Notes on Roughgarden, J. 2009. *The genial gene: deconstructing Darwinian selfishness* University of California Press: Berkeley CA.

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§1: Sexual selection, Falsificationism and Prediction

Roughgarden suggests that sexual selection fails as a scientific theory, since apparent exceptions to it's predictions have been found, therefore "[r]esearch has actually falsified the original Darwinian hypothesis [...] and investigators have, therefore, widened the original sexual-selection hypothesis to accommodate the species that contradicted the original hypothesis. [...] In this way, sexual-selection theory grows bigger and bigger [...] continuously widening sexual-selection theory converts it into a system that becomes increasingly hard to test and impossible to falsify, and so sexual selection slowly morphs from a scientific theory into a doctrine or ideology." (p22) This view of a central theoretical core, protected by changing shield of auxiliary hypotheses neatly describes how philosophers of science think good science is, and ought, to be conducted. The Behaviorists attempted to use falsificationism to purge of Psychology of "witchcraft" (all they thought tied to unfalsifiable ideas, basically everything that wasn't behaviorism). The Behaviorists failure, Falsificationism's last stand, is considered to be a very good thing. It allowed a diversity of research directions to flourish, not least Harry Harlow's work demonstrating the biological need for love. Roughgarden's falsificationistic stance represents the philosophy of science, circa 1960. Exceptions have been found, "How much money, surely many millions of research dollars over the last two decades [...] as been invested in trying to confirm sexual selection only to find that it needs to be redefined yet again? How many thousands of hours by scientists, volunteers, and students have been consumed in field and laboratory [...] Isn't it time to cut losses and move on?" (p60). For Roughgarden, it is very much "three strikes and you're out".

For Roughgarden, a theory that makes correct predictions in some, or even most but not all, species is not "complete and testable" unless it also provides a super-theory which specifies why the exceptional species don't fit the rule (p216). This is a lot to ask of any theory. One of the repeated complaints she raises against the theory of sexual selection is that is fails to explain why homosexuality is not uncommon (e.g. p60, 244). Roughgarden never explains why sexual selection, and not natural selection, is the theory to hold at fault for this failure. It would seem to me that the latter theory has more bearing on the matter than the former. Given that this failure is seen to be so great, how well does Roughgarden's social selection theory do at explaining the mystery of the taxonomic pervasiveness of homosexuality? Roughgarden devotes two sentences to this. They go like this: "According to social selection, homosexuality is natural and adaptive to all participants and both sexes. Homosexuality [...] allows animals to work together as a team — to coordinate actions and tactilely to sense one another's welfare" (p244). this

doesn't really rise to the level of a "just-so" story. It certainly fails to provide a super-theory to the exceptions of the general pattern of heterosexuality. When should it be expected, and when not?

§2: Controversy & Language

The book is described on the flyleaf as "compelling and controversial", and it certainly presents a controversial theory. The original *Science* article prompted a number of critical letters. Those which were published in *Science* are described by Roughgarden as "mostly emotional outbursts" (p226) a "gang of 40 was attempting peer suppression, not peer review, bullying" (p159). She challenges her critics, "the neo-Spencerists to be the scientists that they claim to be, to engage and entertain alternative hypotheses objectively without descending to the personal and homophobic rebukes that have characterized their discourse so far"(p4).

She decries the "cesspool of adjectives inventied ostensibly as descriptions of animal behavior [...] which poisons any aspiration to objectivity" (p30). Examples include "cuckolded" for birds whose nest contains extra pair paternity eggs, "sneaky fuckers" for "males who do not hold territories" and "female mimics" for "feminine males" (p30).

With the belief that the proponents of the dominant paradigm in evolutionary biology are aiding and abetting the oppression of at least half the world's population, Roughgarden is not shy about slinging around some loaded language herself, eg "Sexual conflict is rape in scientific guise, a narrative of males victimizing females. One may find this brave new world championed by the sexual-conflict advocates appealing or repugnant. But is it true and accurate?"(p103), "The issue before us is not whether it is appealing or repugnant that female choice might supply a universal natural system of eugenics, the issue is whether this claim is true"(p52).

