Exploring Male Spatial Placement Strategies in a Biologically Plausible Mating Task

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The mate choice problem in treefrogs

Male treefrogs move at night into swamps where they establish "calling sites" from which the call to attract females

Females pick males based on the male call characteristics and move towards their chosen male...

Some relevant biological questions

- How do female treefrogs pick their mates?
- And based on how they do it, how can male treefrogs place themselves to improve their chances of mating?
- In general, these are open questions in biology as there are several possibilities in a spatially extended environment
- In particular, there are two main competing theories with different predictions for female choice, but also with supporting evidence (none for spatial placements):
- **The Minimum Threshold Strategy:** pick the (closest) male whose quality is above some minimum threshold
- **The Best-of-n Strategy:** pick the best of (the closest) *n* males

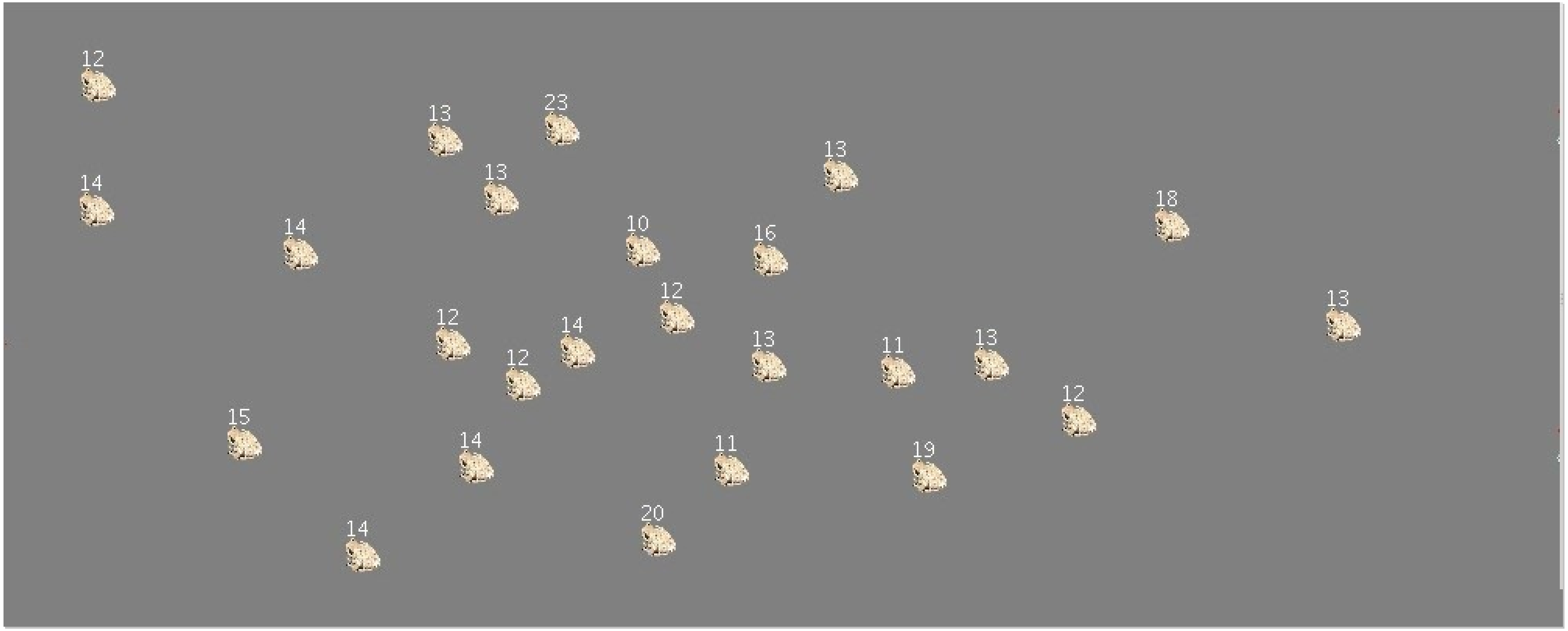
Mate choice as an optimization problem

- The mating problem can be viewed as an optimization problem in a partially observable competitive multi-agent environment
- Given *n* males and *m* females distributed in the environment where some of the males' locations and call qualities are observable (due to their advertisement calls), but locations of silent males and of any female are unobservable, find a mate choice policy for females (based on the perceivable call qualities only) to select a male mate and a male placement strategy (based on the assumed female choice policy) such that the average male call qualities of the mated males is maximized.
- Other optimization measures could be used (e.g., find the policy that will lead to the shortest path to male mates or mating time)

