Multiplayer Evolutionary Games

Chaitanya S. Gokhale

Professor of Theoretical Biology

Center for Computational and Theoretical Biology

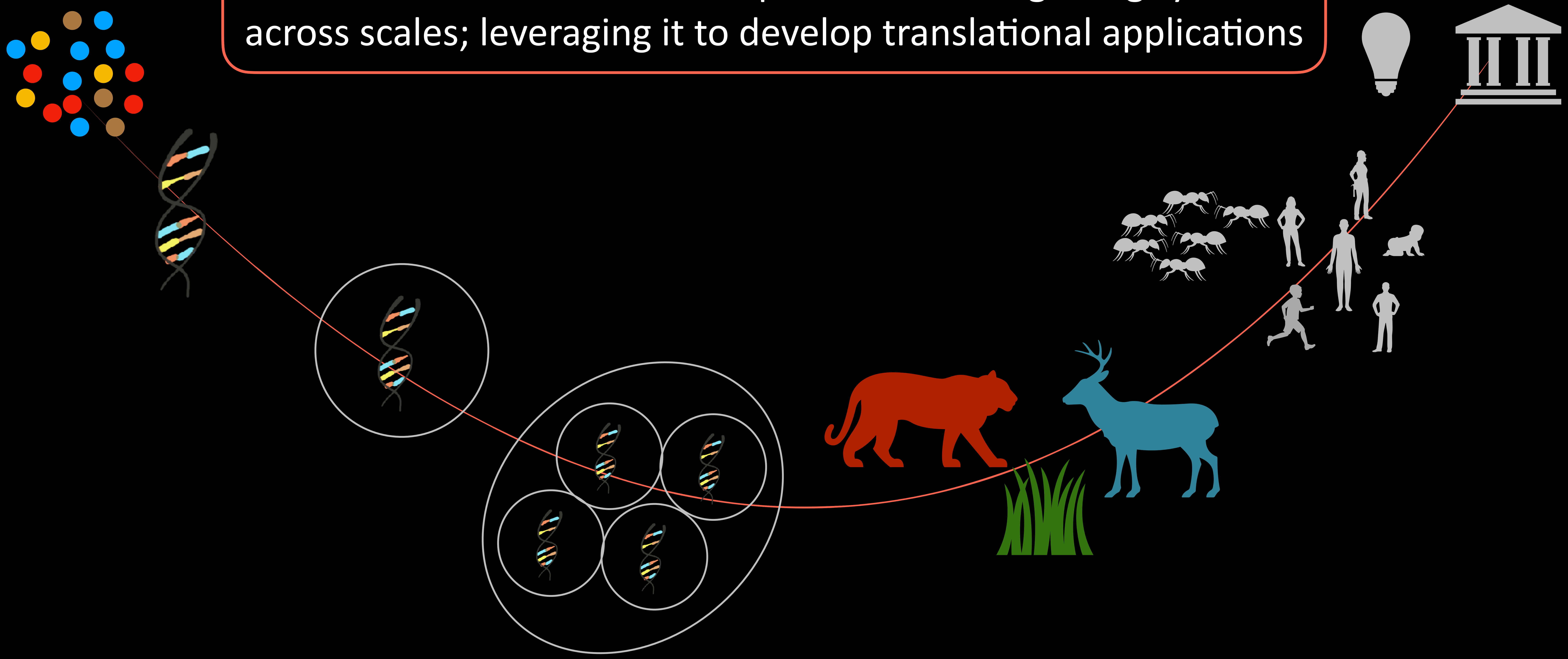
University of Würzburg

Dynamics of Living Systems

From Fundamental Processes to Translational Applications

Dynamics of Living Systems

Understand the fundamental processes driving living systems across scales; leveraging it to develop translational applications



Understand the fundamental processes driving living systems across scales;
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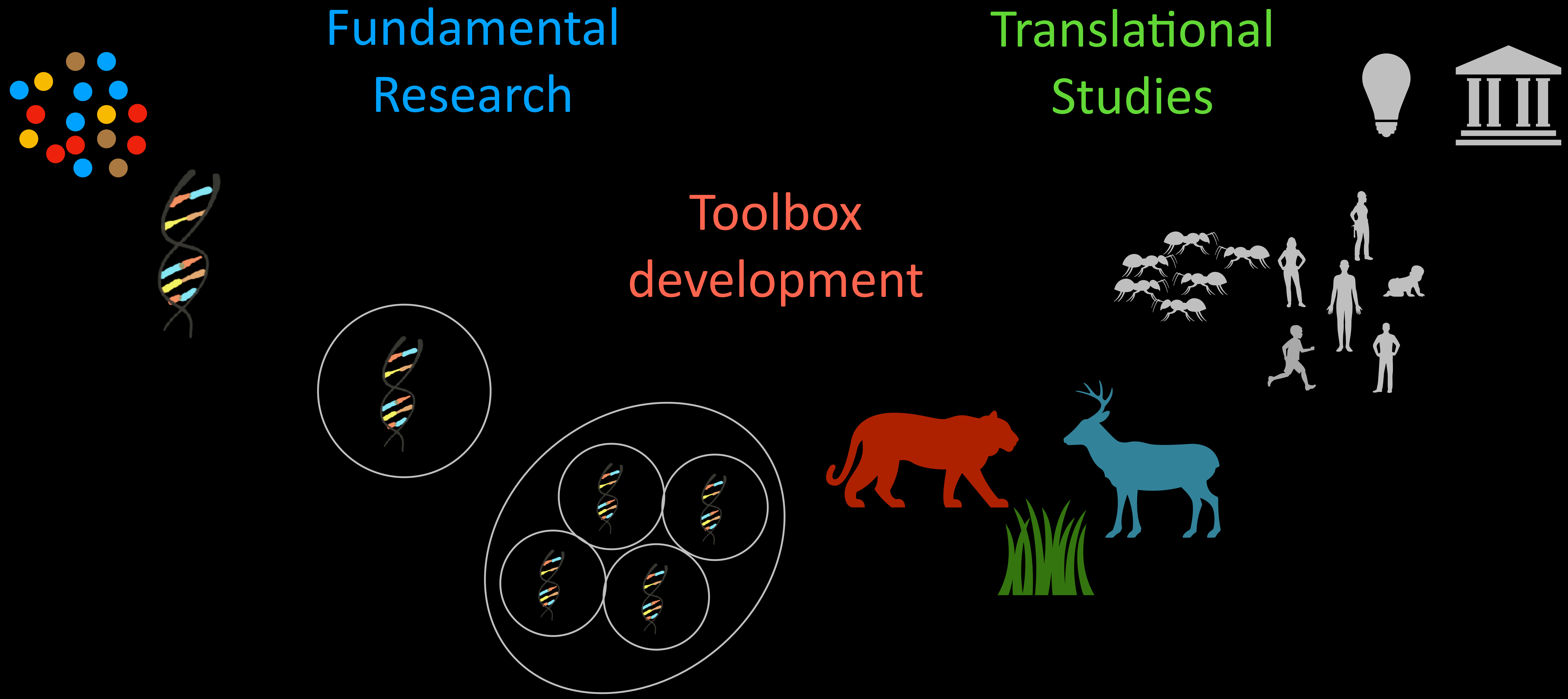
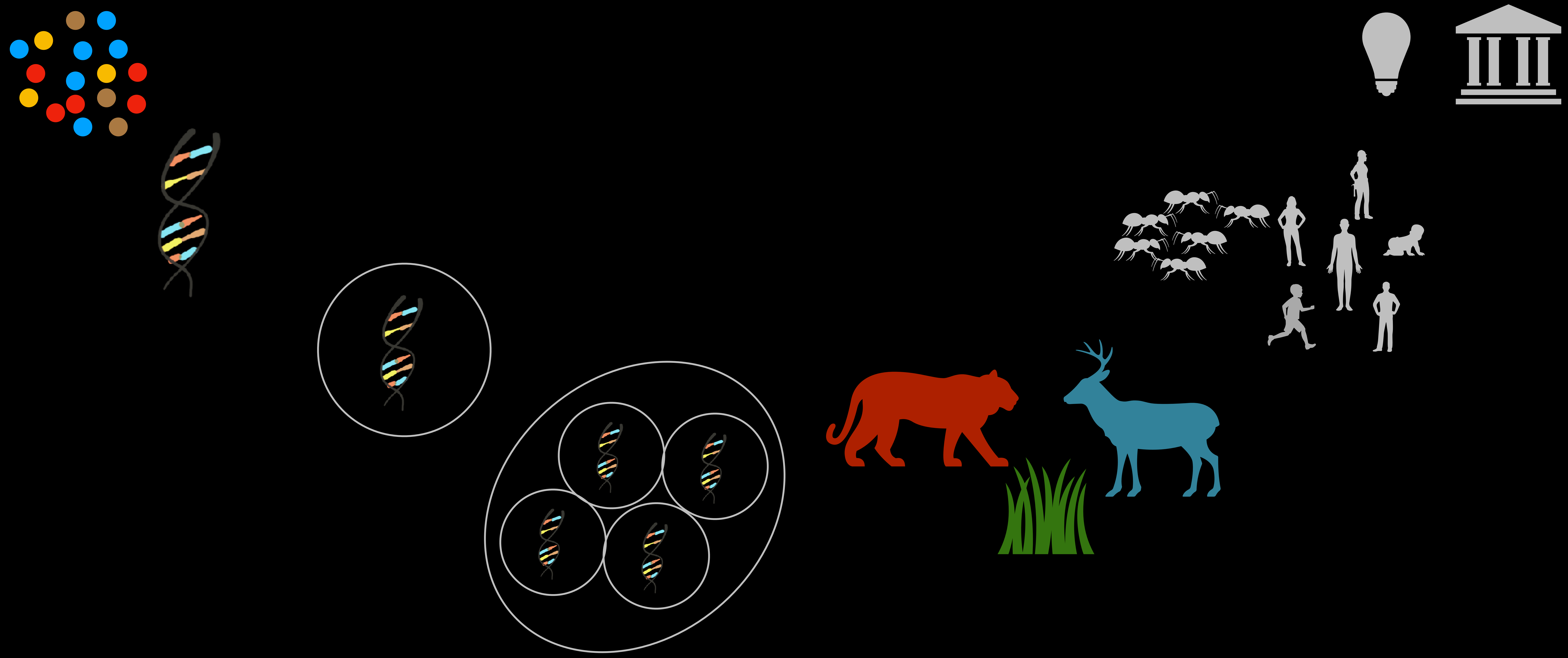


Fundamental Research



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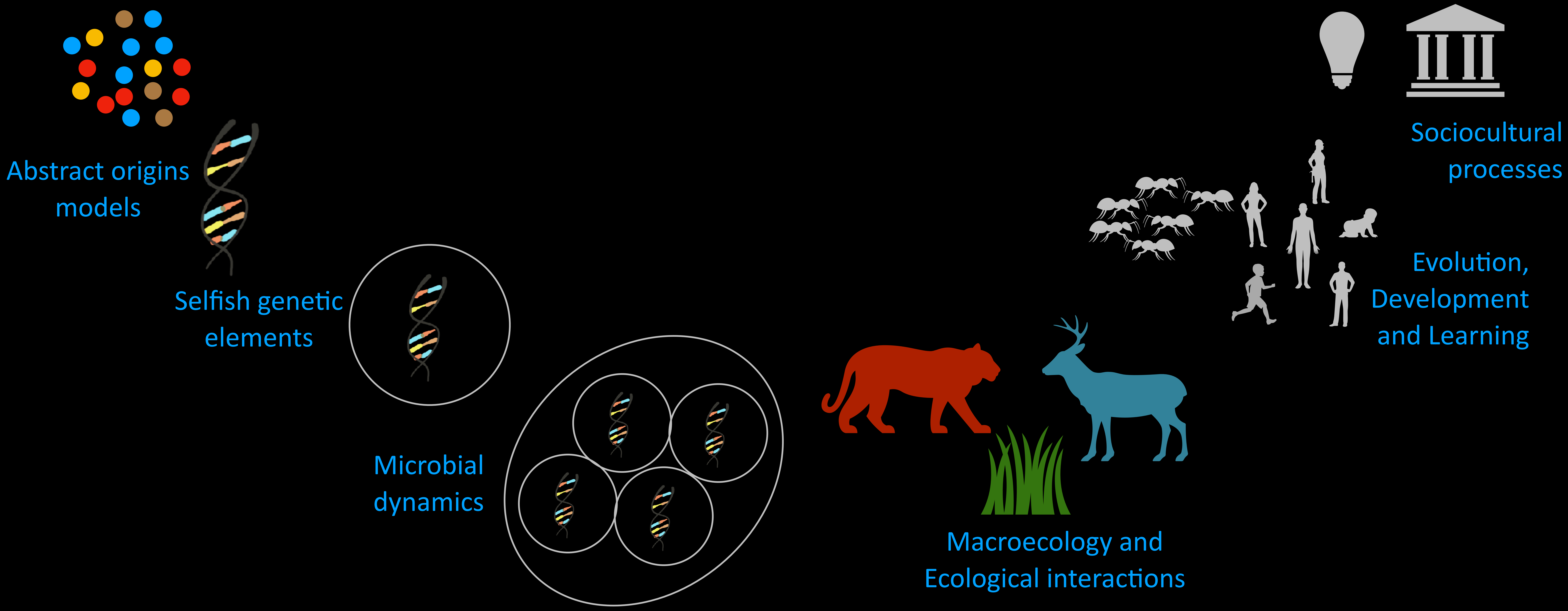

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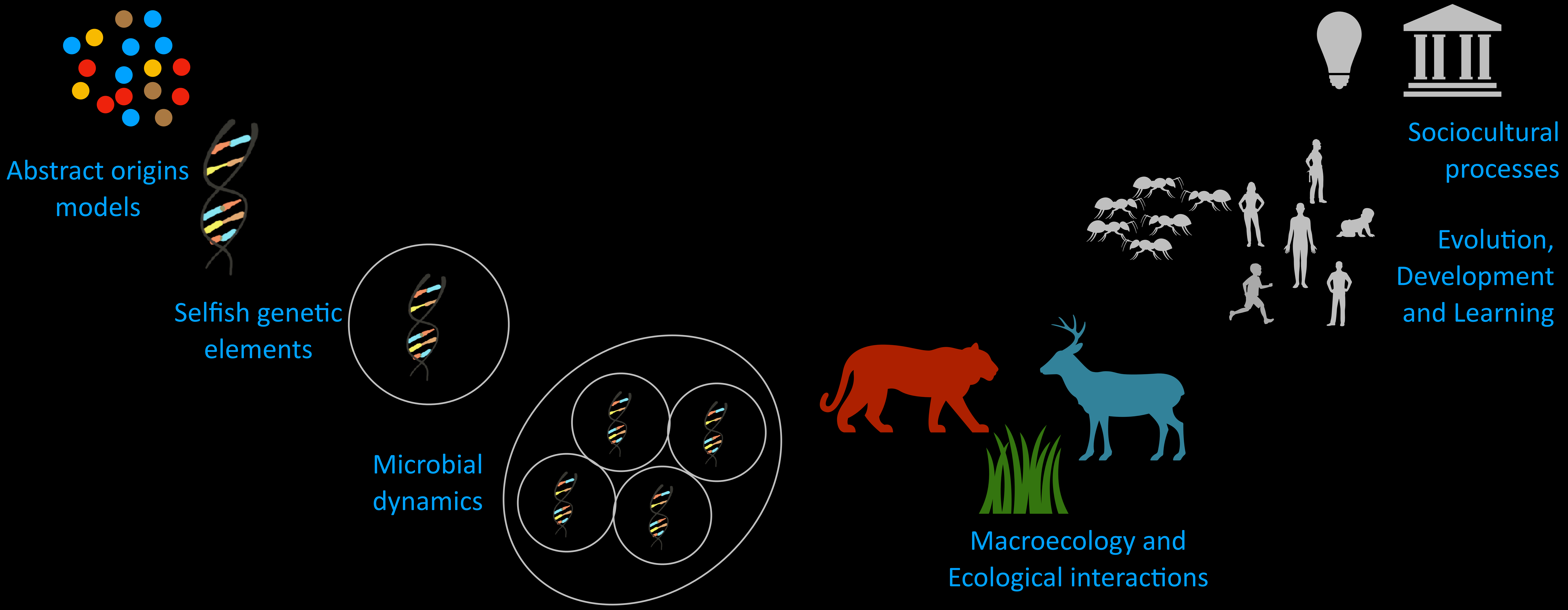
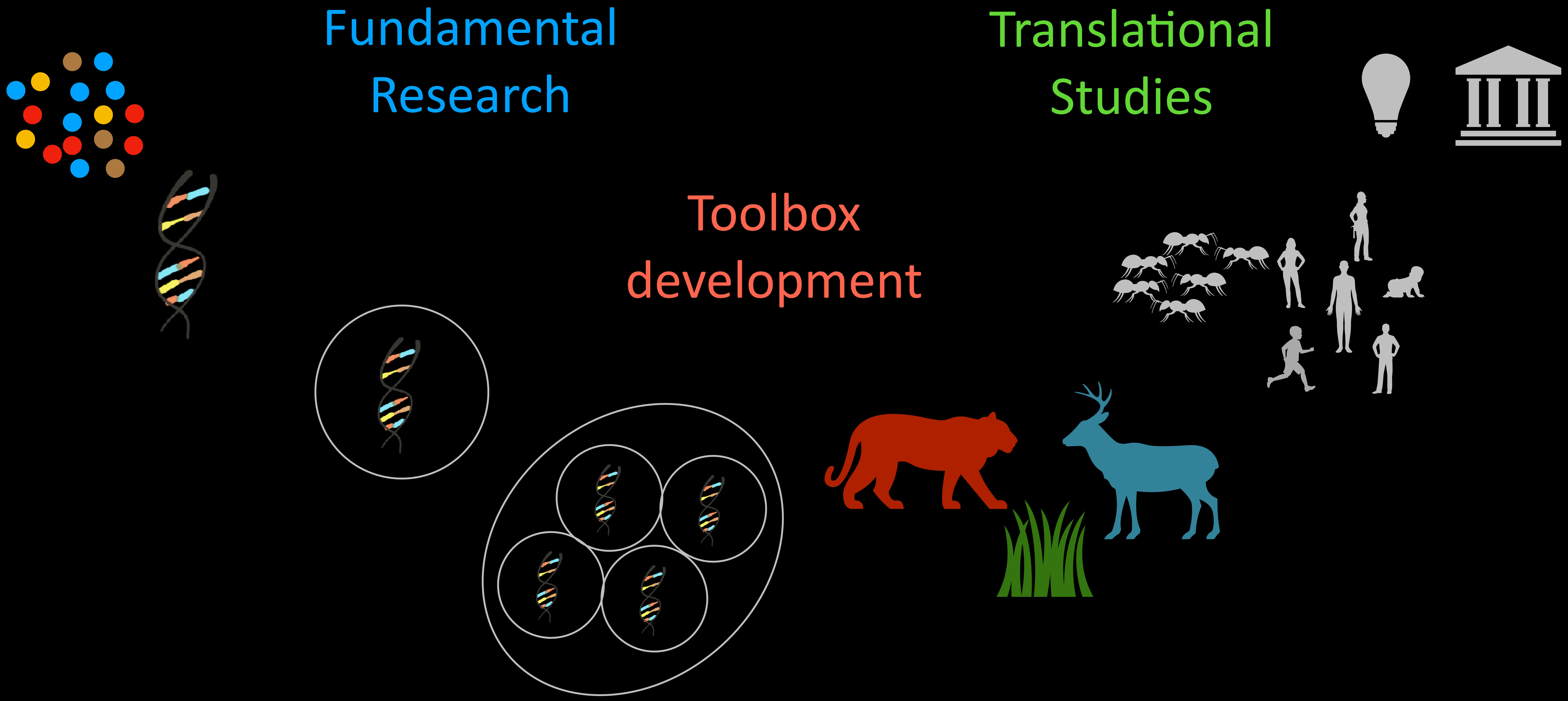
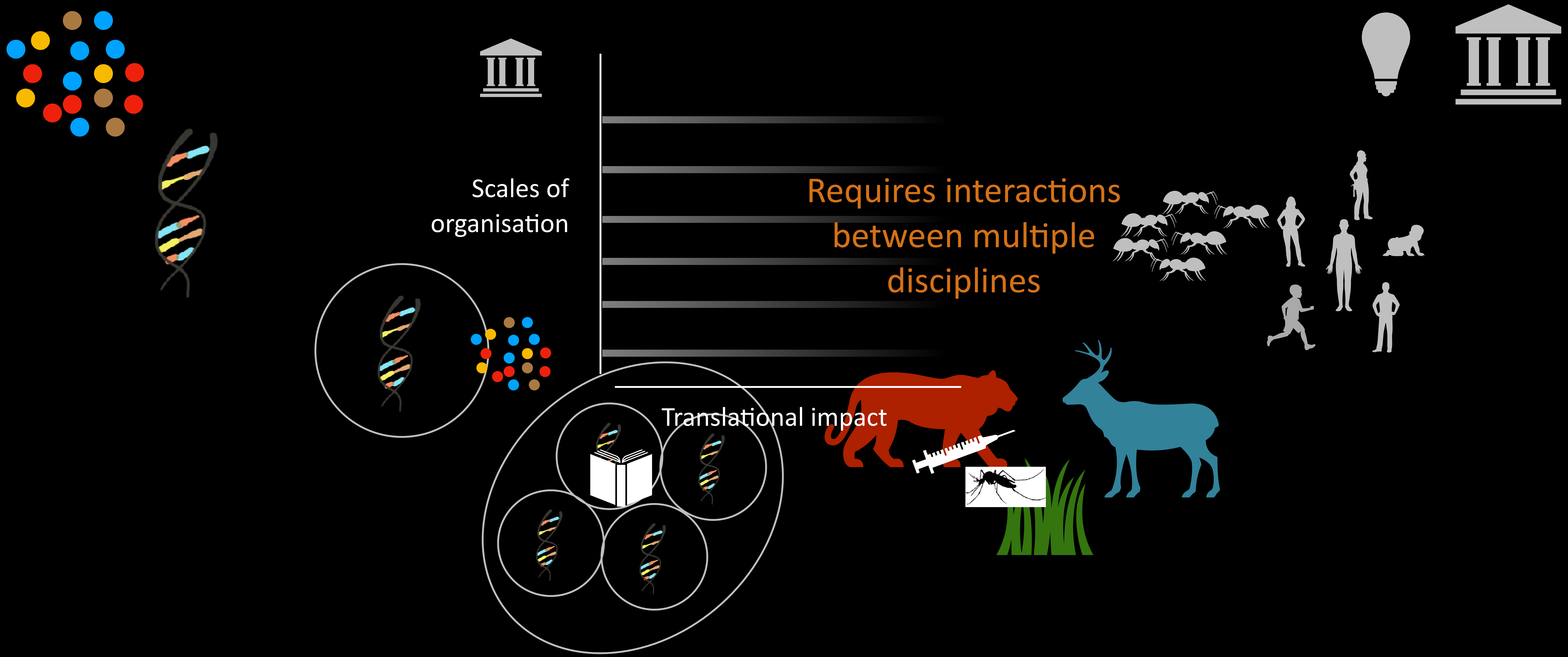