§3 The Naturalistic Fallacy

Says Roughgarden, "If sexual selection theory is indeed true, then [...] the prospect of an egalitarian society is an unrealistic mirage. Alternatively, if sexual selection is not true, it [...] should be explicitly discredited lest sexual selection remain on the books as an obstacle to social justice"(p5)

Roughgarden requires that sexual selection be debunked with maximum force and publicity for the social good. This makes for a very angry book, and explains the book's dedication ("To those who suffer the persecution of science"). There is some "hate the sin, love the sinner" attitude towards her colleagues in evidence here, but it seems to require quite an effort on her part. Prominent Intelligent Design proponent Michael Behe receives conspicuously gentle treatment. I'm really totally mystified by the point of the paragraphs on page 68 discussing the status of the Intelligent Design movement. As I understand it, Roughgarden's point is that Intelligent Design supporters now largely agree with the major points of evolutionary theory, and the rest amounts to little more than "technical arguments about mutation rates"(p68). The good will extended here to the Intelligent Design crowd is in marked contrast to mainstream evolutionary theorists. I would have thought that we face a far greater threat of oppression through the imposition

of patriarchical sex roles from the Intelligent Design crowd than the followers of Darwin, but perhaps that is naive of me.

Really, the oppression of women, gays, lesbians and transexuals is obvious to anyone with eyes or ears. The struggle against oppression, and for social justice must, and will, continue regardless of the strengths or weaknesses of sexual selection theory. No one needs permission from a book about birds and fungi to be convinced that social justice is something that must be worked towards. One reason for this is that one cannot derive morals from facts, to attempt to do so is to commit the naturalistic fallacy. Perhaps the most prominent example of the naturalistic fallacy is the claim that homosexuality is immoral because it is unnatural. One refutation of this claim is to demonstrate (as has been done quite clearly by Bruce Bagemihl[1]) that there is nothing unnatural about homosexuality. But a far stronger refutation is to simply point out that whether or not penguins really are or aren't sometimes gay means absolutely nothing at all to whether or not human rights apply to all humans, or homophobia ought to be tolerated in a just society.

§4: Joint nest building incompatible with previous theory?

"Take two robins, a male and female, who build a nest together. [...] Dawkins sees the evolution of nest-building ability as another success story for some selfish genes. In fact, the nest building results from the relationship developed by the male and female during courtship. Both bring twigs to build the nest. The success of the genes in either bird is zero if the other doesn't do their job [...] Therefore, the genes for nest-building do represent an evolutionary success story, but not success because of selfishness. [...] Moreover, the success of the nest is not decomposable to a sum of the twigs brought by each, because half a nest is useless. No one has yet figured out a useful way to decompose team achievements into individual contributions. [...] In the 30 years since the selfish-gene metaphor has gained traction as a popularization of neo-Darwinian thought, it has yet to emerge as a scientifically operational concept because of the decomposability problem. Still, at this point a selfish-gene advocate typically retorts that a robin who cooperates with another robin in building a nest is helping itself, and so it can be thought of as selfish after all. But that vacates the meaning of selfish. "Selfish gene" and "successful gene" are not the same thing. [...] The explanation for why the male and female robins cooperate to build a nest together cannot be subsumed under kin selection, reciprocal altruism, or group selection. The male and female robins are usually not brother and sister or another close relative, so kin selection does not apply. The female and male robins are not exchanging altruistic acts that directly help each other as individuals, so reciprocal altruism does not apply. And a robin's nest does not bud off other nests, so group selection does not apply either [...]" (pages 11–12)

§5: Roughgarden's odd take on game theory

Roughgarden consistently refers to what is known in standard terminology as "non-cooperative" game theory by her term "competitive" game theory. I began to suspect that this was to discriminate the way she was applying ideas from their standard use (see §6 for more on this point) but this isn't the explanation. She just uses "competitive game" when everyone else uses "non-cooperative game", there doesn't seem to be any point other than retitling this to be more in line with her mistaken views.

Roughgarden continues to twist the differences between cooperative game theory and non-cooperative game theory through totally psychedelic funhouse contortions. Previous criticisms of her misrepresentations of this point [2,3] have had no discernible influence on her writing. By page 143 I stopped wondering if Roughgarden actually believed what she was writing. It was so bizarre that I just stopped caring.

Roughgarden suggests that it is appropriate to use non-cooperative game theory in preference to cooperative game theory "if the organisms cannot discern a better outcome than the one they are experiencing" under non-cooperative game theory predictions (p161). I'm not quite sure how to interpret the word "discern" here, but it is impossible to rephrase this idea with a valid game theoretical interpretation. The idea seems to require the full anthropomorphic appeal to the application of conscious insight implied by "discern".