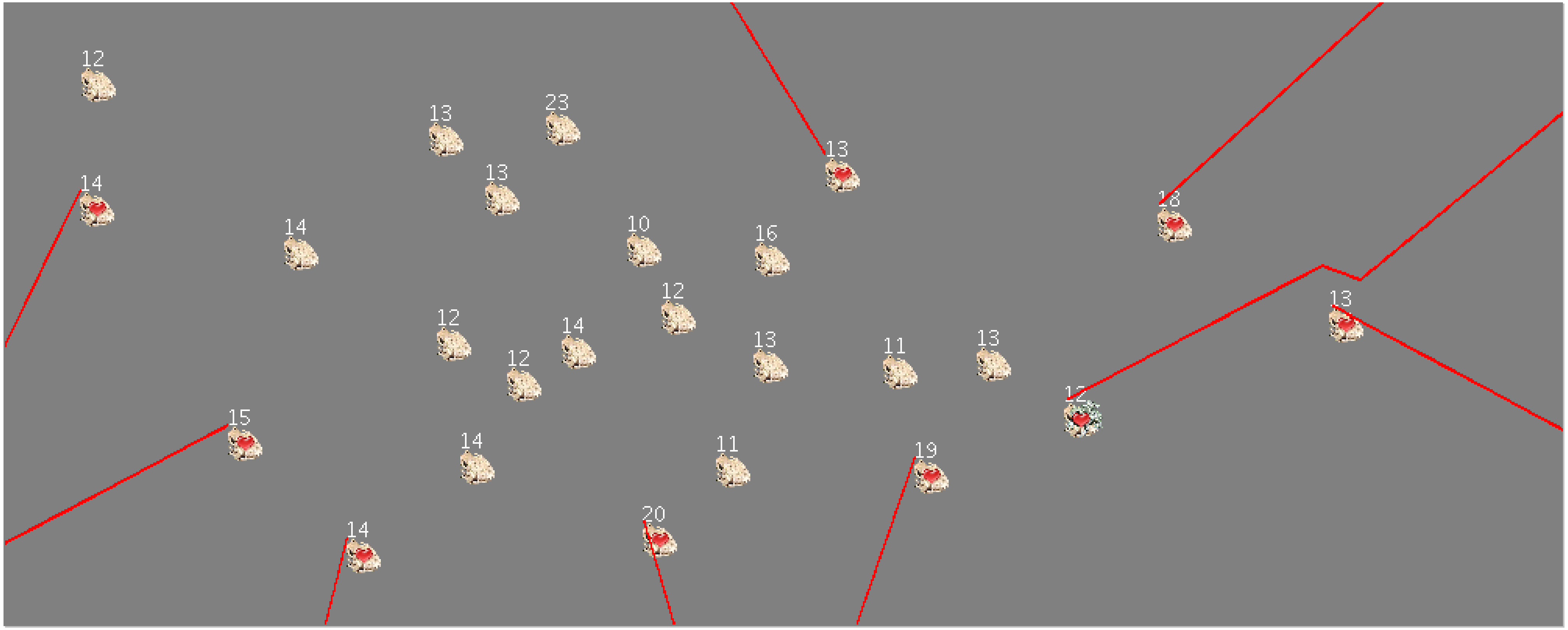
How do investigate the mate problem?

- The mate problem has both individual as well as environmental (including social) parameters
- Individual parameters include male call features and placement strategy, female sensory range and mate choice strategy, etc.
- Environmental parameters include the number and distribution of agents (and thus the distances among them)
- Given the number of parameters and the complex interplay among them, analytic solutions to the mating problem are not feasible (if not impossible)
- Hence, we use simulations of a spatially extended agent-based model to explore the trade-offs among the various individual and environmental parameter for pre-defined ranges

