tomkins & Brown, 2004). Additionally, the neotropical harvestman *Serracutisoma proximum* has a mating system of resource defense polygyny with alternative mating tactics, and sneaker proportion is highly variable among geographically close populations (Munguía-Steyer et al., 2012). Our predictions can also be tested under a phylogenetically comparative framework, which requires information about multiple species within a clade in which there are multiple species with alternative reproductive tactics (ARTs). For instance, populations and species of dung beetles (genus *Onthophagus*: Scarabaeidae) vary in their switchpoint values and are under different selection forces (Moczek et al., 2002, Simmons et al., 2007), presenting an opportunity for testing our predictions in a phylogenetically comparative framework (Garamszegi, 2014).

Finally, the environmental threshold model (ET model), which served as the base of our simulations, has been seen for years as the main model to explain the presence of ARTs in wild populations (Tomkins & Hazel, 2007; Buzatto et al., 2014). The main alternatives are the models of genetically fixed ARTs (which appear to be rare in the wild) and the "status-dependent selection" model, which is essentially a simplified ET model (without switchpoint variation, Shuster & Wade, 2003; Tomkins

& Hazel, 2007). Empirically, in most populations with ARTs, the tactic adopted by a male seems to be determined by its body condition (i.e., status), and within-population variation in the switchpoint is also observed (Hunt & Simmons, 2001; Buzatto et al., 2011), so that the ET model is rightfully seen as adequate for most populations. However, despite the model's wide acceptance, it has very few predictions, probably because most discussions about ART models focus on separating between different models (see Tomkins & Hazel, 2007). Here, we present various predictions about the operation of the ET model, such as: (1) populations in environments that favor higher variation in the body condition will have a higher proportion of sneakers; (2) switchpoint variation is expected to be relatively high; and (3) the proportion of sneakers and the intensity of sexual selection are influenced by various different environmental and populational parameters. In conclusion, switchpoint evolution was strongly influenced by factors that influence the intensity of both pre and post-copulatory selection, but only weakly affected by the interaction between pre and post copulatory processes.

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7. SUPPLEMENTAL MATERIAL

All files necessary to reproduce our simulations. We have the files that are generated at the end of all simulations in the folders "csv" and "fitness", making it possible to carry out additional analyzes.

It is also possible to simulate from scratch and/or do the PRCC analysis, using the codes available in .r.

https://github.com/vmontagner/IBM-ARTs

7.1 Supplementary methods

7.1.1 Sneaker probability of success - additional details

In the main text, we explain that the sneaker probability of success (in copulating) is a function of the promiscuity correlation parameter p and the number of females in the territory/harem the sneaker is invading (harem size H). During the calculation, however, we use an unexpected data transformation, the values of H are ranked, centered and scaled prior to the calculation. Why would we do that? The simple and short answer is that it was the only way we found to ensure that mean sneaker success was not correlated with the value of p. Such a correlation would be highly undesirable in the model, since the "function" of parameter p was to modulate promiscuity correlation and nothing more. Below, we describe in great detail the troubleshooting process that led us to the exquisite solution. Keep in mind, however, that it was a modelling decision: we simply found a mathematical way of producing a biological pattern within the model (in this case, promiscuity correlation). The biological pattern of promiscuity correlation has a biological meaning and importance (as we argue in the main text), but ranking, centering and scaling data had no biological significance, it is just a mathematical modelling trick.

In order to introduce promiscuity correlation in the model, we needed a way to associate a guard's harem size with the probability that the females in his territory would copulate with sneaker males. The simplest way to do this we could think of was: making sneakers find females randomly and then calculating a probability of sneaking success (copulation success) based on harem size. So, we needed a function that would receive as arguments (inputs): (1) the promiscuity correlation

parameter p; and (2) harem size H. We also needed this function to return a value between zero and one, which could be used as a probability.

We decided to base our function on the inverse logit function (also known as *logit^-1*), which is a sigmoid function, that returns values between zero and one, and is frequently used in modelling and statistics. In its simplest form, the inverse logit function can be written as:

$$f(x) = \frac{1}{1 + exp(-x)}$$ **(equation S1)**.