Following on from "competitive game theory" is her use of the term "Nash competitive equilibrium" (NCE) which is much more difficult to translate back to standard terminology. The Nash equilibrium and its refinement, the Evolutionarily Stable Strategy, will be familiar to readers of this journal. Roughgarden defines NCE as the product of the method of iterated best replies that she uses to solve games in the "behavioral tier"* (see §8 for details). She says that unlike the traditional ESS or Nash method, this "doesn't require that the actions be genetic" (p146). This is fundamentally different from the way the Nash equilibria and ESS are thought of in regular game theory. It also produces different equilibrium solutions (eg Game 4, p191, in §8 below). This would all be fine and good, but she then applies the term NCE to historical work where the solutions were ESSs. When she means ESS, she says NCE; when she means Nash equilibrium, she says NCE, and when she says NCE she means Pareto optima in an extensive form game corresponding to the infinitely repeated sequential choice of strategies... at least usually that's what she means, but not always.

Roughgarden bafflingly says of the war of attrition game that is "retains the spirit of individual competitive play and yet permits a cooperative outcome"(p152). The expected payoff for both players in a war of attrition game is zero. The value of the resource at the heart of the war of attrition is completely squandered during play. There is really nothing to be won in this game, I don't see how this can be described as a cooperative outcome.

Another model that Roughgarden gives an unusual interpretation to is Hamilton's "Sex versus non-sex versus parasite" model [4]. After several pages of explaining why she believes Red Queen models are completely wrong she advances her alternative, the Portfolio model [5] which is based upon Hamilton's model. She then spends a page lauding Hamilton's model. A casual reader would never discern from these pages that Hamilton's model is a dyed-in-the-wool Red Queen model.

∗She also interprets that numbers in the payoff matrix to be some sort of rate of return on the time spent in that outcome state during the iteration. This fundamentally changes the whole concept of a payoff matrix. The numbers aren't payoffs anymore. At this point you might as well throw out all of game theory and make it up as you go along, name dropping concepts when you think they might be useful.

§6: "Winning" etc.

In non-cooperative game theory, each player is attempting only to maximize their own payoff. They are indifferent to the other players payoffs, and whether one players payoffs are larger or smaller than the others never enters into the question. Throughout the book, with the exception of a sentence on page 145, non-cooperative game theory is described as if the two players were playing against each other. Roughgarden speaks as if one or the other player is winning". I began to think that this is why she insisted on using the term "competitive game". Only on page 145 do we find that she knows that this is not the way game theory works. This constant portrayal of biological game theory as being concerned with one player versus the other, the constant pitching of the boys against the girls, is particularly jarring in the chapter on the evolution of anisogamy. The idea that males are competing against each other to be the most reproductively successful* male, while females are simultaneously competing against each other to be the most successful, and thereby move towards some evolutionarily stable combination simply doesn't appear in her description of how researchers thought before her theorizing.

∗ Roughgarden states repeatedly (eg pg61, 62, 190) that the theory of sexual selection rests upon the assumption that males act to maximize their numbers of matings, and ignores reproductive success as a metric of fitness.

§7: Team fitness as "Joy"

Roughgarden largely uses the term "team fitness", which I have largely represented as "shared joy" because that is the formulation that makes the most sense to me. This passage on page 156 where she defines the term has largely guided this interpretation.

"Think of a basketball team. The athletes all hold hands, give high-fives before entering the floor, and stay "in touch" with eye contact. Then follows the joy of making a dunk with an alley-oop pass, the pleasure of a successful joint action, more fun than two foul shots which yield the same score. Team success involves a kind of synergy beyond the sum of utilities . When retired athletes who played a team sport are interviewed, they invariably recall missing the camaraderie the most. Successfull teamwork involves *both* coordinated activity *and* the pursuit of a common goal. We hypothesize that intimate physical contact stimulates physiological responses, hormonal and/or neural, that ensures coordinated activity and guides that activity to maximizing team fitness. Here, team fitness, as a product of the individual fitnesses, values the "synergy" to achieving a goal as a team beyond the sum of the two values for the same achievement if attained individually" (emphasis in original)

§8: Sketches on some of the "behavioral tier" models

Game 1: Tasks for Birds at a Nest, p144, Table 3.

This is a discoordination game. Each player gains most when using the strategy that the other does not [6]. This game is most commonly known to biologists as the Hawk-Dove game, and to economists as Chicken. In this version the strategies are, Guard Nest or Catch Worms.

Discoordination Game

Male \ Female	Guard	Worm
Guard	1 \ 1	4 \ 2
Worm	2 \ 4	0 \ 0

Let x be the probability that the female Guards,
Let y be the probability that the male Guards.

