

How to Pick the Right One: Investigating Tradeoffs among Female Mate Choice Strategies in Treefrogs

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Abstract. Two main theories of female mate choice, that females either pick the best from the n closest males (*best-of-n*) or the closest with some minimum quality (*min-threshold*), make different behavioral predictions in some cases, yet both are supported by biological data. We present a computational agent-based model that is well-suited for investigating the differences between the two strategies for the biological model organism *Hyla versicolor* (“gray treefrog”). We show, based on results from systematic simulation studies, that *min-threshold* overall is the dominant strategy, even though *best-of-n* has some areas in parameter space where it dominates *min-threshold*.

Key words: female choice, mating strategies, agent-based modeling

1 Introduction

Most studies of mate choice assume that females “choose” a single mate from a group of eligible males based on some criteria. Female treefrogs, for example, show phonotaxis toward calls of males with higher pulse numbers [4, 10]. Females are thus assumed to make an active choice [11], show a directional bias (more pulses are better [19]), and differentiate between individual males up to a maximum of 5 [9]. While there are several proposed rules for female sampling and decision making [14], the most prevalent theories suggest that females choose either the “best” of the closest $n = 1, \dots, 5$ – *best-of-n* theory [13] – or the first male they encounter whose quality is above a minimum threshold for acceptance – *min-threshold* theory [14].

Yet, as Jennions and Petrie [14] point out “it has proved difficult to distinguish which tactics are used by females in the field”. In fact, there is empirical evidence for both theories, even though they predict different choices in some cases. In this paper, we attempt to contribute to resolving the apparent contradiction in the empirical data using a social agent-based simulation model of female choice in treefrogs.¹

We start by introducing our agent-based model, which consists of frog and environmental models based as much as possible on biological data. Then we present a thorough analysis of the results and show how both *best-of-n* and *min-threshold* strategies dominate each other in different regions of parameter space for different performance measures with *min-threshold* dominating in vast parts of parameter space. The

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subsequent discussion briefly reflects on some biological implications of our findings and proposes an empirically testable hypothesis to resolve the apparent contradiction in the biological data. The conclusion briefly summarizes our findings and proposes some model extensions for future work.

2 The Model

The aim of our agent-based model is to investigate the social interactions of male and female agents in a spatially explicit environment, using amphibians as the biological model organisms. It was specifically designed to generate and evaluate hypotheses about the dynamics of mating with focus on trade-offs among different female mating strategies in both artificial and natural conditions. The model includes only essential variables for the mating scenario: variables for *female choice strategies*, *male-female sex ratio*, and *male call quality* as well as parameters for the *distributions of males and females*. For simplicity, male amphibian social interactions with other males were not investigated at this stage.

We model male and female frogs using “male agents” and “female agents” in a continuous two-dimensional environment called the “swamp”, with dimensions E_x and E_y .² While the goal for all agents is to mate, only females can choose their mate.

Environment. Each male agent i is placed in the swamp at location $\langle i_x, i_y \rangle$ in a territory of radius r_τ according to the male distribution m_δ . Male agents always have to be inside the swamp and cannot be placed in another male’s territory. I.e., the position $\langle i_x, i_y \rangle$ of male agent i must satisfy the following restrictions for all positions $\langle j_x, j_y \rangle$ of males $j \neq i$: $[d(i, j) > 2 \cdot \tau] \wedge [i_x + r_\tau < E_x] \wedge [i_y + r_\tau < E_y] \wedge [i_x - r_\tau > 0] \wedge [i_y - r_\tau > 0]$ where $d(i, j) = \sqrt{(i_x - j_x)^2 + (i_y - j_y)^2}$ is the Euclidean distance between agents i and j (note that male agents do not move). Different from males, female agents are always placed in locations on the border of the swamp according to the female distribution f_δ . Mating between a female agent i and a male agent j always occurs when they are within *mating distance* d_{mate} , i.e., when $d(i, j) \leq d_{mate}$.