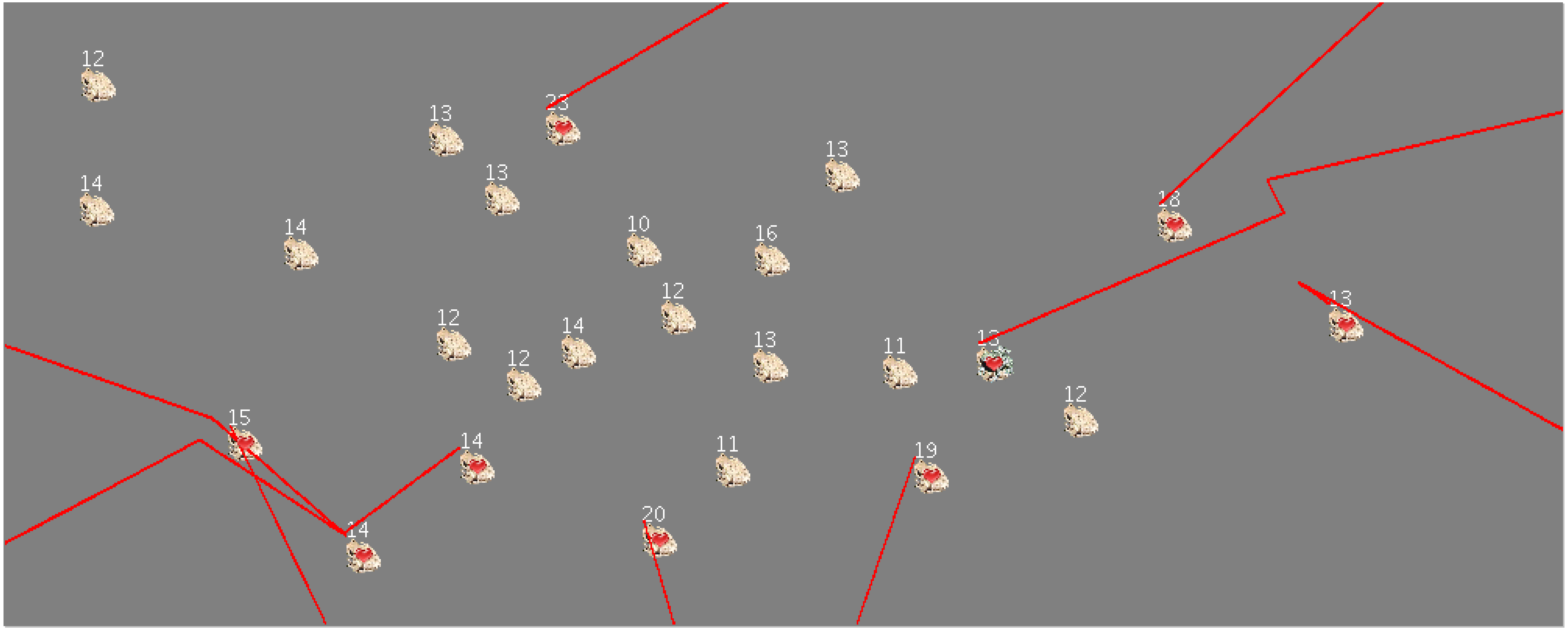
Males in the Swamp



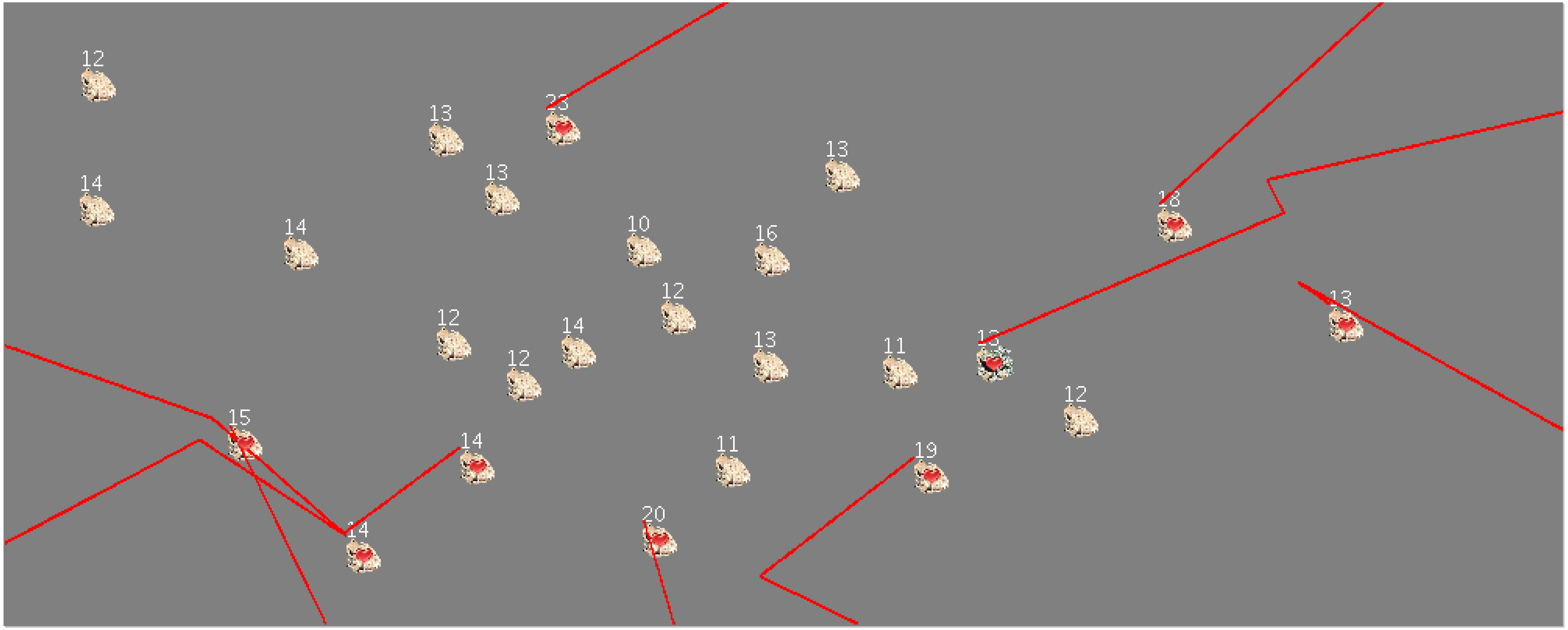
Trajectories for best-of-closest-1



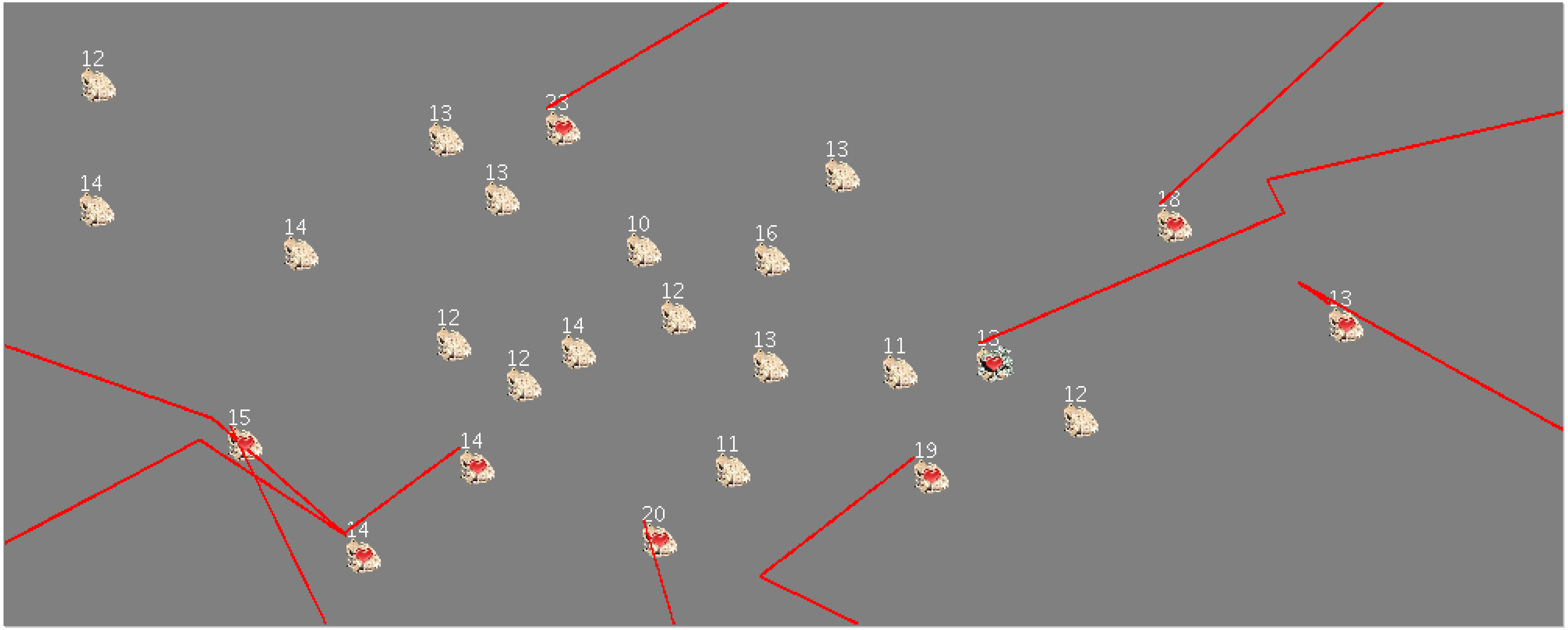
Trajectories for best-of-closest-2



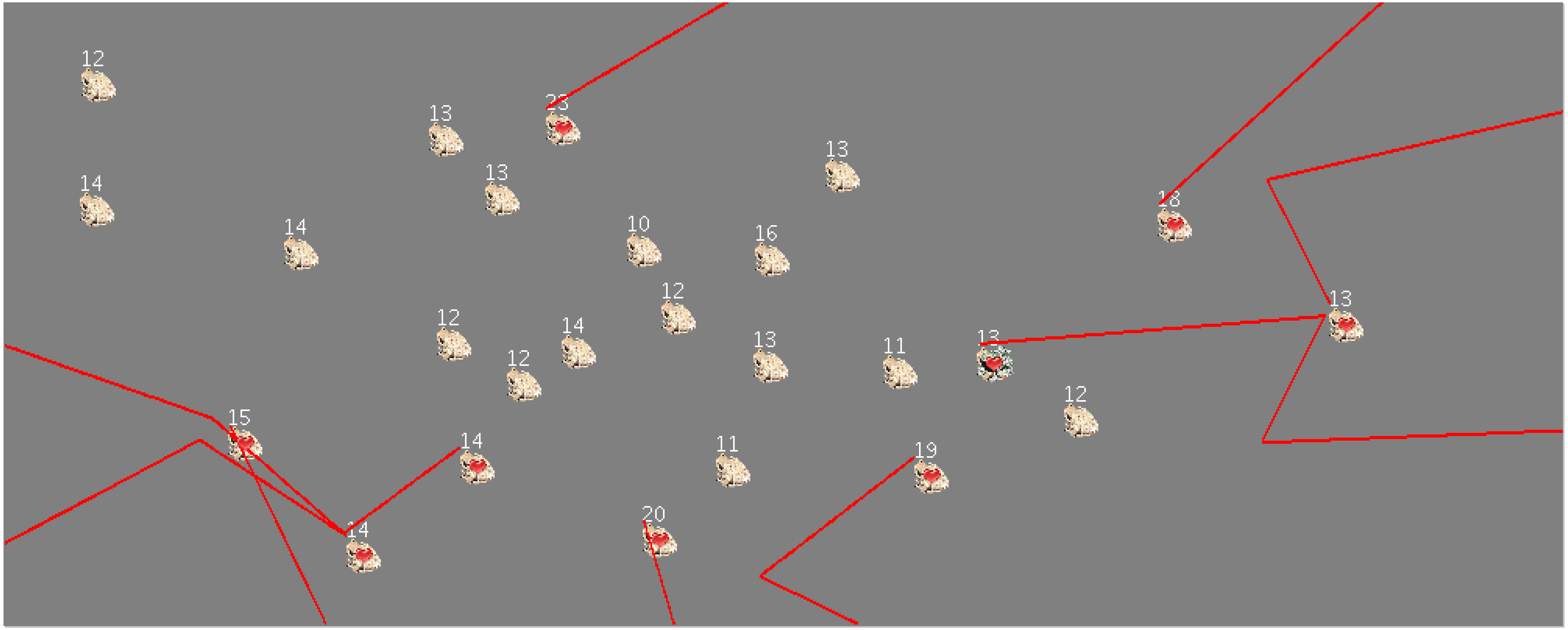
Trajectories for best-of-closest-3



Trajectories for best-of-closest-4



Trajectories for best-of-closest-5



Model parameters

Fixed Environmental Parameters		
E_x	swamp width	(10 m)
E_y	swamp length	(25 m)
d_{mate}	mating distance	(4.5 cm)
