

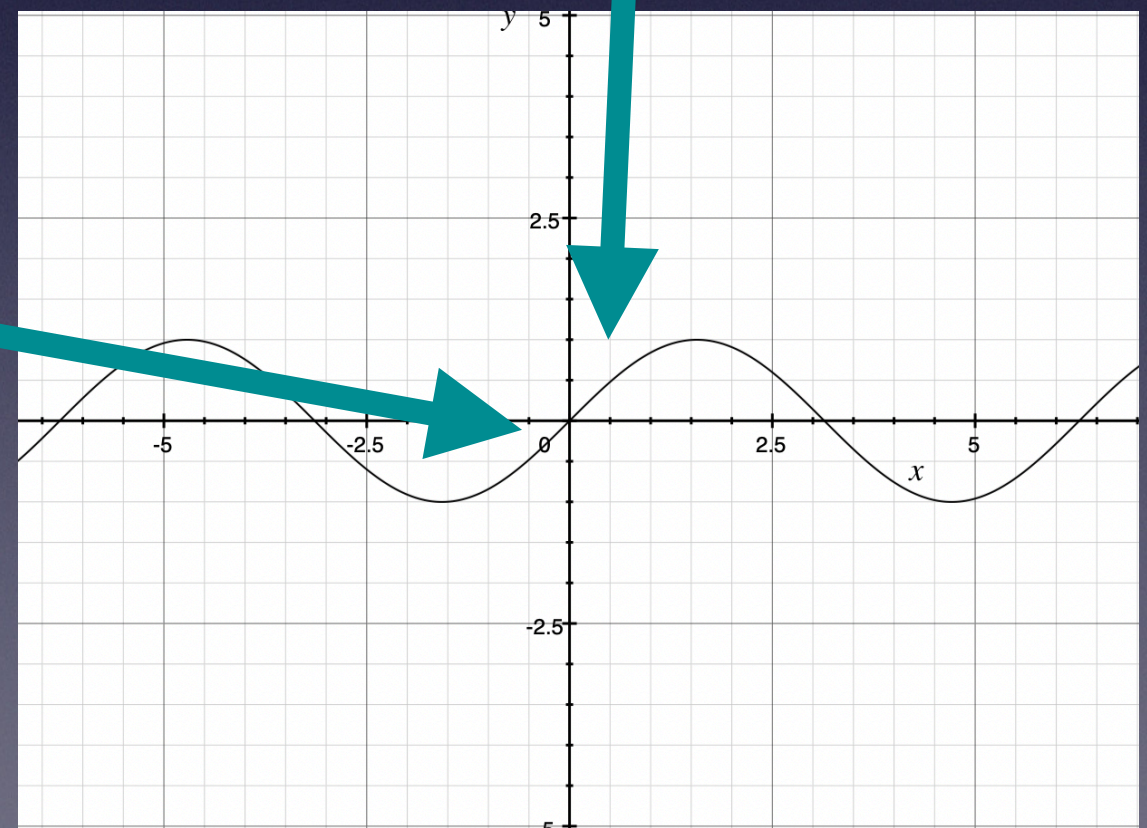
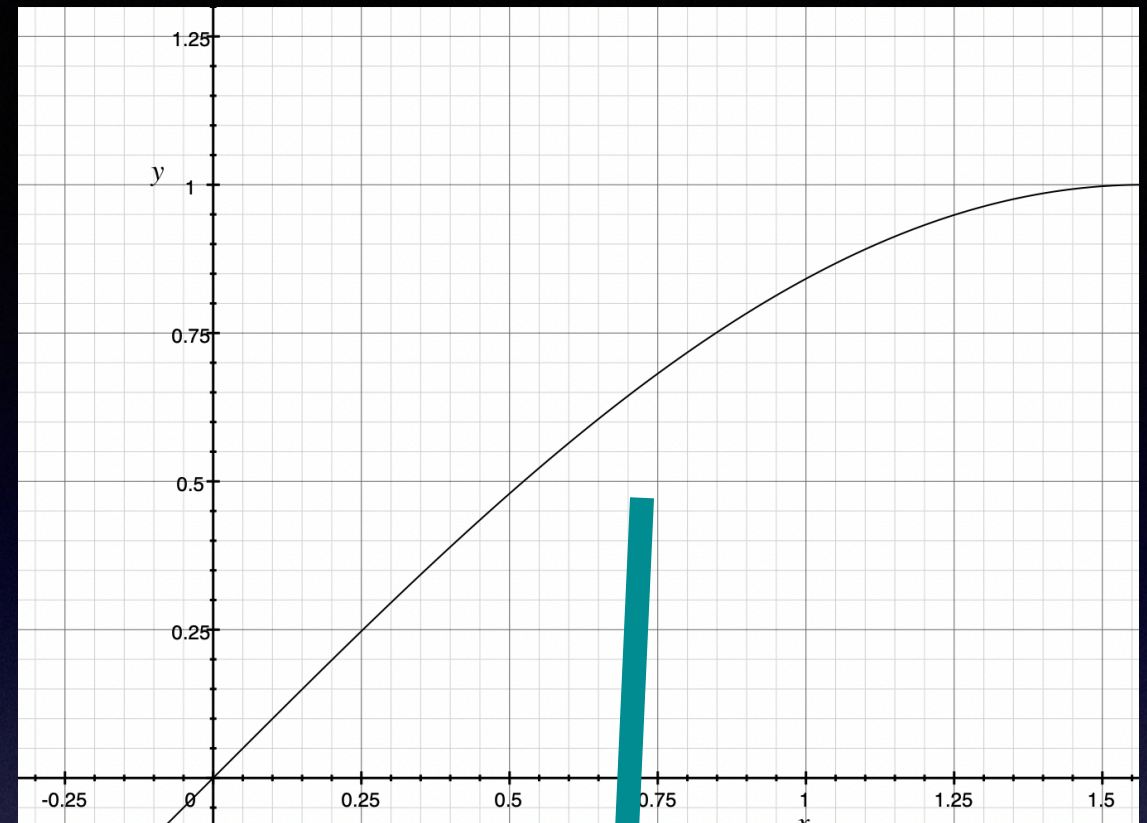