When x equals zero, the inverse logit returns exactly 0.5, negative x values produce probabilities below 0.5, while positive values produce values above 0.5 (see Figure S1).
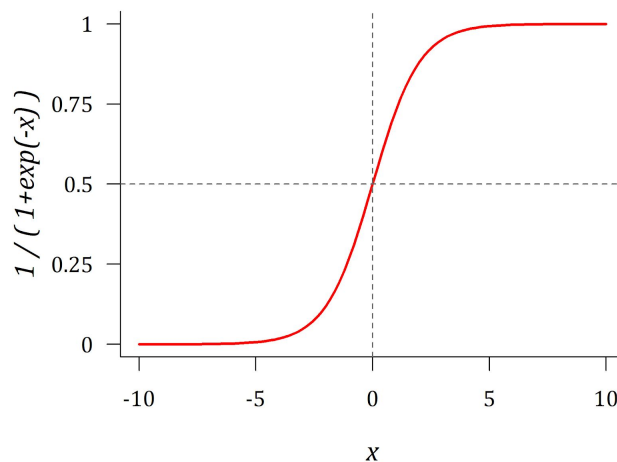

Figure S1 - The inverse logit function is shown as the thick red line and the dotted lines highlight that when *x = 0, f(x)* equals exactly 0.5.

Notice how the inverse logit becomes relatively flat for very positive or very negative x values. If mean sneaker success was very high (or very low), we were at a risk: if all sneaking attempts had a probability of success very close to one or very close to zero, the pattern of promiscuity correlation might not emerge from the model. This would happen because the promiscuity correlation depends on some sneaking

attempts having higher probability of success than others (according to harem size). Therefore, it would be good to keep "mean x" close to zero, because this is the region of the inverse logit curve with the highest variation (y values vary a lot according to x). Based on all this, we decided that the equation for the probability of a sneaker successfully copulating with female j, Q_j, would be as follows (spoiler alert: it almost worked):

$$Qj = \frac{1}{1 + exp(-p(H_j - H'_G))}$$ **(equation S2)**

At first glance, this equation had all we wanted for our model: it theoretically kept mean sneaker success close to 0.5 for various parameter values, and it responded to variation in the p parameter value (see Fig. S2).
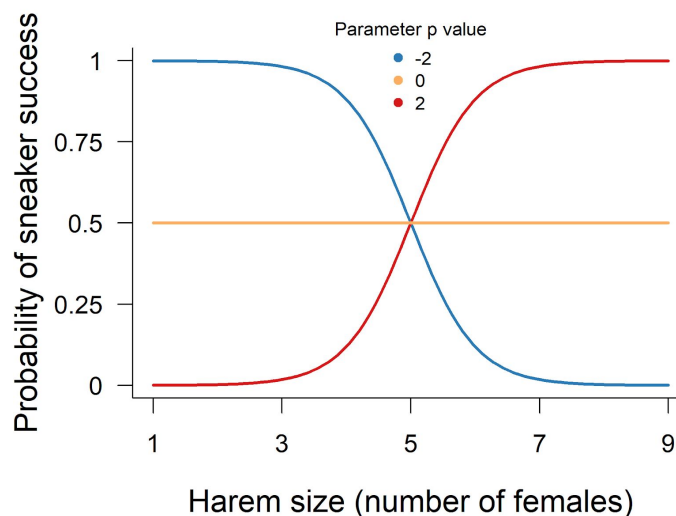
Figure S2 - The "behavior" of equation S2 with mean harem size H'_G = 5. As we wanted, the probability of sneaker success increases with harem size when p is positive and decreases when p is negative.

Before we wrote the code of the "main model"we present in the main text, we wrote a simpler individual-based simulation, just to test if the promiscuity correlation (using equation S2) was working. We will refer to this simpler simulation as *test model*. Each replicate run of the test model represented a single mating season from

a population with alternative mating tactics (guards and sneakers), and followed the simple rules shown below:

- The population is formed by N individuals in a 1:1 sex ratio
- A proportion b of individuals are sneaker males
- Mean harem size is equal to H (so that there are $N/2H$ territories or harems)
- One guard is assigned to each territory, the remaining guards are excluded from the mating pool
- Females are randomly distributed among territories
- Each sneaker attempts to copulate an A number of times
- Sneakers find females randomly, but copulation success is a function of the number of females in the territory (harem size) and the promiscuity correlation parameter.
- At the end of each simulation, we recorded mean sneaker success and the sperm competition intensity correlation ($SCIC$, see main text for details).