r_T	territory radius	(50 cm)
n_{male}	number of males	25

State Variables of Female Agents		
size	size	constant (5.38 cm)
(x,y)	position	begin at edge
ν	velocity	constant (1.86 cm/s)
α	heading	[0,360]degrees
$\pi(n)$	mating strategy	with strategy parameter values

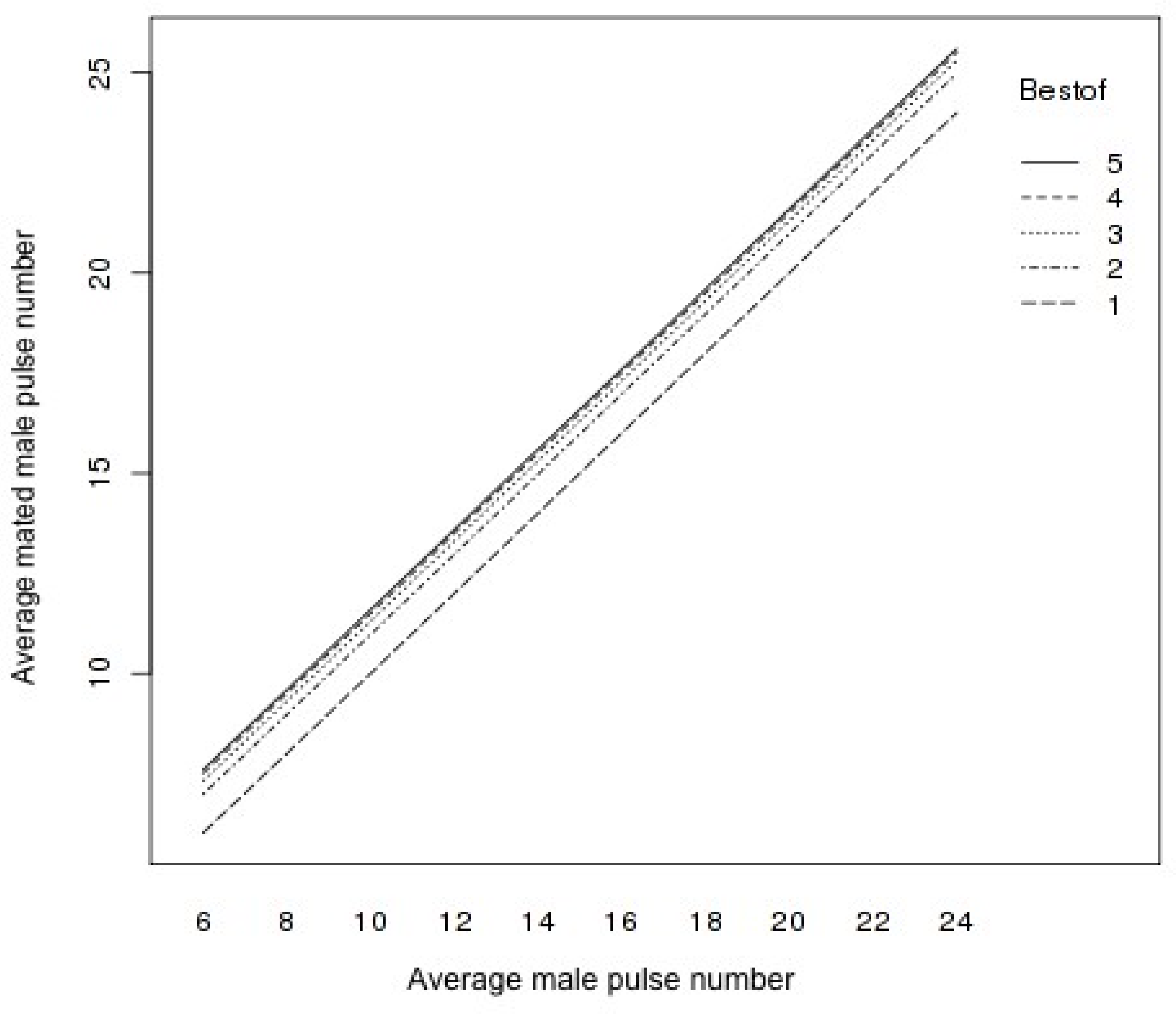
Free Parameters		
n_{female}	number of females	1..20
f_δ	female distribution	random at edges
m_δ	male distribution	Gaussian
μ_{pn}	mean male pulse #	6..24/+2
$\pi(n)$	mating strategy plus parameters	minthresh, bestofn