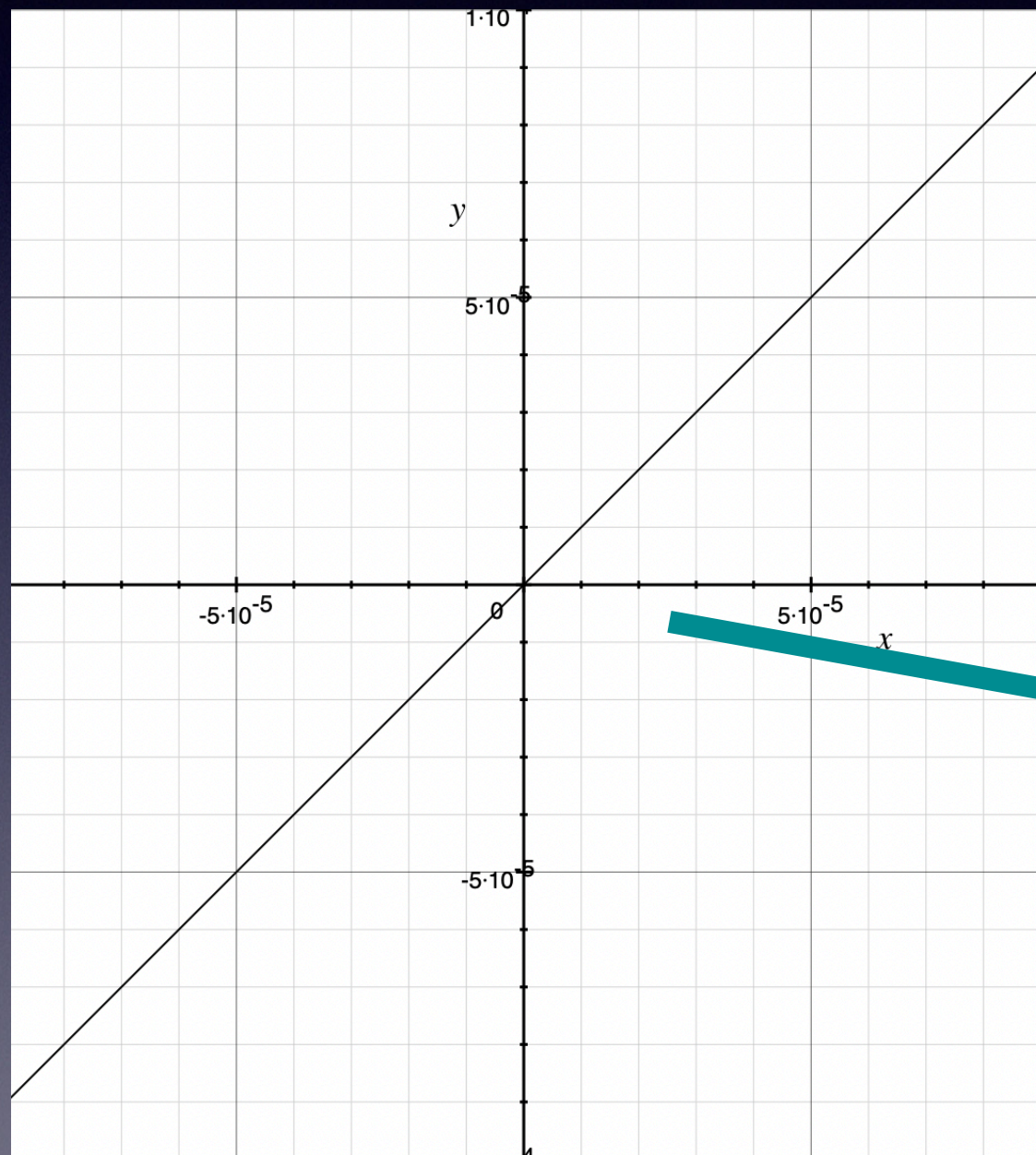
Mathematical Model of Kin Selection and Herd Immunity

