Following Strategies Reduces Accidents, but Makes Outcomes Worse: Evidence from Simulated Treefrog Mating Scenarios

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Abstract

Accidental matings happen in real environments where females end up with males they did not choose. In this paper, we investigate the frequency and changes in mated male fitness in accidental matings specifically in the context of the female choice of the gray treefrogs *hyla versicolor* based on the *best-of-n* and *minthresh strategy*, which are both hypothesized to be widely used in nature. Theoretical considerations as well as results from agent-based model simulations show how and why accidents occur and how the two strategies lead to different accident rates and reduced fitness values of the mated males.

Introduction

Mate choice is a biological selection process that is a critical determinant of the fitness of a species (Welch et al., 1998). Hence, much work in biology has focused on choice strategies, in particular, female choice strategies, and compared the utility of their outcomes, i.e., which strategy fares better based on the selection of the mate (Baugh and Ryan, 2009). However, little work has investigated the negative effects of such strategies when the chosen mate is not the one that ends up mating. This can happen, for example, when an impostor gets to mate instead of the chosen mate, or when an accidental mating occurs.

In this paper, we are particularly interested in investigating the negative outcomes caused by accidental matings in a biologically motivated mating task and compare two main female choice strategies from the literature with respect to the frequency of such accidents as well as the quality of the mates. Specifically, we will investigate how the fitness of male treefrogs changes as a results of accidental matings based on the *best-of-n strategy* (Janetos, 1980) vs. the *minthresh* strategy (Jennions and Petrie, 1997).

The rest of the paper is structured as follows. We start with background information about the task and introduce formal definitions of both strategies, followed by some facts about accidental matings for each strategy. Then we introduce the experimental setup, including the parameter space we investigated, followed by a presentation of the results together with an analysis showing the influence of the param-

eters on the number of accidental matings and also on the fitness of the mated males. Next we discuss when and why accidental matings can happen for each strategy, including the reason why using strategies reduces accidents. Finally, the conclusion summarizes our discoveries and proposes extensions for future work.

Background and Definitions

In previous work (Scheutz et al., 2010), we have investigated two main mate selection strategies using the gray treefrog *hyla versicolor* as an animal model in a biologically plausible mating task where female treefrogs located at the edges of a swamp have to choose a male mate from among a set of calling males situated in the swamp. The first strategy, called *best-of-closest-n* or "best-of-n" for short, requires females to select the best male within the *n* closest males. While how "best" is evaluated in female choice depends on the specifics of the species under investigation, in gray treefrogs females are attracted to the call quality of male callers (Gerhardt, 1994). In particular, the *pulse number* of a male call is a major determinant of the quality of a male treefrog, and this quality has, in fact, been linked to the fitness of the females' offspring (Welch et al., 1998).

The other strategy we have investigated in the past, *closest-above-minimum-threshold* or "min-threshold" for short, requires female treefrogs to select the closest male caller with a call pulse number greater than a *minimum quality threshold* θ. As with the first strategy, females listen to male callers in the swamp and then pick a caller based on the strategy's recommendation. With both strategies, the females sitting at the edges of the swamp will then start moving *in a straight line directly towards* the chosen male and when she arrives at the caller's location will mate with the male.

Next, we will make these notions formally precise. Let $D(f, m)$ denote the straight-line distance between a female f and male m treefrog in the swamp. Let *MALE* be the set of all males in the swamp and *FEMALE* the set of all females at the edges of the swamp, and let m_{pn} denote the pulse number of male $m \in$ *MALES*. Define the set of closest

agents from a given set X to a given agent i as $c(i, X) = \{j \in X | \neg \exists k \in X[D(i, k) < D(i, j)]\}$ and we let $c^n(f, X)$ denote the set of the n closest agents from set X with respect to the location of female f.

Then we can define both strategies formally as in Scheutz et al. (2013):

- *best-of-n.* The selected male agent is $\underset{m \in c^n(f, MALE)}{\operatorname{argmax}} (m_{pn})$ for the female f, i.e., the male with highest pulse number in the set of the closest n males.

- *minthresh.* The selected male agent is $\underset{m \in c(f, \{l \in MALE | l_{pn} \geq f_\tau\})}{\operatorname{argmax}} (m_{pn})$, where f_θ is the minimum threshold of female agent f, i.e., the male with the highest pulse number above the minimum threshold among the closest males.

In our past work, we used an agent-based modeling and simulation environment to investigate various tradeoffs among those strategies, which allows us to both test behaviors observed in empirical experiments and formulate hypotheses for further evaluation in the real world. In Scheutz et al. (2010), for example, we used the simulation environment to determine whether one of the two strategies clearly *dominated* the other, i.e., whether there were parameter settings for *best-of-n* vs. *minthresh* such that one strategy consistently showed better average mated male quality than any of the others. The results from extensive simulations of larger parameter spaces showed that even though females using the *minthresh* strategy perform better for much of the parameter space compared to females using *best-of-n*, *minthresh* did not dominate *best-of-n* because there are regions of the explored parameter space where *best-of-n* performed better than *minthresh* for some parameter values.