Agents. Both male and female agents have states that fully describe their make-up at any given time (Tab. 1 top). The state of a male agent i consists of its location in the swamp $\langle i_x, i_y \rangle$, its size i_{size} , as well as its pulse number i_{pn} . The state of a female agent i consists of its location in the swamp $\langle i_x, i_y \rangle$, its size i_{size} , its velocity i_v , its orientation α and its mating strategy $i_{\pi(n)}$.

2.1 Model parameters

We divide the model parameters into two sets: *fixed* and *free*. Fixed parameters (Tab. 1 middle) were set to known constant values from the literature and kept the same for all simulation experiments. In contrast, free parameters (Tab. 1 bottom) are parameters for

² To avoid confusion between biological and simulated entities, we will refer to simulated frogs as “agents”. We will use the gender attributes “male” and “female” alone if it is clear from the context whether we refer to simulated or real (male or female) frogs.

Symbol	Parameter Meaning	Initial Value	Update/Rationale
Male agents (state var)			
$size$	size	given by m_{size}	constant
$\langle x, y \rangle$	position	based on m_{δ}	constant
pn	pulse number	based on μ_{pn} and σ_{pn}	constant
Female agents (state var)			
v	velocity	given by f_v	constant
$size$	size	given by f_{size}	constant
α	heading $\in [0, 360]$ degrees	based on f_{δ}	calculated
$\langle x, y \rangle$	position	based on f_{δ}	calculated
$\pi(n)$	mating strategy with strategy parameter n	given by f_{π} together with strategy parameter values	constant
Environment (fixed)			
E_x	swamp width	10m	see [17, 6]
E_y	swamp height	25m	see [17, 6]
d_{mate}	mating distance	4cm	model-specific
r_{τ}	(male) territory radius	50cm	model-specific
n_{male}	the number of males	25	model-specific
Individual (fixed)			
m_{size}	male size	4.72 cm	see [7]
f_{size}	female size	5.38 cm	see [18]
f_v	female velocity	1.86 cm/s	see [3]
Environment (free)			
n_{female}	the number of females	1..20	model-specific
f_{δ}	female distribution	random at swamp edge	model-specific
m_{δ}	male distribution	Gaussian	model-specific
Individual (free)			
μ_{pn}	mean male pulse number	6..24 in increments of 2	model-specific
$\pi(n)$	mating rule	$bestofn\ minthresh$	see [3, 4, 10]
Strategy (free)			
θ	minimum threshold	6..24 in increments of 2	model-specific
v	number of sampled males	1..5	model-specific

Table 1. State variables of male and female agents (top), fixed model parameters kept at constant values for all simulations based on the literature (middle), and free model parameters and their variation (bottom).

which there is either no biological data available or no consensus on what the right value is supposed to be. They can be divided into *strategy parameters*, *individual* and *environmental* parameters. *Strategy parameters* concern only the strategy used by female agents in their selection of mates. *Individual parameters* concern the behavior of individual agents, and *environmental parameters* concern the make-up of the swamp, i.e., the number of agents, their locations, and their interactions (e.g., mating). Together, the free parameters form a *multidimensional parameter space* whose dimensions depend on the variations and particular samplings of each free parameter. We will first describe the variations of the free parameters and then provide details of the experimental setup.

Environmental parameters. The swamp is $E_x = 10$ by $E_y = 25$ meters which allows all female agents to sample every male agent. The male agents' territory radius r_{τ} was

fixed at 50 cm. Males were placed in the swamp according to a Gaussian distribution with means $\mu_x = E_x/2$ and $\mu_y = E_y/2$ and standard deviations $\sigma_x = E_x/4$ and $\sigma_y = E_y/4$, respectively, resulting in a greater density of males in the center of the swamp. Since the number of males n_{males} was kept constant for all experiments at 25, the number of females was varied from 1 to 20 yielding different male-female sex ratios (from 0.04 to 0.82) at the beginning of each run (which, of course, changes throughout the run as females and males mate).