Loafing in theoretical biology

“All models are wrong, but some of them are meaningful.”

–Kokko, H. 2007. **Modelling for field biologists and other interesting people**

How to describe it?



Who are they defending for?

- Defence can be costly.
 - Toxin, hair...
- Ineffective.
 - Some toxin releases only when the prey is killed.
 - Wax secreted by aphids.
- Individual hardly gain any fitness.





How do they evolve?

- Personal fitness + inclusive fitness;
- Selfishness vs. group fitness.
- Group protection leads to cheating.
- Multiple driving force in evolution.
- How to balance selfishness and group fitness?
- Kin selection model by Steve Frank(1998).

Assumptions

- The probability of an individual inducing a defence is a **phenotype**, which can be represented as a **continuous** variable.
- **Phenotypes** of individuals are so **closely related** that it can be seen as a **continuous** function.
- The **change in phenotype** is **vanishingly small** in a relatively **short period of time**, such as in tens of generations.

The Storyline of Frank(1998)

1. Preparation

- A sign of possible attack appears
- Individuals either induce a defence or not, with the probability, y .

2. Action

- Pick someone to attack
- Kill the undefended
- Not kill the defended

Average y

Factor of cost

Group protection


$$W(y, z) = (1 - c \cdot y) \cdot [1 - a \cdot (1 - y) \cdot f(z)]$$

Individual phenotype
(Probability of defence)

Rate of attack.

Limitations

- Defended individuals are excluded from attack (unrealistic).
- Attacks are perfect for undefended individuals (unrealistic).
- Undefended individuals are absolutely susceptible (might not be true).
- Defence is permanent (unrealistic).
- Make it persuasive.

New Storyline

1. Preparation

- Invest a defence = higher tolerance to attack
- Not invest a defence = lower tolerance to attack

2. Action

- Attack, attack, attack.....(with an expectation)
- Who get killed?

I DON'T HAVE TIME, ASK ME LATER!!!

$$W(y, z) = (1 - c \cdot y) \cdot [(1 - y) \cdot p_1 + y \cdot p_2] \cdot g(z)$$

$$p = \sum_{i=0}^k e^{-\lambda} \cdot \frac{\lambda^i}{i!}$$

$$p_1 = p|_{k=k_1}$$

$$p_2 = p|_{k=k_2}$$

What is the chance of
the number of attack
not reaching k?