We ran 300 replicates of the test model, in each of them the parameter p (the promiscuity correlation parameter) received a random value between -2 and 2, sampled from a uniform distribution. Other than that, we kept all parameters constant: population size of 2000 individuals; sneaker proportion of 0.5; mean harem size of five females (which resulted in 200 territories); and four sneaking attempts per sneaker male. The results for the promiscuity correlation were highly promising, the parameter p and the $SCIC$ were highly correlated (Pearson correlation coefficient of 0.94, and see Fig S3).
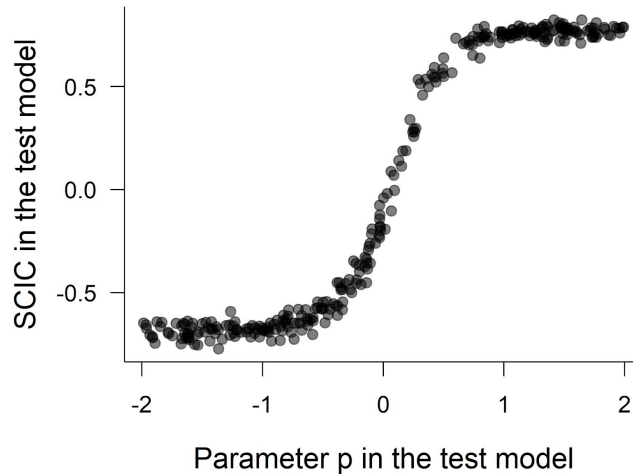
Figure S3 - Relationship between SCIC (the operational measure of promiscuity correlation) and the parameter *p* in the first version of the test model. Each dot is a replicate run of the test simulation.

After verifying that the process of generating promiscuity correlation was working in the model, we looked at the mean sneaker success: it was highly variable among replicate simulations (!); bimodal (!!); and even worse, strongly correlated with the parameter *p*, with a Pearson correlation of 0.95 (!!!), as you can see on Fig. S4.
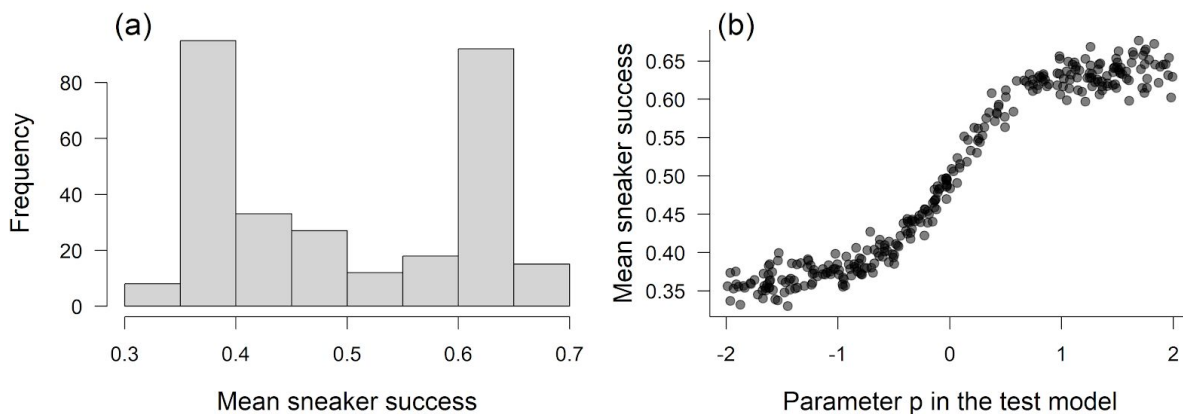
Figure S4 - Here it was clear that the first version of the test model had a problem. (a) Weirdly bimodal distribution of mean sneaker success. (b) Strong correlation between mean sneaker success and the parameter *p*, each dot is a replicate run of the test simulation.

Upon realizing equation S2 was not a good way of modelling the probability of sneaker success, we started looking for a solution. At this point, you may be asking why equation S2 did not work, and we believe it was mostly for two reasons: (1) mean harem size from the point of view of guardians is not the same as mean harem

size from the point of view of sneakers looking for females; and (2) because the distribution of harem sizes is not perfectly symmetric. So, we decided to borrow a few tricks from the statistics handbooks. Since the problem seemed to be that the distribution of harem sizes was "ill behaved", we tried some transformations commonly to "tame" the distribution: centering, scaling and ranking. Centering a continuous variable means to subtract the mean of the data from all observations, so that the mean of the centered variable becomes zero. Scaling means dividing each observation by the standard deviation of the data, so that the standard deviation of the scaled data becomes one. Finally, ranking is a transformation in which the lowest value becomes one, the second lowest becomes two and so on (i.e., values are replaced by ordered integer numbers). Many classical statistical tests use ranked data (including the PRCC we use in the main text).