In other work, we investigated how the two strategies would fare when males were re-positioning themselves in order to create calling sites that could increase their chances of being chosen by females (Scheutz et al., 2013). In this extended setting, males can either call remaining stationary in their chosen position or wander, leaping through the swamp to find a better location for calling that would improve their chance of mating. We hypothesized that staying near a high-quality male caller would increase the chance of mating for a male for two reasons. First, the high-quality caller will likely attract several females that will independently approach him, but once he mates with a female, he will stop calling. Thus, the males near him could become of interest to close-by females that were attracted to the location by the high-quality male. Second, when a female is leaping to the high-quality male, she might accidentally bump into another lower quality male that is close to the high-quality male, but directly in her approach trajectory. To simulate the wandering behavior, we allowed male frogs to use the same two strategies used by females, i.e., either *best-of-n* or *min-threshold*, to

evaluate the quality and location of fellow male callers. The simulation results showed that mate quality overall improves when males are allowed to reposition themselves compared to non-repositioning males, and that this improvement was greater when females and male wanderers use the same strategy (Scheutz et al., 2013). However, it was unclear to what extent these differences were due to females in the area picking their second (or third, etc.) choices after the high-quality male already mated, and to what extent the fitness was actually lower than it could have been due to *accidental matings*, i.e., females bumping into males on their way to the chosen mate.

Specifically, we are now interested in determining the extent to which females mate by accident, i.e., the *frequency of accidental matings*, and the *average fitness of the accidentally mated males* compared to frequency of non-accidental matings and the average fitness for the chosen and mated males. These tradeoffs are not only important for understanding female choice in the context of treefrog matings, but also for evaluating the fitness of these strategies in general biological domains, at least for two reasons: (1) accidental matings could have very negative if not detrimental consequences for females and offspring, hence accidental mating frequency matters; yet, (2) lower quality mates, even though they might have negative consequences in the short term, might be able to preserve the variety in the gene pool in the long term and thus be overall positive for the species. We will, in the following, start with some general observations about accidental matings based on the definitions of the two strategies and then move towards agent-based simulations to be able to quantify tradeoffs that cannot be predicted based on general principles.

Facts about Accidental Matings

Start by defining an *accidental mating* as any mating that occurred involving a male that the female did not select based on her female choice strategy. Note that accidental matings can occur with both strategies when a female is moving towards a chosen male and ends up bumping into another non-chosen male while traversing the swamp.[1] However, accidental matings can also happen when none of the remaining males' call qualities meet the minimum threshold of the remaining females in the swamp using the *minthresh* strategy. For in that case, females will leave the swamp and might also bump into a lower-quality male by accident.

Definition Let m be a male frog and f be a female frog. We denote $F(m)$ as the fitness of the male frog m, and $D(f, m)$ as the distance between a female f and male m. Let d_{mate} be the *mating distance*. So, in order for a mating to occur, $D(f, m) < d_{mate}$.

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[1]Note that treefrogs in that case will always mate, but that it is certainly possible to define a probability of accidentally mating in such cases and that this probability will then determine accidental mating frequency and male quality.

In the following, we will report a few facts about accidental matings. We will let

Fact 1 *Let n be the parameter for best-of-n strategy for all females in* FEMALE. *No female using* best-of-n *with $n = 1$ can mate by accident.*

Proof Suppose f is an accidentally mated female with $n = 1$, that m_{ac} is the male involved in the accidental mating, and that m_b the male chosen by f (both males in *MALES*). Then by definition, $D(f, m_{ac}) < d_{mate}$ and $D(f, m_b) > d_{mate}$. Therefore, $D(f, m_{ac}) < D(f, m_b)$. However, by definition of the *best-of-n* strategy for $n = 1$, the chosen male m_b is the closest male, contradicting $D(f, m_{ac}) < D(f, m_b)$.

Fact 2 *Let θ be the parameter for the* minthresh *strategy for females in* FEMALE. *Then no accidental mating can occur for males $m \in$ MALES with $F(m) > \theta$.*

Proof If $F(m) > \theta$ for all $m \in$ MALES, then by definition of *minthresh* each female using the strategy with θ will pick the closest male. Hence, there cannot be any male between the female and the chosen one (which would be closer).

Fact 3 *Let n be the parameter* for best-of-n strategy *for all females in* FEMALES. *For* best-of-n strategy, *accidental matings lower the average fitness of the mated males.*

Proof Consider the subset $M_f \subseteq$ *MALES* of all males that are the n closest to a given female f and let $m_b = argmax\{F(m)|m \in M_f\}$. Suppose a male m_{ac} accidentally mated with f. Then $D(m_{ac}, f) < m_b$, since females have a direct straight-line approach to males and thus $m_{ac} \in M_f$. By definition of *best-of-n*, $F(m_{ac}) < F(m_b)$. Therefore, the average mated pulses with accidents is strictly lower than without.