Understand the fundamental processes driving living systems across scales leveraging it to develop translational applications



Translational Studies



Translational Studies

Ecosystem Engineering	Darwinian medicine	Darwinian agriculture	Conservation biology/policy

Translational Studies

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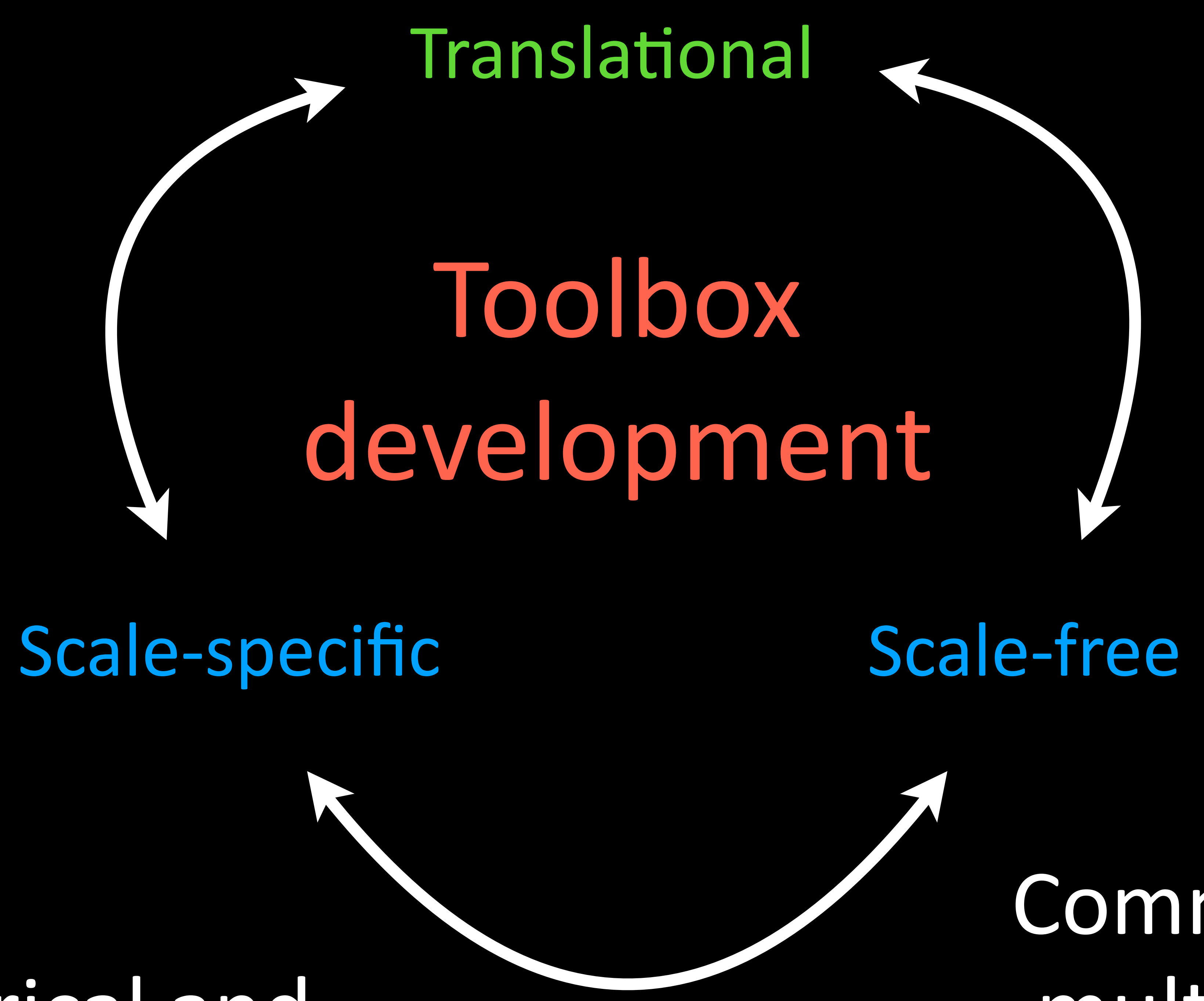
Theoretical Biology

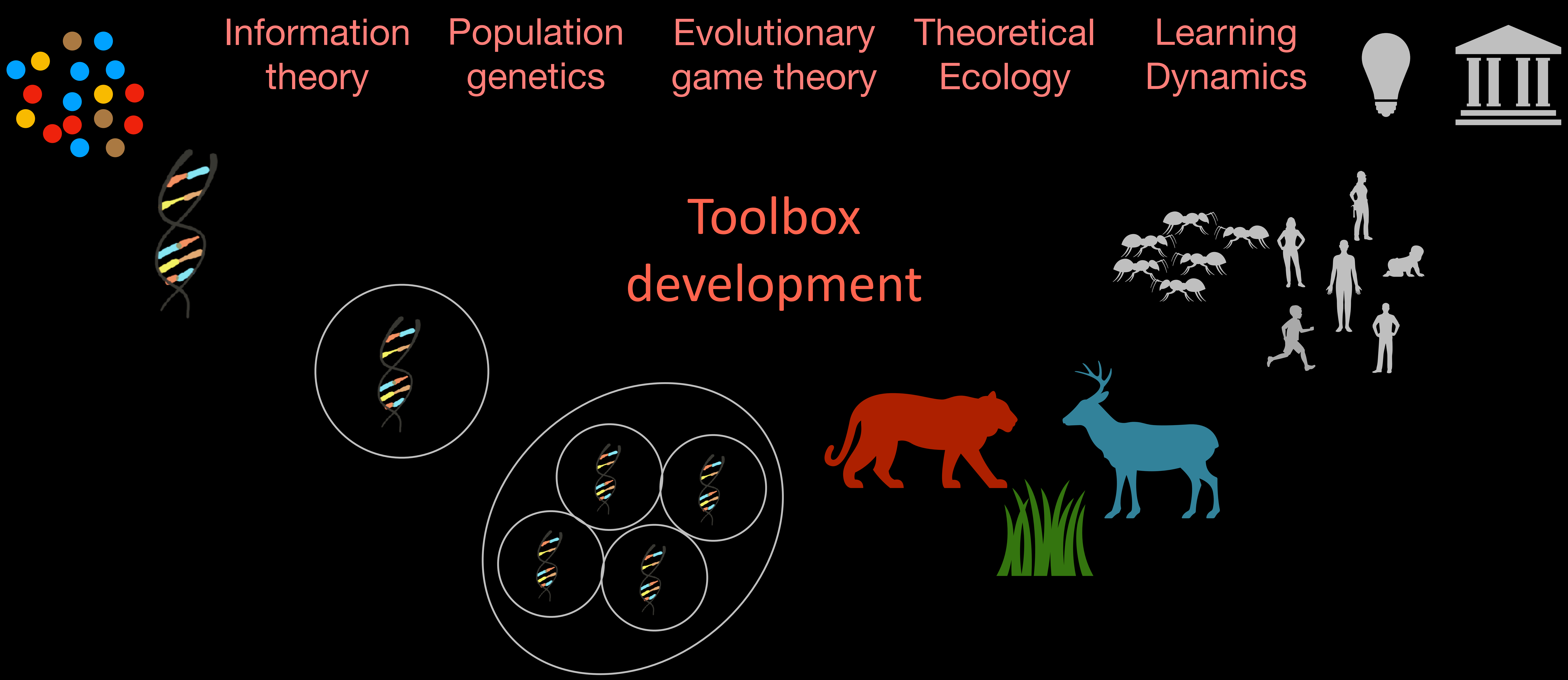
(…as we are pursuing it…)



Feedback between fundamental empirical and theoretical work, and translational fields of research

Communication between multiple disciplines from natural sciences to humanities

Understand the fundamental processes driving living systems across scales leveraging it to develop translational applications



Multiplayer Evolutionary Games

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Lecture 1 - Monday

Introduction to MEGs

Connection to PopGen

Wednesday - Lecture 3

Higher-order interactions

Collective beliefs and trust

Multiplayer evolutionary games (MEGs)

Tuesday

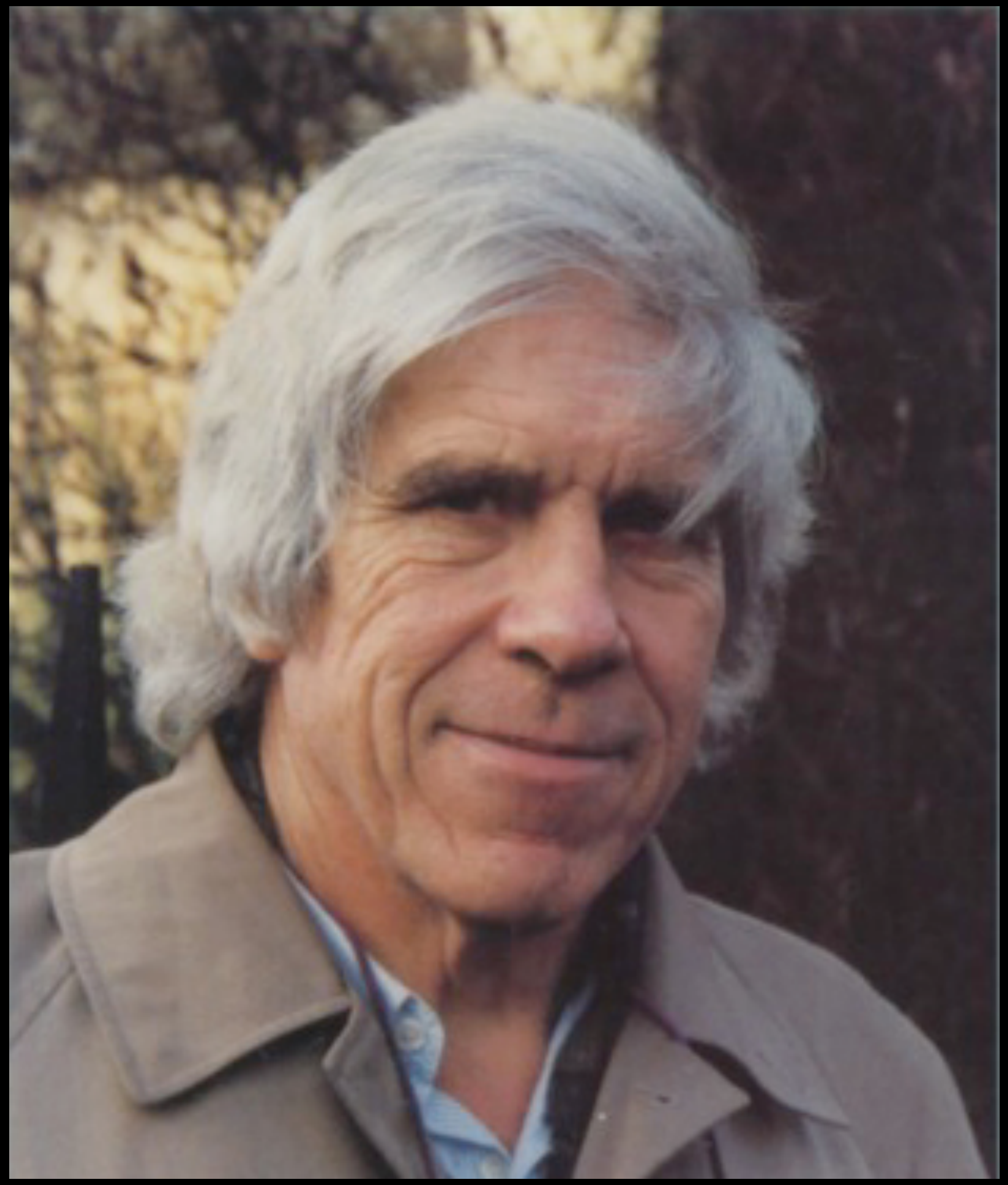
Lecture 2

If .. .when & how of MEGs in the long run

(If time permits)

MEGs in mutualism and

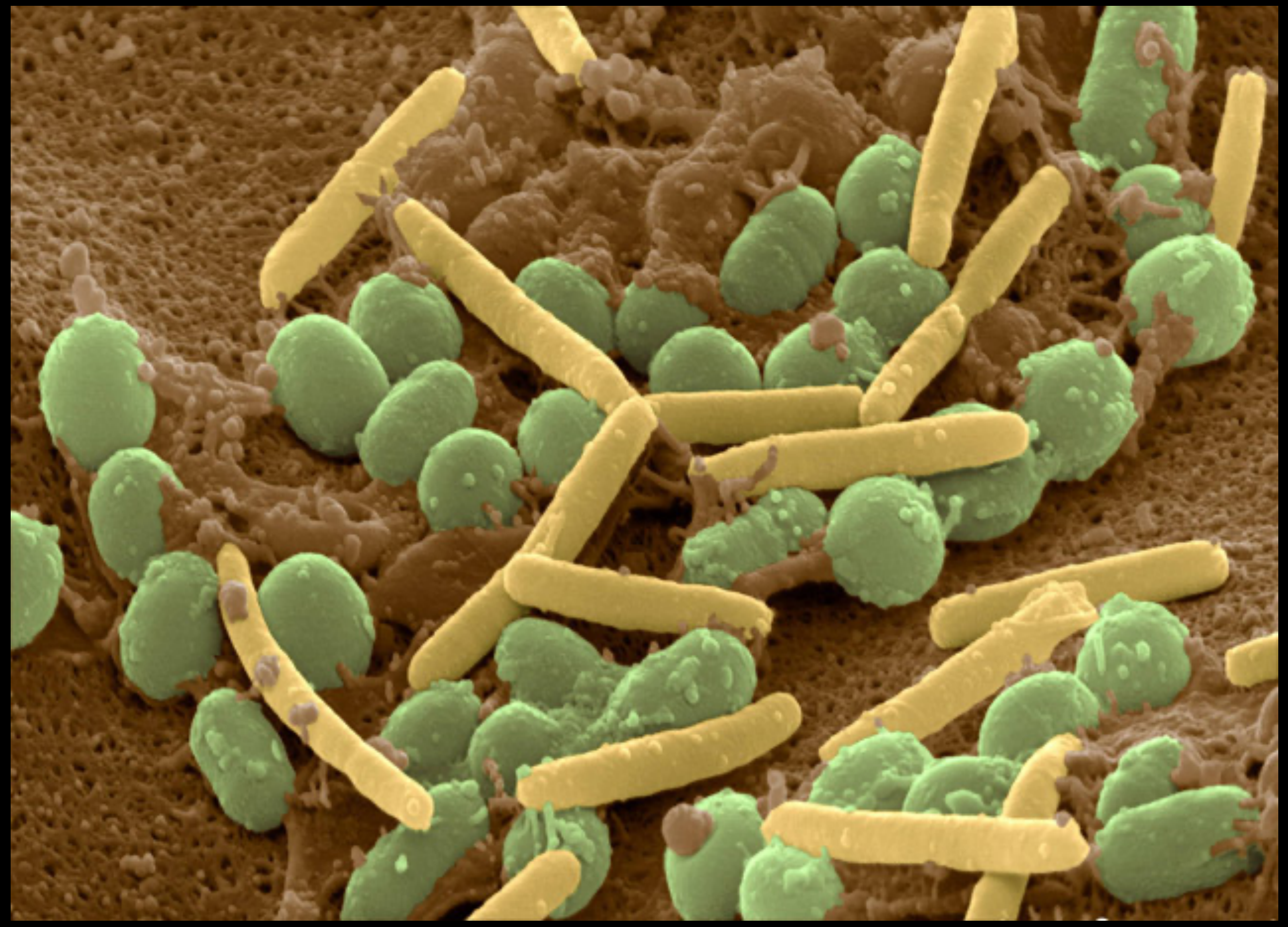
Eco-evolutionary dynamics



W.D. Hamilton

"....human life is a 'many-person game' and not just a disjoined collection of 'two-person games'....."

Its not just human life



Multiplayer evolutionary games

Fundamental tenets

THE UNITS OF SELECTION

4000

R. C. Lewontin

Department of Biology, University of Chicago, Chicago, Illinois

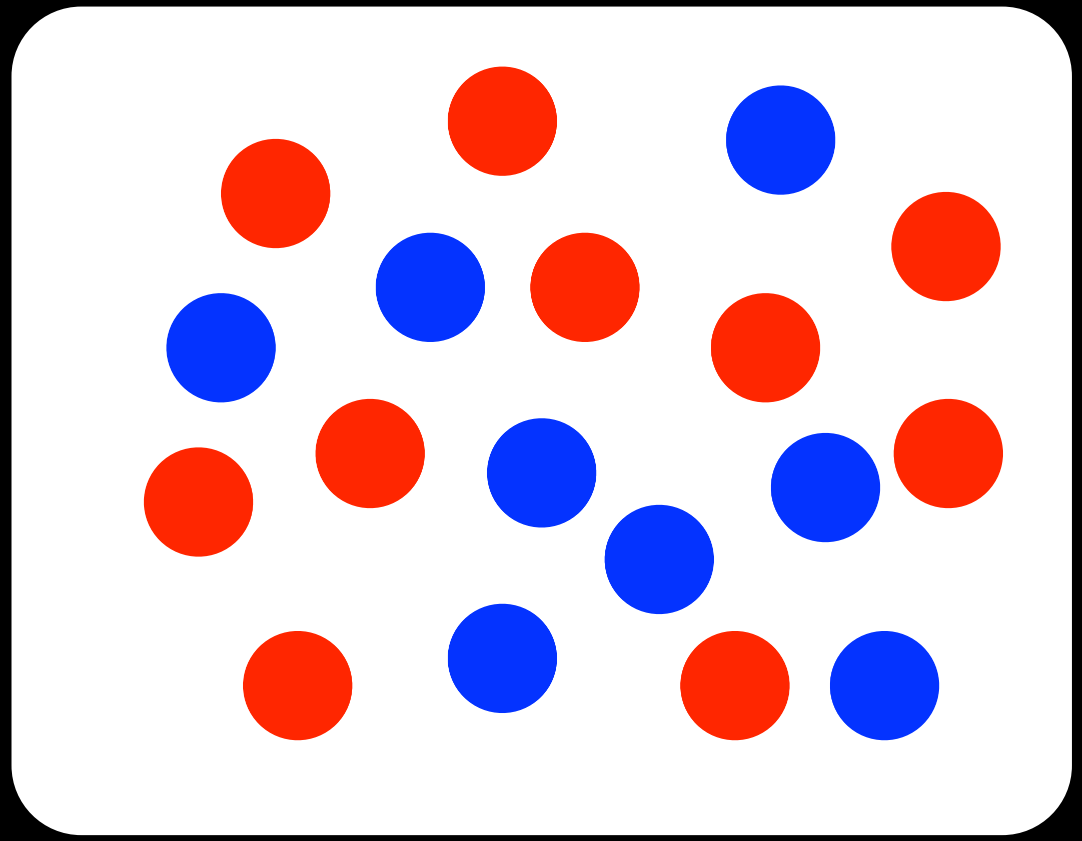
The principle of natural selection as the motive force for evolution was framed by Darwin in terms of a "struggle for existence" on the part of organisms living in a finite and risky environment. The logical skeleton of his argument, however, turns out to be a powerful predictive system for changes at all levels of biological organization. As seen by present-day evolutionists, Darwin's scheme embodies three principles (Lewontin 1):

1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).

These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change.