Thus, we modified the test model so that, within it, the probability of sneaker success would be calculated in three different ways: (1) as described above (equation S2); (2) centering and scaling harem size values; and (3) ranking, centering and scaling harem size values. So we ran the test model 300 additional times, using the same parameter values described above. In this upgraded version, however, at each replicate run we calculated sneaker success probabilities in three different ways, simulated sneaker success separately, and calculated mean sneaker success and *SCIC* separately too. In a way, each replicate run of the test model became a triple simulation. Mathematically, the probability of sneaker success in the test model is calculated in three different ways, as in equation S2 and as in the following equations:

$$Qj = \frac{1}{1 + exp(-p \cdot scale(Hj))} \textbf{(equation S3)}$$

$$Qj = \frac{1}{1 + exp(-p \cdot scale(rank(Hj)))} \textbf{(equation S4)}$$

In equations S3 and S4, Q_j is the probability of a sneaker successfully copulating with female j, p is the promiscuity correlation parameter, and H_j is the number of females in female's j harem; the function *scale()* means centering and scaling the data, and the function *rank()* means ranking the data. Notice equation S4 is just equation 4 from the main text written differently.

The results of these two additional options for calculating the probability of sneaker success (equations S3 and S4) are shown in Fig. S5. On the right column, in light blue, the results for the centered and scaled values (equation S3), and on the left column, in orange, we show the results for ranked, centered and scaled values of harem size H (equation S4). Regarding the modelling of promiscuity correlation, both options (equations S3 and S4) worked well, as can be seen on Figs. S5a and b. In both cases, the Pearson correlation between *SCIC* and parameter p was around 0.96, which is excellent. Also in both cases, the distribution of sneaker success had little variation, and was unimodal, which is also excellent (Figs. S5c and d). Nevertheless, when H was centered and scaled, the probability of sneaker success was still correlated with parameter p (Fig. S5e, Pearson correlation coefficient of -0.51). However, when H was ranked, centered and scaled, the correlation finally disappeared (Fig. S5f, Pearson correlation coefficient of -0.009).
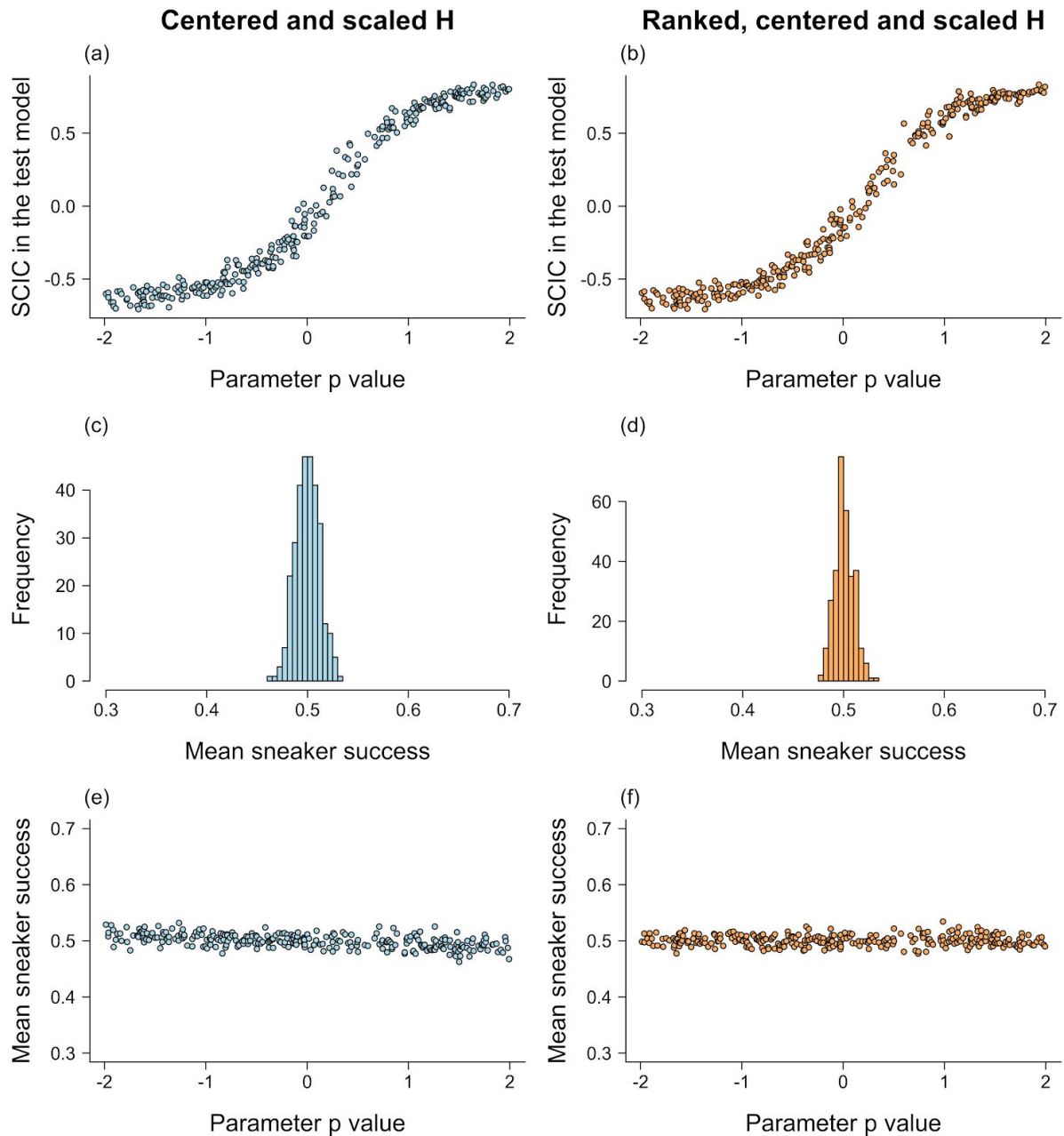
Figure S5 - One last fail (left column) before success (right column). On the left column (**a**, **c** and **e**) we show the results of the test model when harem size *H* was centered and scaled during the calculation of the probability of sneaker success, while on the right column (**b**, **d** and **f**), harem size *H* was ranked, centered and scaled. In both cases, the observed *SCIC* in the test model was highly correlated with parameter *p* (as we desired). Also in both cases, mean sneaker success had little variation among simulations and was unimodal. However, in **(e)**, there is a negative correlation between mean sneaker success and *p*, while on **(f)** there is no correlation.