Fact 4 *Let n be the parameter for* best-of-n strategy *and let θ be the parameter for minthresh strategy. Furthermore, let $M_f \subseteq$ MALES be the subset of all males that are the n closest to a given female $f \in$ FEMALES and let $M_t \subseteq$ MALES the subset of all males that have pulses per call higher than the threshold θ. Then for any female f the worst fitness of an accidental mate for* best-of-n *is equal to the worst fitness of a male $m \in M_f$, while for the minthresh strategy the worst fitness of an accidental mating can be a male $m \notin M_t$ (i.e., any male m with $F(m) < \theta$).*

Proof Assuming a male m_{ac} accidentally mates with f. For *best-of-n*, $m_{ac} \in M_f$ because any accidentally mated male must be closer than the chosen male in M_f, which, in the worst case, has the lowest fitness in M_f. For *minthresh*, the chosen male is the closest with $F(m) \geq \theta$. Hence, any closer male must have worse fitness, hence $m_{ac} \notin Mt$.

The above facts provide a rough qualitative characterization of the differences between the two strategies with respect to accidental matings. We know that accidents can only lower the average mated male fitness, but it is unclear how the two strategies compare quantitatively. Hence, we

next describe the experimental setup of our agent-based simulation model that was used to explore the tradeoffs between the two strategies quantitatively.

Experiments

We built our present investigations on our previous agent-based models (Scheutz et al., 2010, 2013), adding various mechanisms for detecting and recording the different types of accidental matings. To briefly summarize the model, we assume that female agents are initially placed at the edges of a rectangular simulated 2D swamp. For simplicity, we assume that male frogs call all the time and never change their call rate or the quality of their call. This male's call is determined by a pulse number and this is the only measure of the fitness of mates (i.e. more pulses are better). We also assume that females can hear and discern the call qualities of all male frogs and make moment-by-moment decision about where to go. Since males never change their calls, a female will move towards a chosen male as long as the male is calling. When a chosen male stops calling because he mated (which is the only reason why males will stop calling in our model), she will pick another male and start moving towards the new male. Whenever any male is with mating distance, both male and female will mate.

Fixed Parameters

We assume a realistic swamp size of $10m x 25m$ and a frog size of about $5cm$ in length. Furthermore, we assume each female frog moves at a fixed speed of $1.86cm/sec$ when approaching a male and at $1.44cm/sec$ otherwise. We set the mating range to $4cm$ and always use 25 stationary males placed according to a Gaussian distribution with means in the center of the swamp and standard deviations half the distances to the edges. All females are placed uniformly on the edges of the swamp and always followed a single given strategy with fixed strategy parameters. For details about the simulation model and the simulation update algorithm, which is a straight-forward cycle-based discrete event simulation, see (Scheutz et al., 2010).

Varied Parameters

We vary the number of females – 5, 10, 15, or 20 – initially placed on the swamp's edges. We also vary male call rate based on Gaussian distribution means 6, 12, 18, and 24 with a fixed standard deviation of 2. We consider three different female strategies: *best-of-n* with its parameter $n \in \{1, 2, 3, 4, 5\}$ and *minthresh* with $\theta \in \{6, 12, 18, 24\}$. Finally, we also add a third strategy for comparison, the *random* strategy where a female randomly chooses a male and keeps approaching that male until she either mates with him or needs to pick another random male to approach. Note that the *random* strategy can be used as a baseline compared to the two other strategies because we would not expect any difference in the average fitness of accidentally or

non-accidentally mated males when females following the random strategy.

The varied parameters thus span a "parameter space" which we fully explored running 100 simulations with distinct initial conditions for each point in the space for a total of 16000 simulations. The dependent variables were the number of accidental and non-accidental matings as well as the fitness of the accidentally and non-accidentally mated males.

Results

Table 1 shows the overall simulation results for each of the three strategies as well as each strategy parameter for *best-of-n* and *minthresh* averaged of the male call rates and the number of females: column 1 shows the average fitness of mated males, column 2 shows the average fitness of non-accidentally mated males, column 3 shows the average fitness of accidentally mated males, and column 4 shows the frequency of accidental matings.

As can be seen, the random strategy had the highest mean of accidental matings per simulation. Furthermore, although *minthresh* had the lowest mean of accidental matings among the three strategies, it also had the highest influence of accidental matings on the fitness, i.e., when a accident happens, it reduces the fitness drastically.