Individual parameters. The pulse number for individual males was assigned based on sampling a Gaussian distribution with mean μ_{pn} and standard deviation σ_{pn} , where $\mu_{pn} \in \{6, 8, 10, 12, 14, 16, 18, 20, 22, 24\}$ and $\sigma_{pn} = 2$. The two biologically plausible strategies π (kept constant throughout each simulation run) are *best-of-closest-n* (*best-of-n*) and *closest-above-minimum-threshold* (*min-threshold*) [3, 4, 10]. Let $c(i, X) = \{j \in X \mid \neg \exists k \in X [d(k, i) < d(j, i)]\}$, which is the set of the closest agents from set X to the given agent i (usually this will only contain one agent, but there could be multiple agents that are equidistant to i). Let M denote the set of all male agents in the swamp.

- *Bestofn*. Let $c^n(i, X)$ denote the set of the n closest agents from set X with respect to the location of agent i .³ Then the selected male agent is $\operatorname{argmax}_{j \in c^n(i, M)} (j_{pn})$ for the female i , i.e., the male with highest pulse number in the set of the closest n males.
- *Minthresh*. The selected male agent is $\operatorname{argmax}_{j \in c(i, \{l \in M \mid l_{pn} \geq i_\theta\})} (j_{pn})$, where i_θ is the minimum threshold of female agent i , i.e., the male with the highest pulse number above the minimum threshold among the closest males.

Note that we are only considering homogeneous populations of females, so that every female in a given simulation run has the same mating strategy.

Strategy parameters. For *bestofn*, we vary its parameter $v \in \{1, 2, 3, 4, 5\}$ and for *min-threshold*, we vary its parameter $\theta \in \{6, 8, 10, 12, 14, 16, 18, 20, 22, 24\}$ (the upper limit of $v = 5$ was chosen based on prior model results [13] and empirical data [14]).

2.2 Model algorithm and implementation

The model was implemented in the Java programming language within the *Repast Simphony* agent-based simulation environment and run as a discrete-time simulation where each update cycle corresponds to one second in real-time (the pseudo-code of the main simulation loop is given below).

The males' positions and pulse numbers and females' positions and strategies are initialized based on a random seed (in *initializeMales* and *initializeFemales*).⁴ In the main loop, female agents sample male agents at every time step, select a candidate male

³ $c^n(i, X)$ can be defined inductively as follows: $c^0(i, X) = \emptyset$ and $c^{n+1}(i, X) = c^n(i, X) \cup \{j \in X - C^n(i, X) \mid \neg \exists l \in (X - C^n(i, X)) \wedge d(l, i) < d(j, i)\}$.

⁴ Females are incrementally placed, hence the location of the fourth female, for example, will be the same in all simulations with four or more females with the same random seed. This is to allow analyses of females across different male-female ratios.

Algorithm 1 Pseudo code of the model simulation algorithm.

```

Simulation(seed, maleList, femaleList)
  initializeMales(seed, maleList)
  initializeFemales(seed, femaleList)
  terminate  $\leftarrow$  false
  step  $\leftarrow$  0
  while  $\neg$ terminate do
    step  $\leftarrow$  step + 1
    for all  $f \in$  femaleList,  $m \in$  maleList do
      if withinMatingDistance( $f$ ,  $m$ ) then
        report_mated_and_remove( $f$ , femaleList)
        report_mated_and_remove( $m$ , maleList)
      end if
    end for
    for all  $f \in$  femaleList do
      updateState( $f$ )
    end for
    terminate  $\leftarrow$  checkTerminationConditions()
  end while

```

according to their strategy π (and strategy parameters n) and then approach the selected male at their *velocity* [3]. This sequence models the female frogs' behavior of sampling the males, selecting a potential mate, and leaping towards him [11]. The female's heading angle α is updated according to the direction to the chosen male and the female's new position $\langle x, y \rangle$ is updated based on the female's velocity v and heading α . At every step, for every male and female agent, their mating distance is compared to the mating range (*withinMatingDistance*): if a female is within d_{mate} of a male, both are reported as mated and removed from their respective lists (*report_mated_and_remove*), otherwise the female state is updated (*updateState*) (there is no need to update the male state because males neither move nor change their pulse number). Because there are always fewer females than males in all of our simulations [22], the termination condition for the simulation depends on the females' mating strategy: the simulation ends when either all females have mated (as will always be the case in *bestofn*) or when no more males above the female *min-threshold* θ are left (*checkTerminationConditions*), in which case none of the remaining females will ever mate.