Lewontin, R C. "The Units of Selection." *Annual Review of Ecology and Systematics* 1 ,1970

Fundamental tenets



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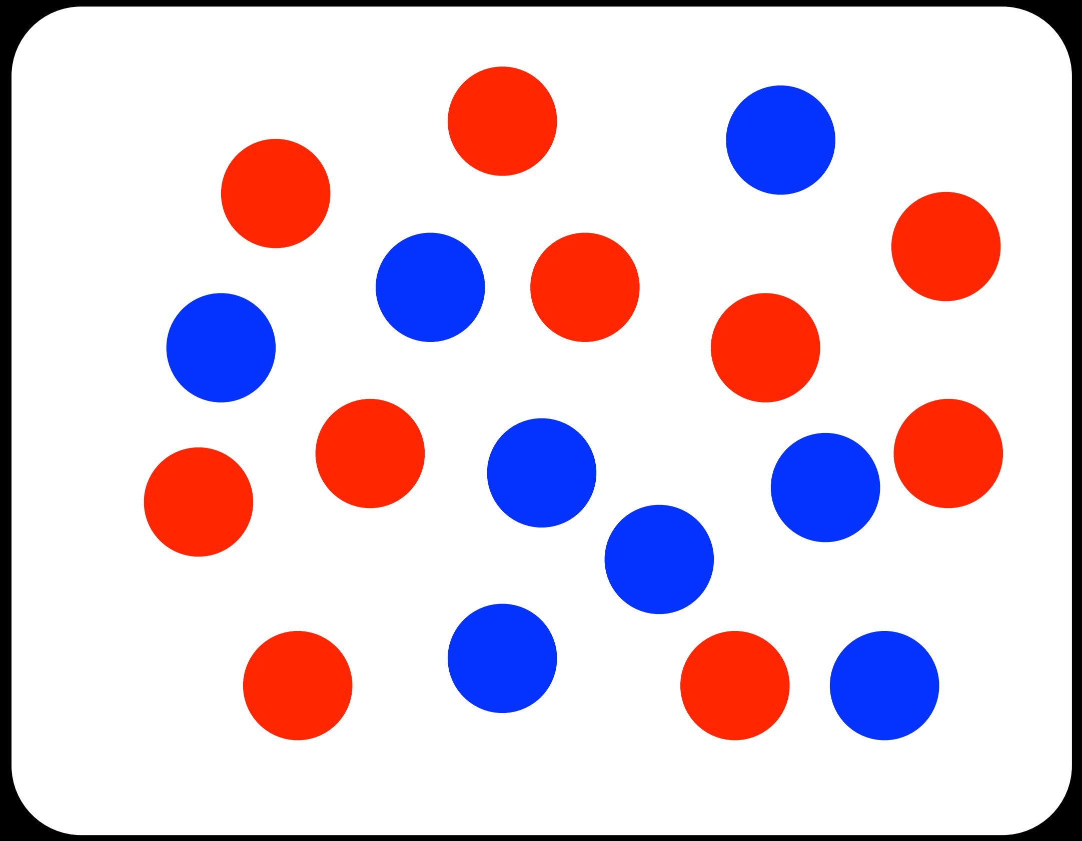

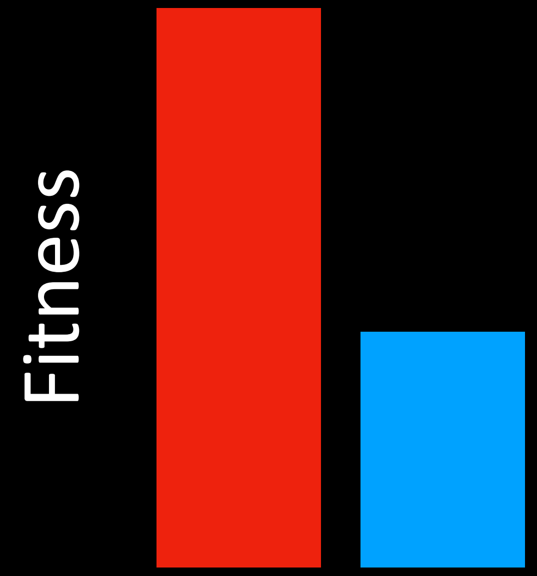

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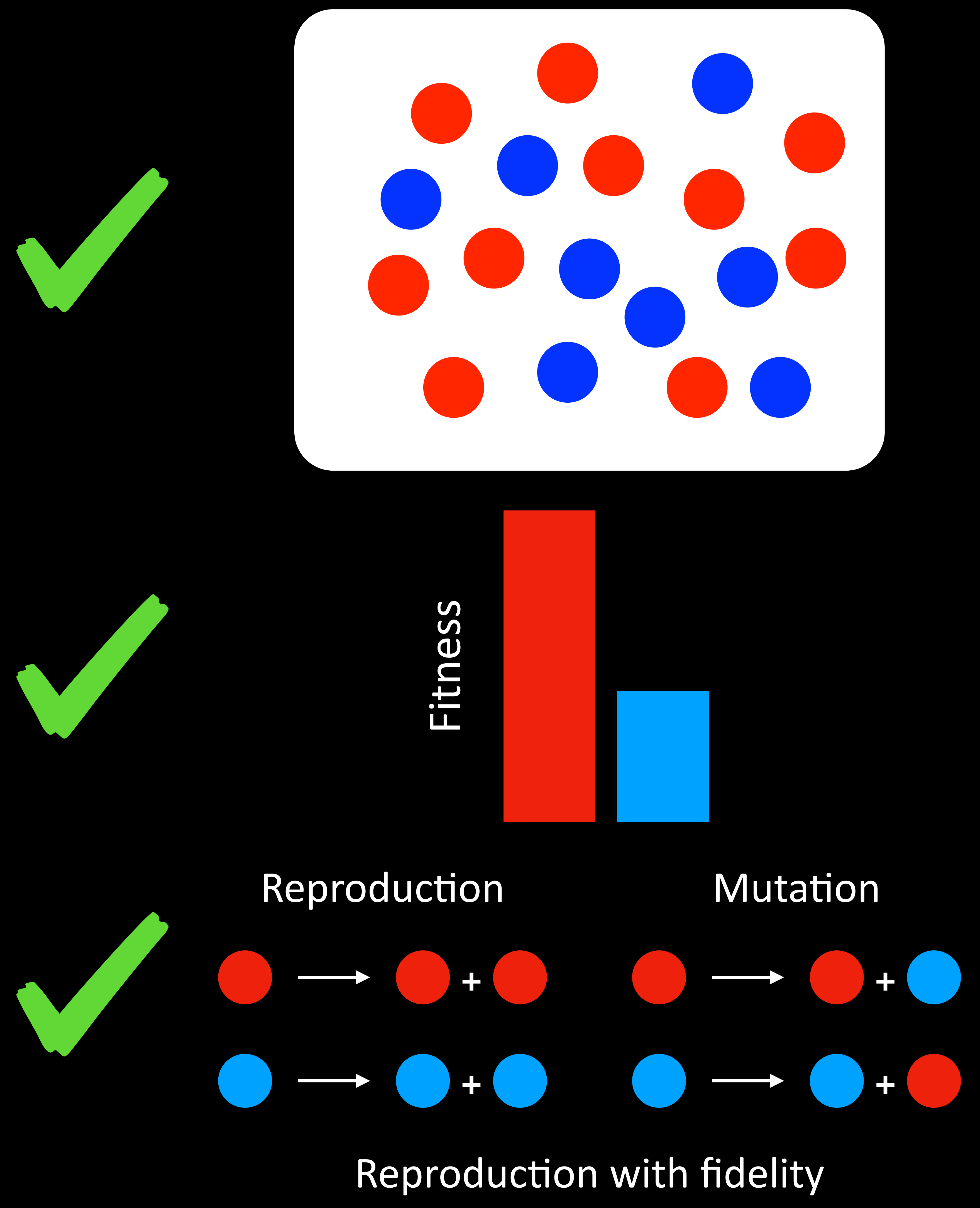

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... there have been updates to this

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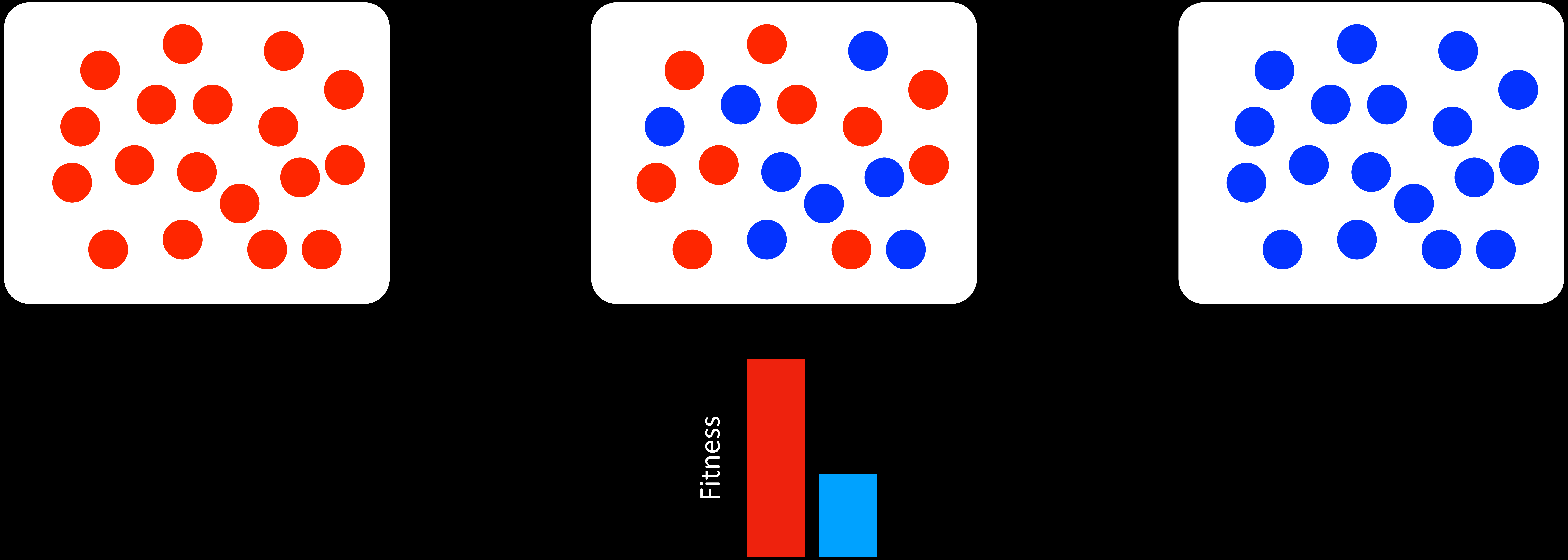
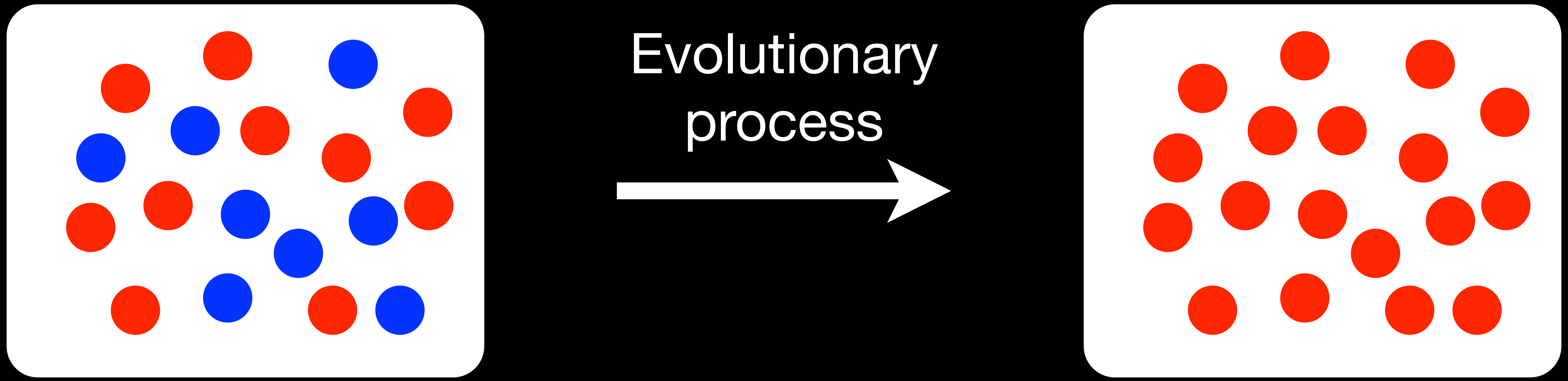
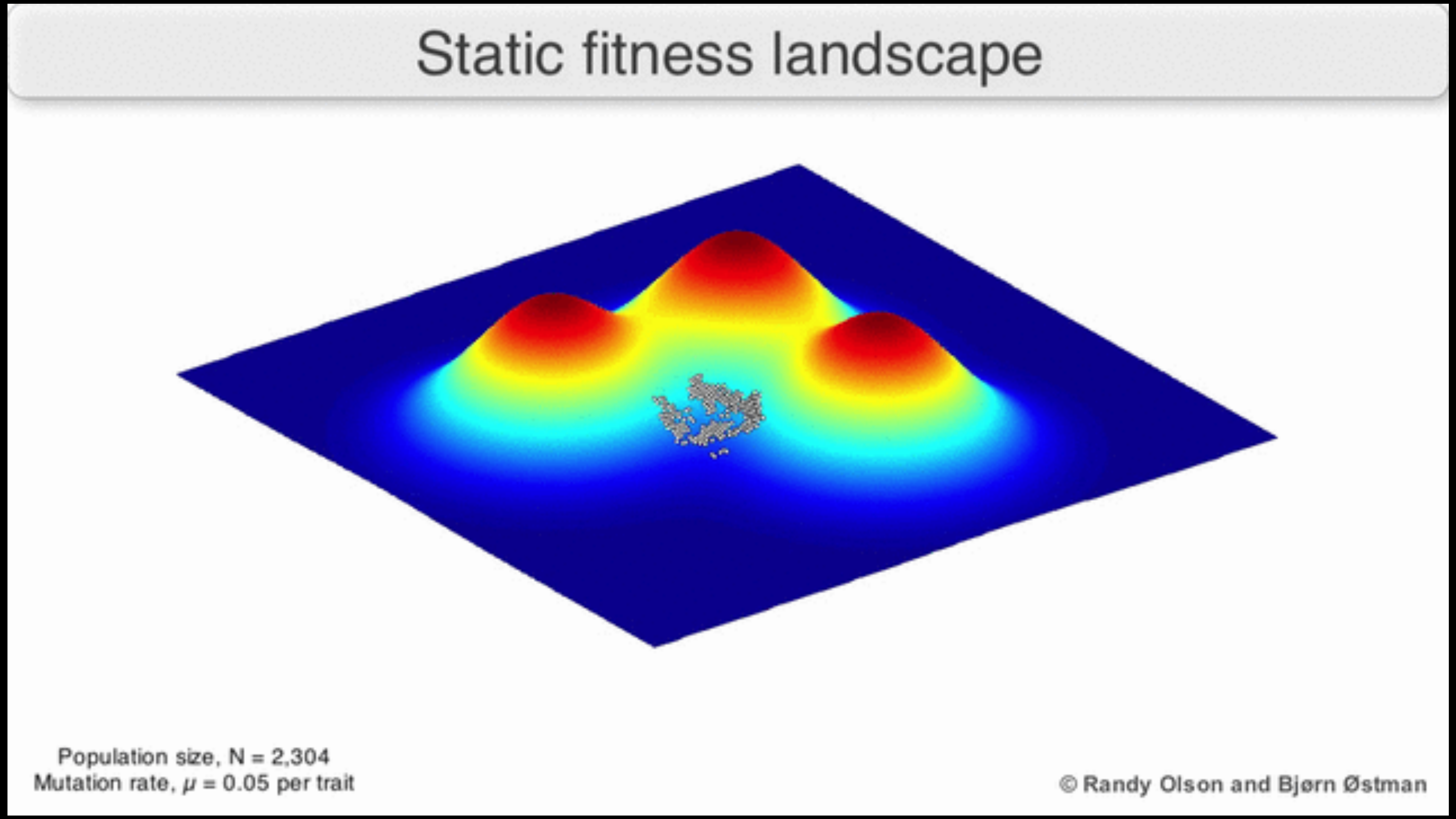

Fitness


Evolutionary
process


Static fitness landscape
Population size, N = 2,304
Mutation rate, μ = 0.05 per trait
© Randy Olson and Bjørn Østman

Multiplayer evolutionary games

Multiplayer evolutionary games

species, or among the whole assemblage of an ecology, may be immensely complex; and at Dr Cavalli's invitation I propose to suggest that one way of making this intricate system intelligible to the human mind is by the analogy of games of skill, or to speak somewhat more pretentiously, of the Theory of Games.

A little more than 20 years ago (1934) I was led to rediscuss an old puzzle in the tactics of card play, which had been discussed in correspondence between Montmort and Nicolas Bernoulli early in the eighteenth century, and of which a rather full account had been given by Todhunter in his *History of the Theory of Probability*. Each of the players could have at one stage of the game, known as Le Her, a significant choice, but whereas it was to the advantage of A that these decisions should be alike, B had something to gain by them being unlike. No course of action seemed unequivocally advisable to a player who wished to assume that his opponent was playing as skilfully as possible, but that his own aim lay in making this skilful play as unsuccessful as might be, within his own range of choice. This general method of looking at such problems has since been called the Minimax Principle. Using it for the game of Le Her, and recognizing that it was not impossible for a player to randomize his decisions, I was able to show that for both players only a randomized strategy would satisfy the condition for playing as well as possible. One could calculate the frequencies of choice appropriate to each, and the general advantage of one of them. Ten years later (1944) the Princeton mathematicians von Neumann and Morgenstern, published a mathematical treatise on the Theory of Games, and developed with great generality both the Minimax Principle and the randomized, or, as they called it, the mixed strategy, to which, indeed, von Neumann had earlier drawn attention in one of the German mathematical journals.

The success of a randomized strategy in games flows from the fact that the players *learn* to anticipate their opponent's customary reactions, and that the adoption of randomization introduces a new degree of uncertainty in such anticipations. A similar measure of uncertainty must be introduced into the reactions of 'natural enemies' in the state of nature, especially by discontinuous variations of the kind made possible by balanced polymorphisms affecting the appearance, or the behaviour.

Now I am comparing whole species, the relations between which are antagonistic, to the players in a game of skill. Among the higher animals there can be no doubt of the important extent to which they learn by experience and adjust their tactics to the normal reactions of their adversary; and in this they are evidently analogous to human contestants at cards or chess. I believe, however, that if we

Fisher, Ronald A. "Polymorphism and Natural Selection."
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J. Theoret. Biol. (1961) **1**, 382–403

Evolution and the Theory of Games

R. C. Lewontin

Dept. of Biology, University of Rochester, Rochester, New York

(*Received* 6 *March* 1961)

The shortcomings of present population genetic theory are discussed as they pertain to problems of speciation, extinction and the evolution of genetic systems. It is suggested that the modern theory of games may be useful in finding exact answers to problems of evolution not covered by the theory of population genetics. An outline of relevant topics in the theory of games is given. It is suggested that the most pertinent utility measure for a population is its one-generation probability of survival and that a strategy or a mixture of strategies corresponding to a *maximin* strategy will be found in natural populations. These notions are applied to a population segregating for two alleles with different norms of reaction in different environments. For the model chosen the optimal strategy is found to be homozygosis for different alleles in different populations due either to inbreeding or genetic isolation. A segregating polymorphism in such populations would be a detriment to the species, although the heterozygotes are more constant in fitness.

The Present State of Evolutionary Theory

The modern theory of evolutionary dynamics is founded upon the remarkable insights of R. A. Fisher and Sewall Wright and set forth in the *loci classici* "The Genetical Theory of Natural Selection" (1930) and "Evolution in Mendelian Populations" (1931). By the time of the publica-

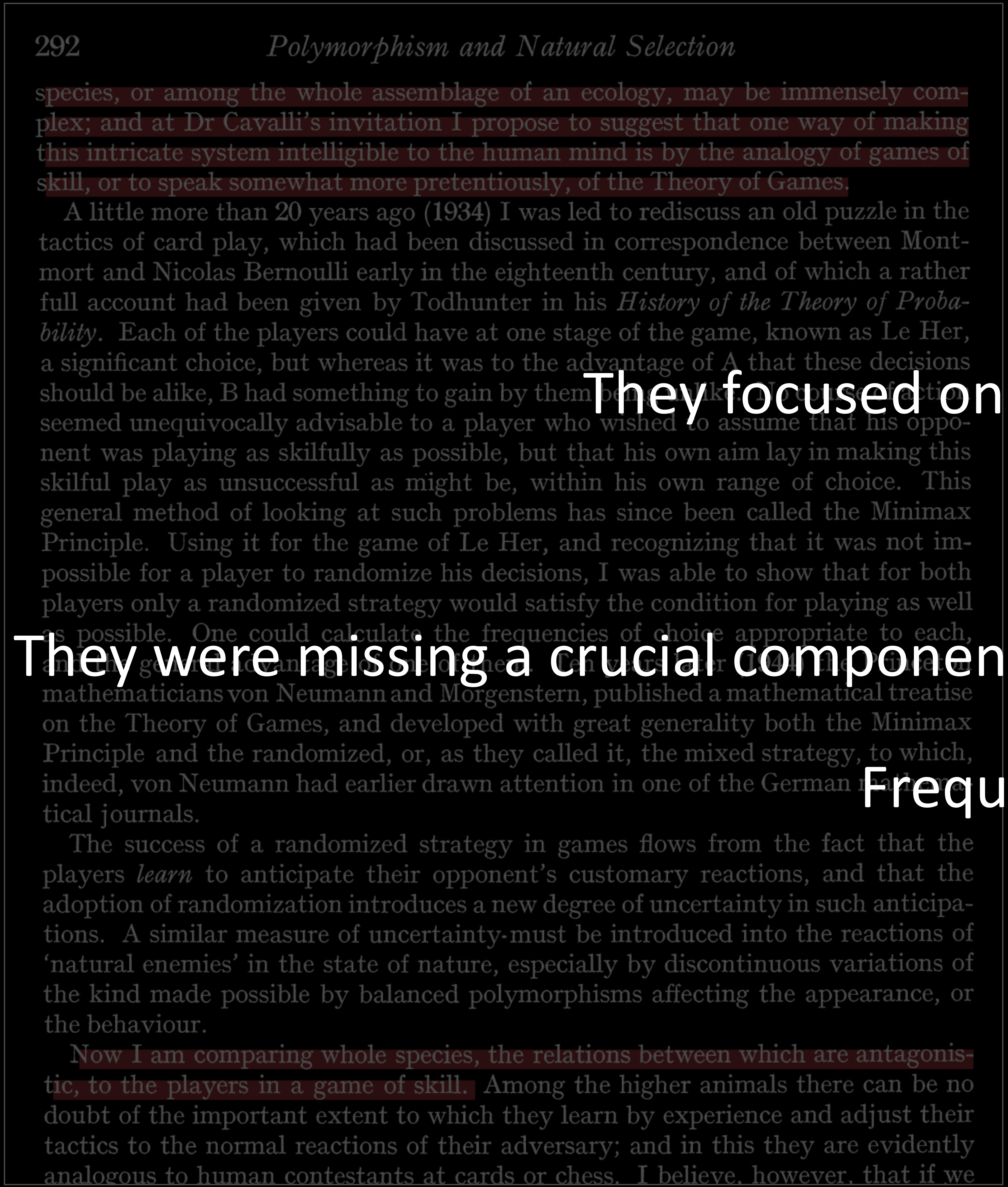
Lewontin, R C. "Evolution and the Theory of Games." *Journal of Theoretical Biology*, no. 3 (1961): 382–403.