Strategy	MM	NAMM	AMM	Freq
random	14.901	14.911	14.803	0.940
best-of-n	15.865	15.909	14.474	0.329
best-of-1	14.847	14.847	NaN	0.0
best-of-2	15.813	15.856	14.032	0.297
best-of-3	16.107	16.150	14.725	0.384
best-of-4	16.237	16.300	14.487	0.456
best-of-5	16.319	16.392	14.536	0.509
minthresh	16.985	18.424	10.661	0.210
minthresh 6	15.187	15.206	3.883	0.064
minthresh 12	17.045	18.270	7.272	0.166
minthresh 18	18.397	21.523	10.449	0.259
minthresh 24	18.617	25.267	13.531	0.352

Table 1: Mean Mating (MM), Non-Accidental Mean Mating (NAMM) and Accidental Mean Mating (AMM) fitness and accident frequency for each strategy and parameter.

To compare the main effects of each independent variable on accidental matings, we performed two ANOVAs with *strategy* (s), *number of females* (nf) and *parameter value* (p) as independent variables, and the *number of accidental matings* (nam) and *average fitness* (af) as the dependent variables for each ANOVA. The results of the ANOVA for the dependent variable nam in Table 2 shows a significant main effects of all independent variables on the number of accidental matings, as well as significant two-way and three-way interactions. This confirms the intuitive expectation that using female strategies drastically reduces the average number of accidental matings, the reasons for which we will discuss in the next section.

Of the three two-way interactions, the effect of parameter changes of strategy performs is to be expected – increasing n will increase the average mated male fitness and so that increasing θ, albeit to different degrees (e.g., the increase is generally steeper with *minthresh* because a minimum threshold is imposed, see also (Scheutz et al., 2010)). Similarly, the interactions between strategy parameters and females, strategy and females, and the three-way interactions involving all independent variables are to be expected: an increase in the number of females leads to different increases in average mated male fitness for the three strategies based on the different parameters. However, as the number of females increases, so does the probability of accidental matings. Critically, as shown in Figure 1, the slopes of the two strategies are lower than that of the random strategy, thus confirming that both strategies, *minthresh* and *best-of-n* significantly reduce the number of accidental matings, with *minthresh* overall doing better than *best-of-n*.

The ANOVA in Table 2 shows that there was a significant main effect of the strategy parameter on the number of accidental matings. As shown in Table 1, as the parameter value increases, it also increases the number of accidental matings. Specifically, the value of θ in the *minthresh* strategy determines whether a female can find a potential mate in the swamp or whether she will leave the swamp without mating. Since males are distributed based on a Gaussian distribution centered in the middle of the swamp, it is less likely for females to accidentally mate on their way out of the swamp compared to the chances of accidentally mating based on the *best-of-n* strategy. While we argued previously that no accidental matings are possible with $n = 1$, the average length of the path traversed by each female before she can mate also significantly increases as n increases, and so does the probability of her accidentally mating.

Variable	Df	F value	Pr(>F)
s	1	193.392	<.001
nf	1	1026.013	<.001
p	1	528.230	<.001
s:nf	1	26.981	<.001
s:p	1	602.676	<.001
nf:p	1	113.222	<.001
s:nf:p	1	150.289	<.001

Table 2: ANOVA table for the model "$nam = s * nf * p$" where "nam" is the number of accidental matings, "s" is the strategy, "nf" is the number of females and "p" is the parameter of the strategy, using the best-of-n strategy.
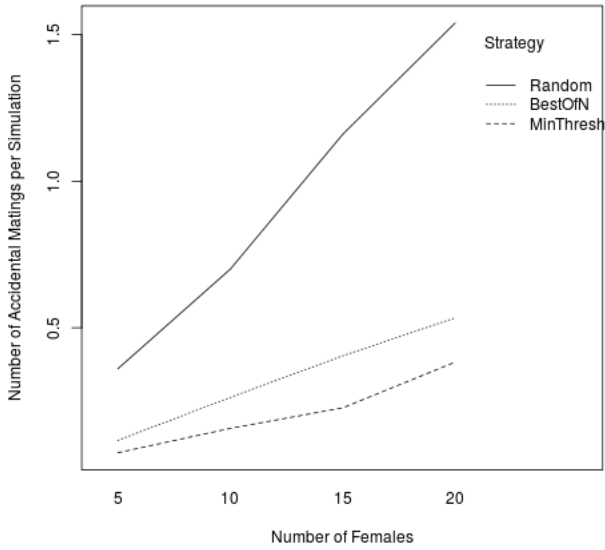
Figure 1: Interaction between the number of females and the number of accidental matings on the three strategies.

Variable	Df	F value	Pr($>$F)
s	1	270.662	$<.001$
nf	1	0.0082	.928
p	1	246.038	$<.001$
s:nf	1	4.870	.027
s:p	1	11.285	$<.001$
nf:p	1	0.164	.685
s:nf:p	1	0.010	.919

Table 3: ANOVA table for the model "$af = s * nf * p$" where "af" is the average fitness of the accidental matings, "s" is the strategy, "nf" is the number of females and "p" is the parameter of the strategy, using the best-of-n strategy.