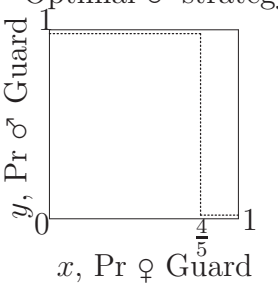
$$w\male(Guard) = 1x + (1-x)4 = 4 - 3x$$
$$w\male(Worm) = 2x + (1-x)0 = 2x$$

$$w\female(Guard) = 1y + (1-y)4 = 4 - 3y$$
$$w\female(Worm) = 2y + (1-y)0 = 2y$$

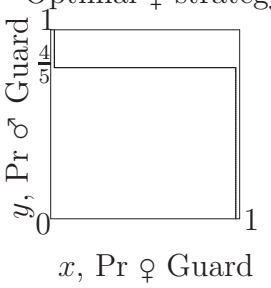
For each player, the two alternative strategies pay equally well when:

$$2x = 4 - 3x$$
$$x = \frac{4}{5}$$

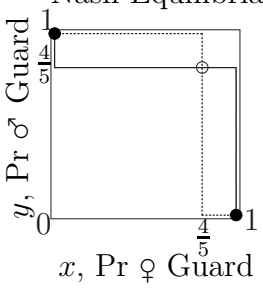
Optimal ♂ strategy



Optimal ♀ strategy

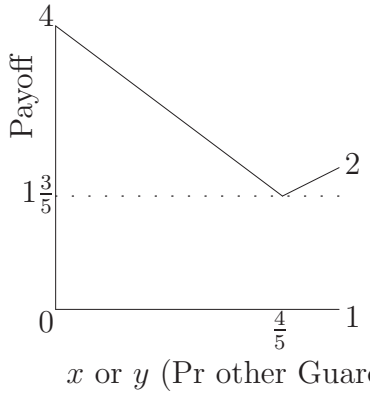


Nash Equilibria



The payoff at the mixing Nash equilibrium is $2x = 2\frac{4}{5} = 1\frac{3}{5}$, payoff at the pure equilibria are 4 to the Guarding player, and 2 to the Worming player.

The payoffs to each player, given optimal strategy choice, as a function of probability that the other player plays Guard is graphed below. The player earns maximum payoff when the other player plays Guard with probability zero (and they play guard with probability one).



The minimum payoff in the figure above is the "threat point", the maximum that the player can gain if the other player is playing so as to be maximally spiteful. Here it is $1\frac{3}{5}$. Note that the ESS to the role-symmetric version of this game, the mixing Nash equilibrium, is where the threat point is located in this game. This game has a role asymmetry, so the mixing Nash equilibrium is not an ESS [3].

Method for determining Nash Bargaining Solution according to Roughgarden, paraphrased from pg. 151.

1. For each player, calculate the difference between payoff and threat point for each strategy.

2. Calculate the play which maximises the product of the two differences above

This method is a bit ambiguous. The assumption that the second point refers to a strategy is incorrect. Roughgarden doen't ever make this clear, but when she talks about "the earnings that come from a choice of time allocations"(p151) she isn't talking about a choice of strategy, but a choice of end points.

When game theorists put payoffs into a matrix, it is taken to mean that players each choose a strategy simultaneously. As part of her "behavioral tier" idea, Roughgarden forces all games to be sequential move games. Game theorists depict games with sequential moves (which they call dynamic games) using the extensive form, not payoff matrices.

But first Roughgarden's solution:

> "Because our bird nest payoff matrix is symmetric to begin with, we know that the optimal compromise will be a 50:50 division of labor" (pg. 150)

We know no such thing. That the payoff matrix is symmetric means that the optimal outcome will be independent of what sex the individual is, but it doesn't mean that "a 50:50 division of labor" is necessarily optimal.

What Roughgarden means by "a 50:50 division of labor" is ambiguous. It could mean that both male and female play the game as a normal form (a simultaneous move, matrix) game and both play Guard and Worm in 50:50 ratio, or (as it turns out that she actually means) it could be that half the time the outcome is male plays Guard and female plays Worm, and the other half of the time male plays Worm and female plays Guard. We'll examine each of these options in turn.