State Variables of Male Agents		
size	size	constant (4.72 cm)
(x,y)	position	fixed; according to distribution
pn	pulse number	based on μ and σ
$\pi(n)$	mating strategy plus parameters	none, minthresh, bestofn
$d_{placement}$	placement distance	(50 cm)

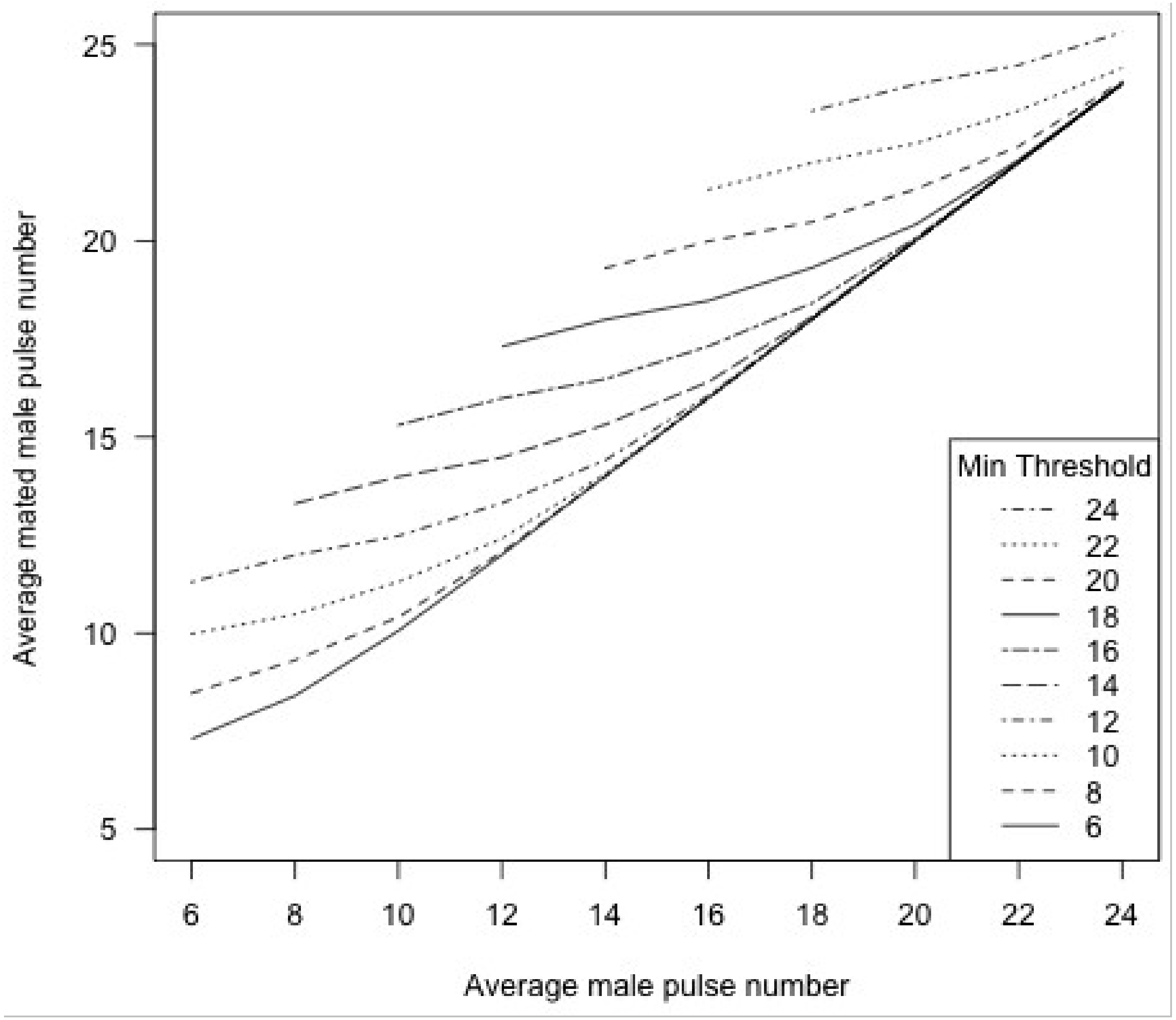
Previous results on female choice strategies (Scheutz et al. 2010)

- Initial conditions:
  - 25 male frogs placed according to a give distribution
  - males remain stationary and call constantly (simplification)
  - females enter from random positions on the swamp's edges
  - female choice strategy w/ parameters is fixed
- Simulation:
  - one update cycle corresponds to one second in real-time
  - females sample all calling males and make a decision in which direction to move on each cycle (simplification)
  - 100 initial conditions are considered for each variation of the parameters
  - female population is homogeneous w.r.t. choice strategy