Examining the ANOVA for the average fitness of accidental matings (af) in Table 3, there was a significant main effect of the strategy on the results. This suggest that even though strategies reduce the number of accidental matings, the average fitness of the accidentally mated males is lower than that of the non-accidentally mated males as shown in Figure 2. This is as expected because given the strategies' boost to the average mated fitness compared to the random strategy, one would expect accidental matings to yield lower average fitness values in exchange.

In addition, the ANOVA shows a significant main effect of strategy parameter on the average fitness of accidental matings. This can be explained by the difference in fitness of the accidental matings for the *minthresh* strategy, because its parameter θ is an upper limit of the accidental matings (fitness of all accidental matings are less then θ). Thus, increasing the value of the parameter, will also increase the fitness of accidental matings, as shown in Figure 3.

Table 4 shows the influence of the number of females and the parameters of each strategy on the average accidentally mated male fitness. For the *best-of-n strategy* (except for $n = 1$), as the number of females increases, both the fitness of mated males and that of the non-accidentally mated males decrease. This sensitivity to the male-female ratio was originally shown in Scheutz et al. (2010) and is confirmed here: the same patterns emerges even when accidental matings are removed. In contrast, the *minthresh* strategy shows an increase in the fitness of the non-accidentally mated males as the number of females increases (as the changes of finding a higher valued female above the threshold increases with higher numbers of females).

Using PPC to denote the mean pulses per call and sd the standard deviation of those pulses for each male, occurring an accidental mating when a female is leaving the swamp is dependent of θ, PPC and sd. As shown in Scheutz et al. (2010), the distribution of pulses per call through the males in the swamp is done by a Gaussian distribution. Since the number of pulses per call was defined as an integer, the probability of existing a male with a value of pulses per call lesser than θ, if $\theta = PPC$ is ≈ 40.1. Therefore, if the male-female ratio is greater than 60.9, it is possible to having an accidental mating when the female is leaving the swamp. If $\theta < PPC$, then - for the interval that we tested ($2 * sd$) - all the females will always mate, therefore no one female will leave the swamp unmated. Finally, if $\theta > PPC$, then - again, for the parameters we tested - no one female will find a mate, therefore all accidental matings happen when the females are leaving the swamp.

Table 5 shows the influence of mean pulses per call on the fitness of the matings without remove the accidental matings and also after removing them. Again, changing the mean pulses per call does not have any influence in the *best-of-n strategy*, only increasing its value in 6. On the other hand, *minthresh* is influenced by mean pulses per call, because, as shown previously, the probability of finding a mate using this strategy is dependent of the value of its parameter and also the mean pulses per call. However, if you fix the value of θ and vary the value of PPC, maintaining the relation $\theta < PPC$, the only difference will be an increment of 6, as in the *best-of-n strategy*. For example, for $\theta = 6$ and $PPC = 12$, we have the fitness of mated equals to 11.846, if we look over $PPC = 18$, the same fitness of mated is 17.846, an increment of 6.

Discussion

It is a known fact that female treefrogs do not try to avoid males from other species of treefrogs (Gerhardt et al., 1994),

Strategy	5 Females		10 Females		15 Females		20 Females	
	MM	NAMM	MM	NAMM	MM	NAMM	MM	NAMM
random	14.851	14.865	14.851	14.861	14.935	14.941	14.968	14.979
best-of-1	14.788	14.788	14.836	14.836	14.861	14.861	14.903	14.903
best-of-2	16.171	16.215	15.889	15.937	15.716	15.762	15.475	15.512
best-of-3	16.607	16.658	16.289	16.328	15.967	16.014	15.565	15.599
best-of-4	16.830	16.900	16.471	16.541	16.075	16.133	15.571	15.625
best-of-5	17.014	17.103	16.574	16.658	16.102	16.163	15.586	15.644
minthresh 6	15.150	15.165	15.180	15.192	15.202	15.216	15.217	15.249
minthresh 12	17.724	18.236	17.130	18.255	16.850	18.280	16.542	18.308
minthresh 18	20.034	21.501	18.596	21.505	17.978	21.531	17.361	21.553
minthresh 24	21.493	25.281	18.909	25.242	18.033	25.270	17.258	25.273

Table 4: Mean Mating (MM) and Non-Accidental Mean Mating (NAMM) fitness for each strategy parameter and number of females in the swamp.