Players Choose a strategy

If each player plays Guard and Worm with 50:50 probability then the payoffs are

$$\begin{aligned} w &= \frac{1}{2}(4 - 3\frac{1}{2}) + \frac{1}{2}(2\frac{1}{2})) \\ &= \frac{1}{2}(2\frac{1}{2}) + \frac{1}{2}1 \\ &= 1\frac{3}{4} \end{aligned}$$

and so both the male and female receive $1\frac{3}{4}$, which is clearly worse than the 2 and 4 they would receive if one played Guard and the other played Worm. If we subtract the value of the threat point from all payoffs, then the 50:50 payoffs are $1\frac{3}{4} - 1\frac{3}{5} = \frac{3}{20}$ (and so the product of the two players payoffs is $\frac{9}{400} = 0.0225$) while the product of the payoffs to the one-stay-at-home equilibrium is $(2 - 1\frac{3}{5}) \times (4 - 1\frac{3}{5}) = \frac{44}{25} = 0.96$. In this case, the one-parent-stays-at-home strategy is superior to the 50:50 division of labor. It doesn't matter which parent takes which role, because the payoff matrix is symmetric, but symmetric doesn't equate with equal. In any case, this is academic because Roughgarden intends for us to understand that "50:50 division of labor" means something different, that players chose each of two outcomes with equal probability.

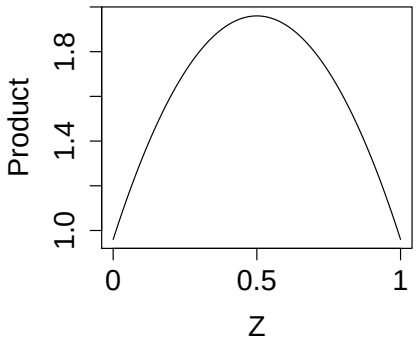
Players Choose an Outcome

The optimal cooperative outcome according to Roughgarden is that half the time the male Worms while the female Guards, and the other half of the time the reverse happens. The method behind this is simply to choose the two Pareto optima. What Roughgarden would do if the game were not to have a Pareto optima, I cannot guess (wait, see game 4 below).

The payoff to each player is then $\frac{1}{2}4 + \frac{1}{2}2$, and the product of the payoffs minus the threat point is

$$\begin{aligned} w &= (\frac{1}{2}4 + \frac{1}{2}2 - 1\frac{3}{5}) \times (\frac{1}{2}2 + \frac{1}{2}4 - 1\frac{3}{5}) \\ &= 1\frac{2}{5} \times 1\frac{2}{5} \\ &= \frac{49}{25} \\ &= 1.96 \end{aligned}$$

Which does surpass the pure one-parent-stays-at-home outcome payoff of 0.96 (see previous section). The product of the payoffs minus threat points is plotted below as a function of the z, which is proportion the time that the outcome is male worm & female guard, and the assumption is then that the outcome female worm & male guards happens with probability $1 - z$.



Tasks for Birds at a Nest, v2, p150, Table 5.

Same as the last game, but with a sexual dimorphism; payoff to a male when both players guard the nest has been lowered to zero.

Discoordination Game

Male \ Female	Guard	Worm
Guard	0 \ 1	4 \ 2
Worm	2 \ 4	0 \ 0

Let x be the probability that the female Guards,
Let y be the probability that the male Guards.

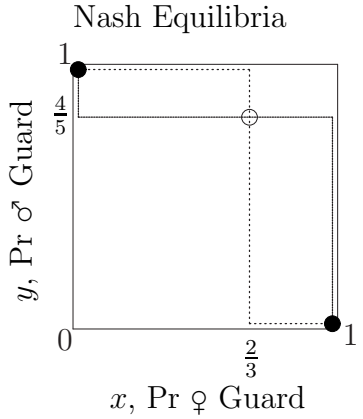
$$w\male(Guard) = 0x + (1-x)4 = 4 - 4x$$
$$w\male(Worm) = 2x + (1-x)0 = 2x$$

$$w\female(Guard) = 1y + (1-y)4 = 4 - 3y$$
$$w\female(Worm) = 2y + (1-y)0 = 2y$$

For the male, the two alternative strategies pay equally well when:

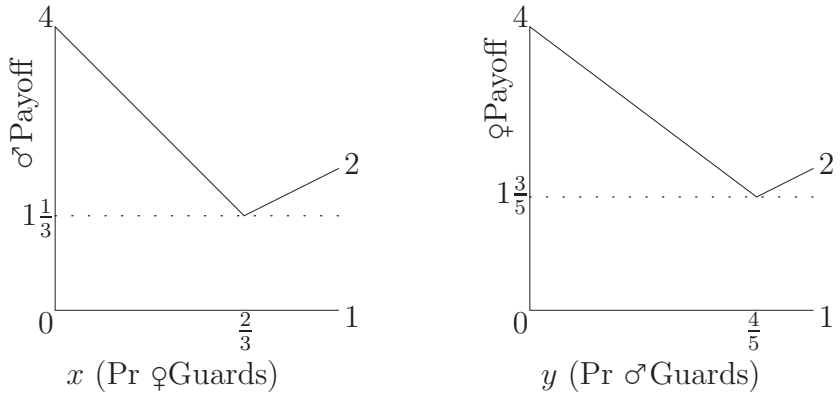
$$2x = 4 - 4x$$
$$x = \frac{4}{6}$$

The best response mapping is then



and the males' payoff at the mixing Nash is $1\frac{1}{3}$. The female's payoff at the mixing equilibrium remains $1\frac{3}{5}$.