Rate of change

- Make a connection between the two variables.
- Analyse the optimal state of the two variables as a whole.
- At some point the rate of change is 0.

$$\frac{dW}{dx} = \frac{\partial W}{\partial y} \cdot \frac{dy}{dx} + \frac{\partial W}{\partial z} \cdot \frac{dz}{dx}$$

W - fitness

x - group genotype

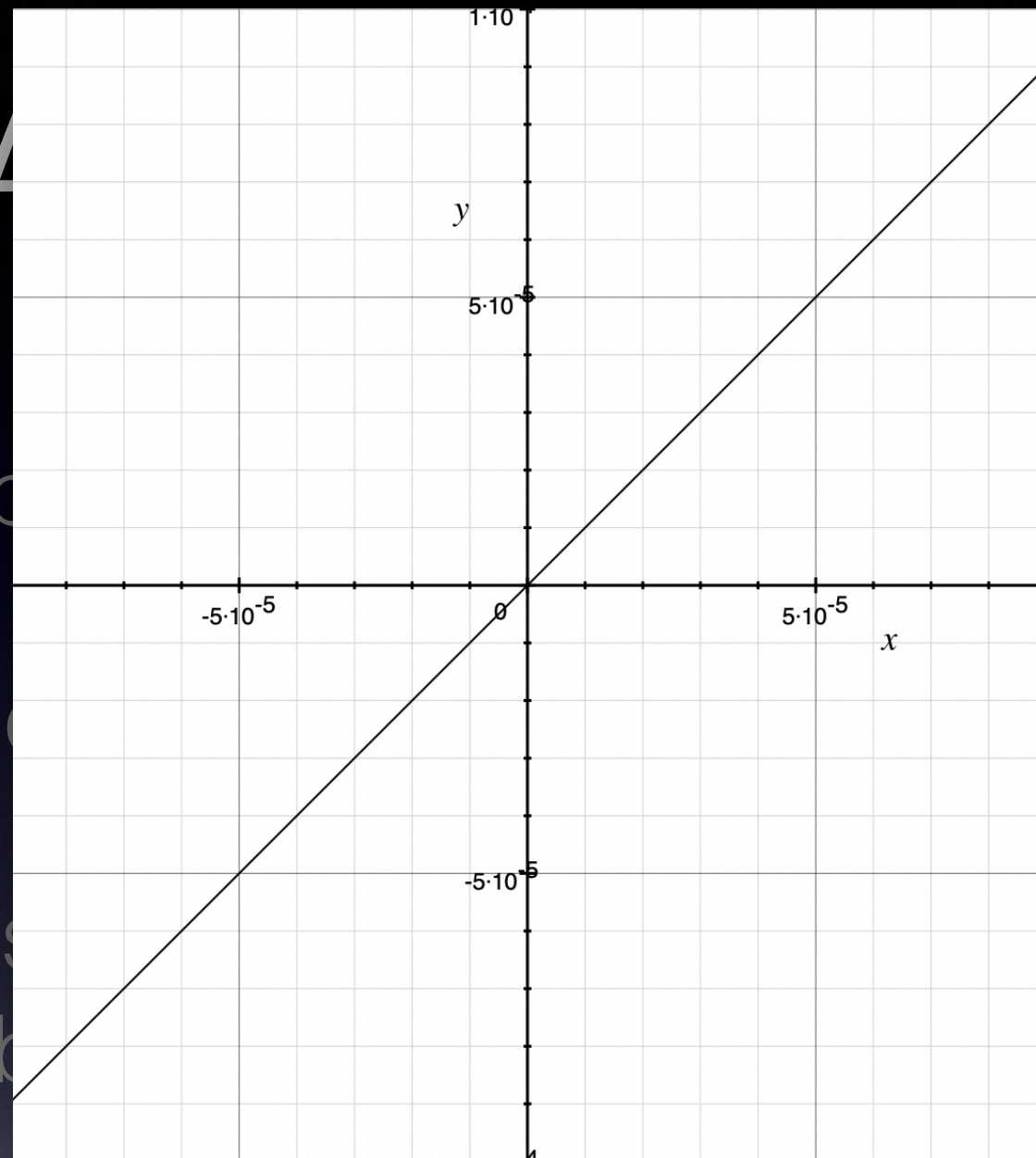
y - individual phenotype

z - group average of phenotype

$$\frac{dW}{dx} = \frac{\partial W}{\partial y} \cdot \frac{dy}{dx} + \frac{\partial W}{\partial z} \cdot \frac{dz}{dx}$$

$$\frac{dW}{dy} = \frac{\partial W}{\partial y} + \frac{\partial W}{\partial z} \cdot \frac{dz}{dy}$$

$$r = \frac{dz}{dy}$$



- The probability of a change in phenotype occurring a relatively short period of time, such as in tens of generations, is vanishingly small.
- Phenotypes are closely related to the genotype, so that it can be represented by a function.
- The change in phenotype is vanishingly small in a relatively short period of time, such as in tens of generations.