They focused on species and not populations

And

They were missing a crucial component of evolutionary games as we know of them today

Frequency dependence



292 *Polymorphism and Natural Selection*

species, or among the whole assemblage of an ecology, may be immensely complex; and at Dr Cavalli's invitation I propose to suggest that one way of making this intricate system intelligible to the human mind is by the analogy of games of skill, or to speak somewhat more pretentiously, of the Theory of Games.

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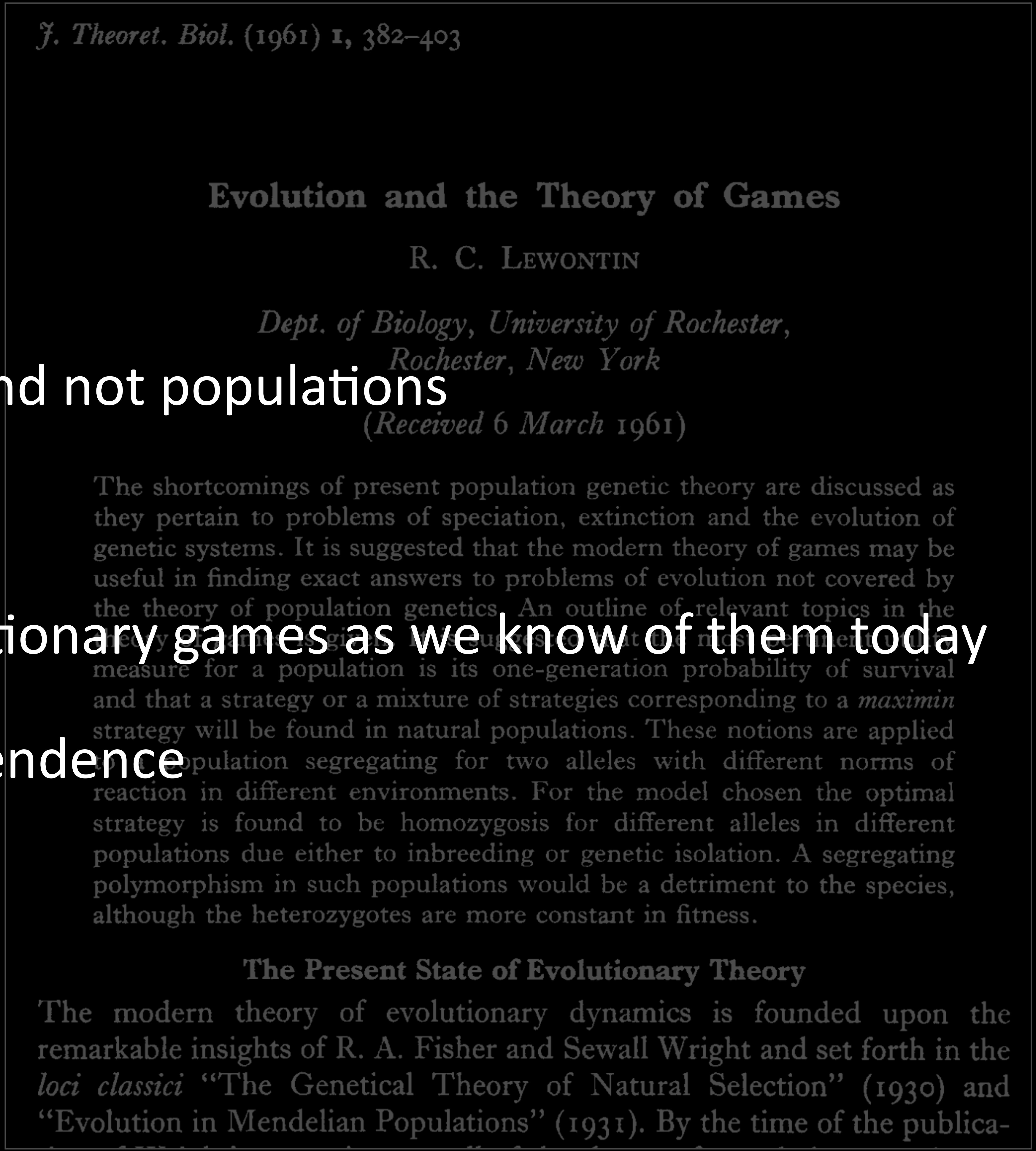

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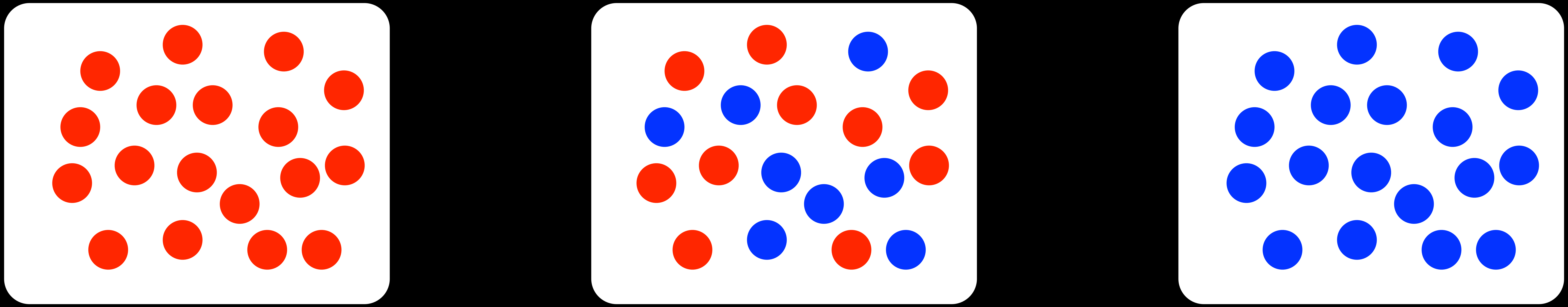
Possible population states



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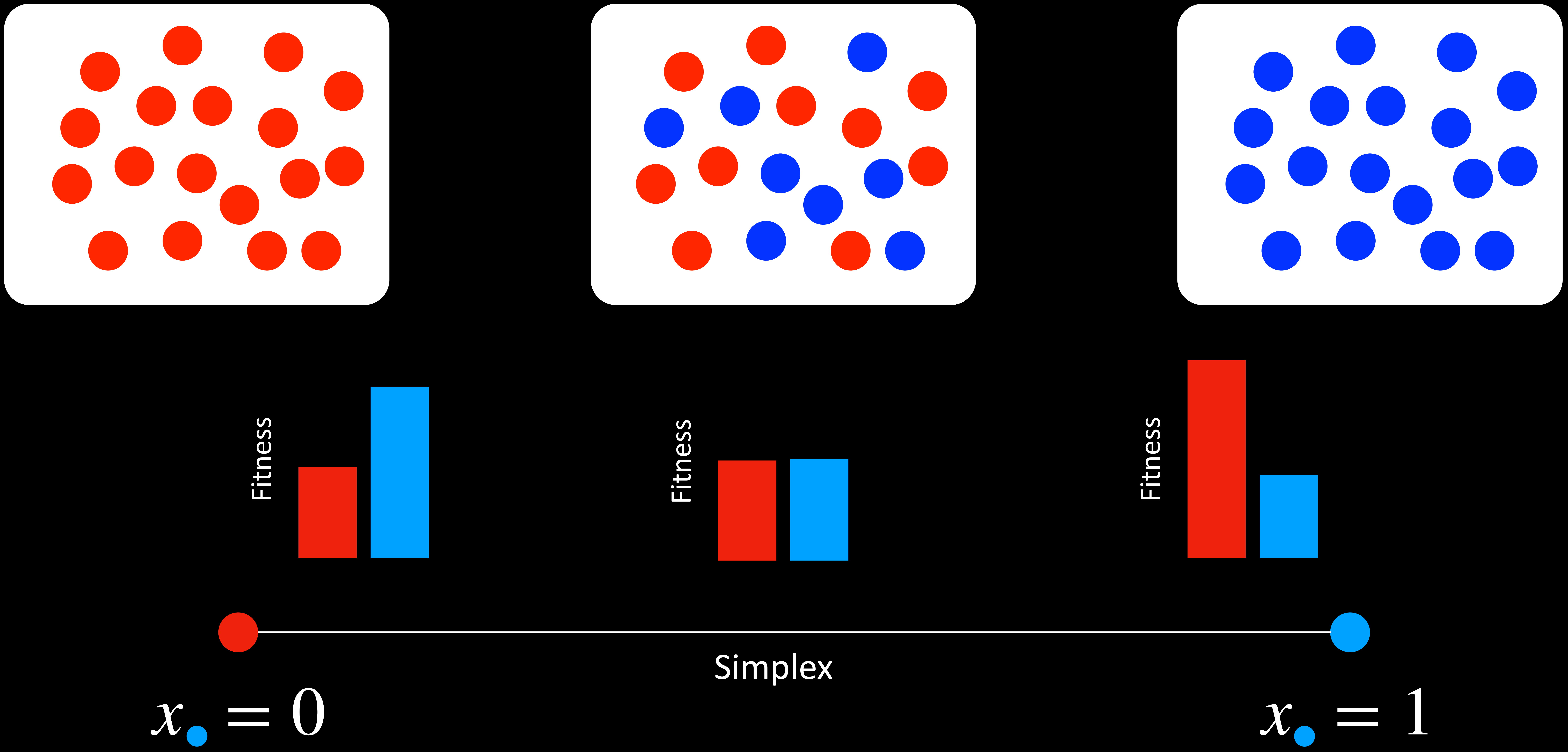
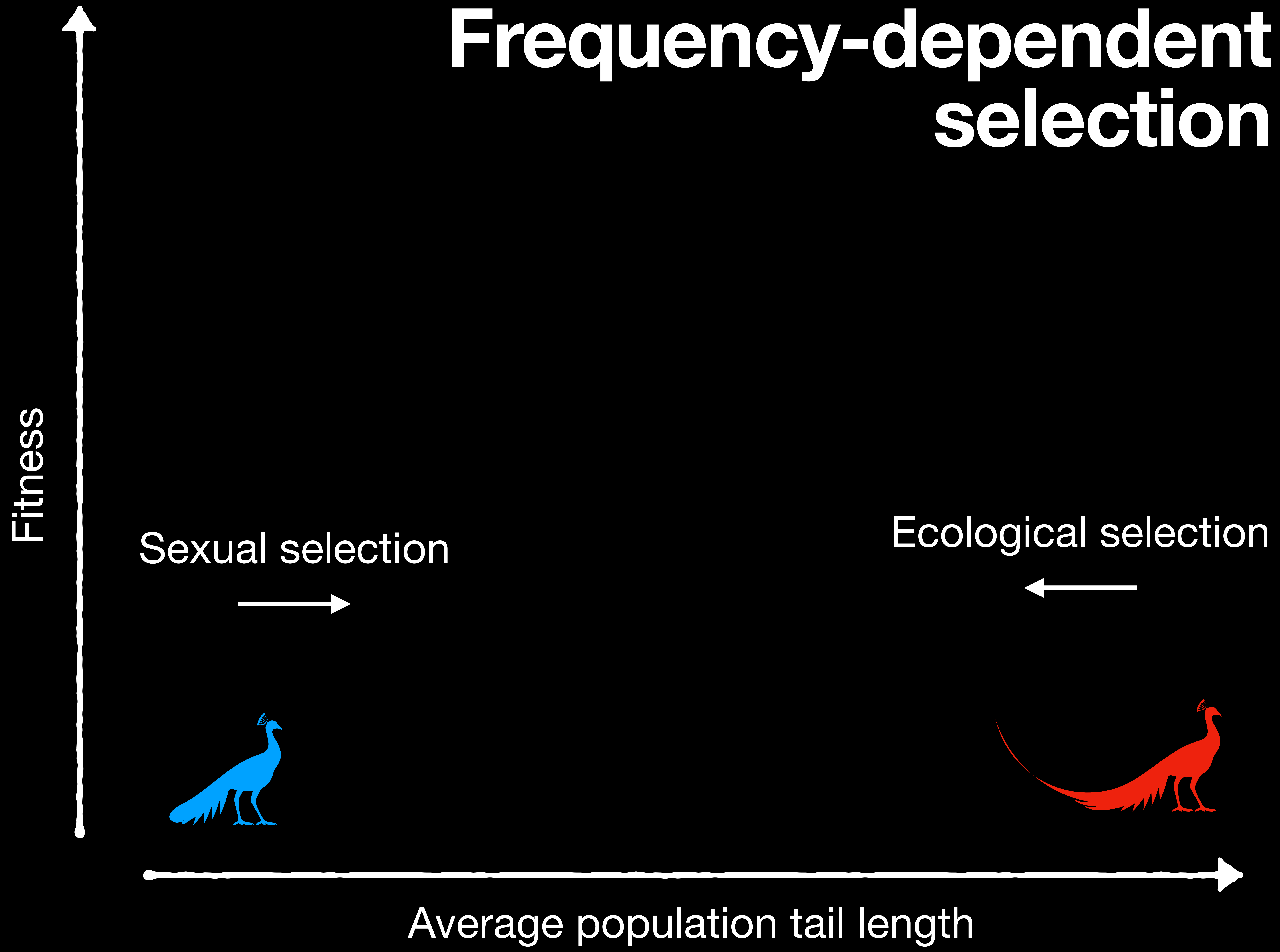
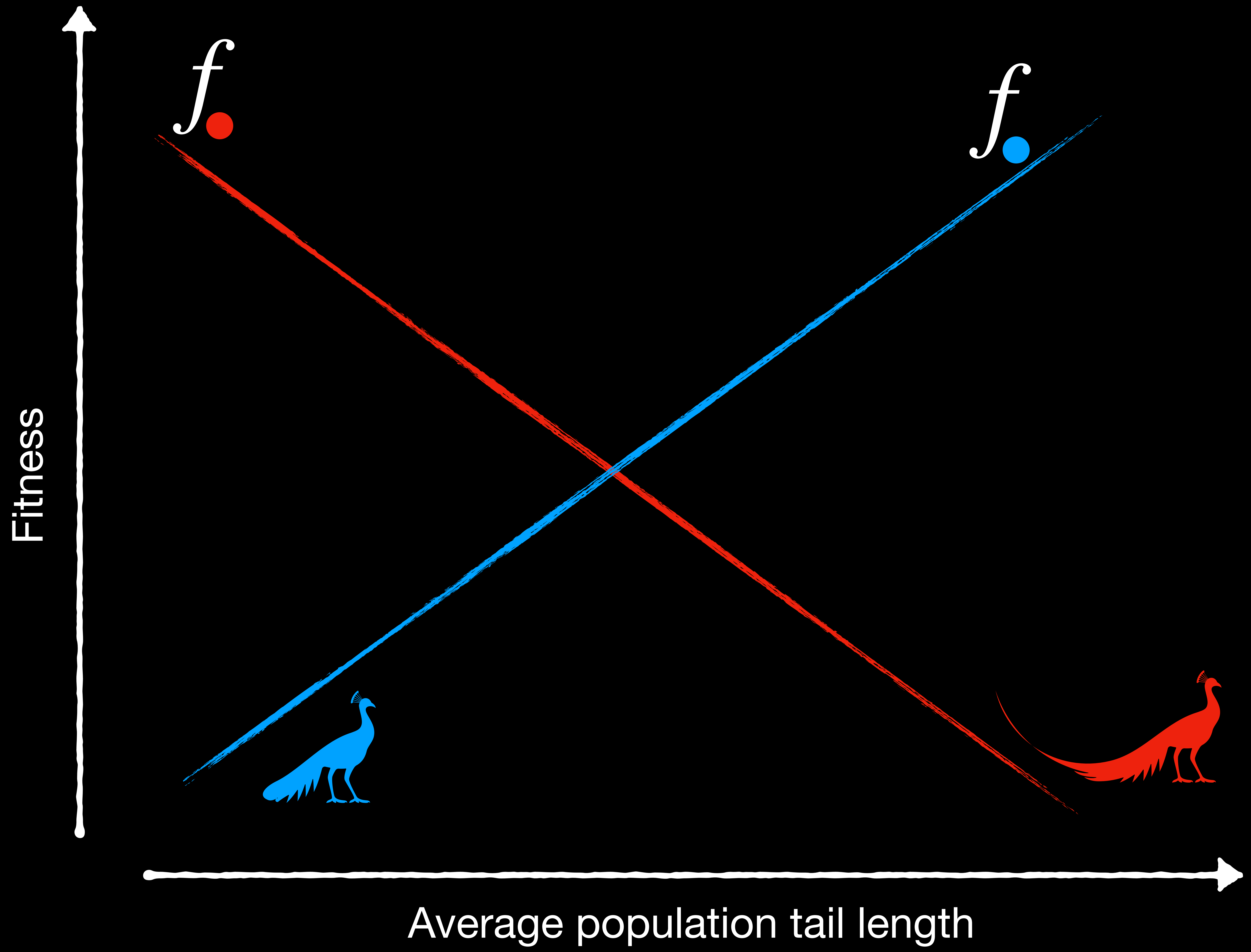


However now fitness is dynamic! It changes according to what others are doing

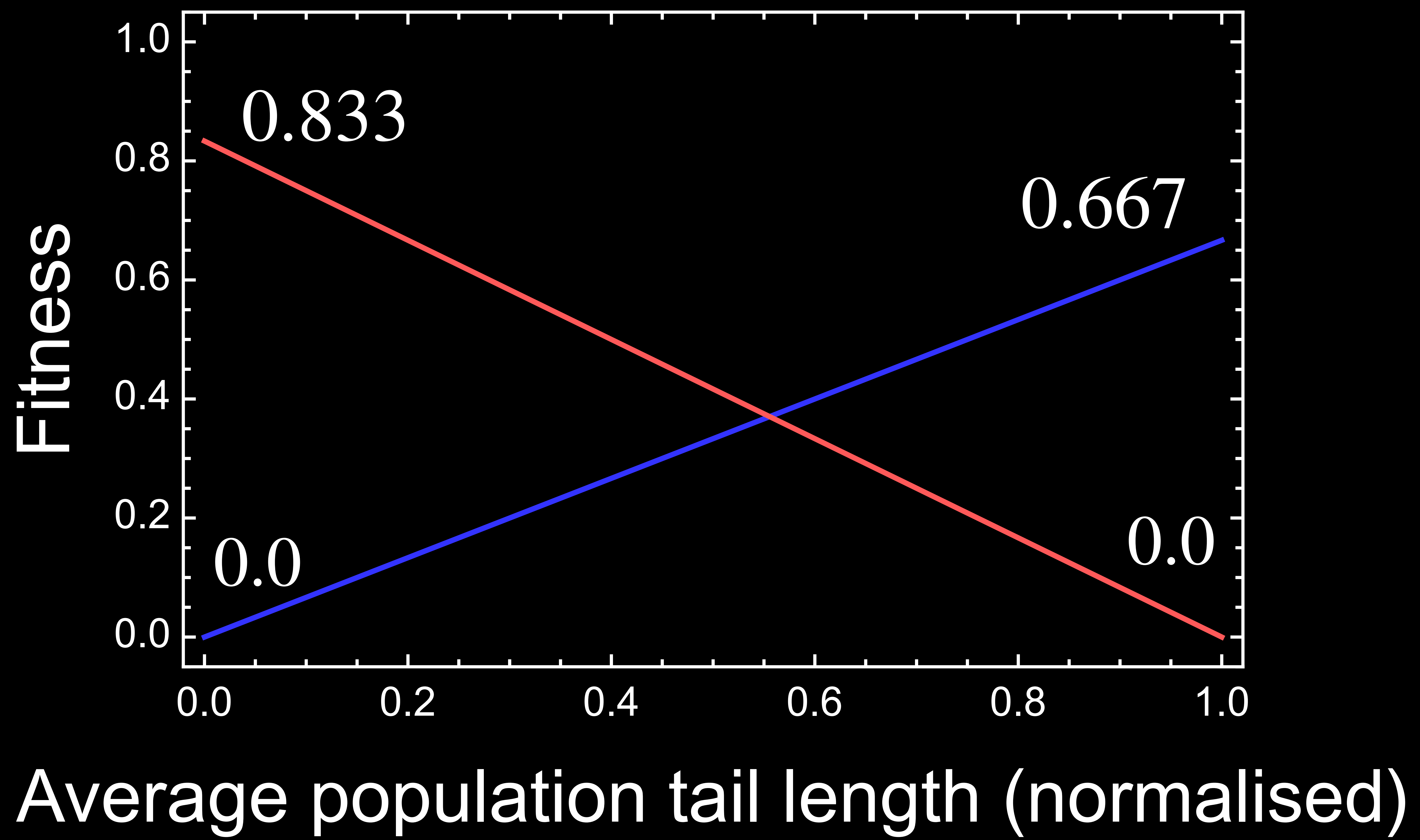
Beauty Contest


Frequency-dependent selection
Fitness
Sexual selection
Ecological selection
Average population tail length