3 Results

We ran 100 simulations with different random initial conditions (based on different random seeds) for each point in the multidimensional parameter space given by the free model parameters for a total of almost 1 million simulations. An analysis of variance (ANOVA) of the results with *number of females* (nf), *male pulse number* (pn), *strategy* (strat) and *strategy parameter* (sp) as independent variables, and *male quality* as dependent variable, shows highly significant main effects for all four variables, highly significant two-way interactions (except for $nf \times pn$, which was not significant as

Variable	Df	F value	Pr(>F)	Variable	Df	F value	Pr(>F)
nf	1	406.17	<.001	nf×sp	1	289.73	<.001
pn	1	1098300	<.001	pn×sp×strat	1	1028.2	<.001
sp	1	168090	<.001	nf×sp×strat	1	248.73	<.001
strat	1	8384.5	<.001				
nf×strat	1	265.25	<.001	nf×pn	1	1.12	.29
pn×strat	1	3765.2	<.001	nf×pn×strat	1	0.002	.96
sp×strat	1	10972	<.001	nf×pn×sp	1	0.72	.39
pn×sp	1	45679	<.001	nf×pn×sp×strat	1	0.01	.92

Table 2. The results of the full ANOVA model for average mated male pulse number as dependent variable (see text for details). The bold-face values are highly significant p-values.

expected), and two highly significant three-way interactions (pn×strat×sp, as well as nf×strat×sp); the four-way interaction was not significant (see Tab. 2).

Overall, the average quality of mated males using *best-of-n* is sensitive to the male-female sex ratio (Fig. 1 top), different from *min-threshold* where females do not mate below their threshold (leading to no matings in setups where the *min-threshold* exceeds the male pulse number). Both strategies show (almost) linear increase in mated male quality as a function of average male pulse number (Fig. 1 middle), with *best-of-n* having a steeper slope than *min-threshold*.

To be able to compare the two strategies directly, we introduce the notion of “dominance” where a strategy S with parameter value set P is said to *dominate* a strategy T with parameter value set Q if there exists a parameter value p for strategy S such that for all parameter values q for strategy T it is the case that S_p (i.e., S with parameter value p) leads to significantly higher performance (at a given α level) than T_q (i.e., T with any of its parameter values q); symbolically, $\exists p \in P \forall q \in Q \text{ Perf}(S_p) >_{\alpha} \text{Perf}(T_q)$, where $\text{Perf}(S_p)$ is the performance of S with parameter value p (in the mating task) and $>_{\alpha}$ denotes a statistically significant ordering at the α level (e.g., p-values $< \alpha = 0.05$ in a paired t-test). This notion of dominance is of particular interest from an evolutionary perspective because a dominant strategy is one that will likely evolve in competition with other strategies (because there is no parameter value for the non-dominant strategy that will lead to even equal performance). Comparing the dominance of *min-threshold* and *best-of-n*, we can see (Fig. 1 bottom left) that for average mated male quality *min-threshold* dominates *best-of-n* for most male pulse number and male-female ratios, only leaving the small area for the highest average male pulse number and low to medium male-female ratios for *best-of-n* to dominate.⁵ Moreover, *min-threshold* is also superior in terms of time-to-mating (Fig. 1 bottom right), with no place for *best-of-n* to dominate. Note, however, that both parameter spaces have areas where neither strategy dominates.

⁵ Note that the small region of domination for *best-of-n* seems to be in conflict within the top plots of Fig. 1 as *min-threshold* seems to lead to overall better average mated male quality than *best-of-n* for all sex ratios. However, the numbers for *min-threshold* are as high because in the averages across the 100 random conditions we excluded those runs where *min-threshold* did not lead to any mating. Yet, in the dominance plots those simulations are taken into account in the statistical comparison.