The maximum payoffs for each player as a function of the probability that the other player chooses Guard is graphed below.



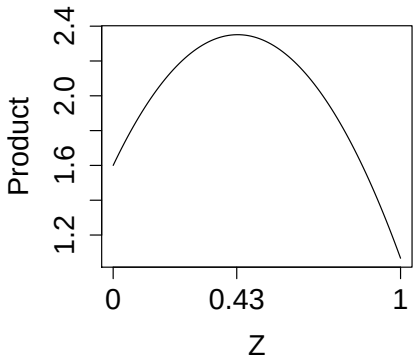
Roughgarden says:

> "The threat point for the male, which is the maximum the male can earn when the female is trying to hurt him the most, is now $1\frac{1}{3}$ fitness units, which is attained when he is guarding $\frac{1}{3}$ of the time and independently she is guarding $\frac{2}{3}$ of the time" (pg. 150)

which is not quite correct, if the female plays Guard with probability $\frac{2}{3}$ then it does not matter what the male does, the payoff is the same. This is because $x = \frac{2}{3}$ is where Guard and Worm pay equally for the male (recall it is the mixing equilibrium female strategy). It is the undefined (vertical) segment in the best response mapping above. Presumably, Roughgarden arrives at the conclusion that the male guards with probability $\frac{1}{3}$ here because she has limited her solution space to the combination $x + y = 1$. That might make sense if she's thinking that the mix of Guard/Worm and Worm/Guard outcomes add to one, but here we are talking about mixed strategies, and there is no reason that the players have to choose a mix that adds to one.

Roughgarden's cooperative optimum is a mix of the two pure equilibria outcomes. Where the product payoffs at the selected outcomes is maximized, where the male payoff (minus $1\frac{1}{3}$) times the female payoff (minus $1\frac{3}{5}$).

Product of the payoffs minus threat points, again z is the proportion of the time that the outcome is male worm & female guard, and $1 - z$ is the proportion of the time that the outcome is female worm & male guard.



Note that the change in the original payoff matrix, lowering male fitness to zero when both play Guard, has resulted in both a decrease in the relative proportion of the time that the male guards, and an increase in the product of their payoffs. If this product is assumed to be joy, then it seems odd that decreasing the male's payoff for one outcome leads to greater joy. The reason for this is that the joy measure is not absolute. Multiplying the payoffs (minus threat point) is just a way of determining some equitable split between the two Pareto optima endpoints of z. The product is "funny money", and thus Roughgarden always speaks of the payoffs to the individual players (the standard reproductive success currency ones used throughout biological game theory modelling) when discussing the joy maximizing outcomes. This raises the key question, if an individual chooses a lower payoff (in reproductive success currency) in order to maximize the joy currency, doesn't natural selection then disfavor them for exhibiting that phenotype? (Roughgarden speaks as if the two-tier model addresses that question, it doesn't, see §5.)

Game 4: Controlling access at the nest, p191

This is the game known in economics as the matching-pennies game. Unlike the tasks at a nest games it has no Pareto optima, and is therefore much more problematic for her iterated best reply method. There is also therefore no nice clear line, the "z" dimension, between the two Pareto optima. In the models above, this line formed a clear continuum of trade-offs between outcomes that the best interests of the two players individually. Such a line and was most amenable to the "product of the payoffs" method, here things are different.

Male	Female	
	Share Access	Control Access
Help	6 \ 6	1 \ 8
Abandon	3 \ 3	2 \ 2

Let x be the probability that the female shares access,
Let y be the probability that the male helps.

$$w\male(Help) = x6 + (1-x)1 = 5x + 1$$
$$w\male(Abandon) = x3 + (1-x)2 = x + 2$$