Fitness
f
f
Average population tail length

Let us put in some numbers



Biological interactions formalised in the payoff matrix

When you mostly encounter

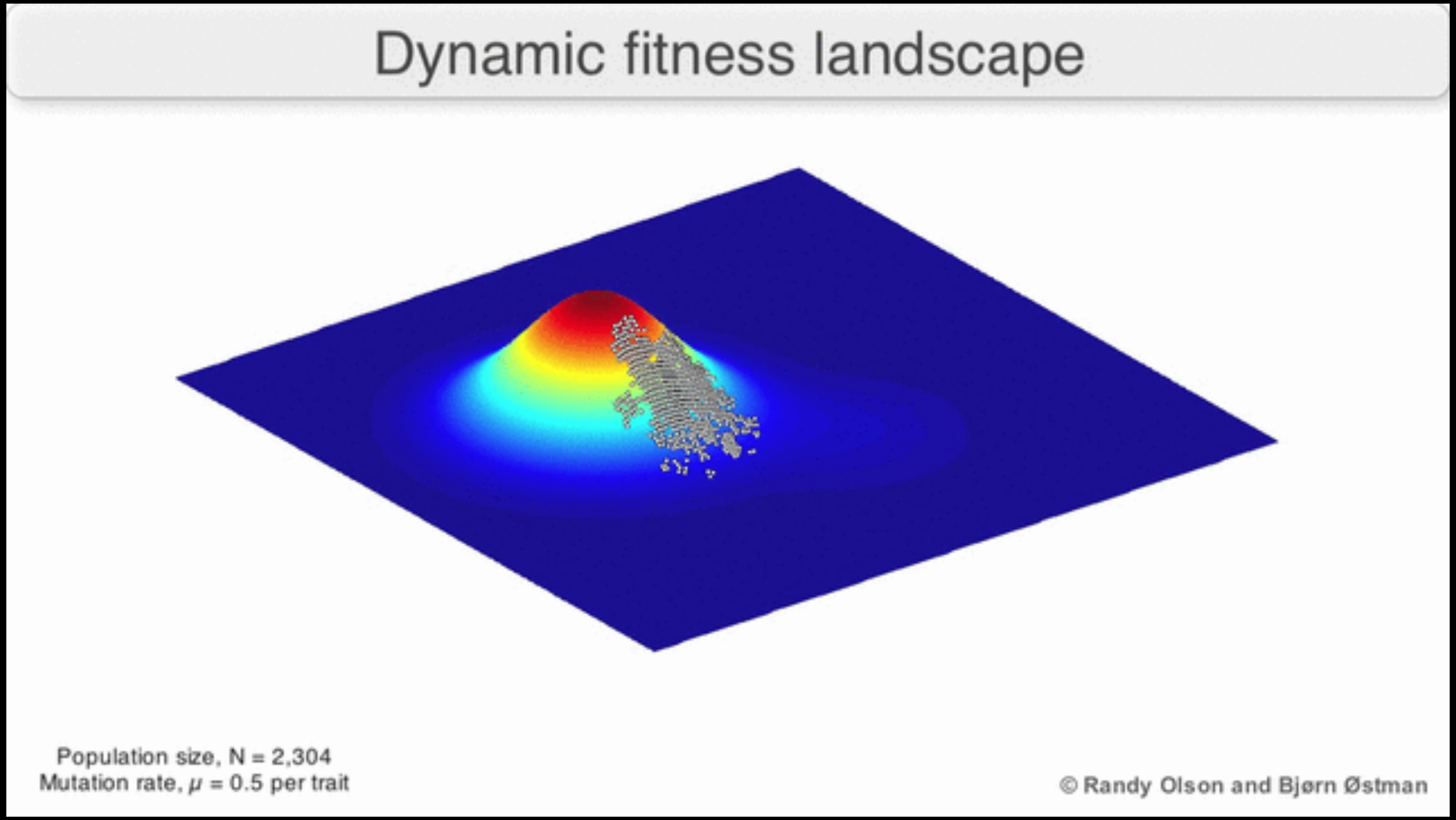
What is your fitness?

$$\begin{pmatrix} 0.0 & 0.667 \\ 0.833 & 0.0 \end{pmatrix}$$

“Evolutionary game theory is a way of thinking about evolution at the phenotypic level when the fitnesses of particular phenotypes depend on their frequencies”

...not strictly true, we will come back to this

John Maynard Smith



Maynard Smith, Evolution and the Theory of Games (1982)

Multiplayer evolutionary games

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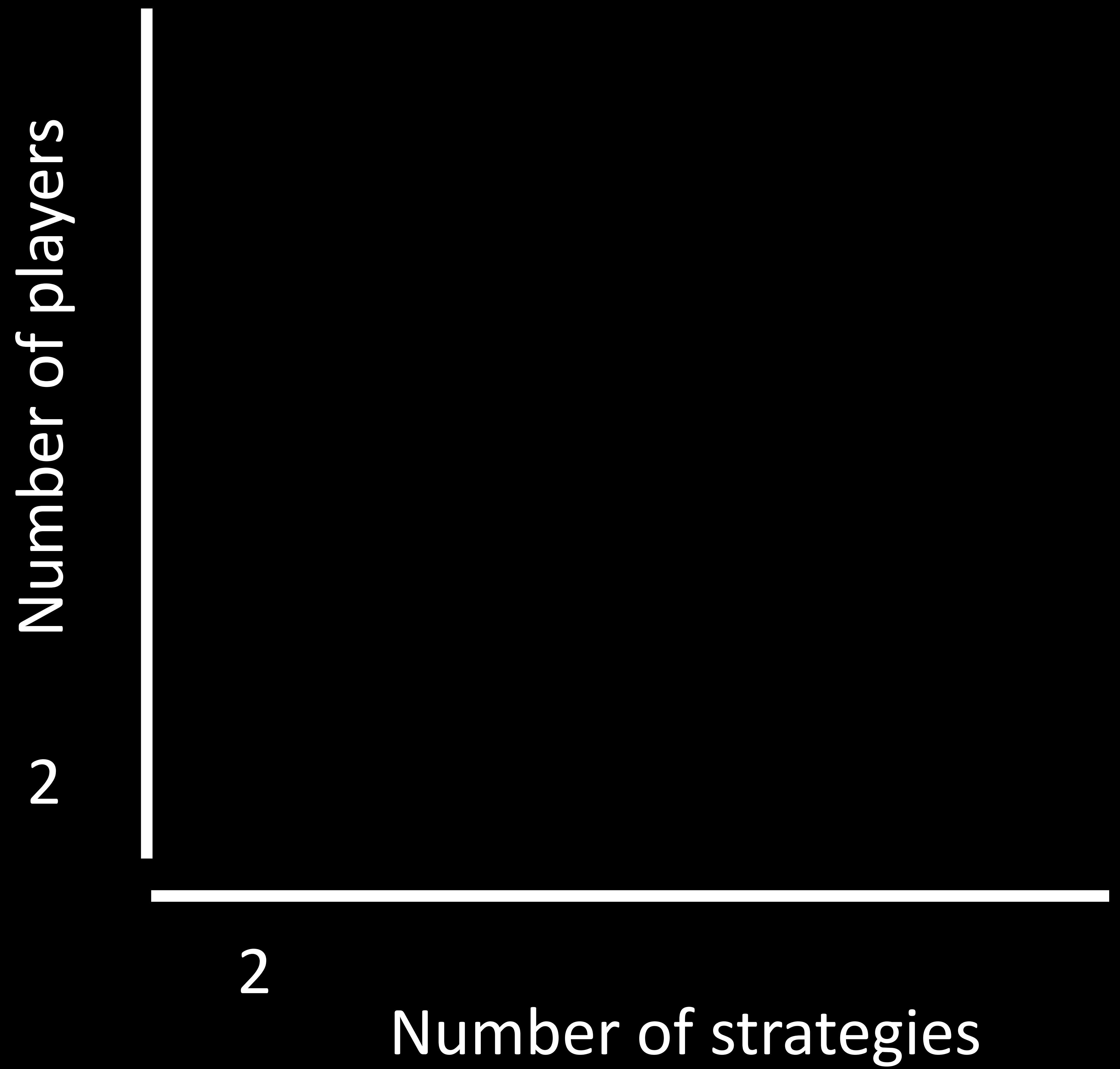
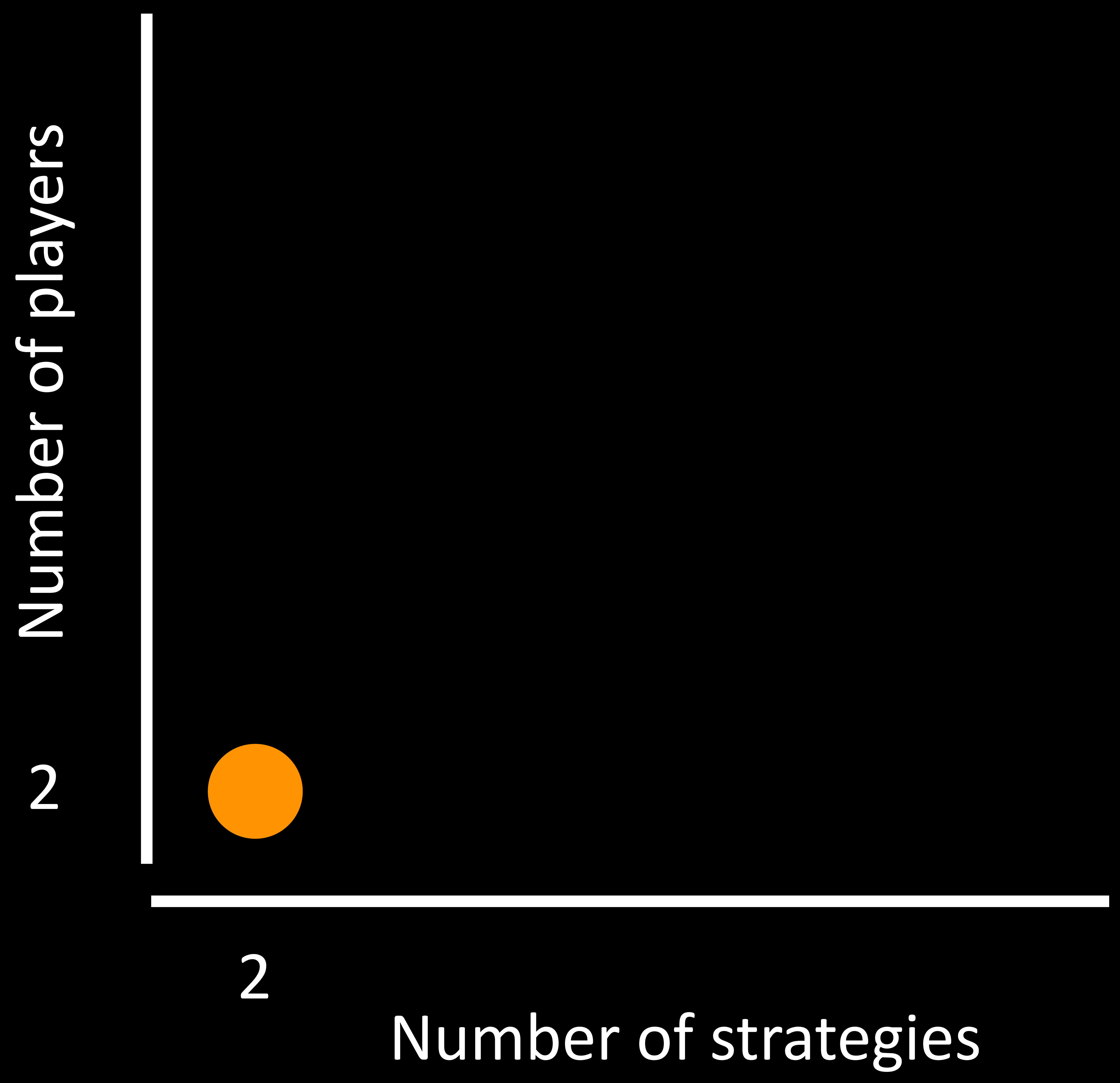
Starting simple…



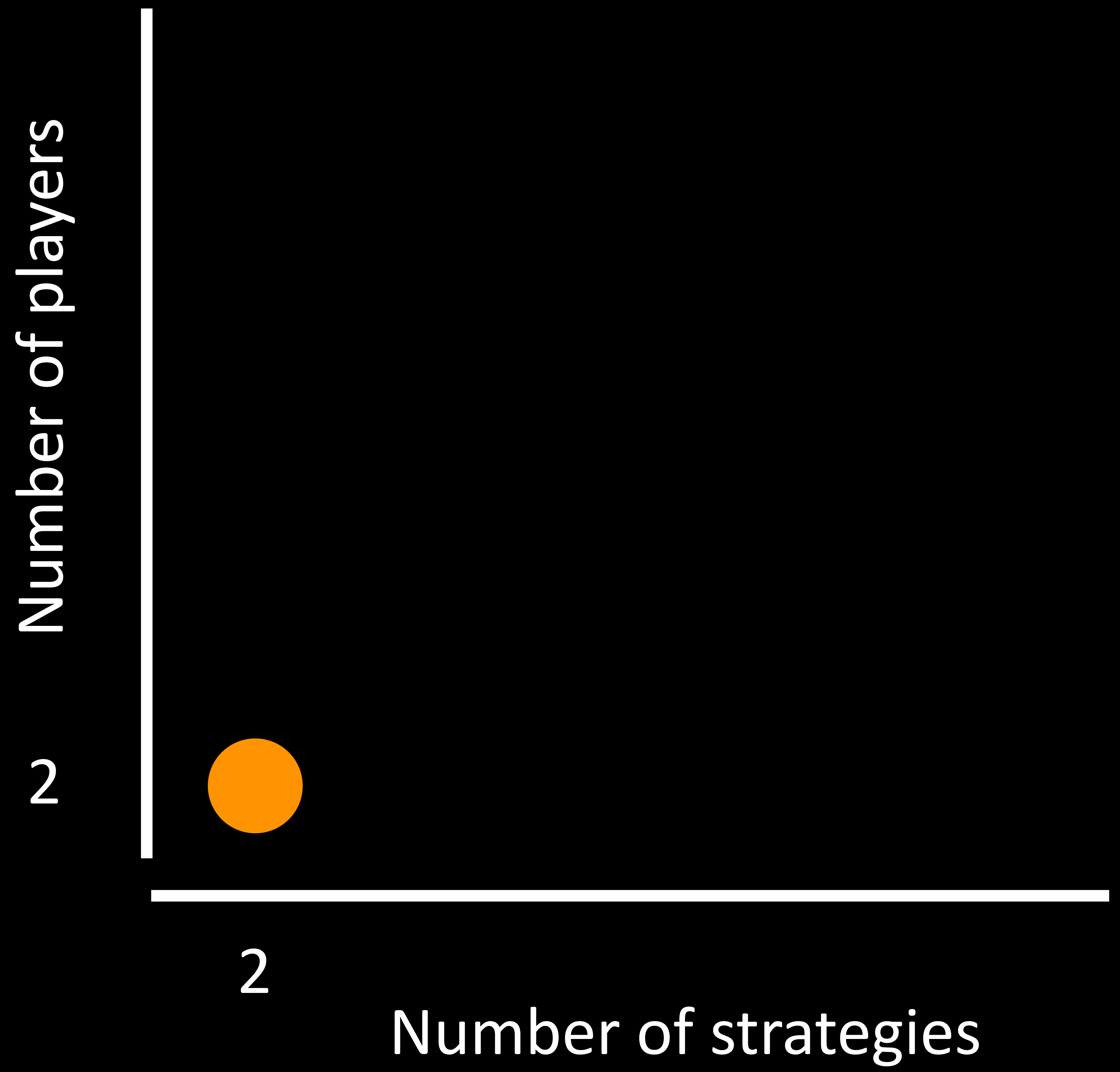
Starting simple...



Starting simple...

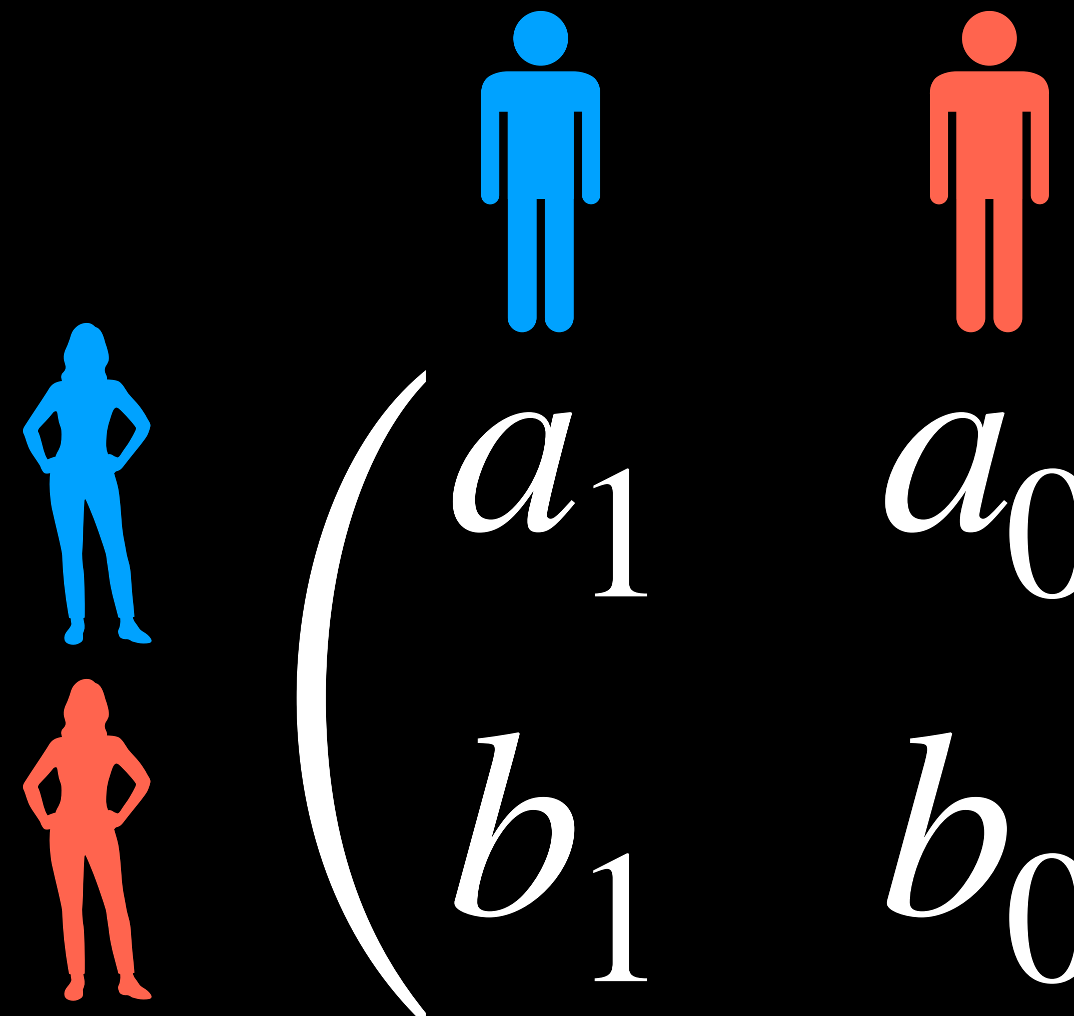
two player games with two strategies

$$2 \times 2$$



What does your partner do?

What do you do?



$$\begin{pmatrix} a_1 & a_0 \\ b_1 & b_0 \end{pmatrix}$$

Starting simple…

Not always

This follows from the arguments used in a forthcoming paper.[13] It is proved by constructing an "abstract" mapping cylinder of λ and transcribing into algebraic terms the proof of the analogous theorem on CW-complexes.

* This note arose from consultations during the tenure of a John Simon Guggenheim Memorial Fellowship by MacLane.

[1] Whitehead, J. H. C., "Combinatorial Homotopy I and II," *Bull. A.M.S.*, **55**, 214–245 and 453–496 (1949). We refer to these papers as CH I and CH II, respectively.

[2] By a complex we shall mean a connected CW complex, as defined in §5 of CH I. We do not restrict ourselves to finite complexes. A fixed 0-cell $e^0 \in K^0$ will be the base point for all the homotopy groups in K.

[4] MacLane, S., "Cohomology Theory in Abstract Groups III," *Ann. Math.*, **50**, 736–761 (1949), referred to as CT III.

[5] An (unpublished) result like Theorem 1 for the homotopy type was obtained prior to these results by J. A. Zilber.

[6] CT III uses in place of equation (2.4) the stronger hypothesis that λB contains the center of A, but all the relevant developments there apply under the weaker assumption (2.4).

[7] Eilenberg, S., and MacLane, S., "Cohomology Theory in Abstract Groups II," *Ann. Math.*, **48**, 326–341 (1947).

[8] Eilenberg, S., and MacLane, S., "Determination of the Second Homology . . . by Means of Homotopy Invariants," these PROCEEDINGS, **32**, 277–280 (1946).

[9] Blakers, A. L., "Some Relations Between Homology and Homotopy Groups," *Ann. Math.*, **49**, 428–461 (1948), §12.

[10] The hypothesis of Theorem C, requiring that ν^{-1} (1) not be cyclic, can be readily realized by suitable choice of the free group X, but this hypothesis is not needed here (cf. [6]).

[11] Eilenberg, S., and MacLane, S., "Homology of Spaces with Operators II," *Trans. A.M.S.*, **65**, 49–99 (1949); referred to as HSO II.

[12] $C(\tilde{K})$ here is the $C(K)$ of CH II. Note that $\tilde{K}$ exists and is a CW complex by (N) of p. 231 of CH I and that $p^{-1}K^n = \tilde{K}^n$, where p is the projection $p: \tilde{K} \to K$.

[13] Whitehead, J. H. C., "Simple Homotopy Types." If $W = 1$, Theorem 5 follows from (17:3) on p. 155 of S. Lefschetz, *Algebraic Topology*, (New York, 1942) and arguments in §6 of J. H. C. Whitehead, "On Simply Connected 4-Dimensional Polyhedra" (*Comm. Math. Helv.*, **22**, 48–92 (1949)). However this proof cannot be generalized to the case $W \neq 1$.