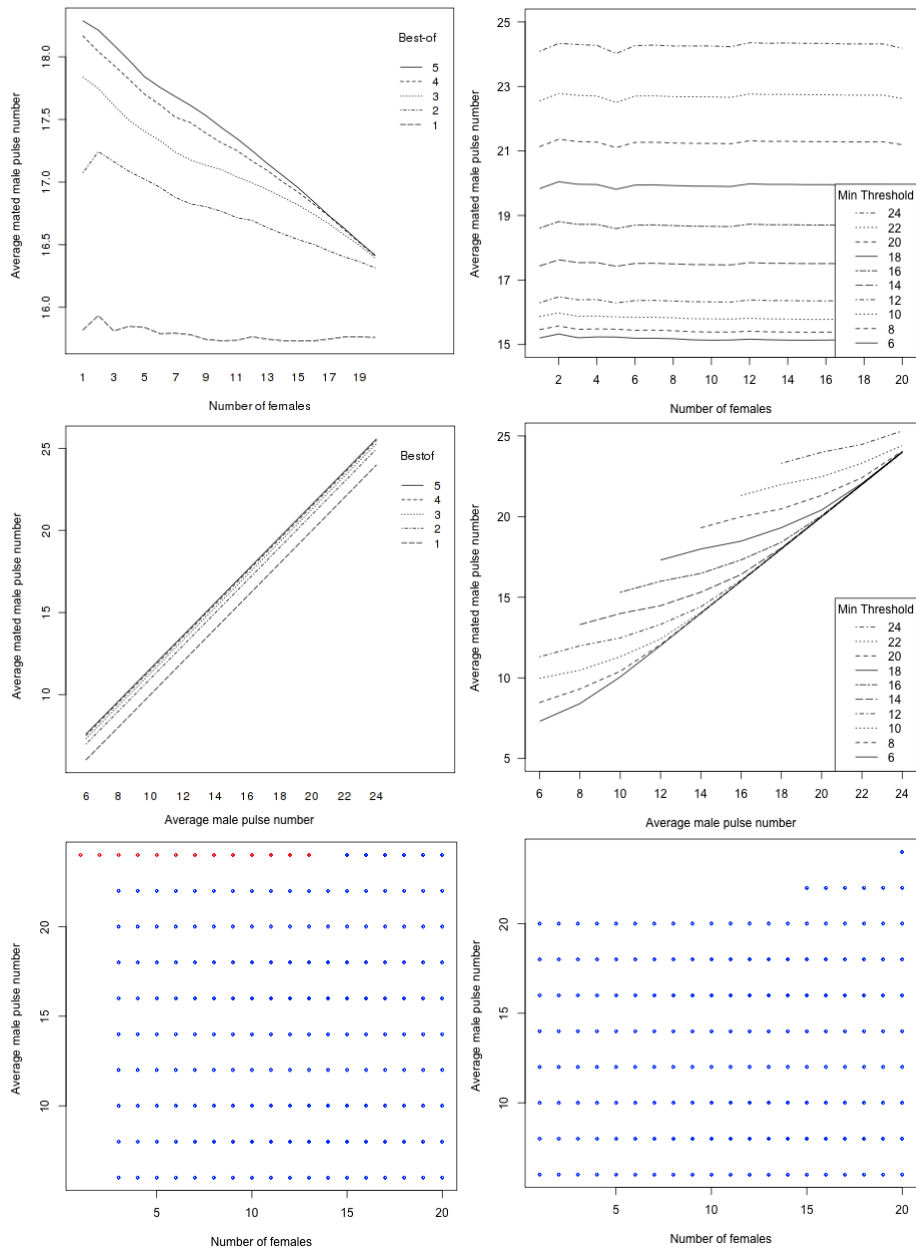


Fig. 1. Interactions for *best-of-n* (top) and *min-threshold* (middle) for average quality of mated males. The missing line segments in *min-threshold* (middle right) for some x-values indicate that there were scenarios without matings because *min-threshold* exceeds the male pulse numbers. The bottom shows dominance plots for *best-of-n* (red) and *min-threshold* (blue) for average male quality (bottom left) and average time-to-mating (bottom right).

4 Discussion

The above results suggest that the *min-threshold* strategy is very attractive from an evolutionary perspective. Females should be able to adjust their level of choosiness, given the lack of predictability in available mates and other aspects of natural environments [1]. The *min-threshold* strategy allows animals to change the threshold without changing the strategy itself, while requiring little complexity in terms of the cognitive architecture. In fact, empirical evidence in female frogs suggests that thresholds are not set via an active cognitive process (e.g., not via comparison of memories of calls heard in the past), but by hormonal changes [15]). This may explain why female frogs sometimes do not find mates – hormone levels may vary independently of the quality of the male population. On the other hand, the memory and neural integration requirements of *best-of-n* (e.g., in the case of $n = 5$) would be substantial, requiring females to remember the quality and location of males heard in the past [13].