Strategy	6 PPC		12 PPC		18 PPC		24 PPC	
	MM	NAMM	MM	NAMM	MM	NAMM	MM	NAMM
random	5.918	5.929	11.896	11.906	17.896	17.906	23.896	23.906
best-of-1	5.851	5.851	11.846	11.846	17.846	17.846	23.846	23.846
best-of-2	6.816	6.859	12.812	12.855	18.812	18.855	24.812	24.855
best-of-3	7.111	7.154	13.106	13.148	19.106	19.148	25.106	25.148
best-of-4	7.241	7.305	13.235	13.298	19.235	19.298	25.235	25.298
best-of-5	7.325	7.398	13.317	13.390	19.317	19.390	25.317	25.390
minthresh 6	7.211	7.284	11.846	11.846	17.846	17.846	23.846	23.846
minthresh 12	5.963	12.667	13.210	13.285	17.846	17.846	23.846	23.846
minthresh 18	5.664	NaN	11.963	18.667	19.210	19.285	23.846	23.846
minthresh 24	5.664	NaN	11.664	NaN	17.963	24.667	25.210	25.285

Table 5: Mean Mating (MM) and Non-Accidental Mean Mating (NAMM) fitness for each strategy parameter and pulses per call (PPC).

thus sometimes inter-species accidental matings occur; however, often the hybrids are sterile (Johnson, 1963) or do not survive until sexual maturity (Schlefer et al., 1986). Although we modeled the simulation with only one species of treefrogs, the negative influence of accidental matings is also sustained on observations of their behavior in nature. Using strategies to select a mate is, therefore, overall beneficial in that it can drastically reduce the probability of an accidental mating to occur, as shown by our results. Moreover, while the *best-of-n* strategy leads to more accidental matings than the *minthresh* strategy, the accidents that happen using *minthresh* have a higher influence on the average mated male fitness than those that occur with *best-of-n*. Hence, we next analyze how and why these accidents occur.

Analysis: The Nature of Accidents

Figure 1 showed that the number of females has an influence on the number of accidental matings and that the use of a strategy to choose a male to mate significantly reduces the number of accidental matings, which we call the *strategy effect*. Furthermore, we call the fact the *minthresh* strategy has a lower number of accidental matings compared to the *best-of-n strategy* the *minthresh effect*.

Both effects can be explained by considering the probability P_a of an accidental mating to occur. In order to calculate P_a, we can define a vector L_f which in its i-th position contains 1 if and only if another male is on the path of f to the male m_i and 0 otherwise. To generate this vector, we can trace straight lines from f to all males in the environment and verify if the line intersects another male (within mating range). Let P_{random}^i be the probability of a male i be chosen by the random strategy, $P_{random}^i = \frac{1}{|MALE|}$ for all males in the swamp. Let $P_{bestofn}^i$ be the probability of a male in position i be chosen based on the parameter n on the *best-of-n* strategy. Finally, let $P_{minthresh}^i$ be the probability of a male i be chosen based on the parameter θ from the *minthresh* strategy. Generically, we denote $P_{strategy}^i$ the probability of
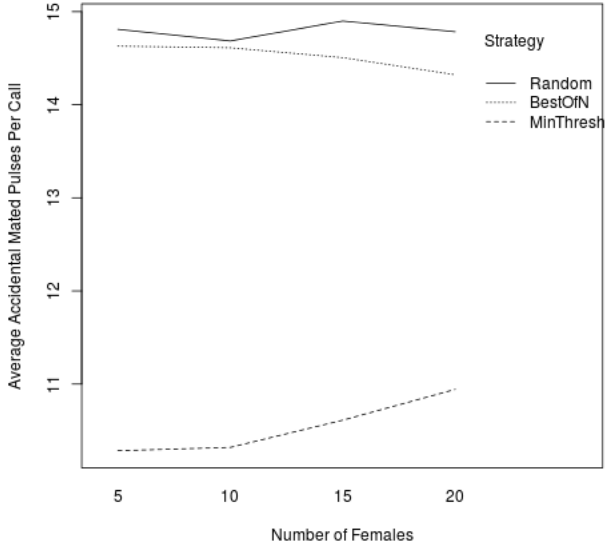
Figure 2: Interaction between the number of females and the fitness of the accidental matings on the three strategies.

Figure 3: Interaction between the parameters and the fitness of the accidental matings on the three strategies.

male i to be chosen by a *strategy*.

Given the state of the swamp at any point in time, the probability of a female accidentally mating with a male during the simulation is determined by $P_a = \sum_{i=1}^{|MALE|} (P_{strategy}^i \cdot L_f[i])$.

To elucidate the difference in P_a for distinct strategies, we consider two configurations of the swamp with just a slight change on the position of one male, as shown in Figure 4(a) and in Figure 4(b). Both figures contain one female f at the bottom and the three males closest to f. Let the fitness of the three males be $F(m_1) > F(m_2) > F(m_3)$ and let $D(f, m_{leftmost}) > D(f, m_{rightmost} > D(f, m_{central})$. The number of distinct arrangements of the three males with the different different fitness values is $3! = 6$.

Now consider the configuration in Figure 4(a). First, we need to define the vector L_f which represents the existence of another male on the path toward the chosen one. Let the first position contain the leftmost male frog, the second position contains the rightmost male frog and the third filled with the central frog in the environment. Thus, $L_f = \{0, 1, 0\}$.

For the *random* strategy, it is clear that, independently of which male has the best fitness, $P_{random}^i = \frac{1}{3}$. Consequently, $P_a = (\frac{1}{3} \cdot 0) + (\frac{1}{3} \cdot 1) + (\frac{1}{3} \cdot 0) = \frac{1}{3}$.