EQUILIBRIUM POINTS IN N-PERSON GAMES

By John F. Nash, Jr.*

Princeton University

Communicated by S. Lefschetz, November 16, 1949

One may define a concept of an n-person game in which each player has a finite set of pure strategies and in which a definite set of payments to the n players corresponds to each n-tuple of pure strategies, one strategy being taken for each player. For mixed strategies, which are probability

distributions over the pure strategies, the pay-off functions are the expectations of the players, thus becoming polylinear forms in the probabilities with which the various players play their various pure strategies.

Any n-tuple of strategies, one for each player, may be regarded as a point in the product space obtained by multiplying the n strategy spaces of the players. One such n-tuple counters another if the strategy of each player in the countering n-tuple yields the highest obtainable expectation for its player against the $n - 1$ strategies of the other players in the countered n-tuple. A self-countering n-tuple is called an equilibrium point.

The correspondence of each n-tuple with its set of countering n-tuples gives a one-to-many mapping of the product space into itself. From the definition of countering we see that the set of countering points of a point is convex. By using the continuity of the pay-off functions we see that the graph of the mapping is closed. The closedness is equivalent to saying: if $P_1, P_2, \ldots$ and $Q_1, Q_2, \ldots, Q_n, \ldots$ are sequences of points in the product space where $Q_n \to Q$, $P_n \to P$ and Q_n counters P_n then Q counters P.

Since the graph is closed and since the image of each point under the mapping is convex, we infer from Kakutani's theorem[1] that the mapping has a fixed point (i.e., point contained in its image). Hence there is an equilibrium point.

In the two-person zero-sum case the "main theorem"[2] and the existence of an equilibrium point are equivalent. In this case any two equilibrium points lead to the same expectations for the players, but this need not occur in general.

* The author is indebted to Dr. David Gale for suggesting the use of Kakutani's theorem to simplify the proof and to the A. E. C. for financial support.

[1] Kakutani, S., *Duke Math. J.*, **8**, 457–459 (1941).

[2] Von Neumann, J., and Morgenstern, O., *The Theory of Games and Economic Behaviour*, Chap. 3, Princeton University Press, Princeton, 1947.

*REMARK ON WEYL'S NOTE "INEQUALITIES BETWEEN THE TWO KINDS OF EIGENVALUES OF A LINEAR TRANSFORMATION"**

By George Polya

Department of Mathematics, Stanford University

Communicated by H. Weyl, November 25, 1949

In the note quoted above H. Weyl proved a Theorem involving a function $\varphi(\lambda)$ and concerning the eigenvalues α_i of a linear transformation A and those, κ_i, of A^*A. If the κ_i and $\lambda_i = |\alpha_i|^2$ are arranged in descending order,

Nash, John F Jr. "Equilibrium Points in N-Person Games." PNAS 36, (January 1950): 48–49.

Starting simple…

Not always

Theory of games and economic behaviour, 1944

Deals with human decision-making among interacting individuals.

Nash, John F Jr. "Non-Cooperative Games." *Annals of Mathematics, Second Series* 54, no. 2 (September 1, 1951): 286–95

ANNALS OF MATHEMATICS
Vol. 54, No. 2, September, 1951

NON-COOPERATIVE GAMES

JOHN NASH

(Received October 11, 1950)

Introduction

Von Neumann and Morgenstern have developed a very fruitful theory of two-person zero-sum games in their book *Theory of Games and Economic Behavior*. This book also contains a theory of n-person games of a type which we would call cooperative. This theory is based on an analysis of the interrelationships of the various coalitions which can be formed by the players of the game.

Our theory, in contradistinction, is based on the *absence* of coalitions in that it is assumed that each participant acts independently, without collaboration or communication with any of the others.

The notion of an *equilibrium point* is the basic ingredient in our theory. This notion yields a generalization of the concept of the solution of a two-person zero-sum game. It turns out that the set of equilibrium points of a two-person zero-sum game is simply the set of all pairs of opposing "good strategies."

In the immediately following sections we shall define equilibrium points and prove that a finite non-cooperative game always has at least one equilibrium point. We shall also introduce the notions of solvability and strong solvability of a non-cooperative game and prove a theorem on the geometrical structure of the set of equilibrium points of a solvable game.

As an example of the application of our theory we include a solution of a simplified three person poker game.

Formal Definitions and Terminology

In this section we define the basic concepts of this paper and set up standard terminology and notation. Important definitions will be preceded by a subtitle indicating the concept defined. The non-cooperative idea will be implicit, rather than explicit, below.

Finite Game:

For us an *n-person game* will be a set of n *players*, or *positions*, each with an associated finite set of *pure strategies*; and corresponding to each player, i, a *payoff function*, p_i, which maps the set of all n-tuples of pure strategies into the real numbers. When we use the term *n-tuple* we shall always mean a set of n items, with each item associated with a different player.

Mixed Strategy, s_i:

A *mixed strategy* of player i will be a collection of non-negative numbers which have unit sum and are in one to one correspondence with his pure strategies.

We write $s_i = \sum_\alpha c_{i\alpha}\pi_{i\alpha}$ with $c_{i\alpha} \geqq 0$ and $\sum_\alpha c_{i\alpha} = 1$ to represent such a mixed strategy, where the $\pi_{i\alpha}$'s are the pure strategies of player i. We regard the s_i's as points in a simplex whose vertices are the $\pi_{i\alpha}$'s. This simplex may be re-

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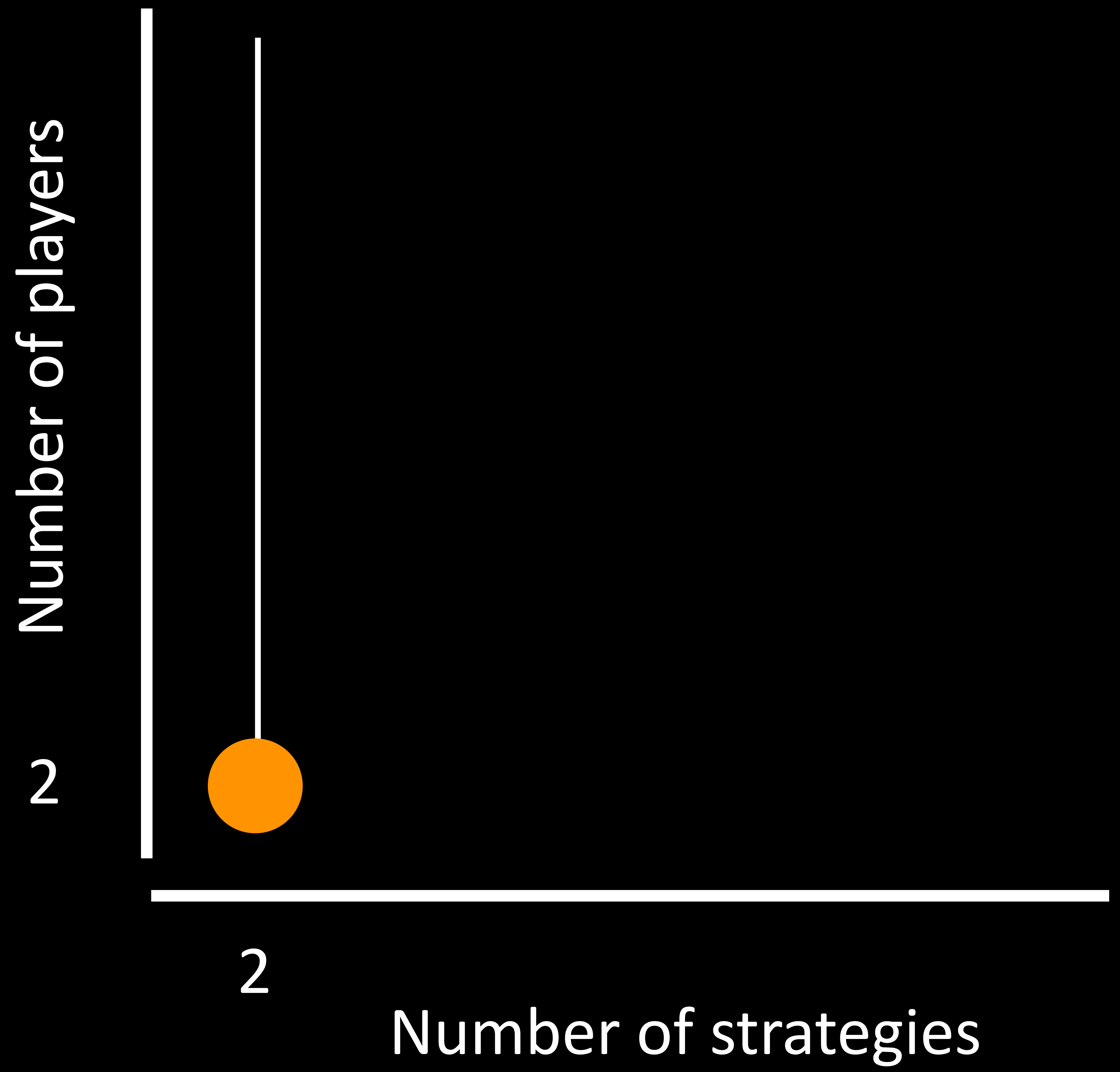
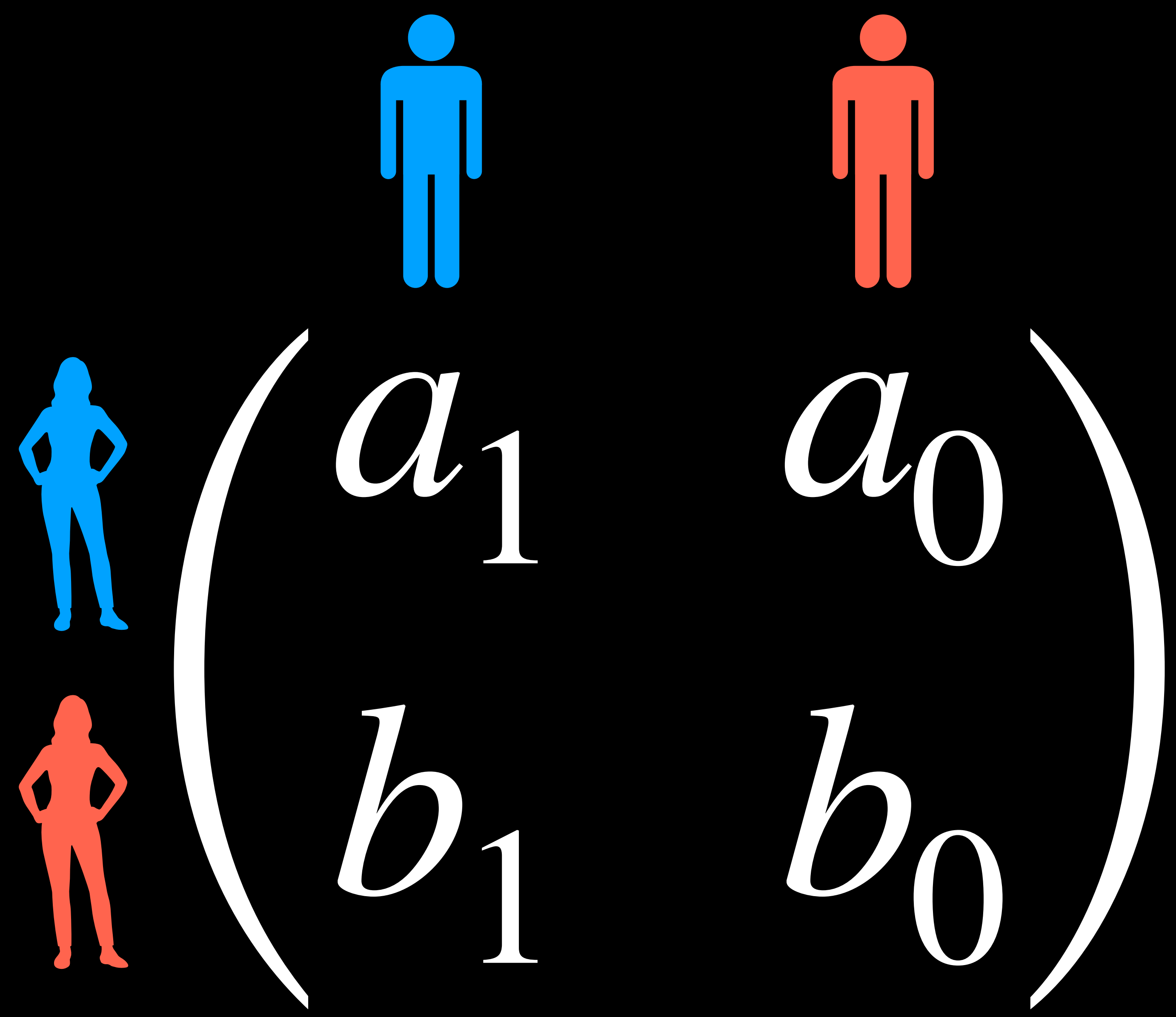
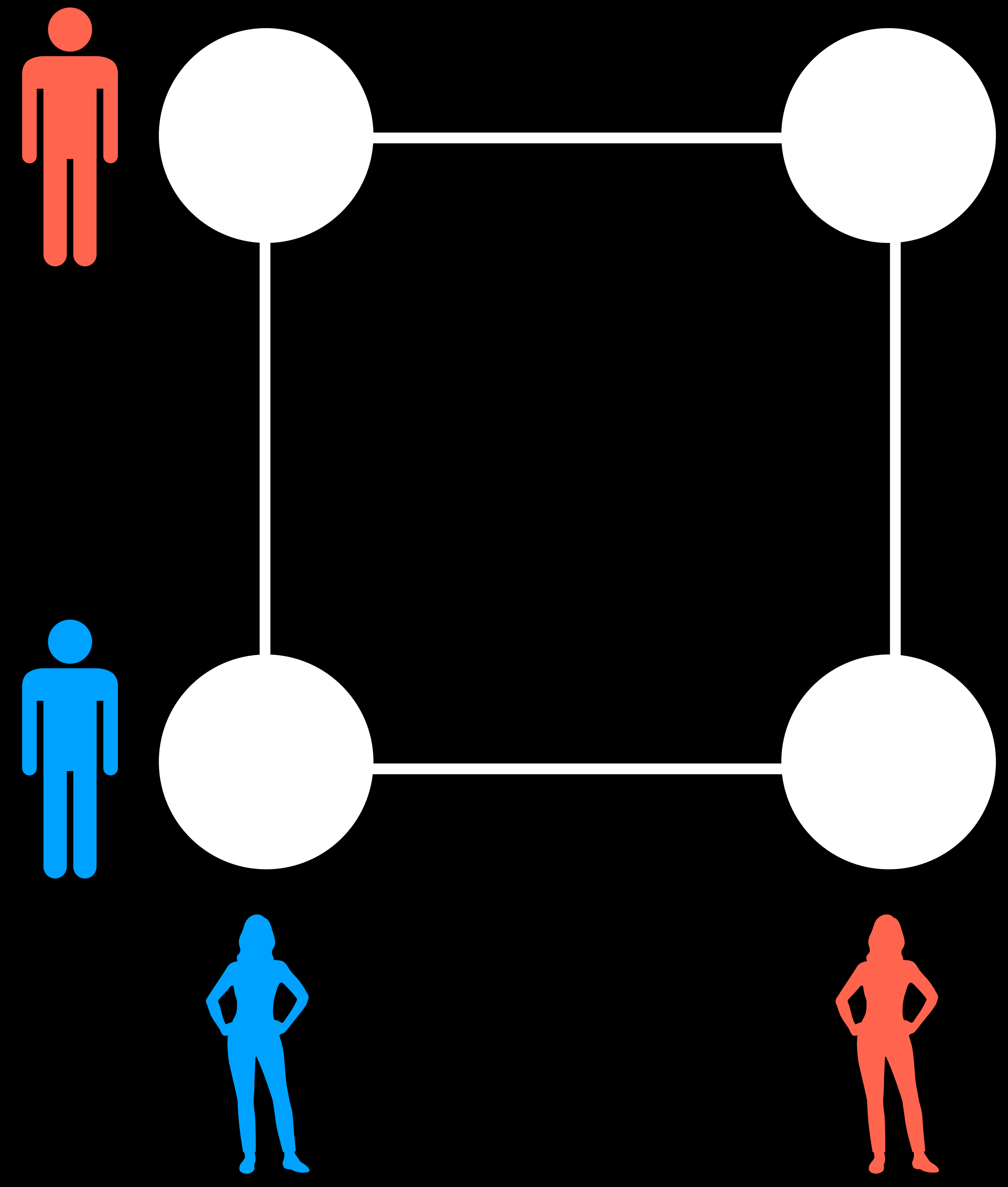
Thinking beyond the dyad