The *min-threshold* strategy should also be adopted when the costs of comparing multiple mates is high [24]. Our simulation included no costs to sampling. Therefore, our study shows that the *min-threshold* strategy can be superior even in an environment without sampling costs. Another critical aspect is the time an animal spends searching for a mate. Not only are energy resources used during the search, but the individual may be at greater risk (e.g., from predation) and/or physiological processes might limit fertile times [14]. A unique feature of our spatially-explicit model is that time-to-mating is an outcome of the simulation (rather than a cost predicted a priori).

So why is it then that there is empirical evidence for *best-of-n* when *min-threshold* is superior in all the above respects? We believe the answer might lie in the fact that female treefrogs are usually only present at the breeding site on the night they mate and lay eggs. Decisions made on a single night will thus have significant impact on male fitness. And if a female’s threshold is set too high so that none of the males in the swamp can meet it, she will not be able to mate. This is the point where switching strategies might help, i.e., if a female even after lowering her threshold over time can still not find an eligible male, then switching to *best-of-n* (for $n > 1$) will at least guarantee that she will find a partner close to the (remaining) male population’s average pulse number (Fig. 1 top left). Mating with one of the remaining “average males” might in the end still be better than not mating at all, for females can only mate over a very limited time period, or they lay their eggs unfertilized. If females did switch strategies for the above reason, then it would not be surprising that some past empirical studies have found female choices to be consistent with the *best-of-n* strategy.

5 Related Work

Female choice has been extensively studied in a variety of scenarios, ranging from simulated mating strategy in animals such as fruit flies [16] to humans [21, 12, 5]. In the context of frogs, for example, Baugh and Ryan [2] investigated the propensity of a female to follow one mate selection strategy versus another. Tárano [23] researched the spacial orientation of male treefrogs during mating time. Our research leverages such empirical work to build models of our agents and the factors that play a critical role in the mating scenario.

There have also been attempts using neural network simulations to understand general mechanisms dictating mating preferences based on evolved sensory bias. Fuller [8], for example, shows modest connections between sensory bias and mate selection. Similarly, our work explores the range of sensory bias level (*min-threshold*) of female treefrogs when selecting a mate based on male call features. However, our study is less focused on how such biases develop and more focused on the ramification of such biases on overall utility of the resulting mate selection strategy.

While these studies focus on different aspects and properties of the mate choice at different levels of detail for different reasons, our study is the first that investigates female choice in the context of treefrogs in great detail over a large parameter space in order to contribute to the resolution of an open biological question, namely which strategy – *min-threshold* or *best-of-n* – female treefrogs might use to select their mates.

6 Conclusion and Future Work

The spatially-explicit frog mating simulation provides a unique and powerful method for testing predictions about mate choice behavior. The comprehensive investigation of two female choice strategies, *min-threshold* and *best-of-n*, across a large parameter space demonstrated that *min-threshold* is a superior strategy with respect to average mated male quality and time-to-mating. The main downside of *min-threshold* seems to be the lack of mating in cases where male call rates are lower than the female's threshold. We speculated that frogs might at some point switch strategies in order to be able to mate at all, which would explain the apparent inconsistency found in the empirical data. With the current results in hand, it is now possible to design empirical experiments with real frogs and arrays of speakers mimicking male callers in order to test specific predictions of behavior in a complex environment.

In the future, we plan to extend the agent-based model in several ways. For one, we only investigated one male distribution here, but it might be interesting to see if the above results will still be valid for other possible male (and also female) distributions. Moreover, we will also extend the model to include a male aggression model together with strategies for handling aggressive encounters (e.g., based on our previous general aggression model [20]). Finally, it would also be interesting to investigate evolutionary scenarios with multiple generations of frogs and possibly additional female strategies in order to compare the outcomes to the results of this study.

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