$$\frac{dW}{dy} = \frac{\partial W}{\partial y} + \frac{\partial W}{\partial z} \cdot r = 0$$

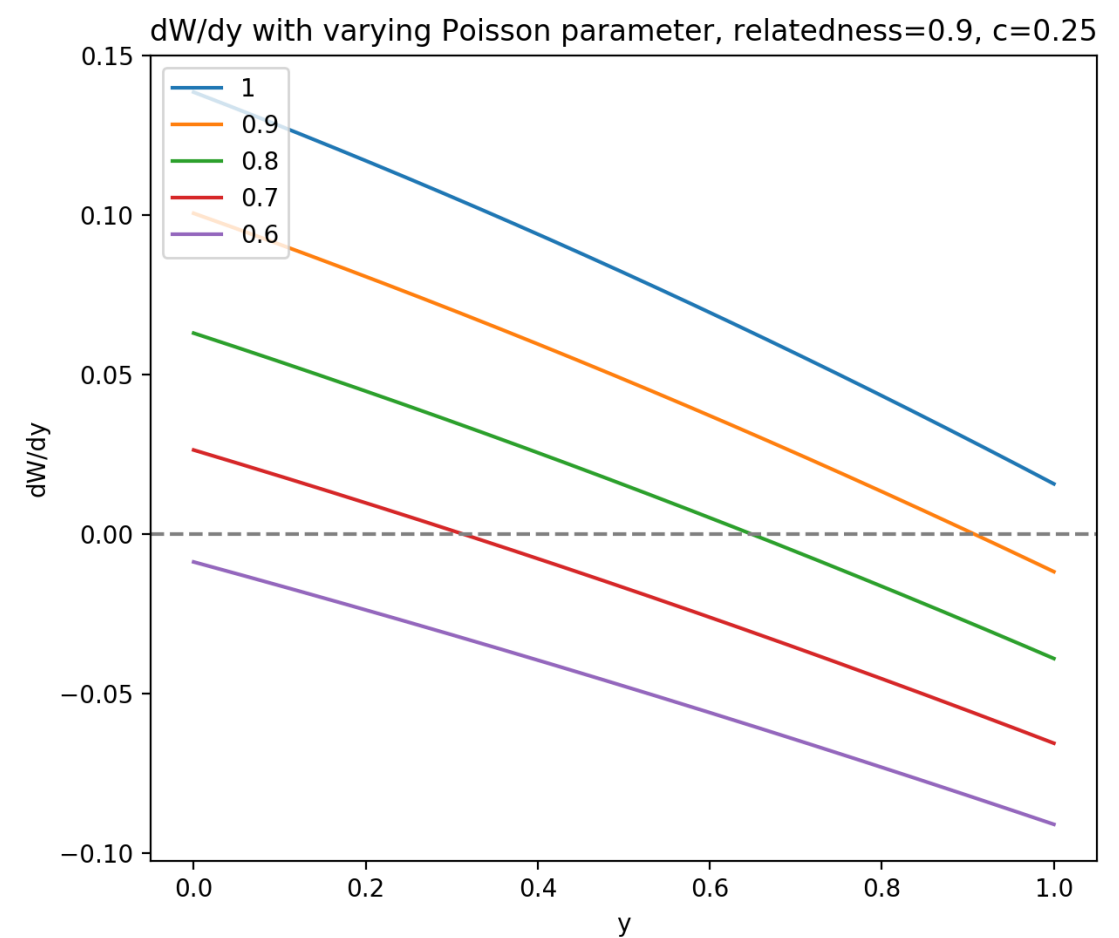
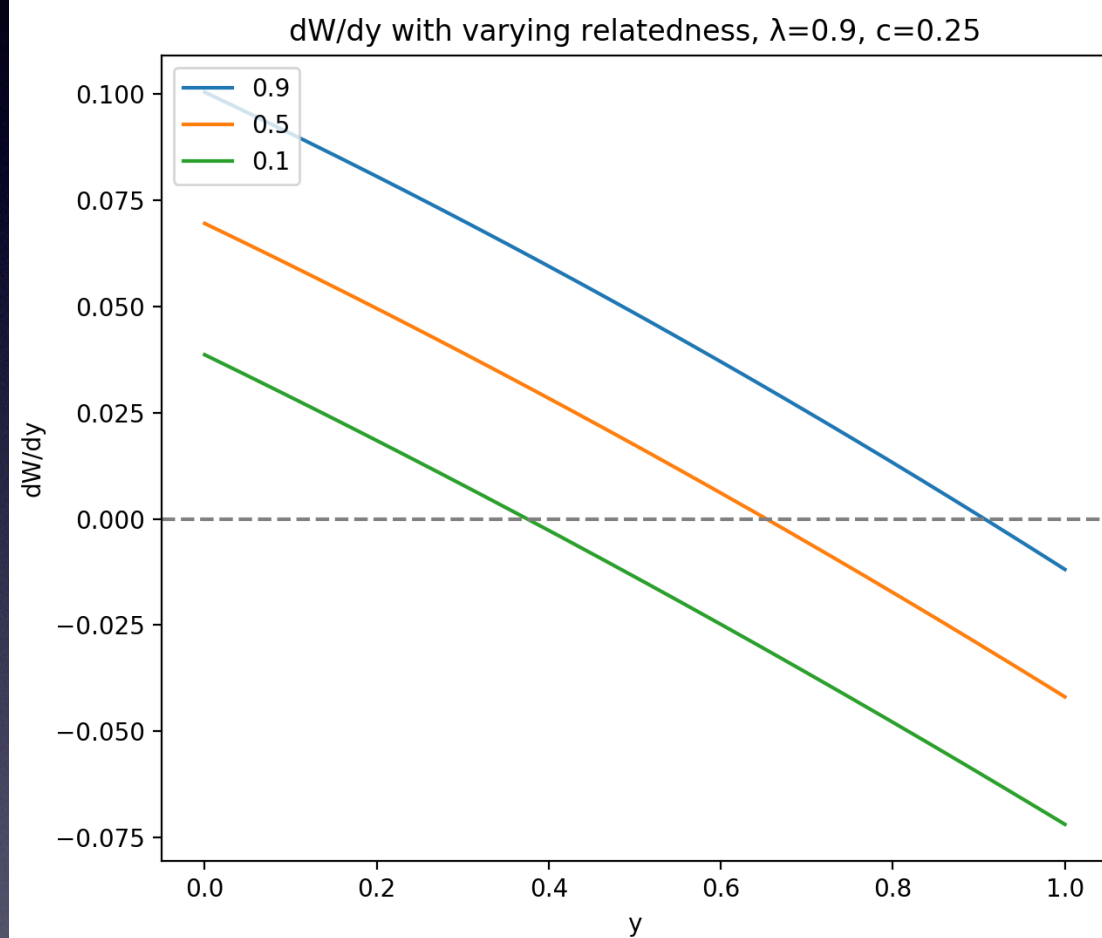
$$r = \frac{dz}{dy}$$