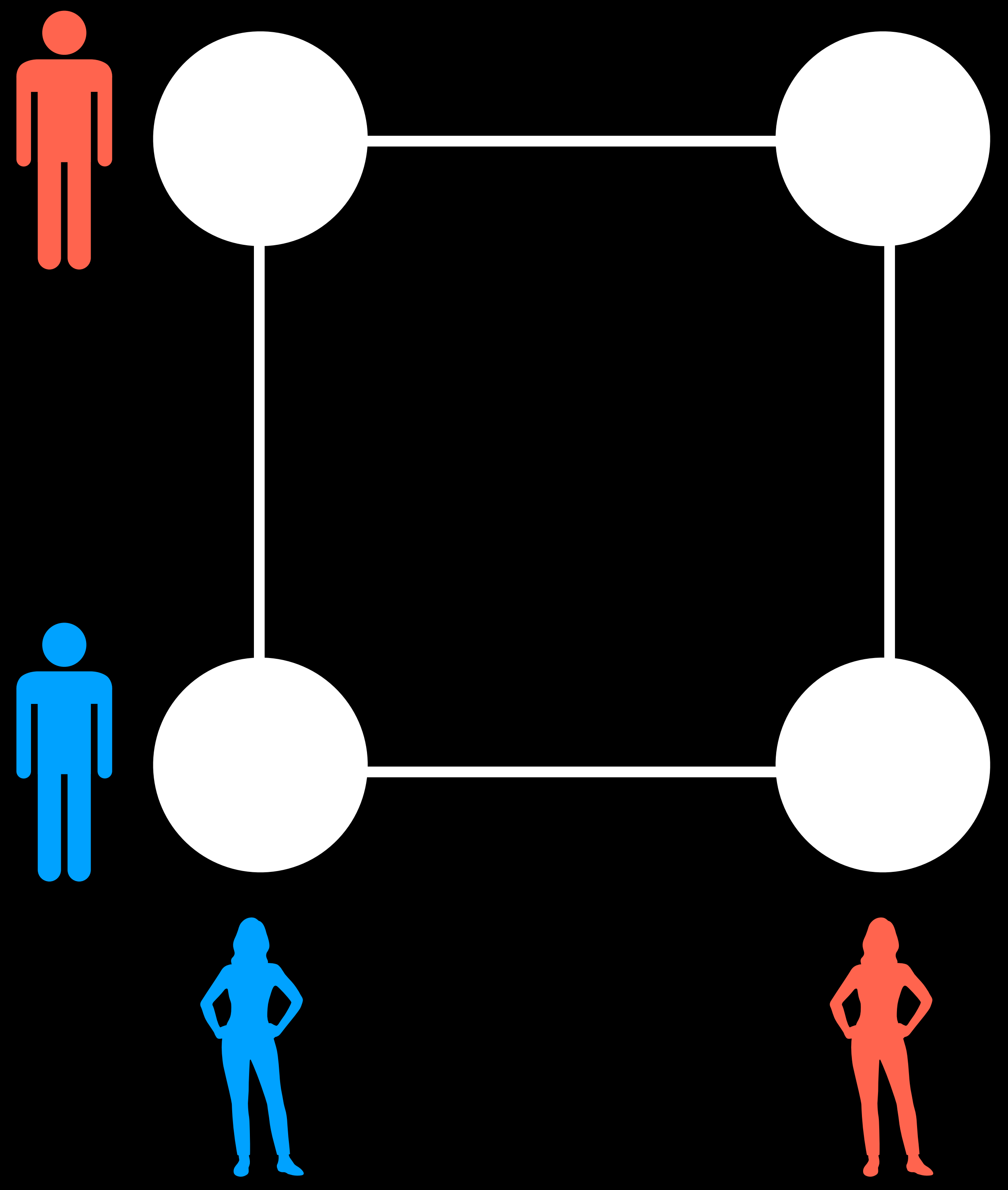


Thinking beyond the dyad



$$\begin{pmatrix} a_1 & a_0 \\ b_1 & b_0 \end{pmatrix}$$

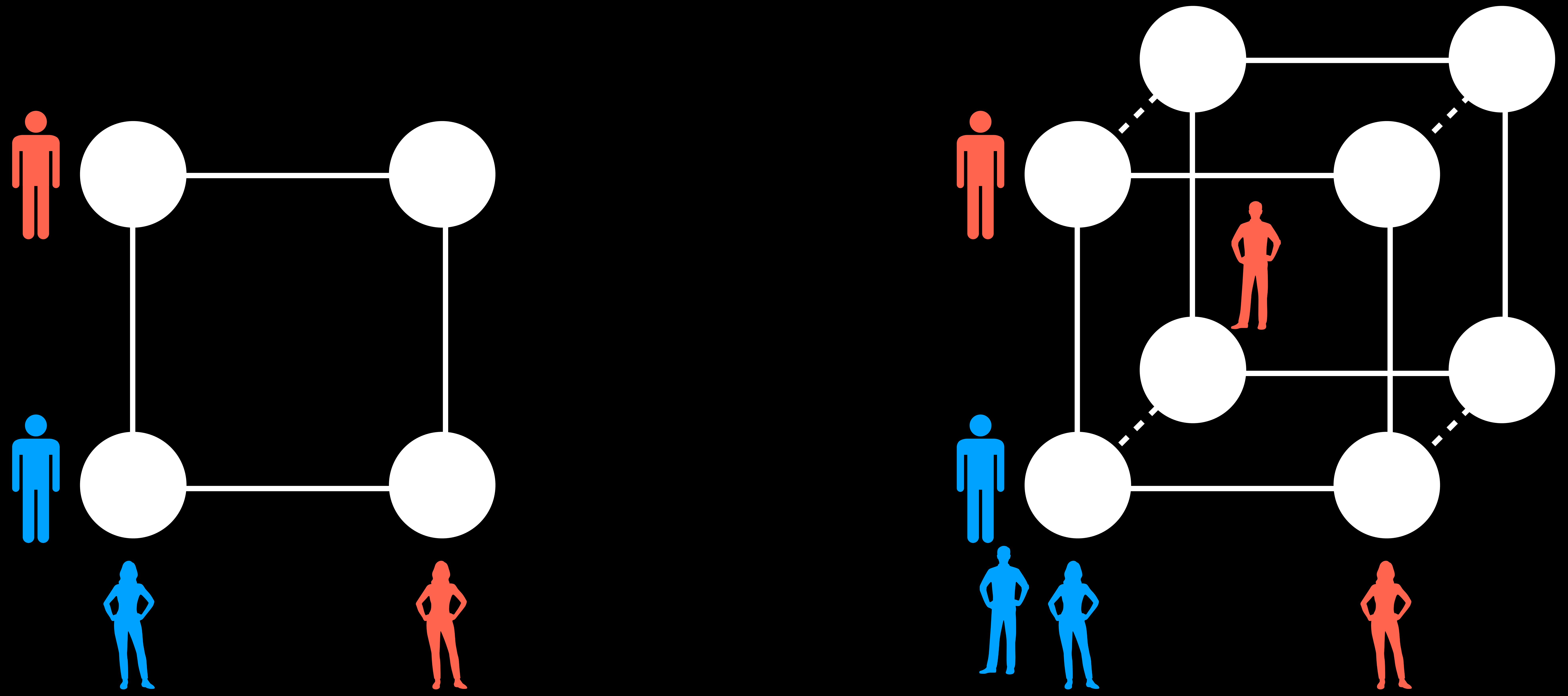




2×2

Three player game with two strategies

Adding the third player



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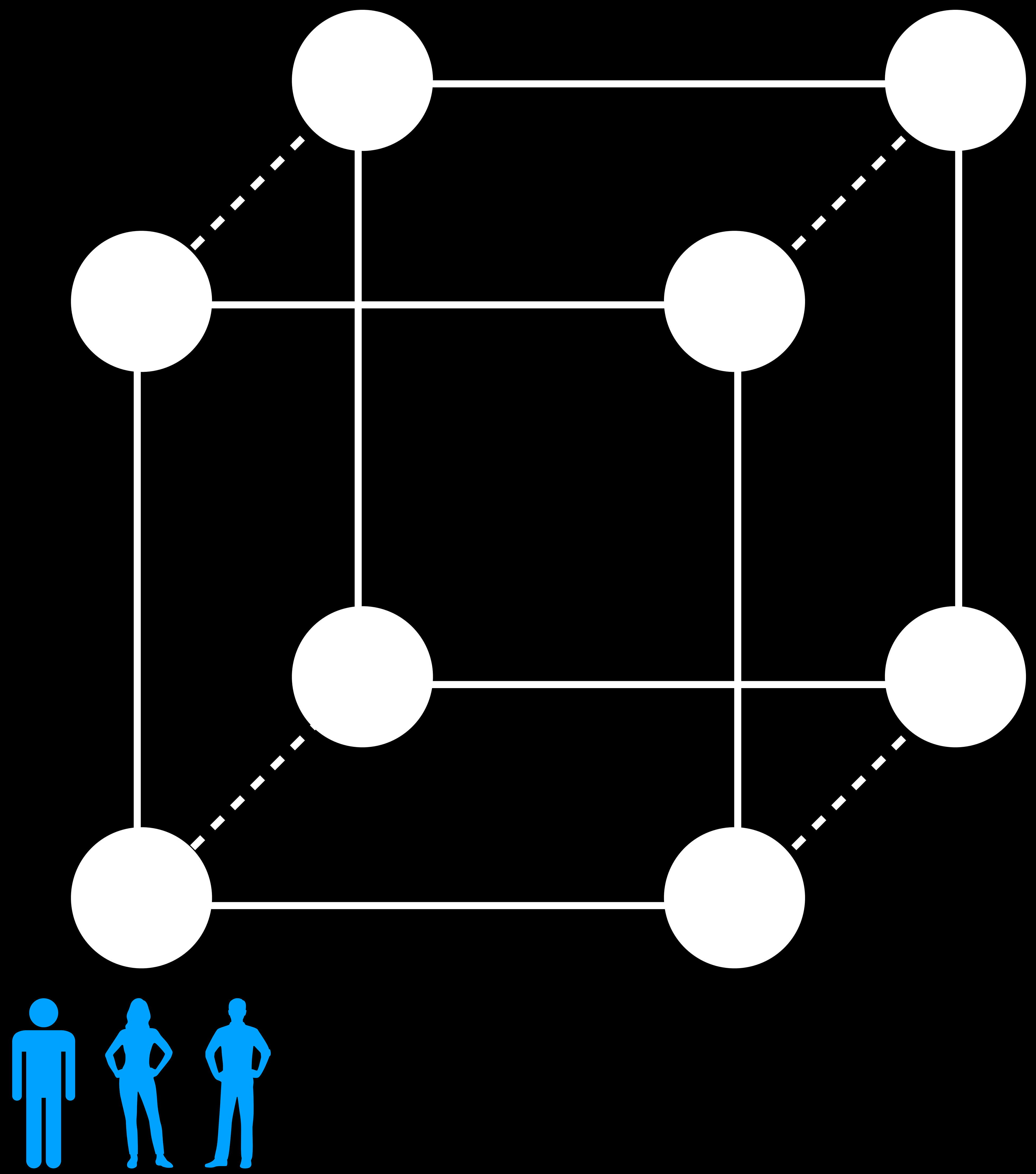
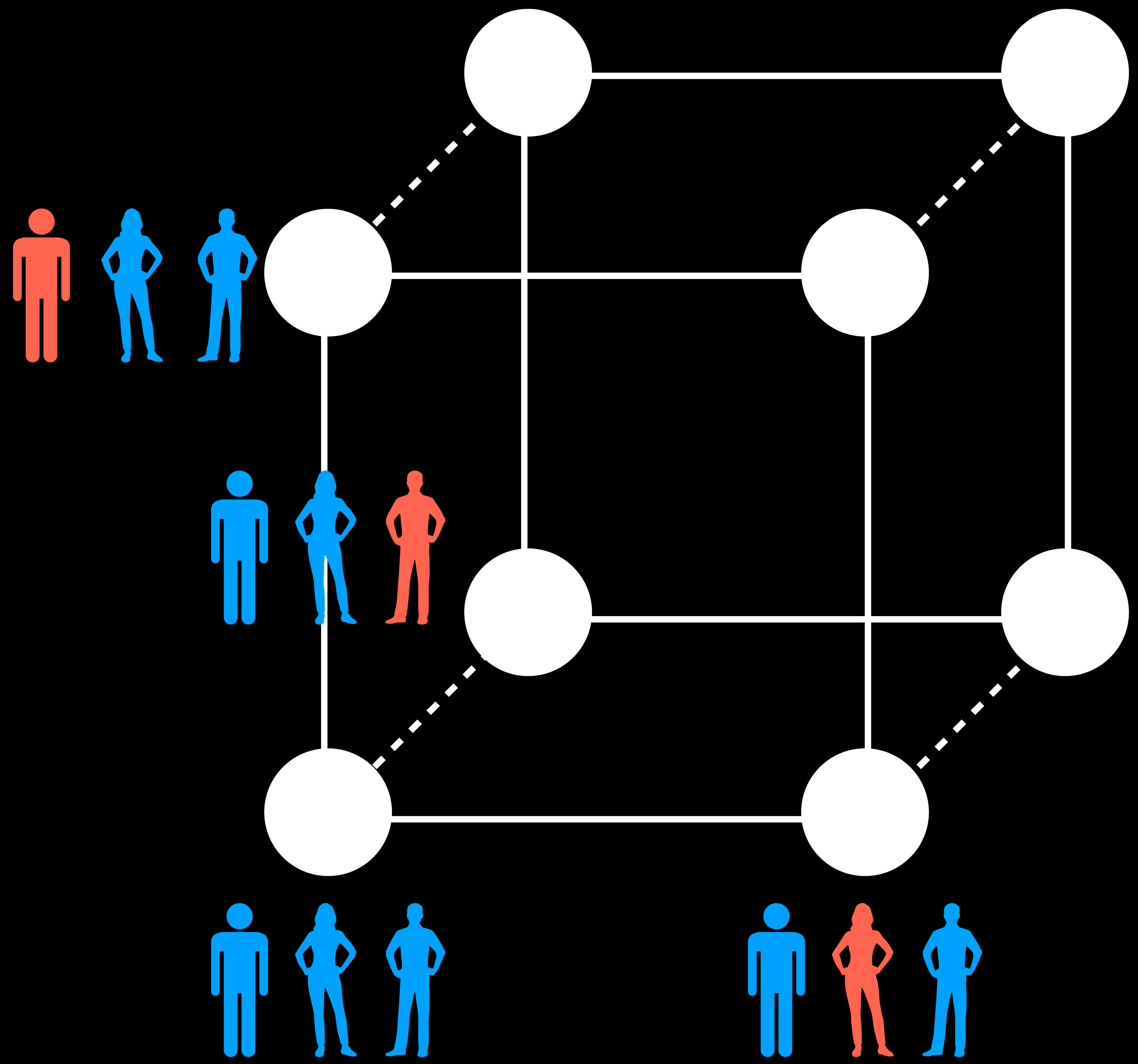


$2 \times 2 \times 2$



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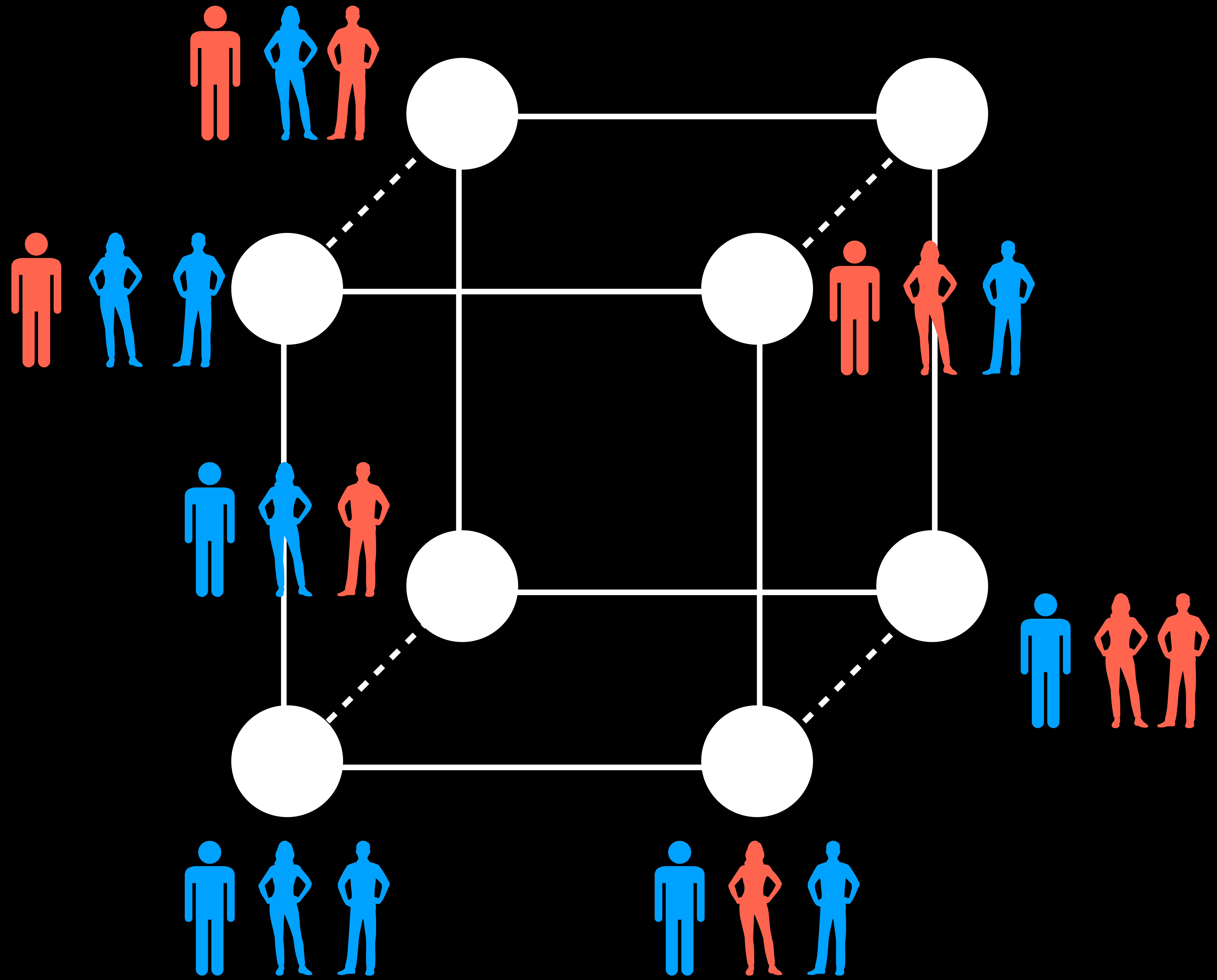
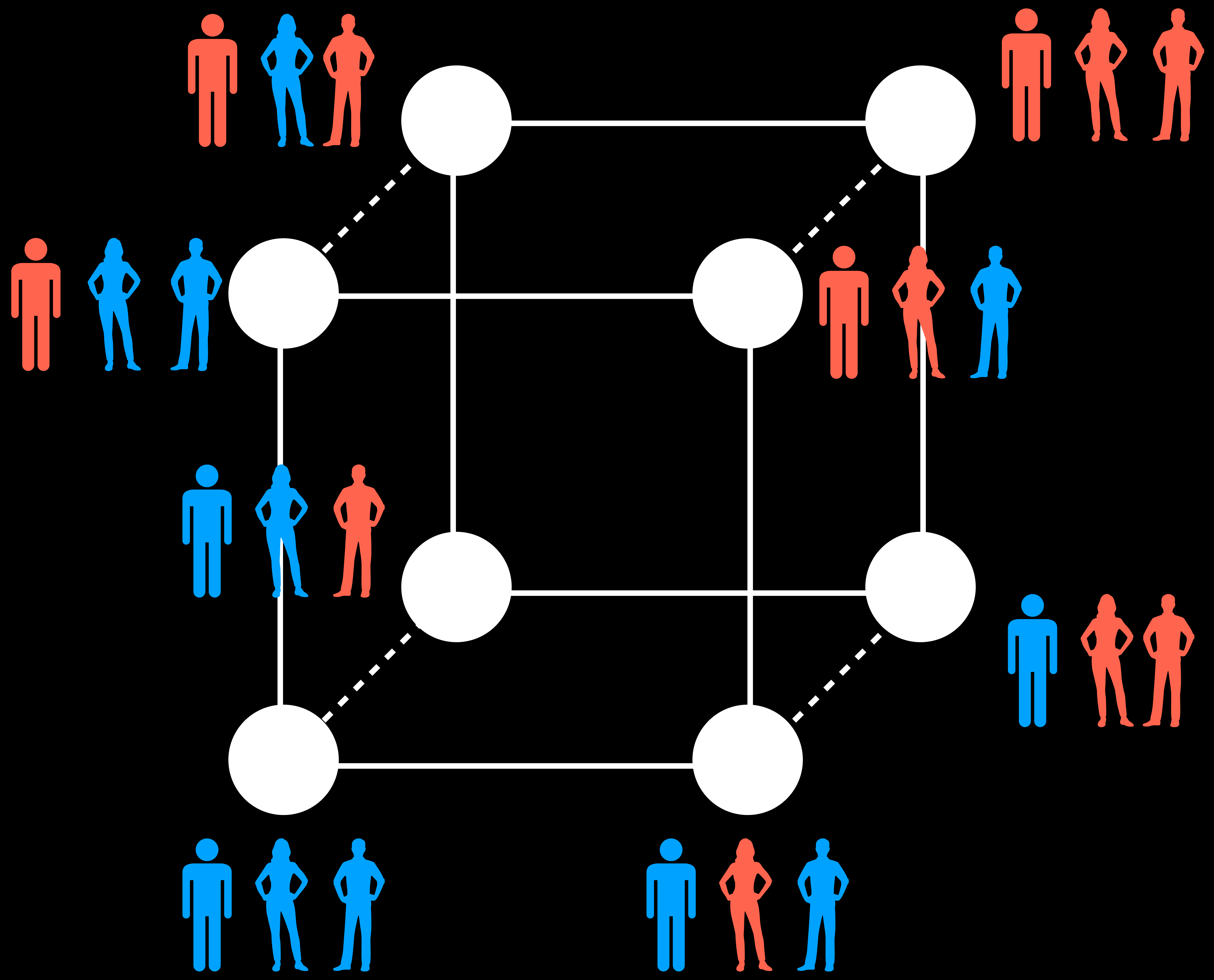
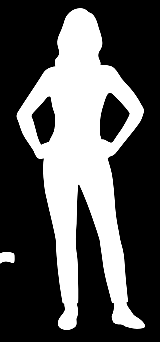


2 × 2 × 2

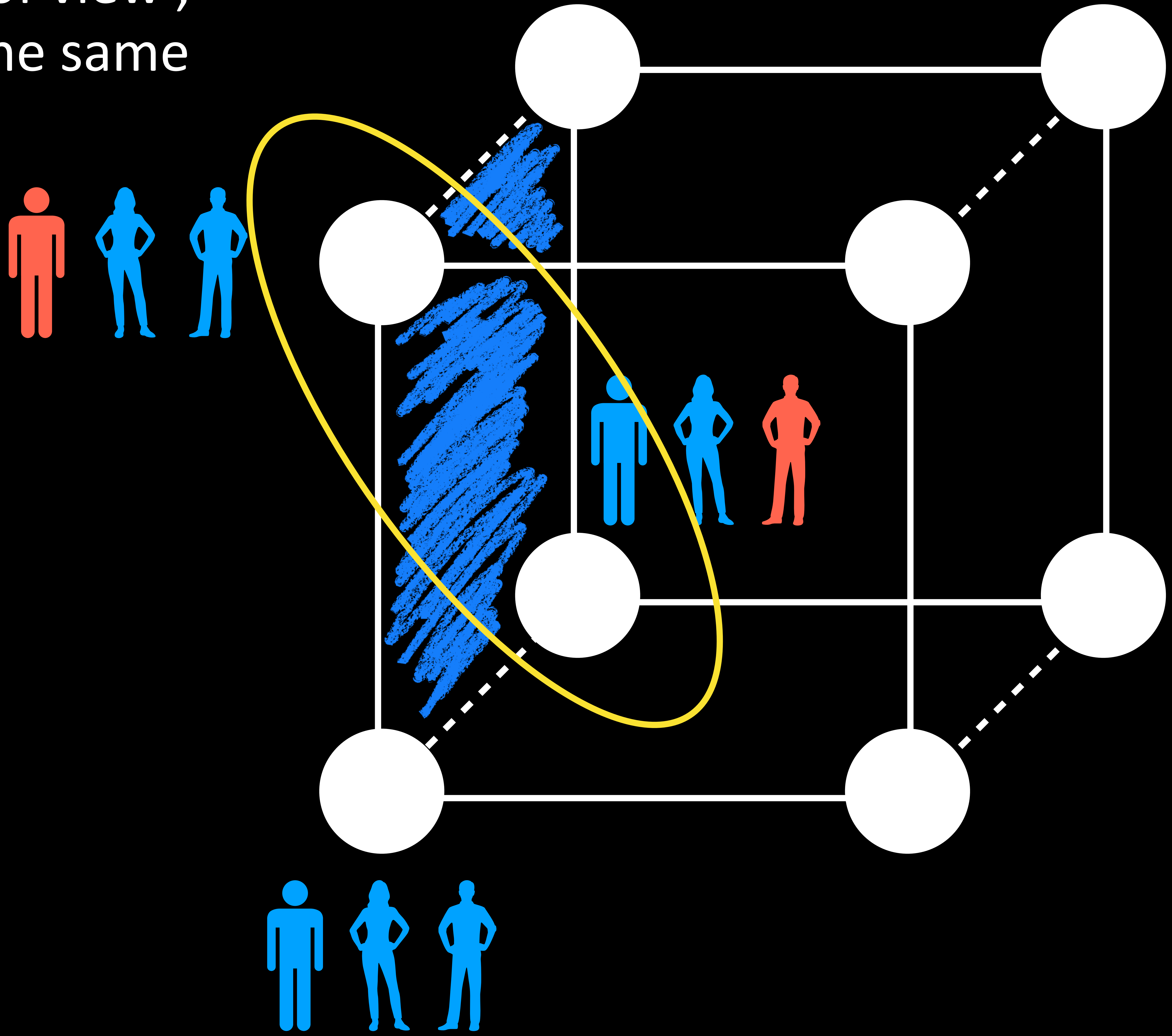
If the identity of the players matters



$2 \times 2 \times 2$

If Player  is blue then from her point of view , these two are the same

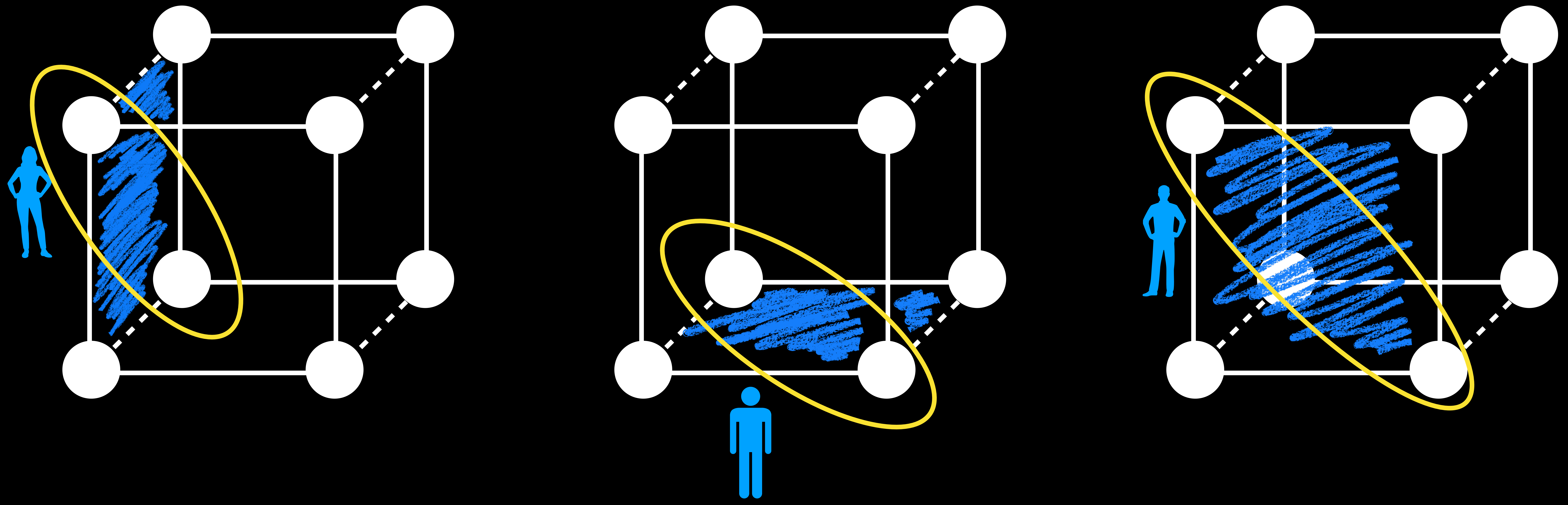
If the identity of the players does NOT matter