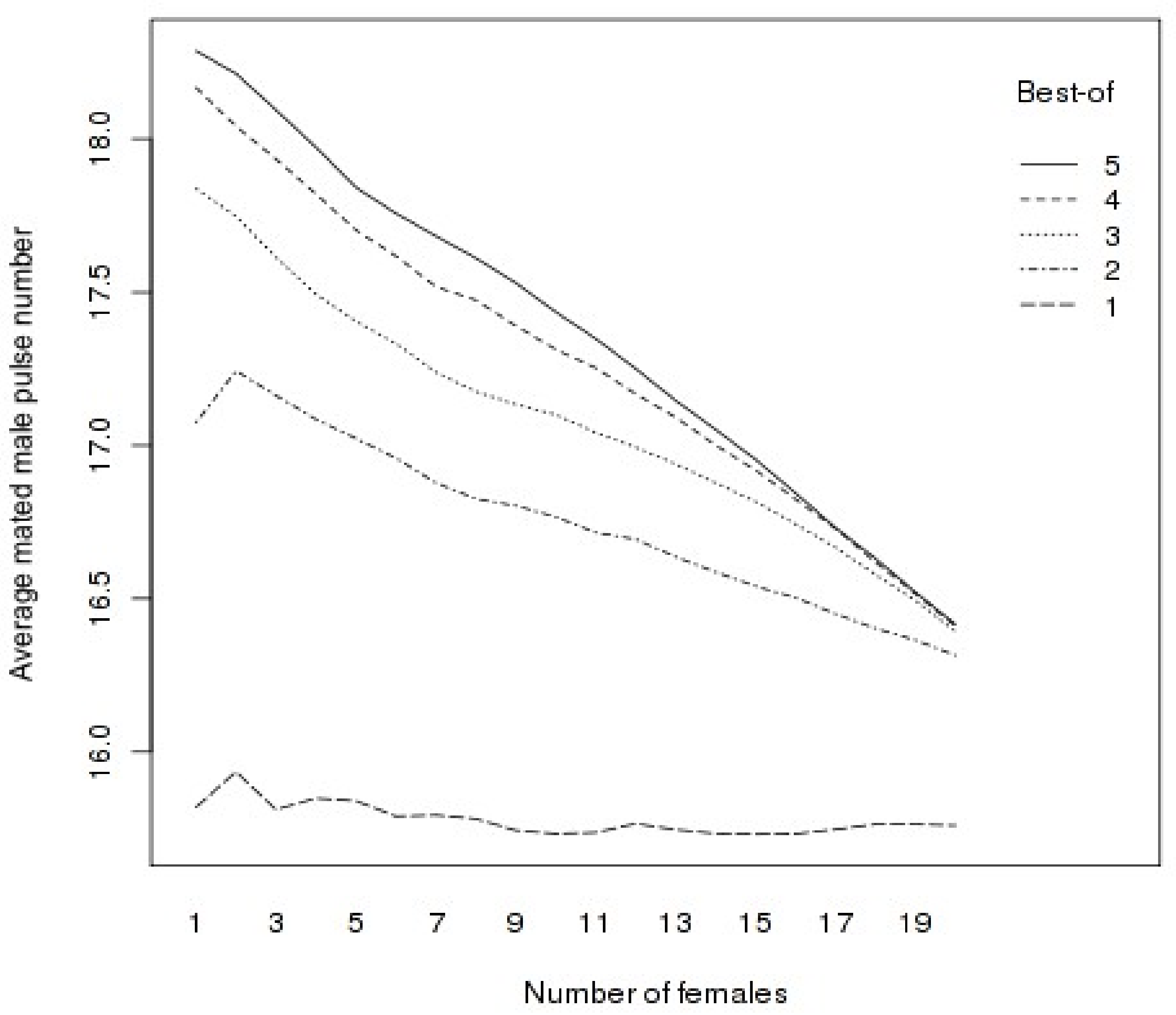
Females find better quality mates as the population mean increases