Constant



- If the best choice for one individual is not being the average, the best choice for everyone is not being the average.
- Then active selection is happening.
- Thus at equilibrium, hidden rule $y^*=z^*$.

$$\frac{dW}{dy} = [p_1(2cy - c - 1) + p_2(1 - 2cy)]g(y) + r(1 - cy)[p_1(1 - y) + p_2y]g'(y)$$



No error bar!

Conclusion

- The goal is achieved. We made a more general model.
- Result accord with the original model.
- Possible applications in public health and economy.

“A theory is the more impressive the greater the simplicity of its premises is, the more different kinds of things it relates, and the more extended is its area of applicability.”

–Albert Einstein

Reference

- Frank, S. A. 1998. Inducible defence and the social evolution of herd immunity. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265 (1408), 1911-1913.
- Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7 (1), 17-52.
- Hamilton, W. D. 1972. Altruism and Related Phenomena, Mainly in Social Insects. *Annual Review of Ecology and Systematics*, 3 (1), 193-232.
- Ruxton, G. D., Sherratt, T. N. and Speed, M. P. 2004. *Avoiding Attack*, Oxford University Press.
- S. Jones, R., C. Davis, S. and Speed, M. P. 2013. Defence Cheats Can Degrade Protection of Chemically Defended Prey. *Ethology*, 119 (1), 52-57.
- Taylor, P. D. and Frank, S. A. 1996. How to make a kin selection model. *Journal of Theoretical Biology*, 180 (1), 27-37.
- Wu, G. M., Boivin, G., Brodeur, J., Giraldeau, L. A. and Outreman, Y. 2010. Altruistic defence behaviours in aphids. *BMC Evolutionary Biology*, 10 (1), 19.