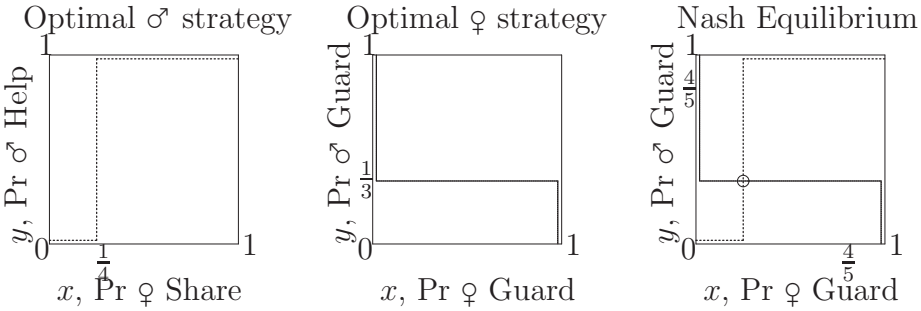
$$w\female(Share) = y6 + (1-y)3 = 3y + 3$$
$$w\female(Control) = y8 + (1-y)2 = 6y + 2$$

For the male, the two alternative strategies pay equally well when:

$$5x + 1 = x + 2$$
$$x = \frac{1}{4}$$

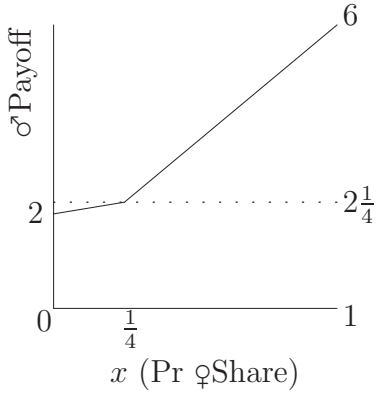
For the female, the two alternative strategies pay equally well when:

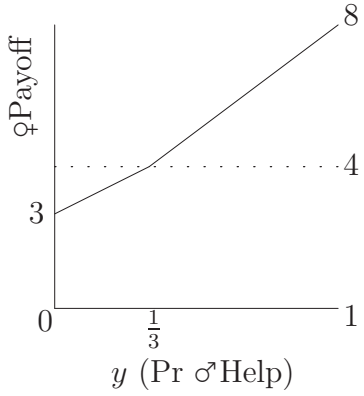
$$3y + 3 = 6y + 2$$
$$y = \frac{1}{3}$$



The mixing point is an unstable equilibrium. The solution she presents for this game is the standard Nash equilibrium solution. Applying Roughgarden's iterated best reply method to this game results in an endless circling through the corners of the game. The flow dynamics diagram she presents in Table 12 (pg 192) should have no arrows pointing inwards at the corners. Instead, the corner arrows ought to point horizontally or vertically towards to form a rectangle with clockwise directions around the outside boundary. She's either glossed over the fact that this "NCE" doesn't exist by her method and calculated the Nash equilibrium using the standard method, or she thinks that the NCE and Nash are equivalent concepts.

The maximum payoffs to each player can earn as a function of the other players strategy is graphed below:





§9: The two-tier game, p166

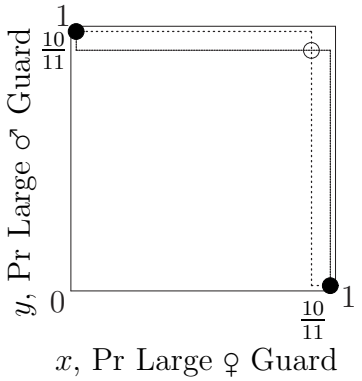
This is the only "two tier" game presented in the book, this adds variation in body size to the task-at-a-nest game. The version on page 144 Table 3 (Game 1 above) serves as the payoffs when both male and female are small (here I am assuming that the "Female A_1A_2" in the column header of table 8, page 166 is a typo, and ought to read "Female A_1A_1"). Size is determined by a one locus, two allele, system, with allele A_2 conferring larger size, so that A_1A_1 is small, A_1A_2 is medium, and A_2A_2 is large.

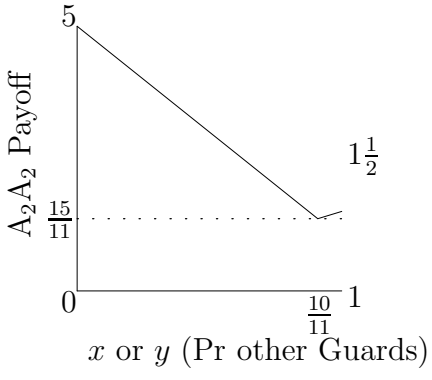
Payoff matrices for pairs of Large individuals are given, a priori, as