7.1.2 Opportunity for sexual selection I_s - additional details

In the main text, we present the formula for I_S, the potential for sexual selection, and say that, in our simulations the mean expected I_S in the absence of sexual selection is 0.5. Where did this null expectation come from? This null expectation comes from the mathematical solution of the I_S formula in a scenario of completely random mating and fertilization. As we mention in the main text, the potential for sexual selection is a measure of variation in the fitness *w* among males (see also Shuster & Wade 2003, cited in the main text). Another way to express the I_S formula is as follows:

$$I_s = var(w)/mean(w)^2$$ **(equation S5)**

Fitness (*w*) is measured as the number of offspring per male, so that it is a discrete variable. So, if mating and fertilization were totally random among males, the distribution of offspring paternity among males would be essentially a Poisson process: a process in which discrete events occur randomly. The Poisson process (not surprisingly) generates a Poisson distribution of events and, in this case, the event is the siring of offspring. So, if there was no sexual selection at all, the number of offspring per male would follow a Poisson distribution. Lucky for us, the Poisson distribution is very well-behaved and has a single parameter: λ. The parameter λ represents the mean of the Poisson distribution, but it also represents the variance! Yes, in the Poisson distribution the variance is equal to the mean.

In our simulations, population size is the same in all generations, with 1000 males and 1000 females, and there is no mortality prior to reproduction, all males enter the mating pool. This means that at any generation there are 1000 males, and at the end of the generation 2000 offspring are generated (100 males and 1000 females). Thus, each male will have, on average, two offspring, so mean fitness *w* equals 2. Therefore, due to the properties of the Poisson distribution, mean and

variance of *w* in a population with totally random mating and fertilization is equal to two. Thus, the expected I_s solution in the absence of sexual selection is:

$$I_S = \frac{\lambda}{\lambda^2} = \frac{1}{\lambda} = \frac{1}{2} = 0.5$$ **(equation S6)**