For the *best-of-n* strategy, we need to define the parameter n in order to calculate the probability of an accidental mating to occur. For $n = 1$, we showed in Fact 1 that accidental matings are impossible. Hence, for $n = 2$,
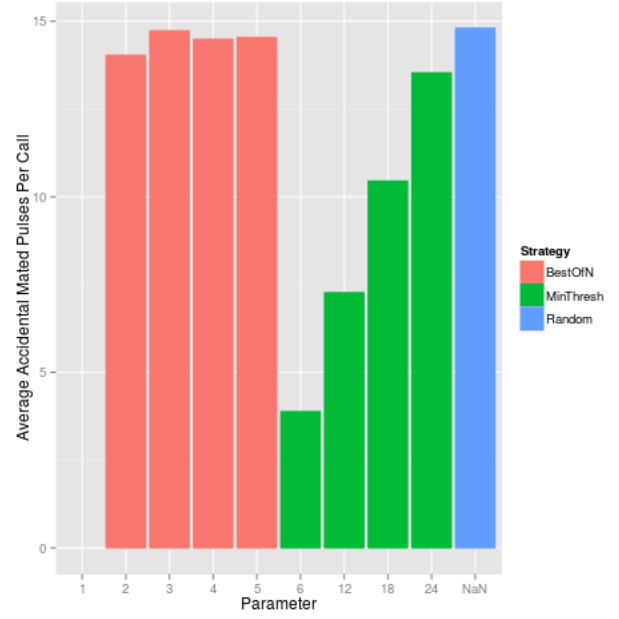
we can calculate the value of $P_{bestofn}^i$. First, selecting the leftmost frog, the probability of him being chosen is 0 because there are two other males that are closer to f. Now, selecting the rightmost frog, there are three distinct arrangements out of six possible ones in which he will be chosen: $(\{m_1, m_2, m_3\}, \{m_2, m_1, m_3\}, \{m_3, m_1, m_2\})$. Therefore, the probability of the rightmost being chosen is $\frac{1}{2}$. Finally, there are three distinct arrangements in which the central frog will be chosen $(\{m_1, m_3, m_2\}, \{m_2, m_3, m_1\}, \{m_3, m_2, m_1\})$, consequently the probability of the central frog being chosen is also $\frac{1}{2}$. As a result, for $n = 2$, $P_a = (0 \cdot 0) + (\frac{1}{2} \cdot 1) + (\frac{1}{2} \cdot 0) = \frac{1}{2}$. For $n = 3$, the probability of the rightmost being chosen is $\frac{1}{3}$, as is the one for the leftmost and the central one. Therefore, for $n = 3$, $P_a = (\frac{1}{3} \cdot 0) + (\frac{1}{3} \cdot 1) + (\frac{1}{3} \cdot 0) = \frac{1}{3}$.

On the other hand, for the *minthresh strategy*, we define $\theta = F(m_2)$, thus only two males have a fitness greater or equal than the threshold. Selecting the leftmost frog, the probability of him being chosen is 0 because for every male there exists at least one more with a fitness value greater or equal to the threshold, but that is closer to the female than the leftmost. Choosing the rightmost, we have two arrangements in which he will be picked: $(\{m_1, m_2, m_3\}, \{m_2, m_1, m_3\})$, thus the probability of him being chosen is $\frac{1}{3}$. Lastly, the central frog has a probability of $\frac{2}{3}$ of being chosen, or four arrangements: $\langle m_1, m_3, m_2 \rangle, \langle m_2, m_3, m_1 \rangle, \langle m_3, m_1, m_2 \rangle, \langle m_3, m_2, m_1 \rangle$. Therefore, $P_a = (0 \cdot 0) + (\frac{1}{3} \cdot 1) + (\frac{2}{3} \cdot 0) = \frac{1}{3}$.

In sum, $P_{a,random} = \frac{1}{3}$, $P_a^{n=2} = \frac{1}{2}$, $P_a^{n=3} = \frac{1}{3}$, $P_{a,minthresh} = \frac{1}{3}$. However, if we look at Figure 4(b), although the $P_{strategy}$ values are the same for every strategy, we need to define a new vector $L_f = \{1, 0, 0\}$, as a consequence, the probabilities P_a can be different. Hence, we get $P_{a,random} = (\frac{1}{3} \cdot 1) + (\frac{1}{3} \cdot 0) + (\frac{1}{3} \cdot 0) = \frac{1}{3}$, $P_a^{n=2} = (0 \cdot 1) + (\frac{1}{2} \cdot 0) + (\frac{1}{2} \cdot 0) = 0$, $P_a^{n=3} = (\frac{1}{3} \cdot 1) + (\frac{1}{3} \cdot 0) + (\frac{1}{3} \cdot 0) = \frac{1}{3}$ and $P_{a,minthresh} = (0 \cdot 1) + (\frac{1}{3} \cdot 0) + (\frac{2}{3} \cdot 0) = 0$.
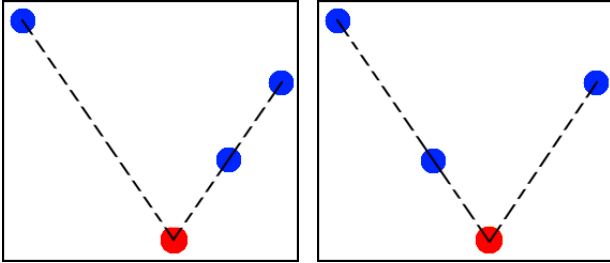