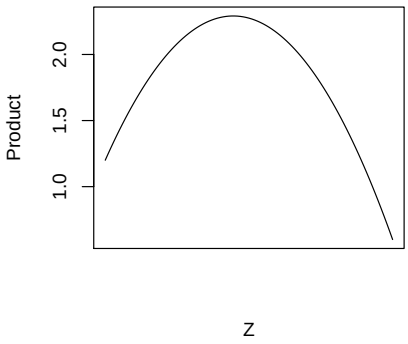
Large Male & Large Female

Male \ Female	Guard	Worm
Guard	1 \ 1	5 \ 1.5
Worm	1.5 \ 5	0 \ 0

Nash Equilibria



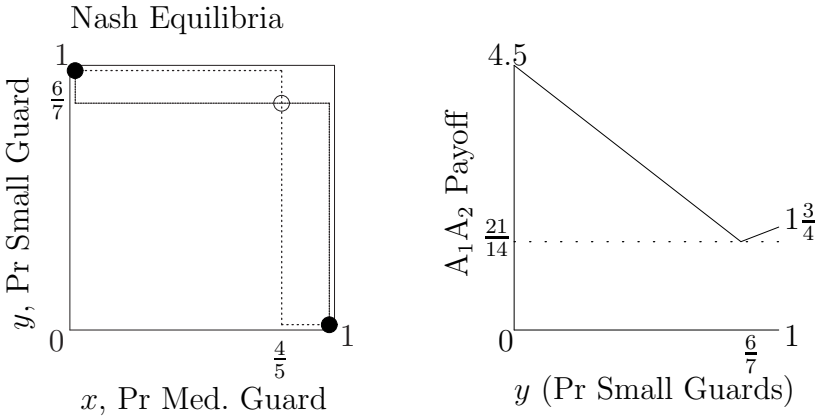


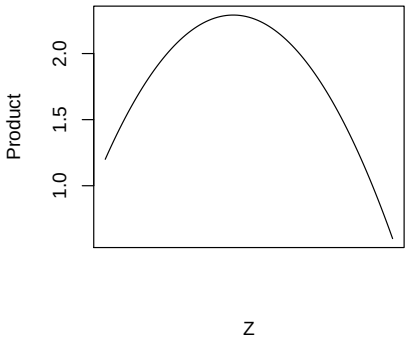


Payoffs for Small and Medium individuals (of either sex) when paired together are:

Payoff for Medium & Small player

Small	Medium: Guard	Medium: Worm
Guard	1 \ 1	4 \ 1.75
Worm	2 \ 4.5	0 \ 0





Payoff for the medium sized player at the mixing point is $\frac{21}{14}$.

Roughgarden models evolution of the A_1 and A_2 alleles by comparing payoffs at the equilibria for each of these matrices. Since the payoffs are larger at the equilibrium in the Small/Medium than in the Small/Small, then A_2 will replace A_1 in the population. An elipsis later and we reach the conclusion that A_2 will go to fixation and that the Large/Large pairing matrix is "an evolutionarily stable payoff matrix" (pg 169). There is no feedback from the "evolutionary tier" to the behavioral. There is no change in behavior resulting from events in the "evolutionary tier" beyond the obvious one that one of the many payoff matrices devised beforehand becomes identified as the outcome, simply because the payoffs within it are larger. There is no evolution of the payoff matrix, there is no natural selection on how joy is derived from behavioral interactions.

The advantage of making the population genetics explicit is totally undermined by having it be so simple. There is no cost to having the model assume phenotypic variation happens by unknown genetic mechanisms. It does not become more realistic, or more robust, if we force it to have a genetic mechanism we know is false. The question addressed by this model would be more directly answered by making male and female sizes into phenotypic variants. This would allow for sexual dimorphism, which is a realistic effect to include. Re-framing the "two-tier" game as a simultaneous move phenotypic variation game with these effects would look something like this:

Male		Female									
		Small				Medium				Large	
Size	Behavior	Guard		Worm		Guard		Worm		Guard	Worm
Small	Guard	1 \ 1		4 \ 2		1 \ 1		4 \ 1.75		\	\
	Worm	2 \ 4		0 \ 0		2 \ 4.5		0 \ 0		\	\
Medium	Guard	1 \ 1		4.5 \ 2		\		\		\	\
	Worm	1.75 \ 4		0 \ 0		\		\		\	\
Large	Guard	\		\		\		\		1 \ 1	5 \ 1.5
	Worm	\		\		\		\		1.5 \ 5	0 \ 0

In order for a two tier model to work in the way intended here we need to have something more added. There needs to be more than one "behavioral tier" game (more like Max Wolf's model of personality [7]), and the way in which the maximized payoff is calculated ought to be subject to selection based on the reproductive success. Without this there is no answer to "why should natural selection choose joy over reproduction?", and without that answer, "joy" is simply "for the good of the group".

Acknowledgments

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