7.2 Supplementary results
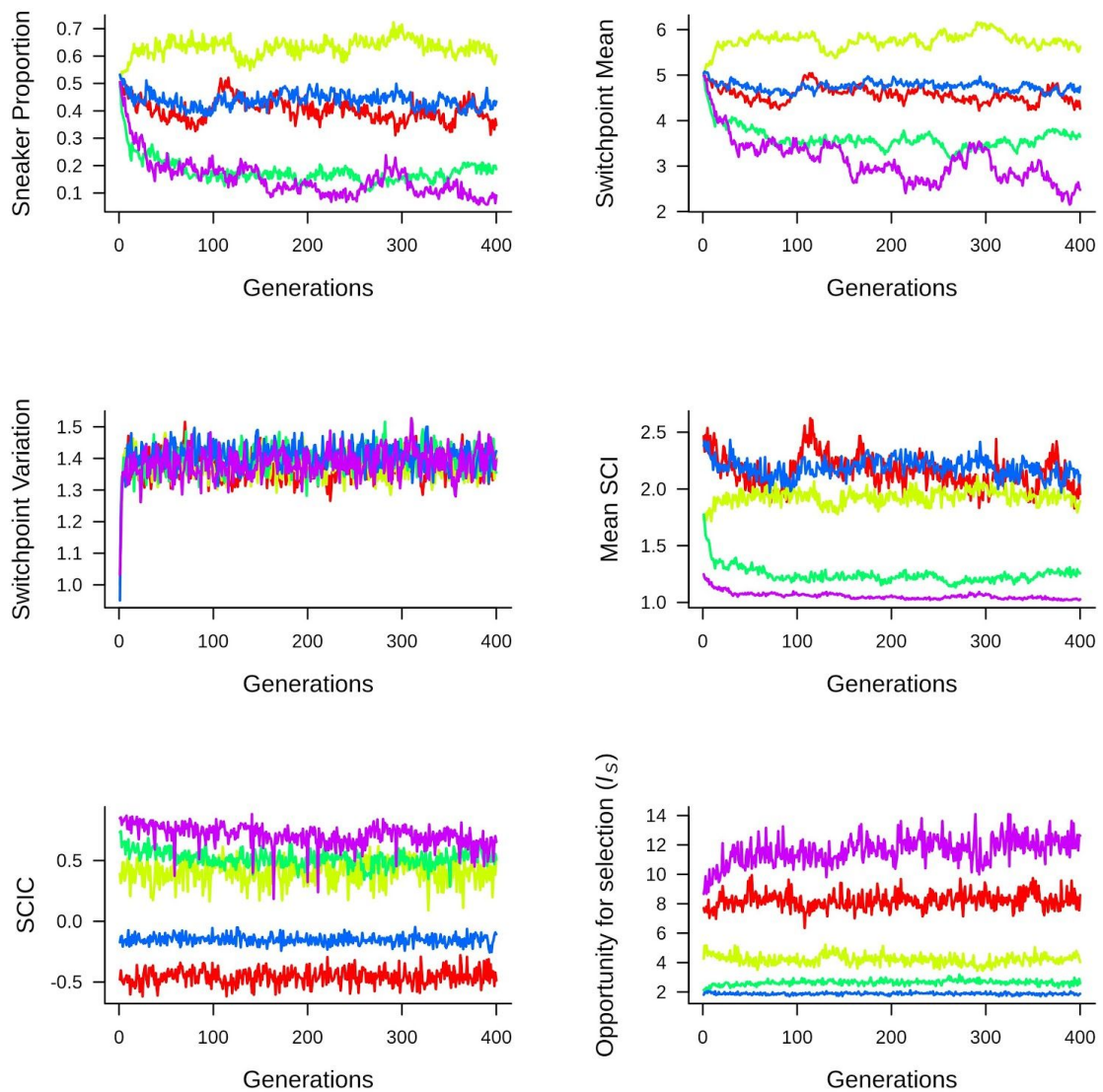
Figure S6 - Values of 6 variable responses over 400 generations. 5 simulations were chosen randomly and each color represents a simulation. All variables and simulations stabilize after 300 generations, so we let another 100 generations pass as a safety margin, stopping simulations in generation 400. In the graphs, we show a reduced number of simulations for better visualization.
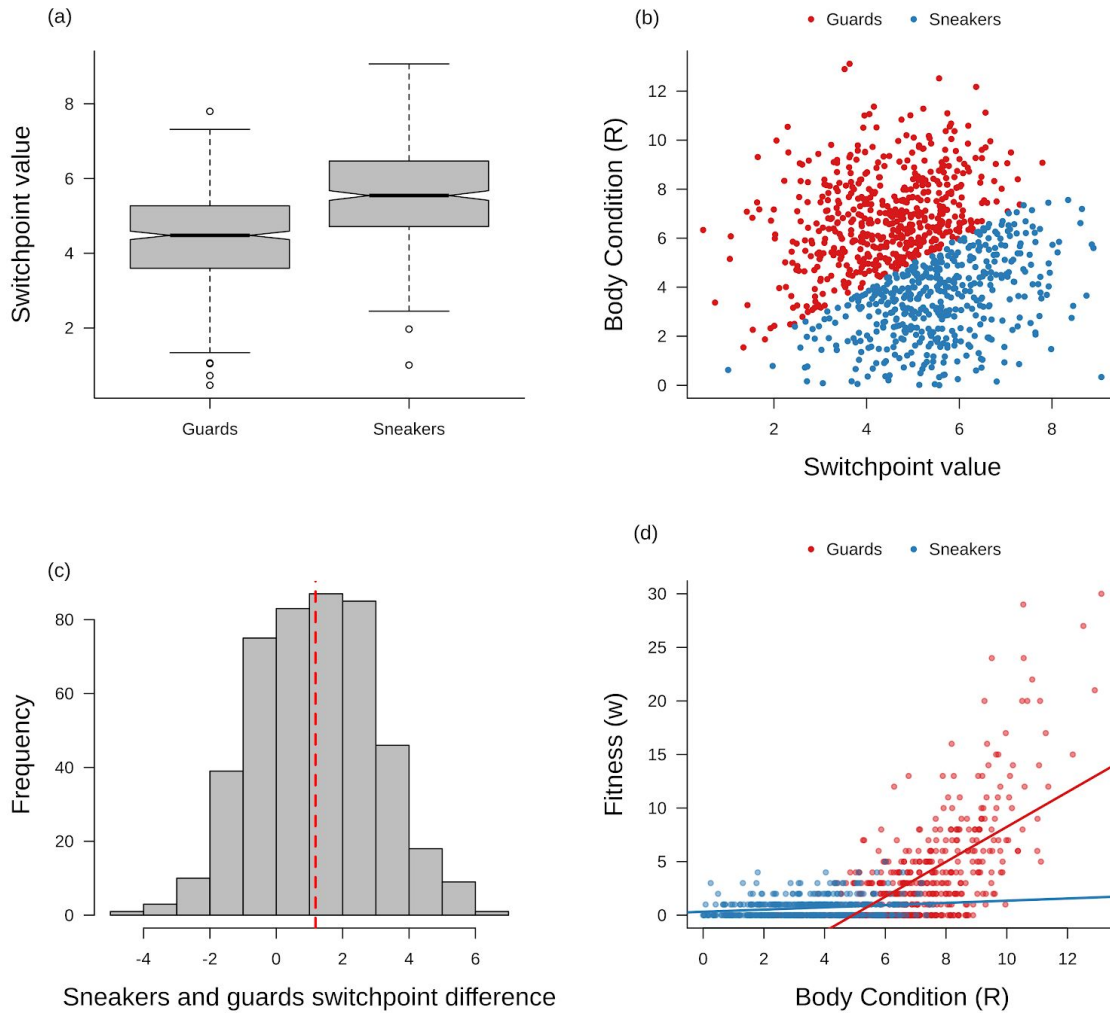
Figure S7 - Differences in the switchpoint values between guards and sneakers in a given drawn simulation. We raffled the simulations with proportion of sneakers between 0.4 and 0.6. The pattern presented here is repeated in the other simulations. (a) We observed a distribution of similar values, but sneakers have a higher concentration of individuals with a high switchpoint value. (b) Sneakers have the cloud of points shifted to higher values, also have body condition (R) generally smaller than guards. (c) The difference in switchpoint values between sneakers and guards, the red dashed line being the mean of the difference. A mean = 0 would be expected if there was no difference in the switchpoint values. (d) Graph that shows the relationship between fitness and the individuals' body condition. Lines were generated by a linear model. In the region of lines intersection, there are individuals who assume both tactics, demonstrating a possible switch zone, and not a switch point.