Figure 4: Two examples of different swamp states. The dashed lines represent distinct trajectories of the female treefrog and are used to create the L_f vector.

We now can compare the mean of the probabilities of accidental matings in the two configurations. For the random strategy, the mean will be $\frac{1}{3}$, for the *best-of-n* strategy using $n = 2$ the mean will be $\frac{1}{4}$ and using $n = 3$ the mean will be $\frac{1}{3}$. And for the *minthresh* strategy, the mean will be $\frac{1}{6}$. Therefore $P_{a,random} = P_a^{n=3} > P_a^{n=2} > P_{a,minthresh}$. Although the results of random and $n = 3$ were the same, it is clear that if the number of males in the swamp was greater than n, $P_{a,random}$ will be greater than any n showing then the *strategy effect*. If we compare the probabilities P_a^n and $P_{a,minthresh}$ we can verify the *minthresh effect* as well.

Conclusion and Future Work

Accidental matings happen in real environments where females end up with males they did not choose. In this paper, we have investigated the frequency and changes in mated male fitness in accidental matings specifically in the context of the female choice of the gray treefrogs *hyla versicolor* based on two main strategies hypothesized to be widely used in nature. Our simulation results showed that the *best-of-n* strategy had a less preferable, higher incident rate of accidental matings compared to the *minthresh strategy*, while also having a preferable, higher average mated male fitness. We demonstrated how and why these two dimensions trade off both based on strategy parameters and on the male-female ratio in the swamp when males are distributed in the swamp according to a Gaussian distribution.

As a next step, we intend to investigate how different male distributions in the swamp could have an impact on the results, i.e., in particular on the probability of females accidentally bumping into a non-chosen male. For example, we would expect that different distributions might change the

relative likelihood of accidental matings among the strategies (e.g., a uniform or inverse Gaussian male distribution might be an equalizer between *best-of-n* and *minthresh strategy* regarding the frequency of accidents). We are also interested in evaluating the accident rates when males are allowed to reposition themselves as previously investigated in Scheutz et al. (2013). For example, it is currently unclear where repositioning will increase or decrease accidents, but the overall expectation is that accidents can be increased based on the positioning strategy chosen by the males. In particular, one would expect that so-called "satellite males", i.e., males that do not call at all, might use a strategy that favors accidental matings (which is in their favor because they cannot be detected otherwise). Finally, it would be interesting to derive more detailed general principles about strategy-dependent accidental matings that might inform theories of female choice independent species-specific details.

Acknowledgements

References

Baugh, A. T. and Ryan, M. J. (2009). Female tungara frogs vary in commitment to mate choice. *Behavioral Ecology*, page arp120.

Gerhardt, H. C. (1994). Selective responsiveness to long-range acoustic signals in insects and anurans. *American zoologist*, 34(6):706–714.

Gerhardt, H. C., Dyson, M. L., Tanner, S. D., and Murphy, C. G. (1994). Female treefrogs do not avoid heterospecific calls as they approach conspecific calls: implications for mechanisms of mate choice. *Animal Behaviour*, 47(6):1323–1332.

Janetos, A. C. (1980). Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology*, 7(2):107–112.

Jennions, M. D. and Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, 72(2):283–327.

Johnson, C. (1963). Additional evidence of sterility between call-types in the hyla versicolor complex. *Copeia*, pages 139–143.

Scheutz, M., Harris, J., and Boyd, S. K. (2010). How to pick the right one: Investigating tradeoffs among female mate choice strategies in treefrogs. In *Proceedings of the Eleventh International Conference on Simulation of Adaptive Behavior - SAB 2010*, Paris - Clos Luc, France.

Scheutz, M., Smiley, M., and Boyd, S. (2013). Exploring male spatial placement strategies in a biologically plausible mating task. In *IEEE Symposium on Artificial Life*.

Schlefer, E. K., Romano, M. A., Guttman, S. I., and Ruth, S. B. (1986). Effects of twenty years of hybridization in a disturbed habitat on hyla cinerea and hyla gratiosa. *Journal of herpetology*, pages 210–221.

Welch, A. M., Semlitsch, R. D., and Gerhardt, H. C. (1998). Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, 280(5371):1928–1930.