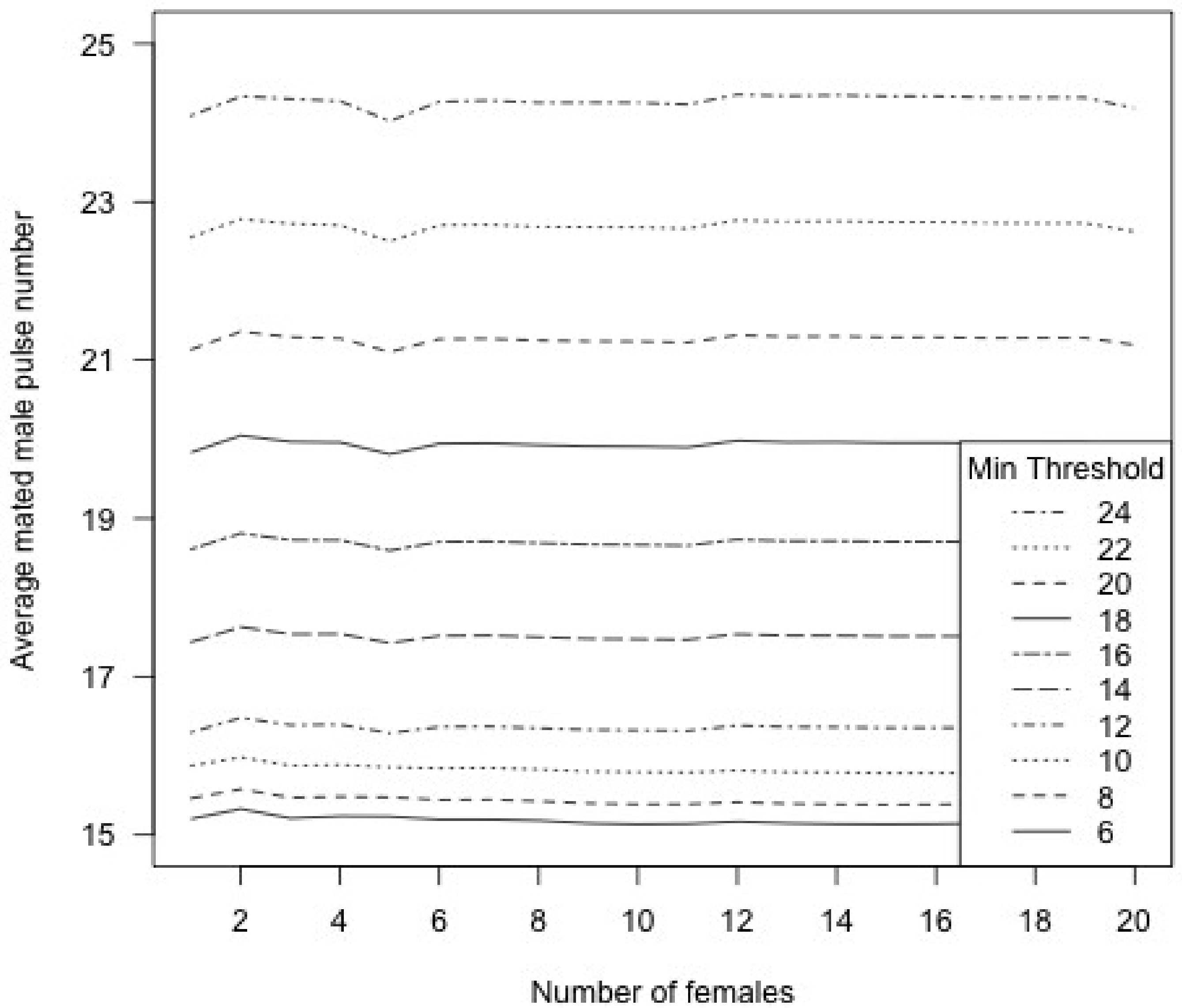
If min-thresh is too far above the population average, no females find mates



Female competition significantly affects mate quality for best-of-closest-n (n>1)



No influence of female competition is seen with the min-thresh strategy



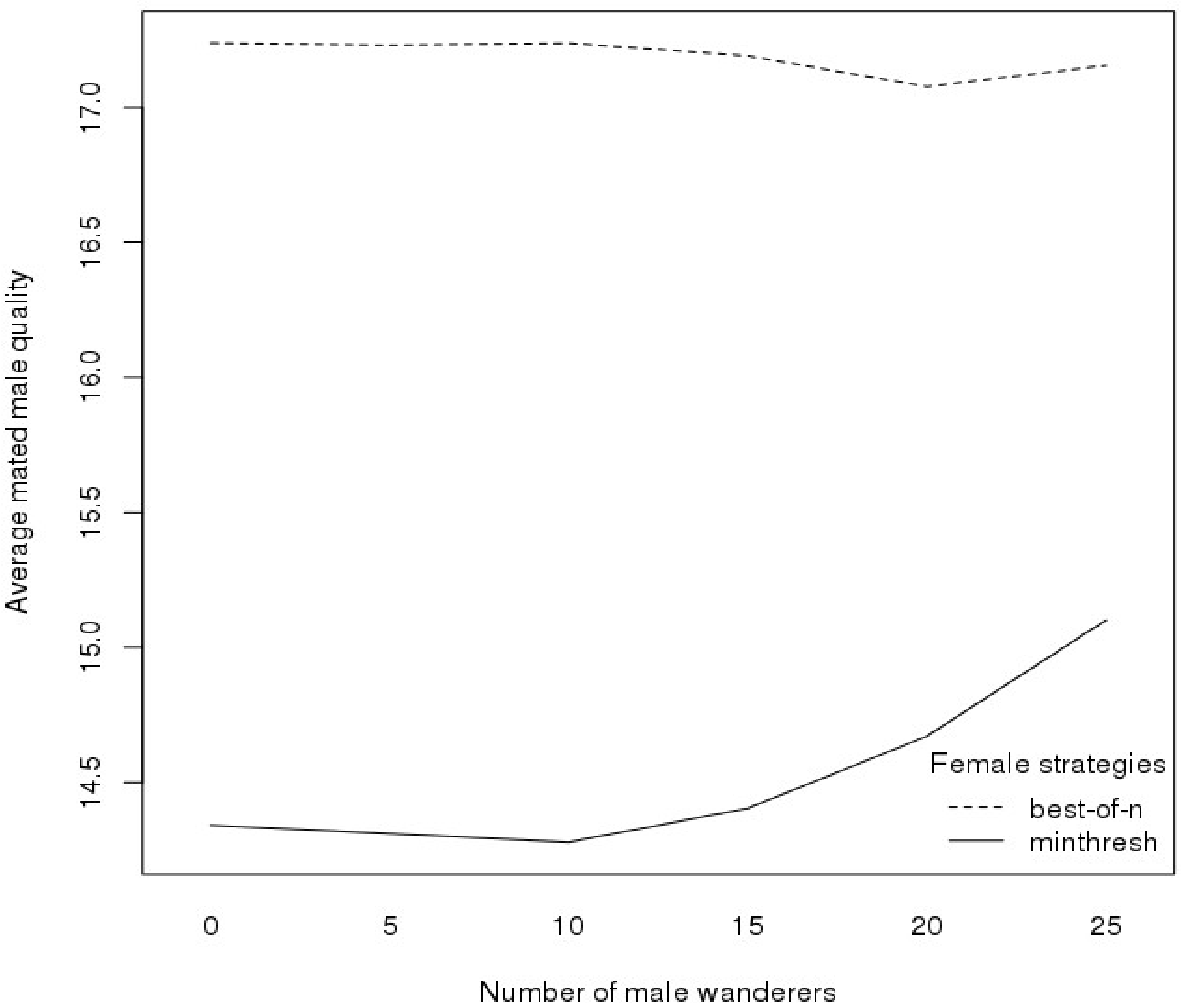
New male placement strategies

- **Idea:** let males use the same strategy for placement as females for mate choice (i.e., for approaching a fit male caller)
- This should lead to groups of agents surrounding fit males (which attract females with either choice strategy) and thus increase the chance of mating for agents that are eligible based on female criteria but are not the best choice
- **Best-of-n:** pick the (calling) male with call quality in the set of the closest *n* males (if the agent itself has the highest call quality, then it does not wander)
- **Min-thresh:** pick the closest male with the call quality above the minimum threshold (if agent itself is below threshold)
- Wandering males approach other males based on their strategy until they come within placement range, then they stop moving and start calling themselves

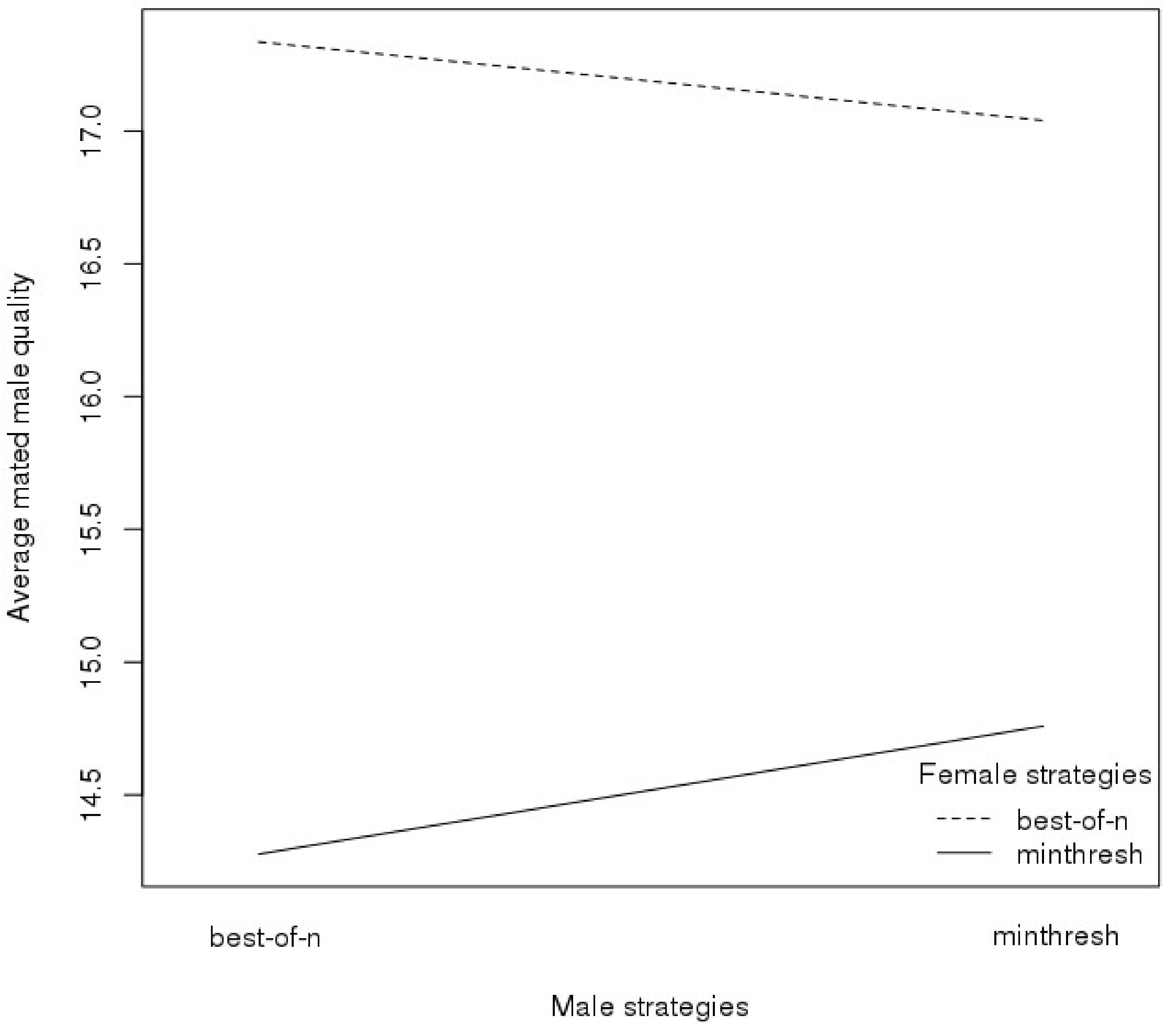
New simulations testing the effects of male placement strategies

- Initial conditions:
  - 25 male frogs placed according to a Gaussian distribution with mean call pulse number of 16 (std 2), some proportion of which are initial wanderers with a placement strategy
  - females enter from random positions on the swamp's edges
- Five dimensional parameter space (with 24 replications):
  - male-female ratio – 4 values (5,10,15,20)
  - percentage of wanderers – 6 values (0,5,10,15,20,25)
  - min threshold – 5 values (14,16,18,20,22)
  - male wandering strategy – 2 values (best-of-5, minthresh)
  - female mate choice strategy – 2 values (best-of-5, minthresh)

Number of initial wanders affects minthresh but not best-of-closest-n



Males do better when they use the same strategy as females



Discussion

- We explored for the first time the hypothesis that male treefrog chorus structure is an outcome of decision-making processes used by males to acquire calling sites
- Previously we found that (by and large) females using the closest-above-min-threshold strategy found better quality mates than those using the best-of-closest-n strategy
- The present results suggest that this performance can be significantly improved based on the number of wandering males
- The risk of minthresh, however, is that females might not mate at all (but could add mechanism to lower threshold over time)
- Wandering also often resulted in clusters of lower quality males around high quality males, which has been observed in nature

Current and future work

- We are currently investigating the effects of different initial male distributions on mating success with different numbers of male wanderers and are testing the results in real settings
- We are also analyzing the potential effects of “accidental matings” based on the wandering strategy
- And we are looking at effects of heterogeneous groups where males and females can use themselves different strategies
- Finally, we are planning to extend the model to allow males to adapt their calls over time based on their perceptions of the calls of their neighbors (which will require the introduction of a male calling strategy, possibly depending on the male energy budget)
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