$2 \times 2 \times 2$

If the identity of the players does NOT matter

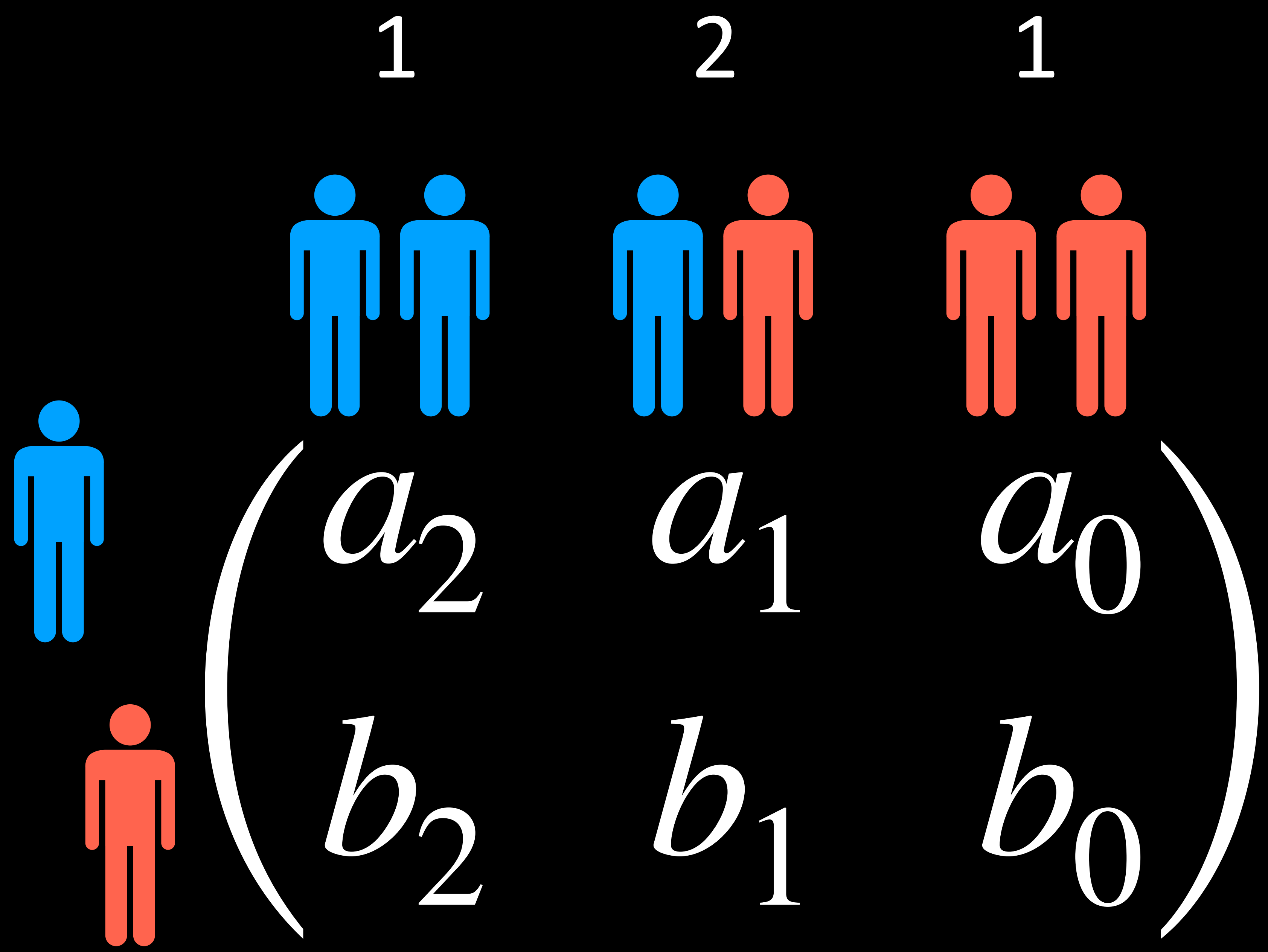
This is true for all the players



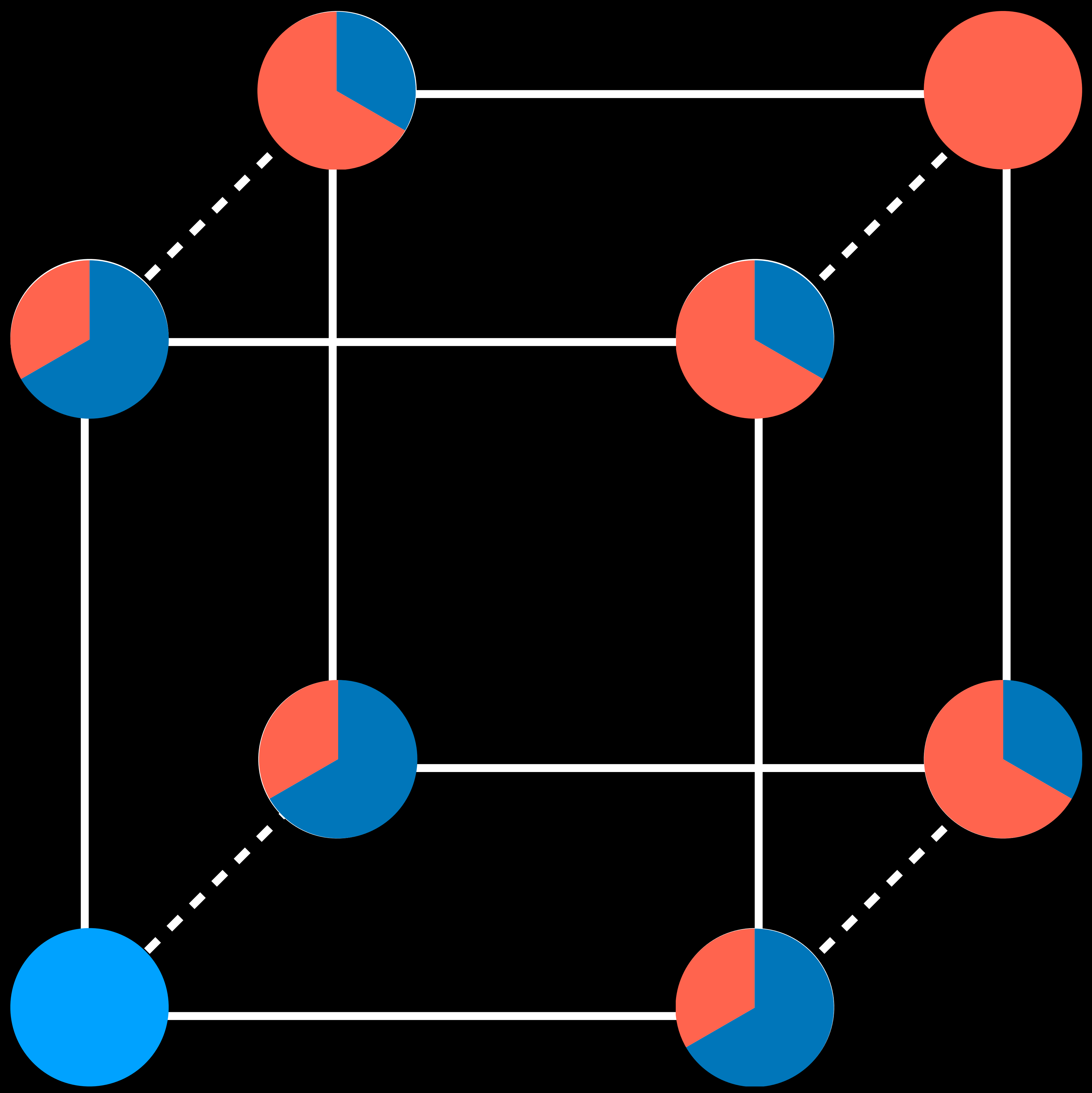
And since we are dealing with

$2 \times 2 \times 2$

Assuming that the identities do NOT matter



$$\begin{pmatrix} a_2 & a_1 & a_0 \\ b_2 & b_1 & b_0 \end{pmatrix}$$



$2 \times 2 \times 2$

Thinking beyond the dyad

$d-$player game with 2 strategies

$d-1$ $\qquad\qquad\qquad\qquad$ $d-1$

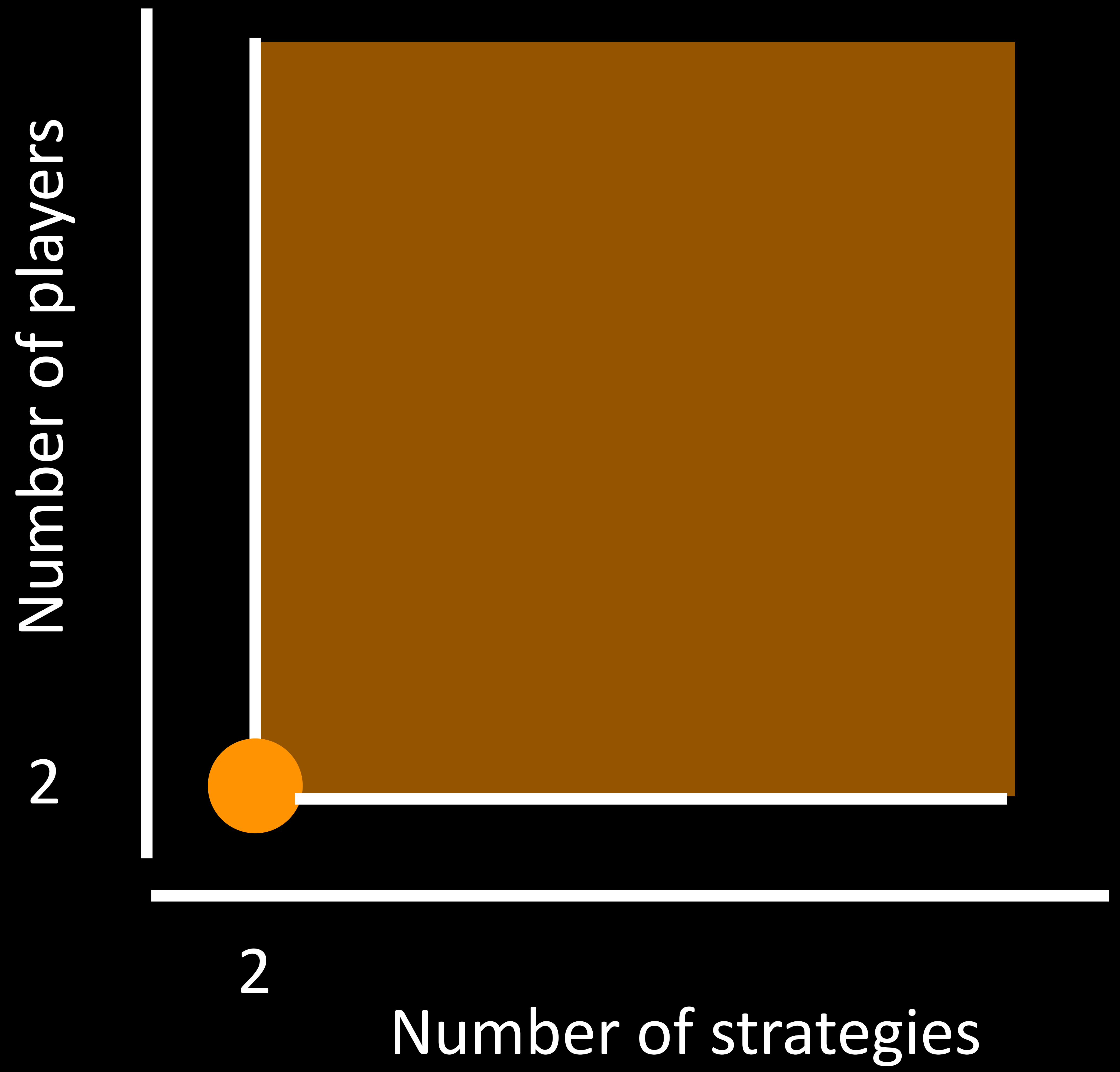
$$\begin{pmatrix} a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_1 & a_0 \\ b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_1 & b_0 \end{pmatrix}$$

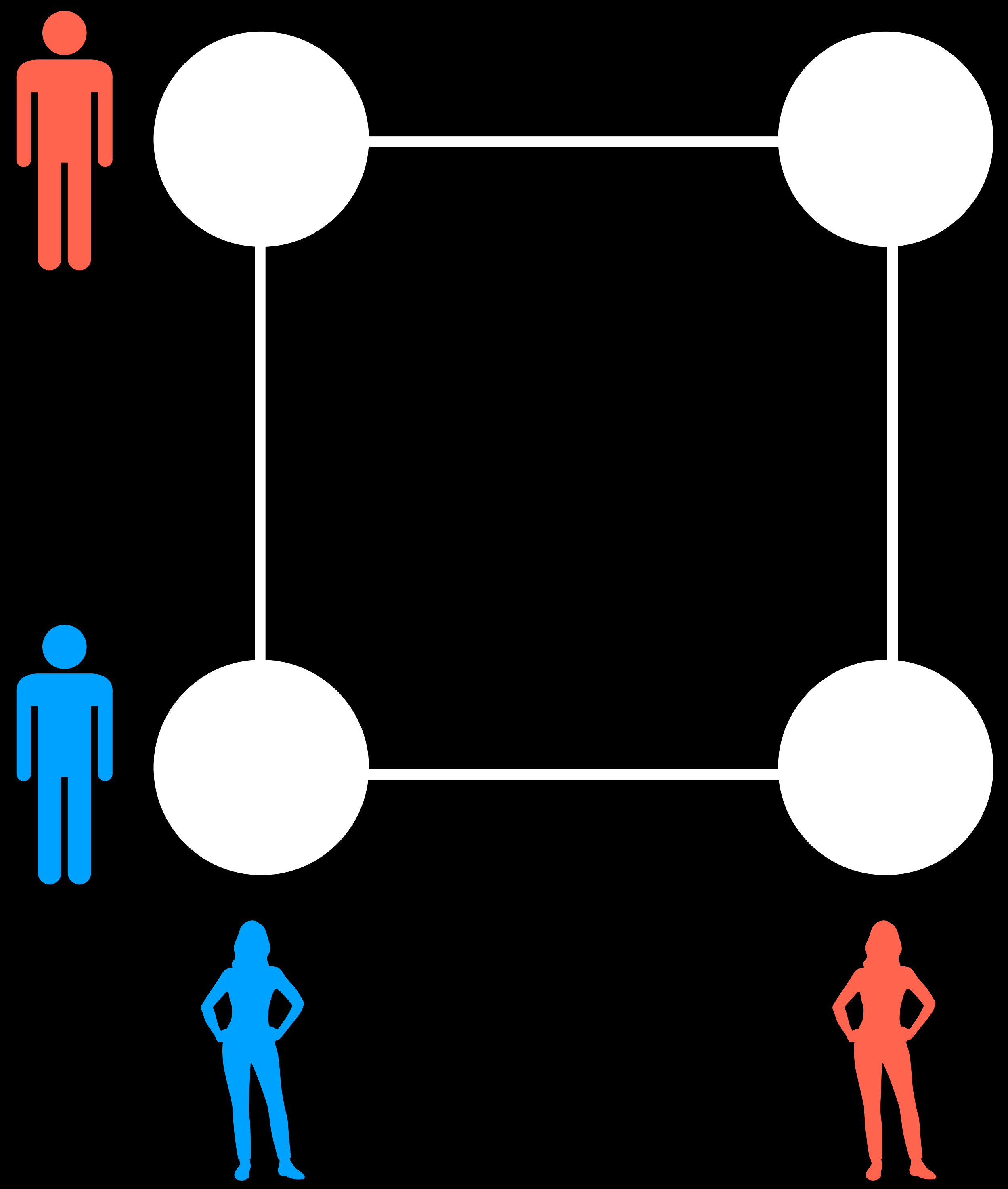
$$\underbrace{2 \times 2 \times \ldots \times 2}_{d}$$

All the results that we will talk about are valid for the generic case

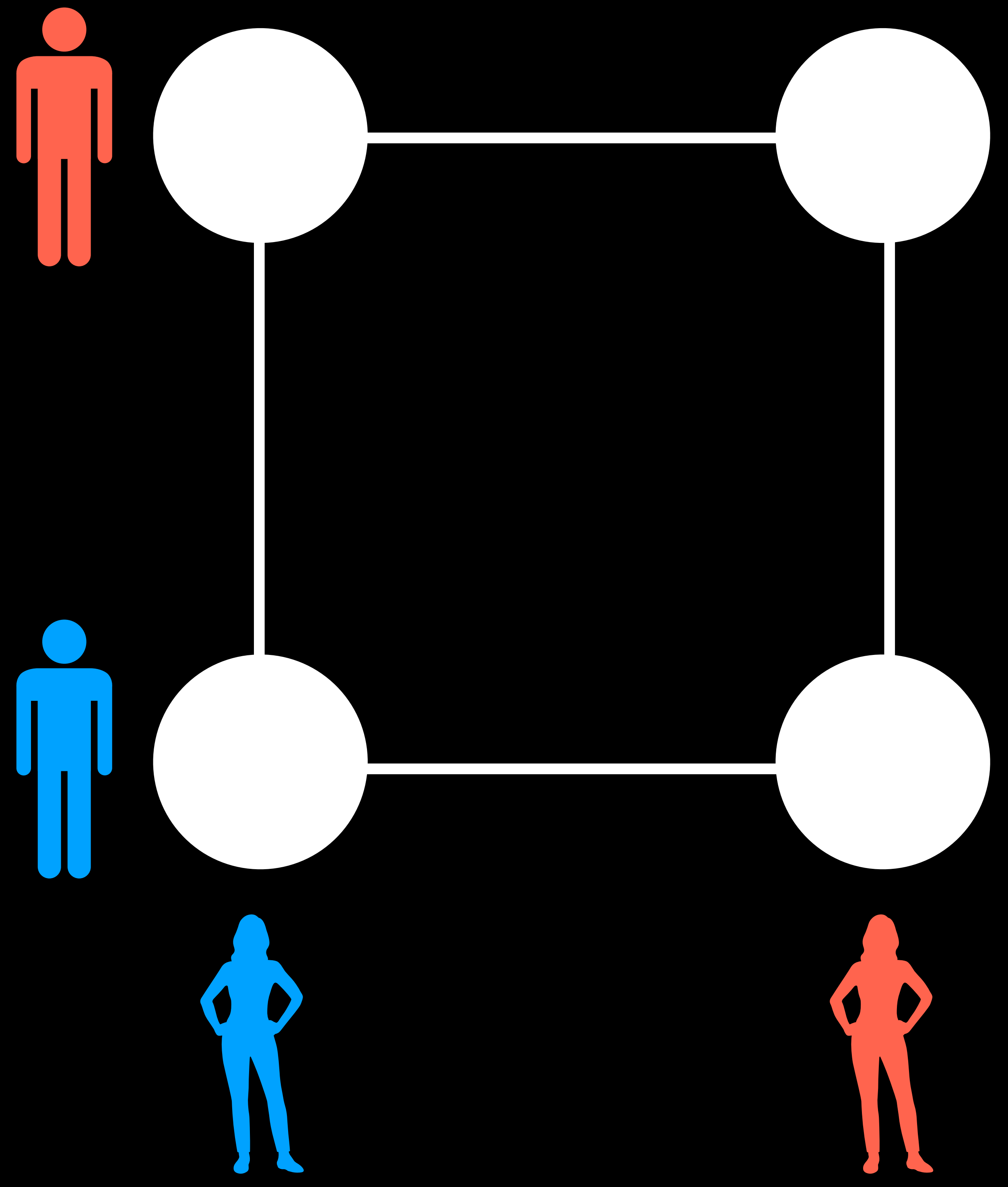
What about multiple strategies?

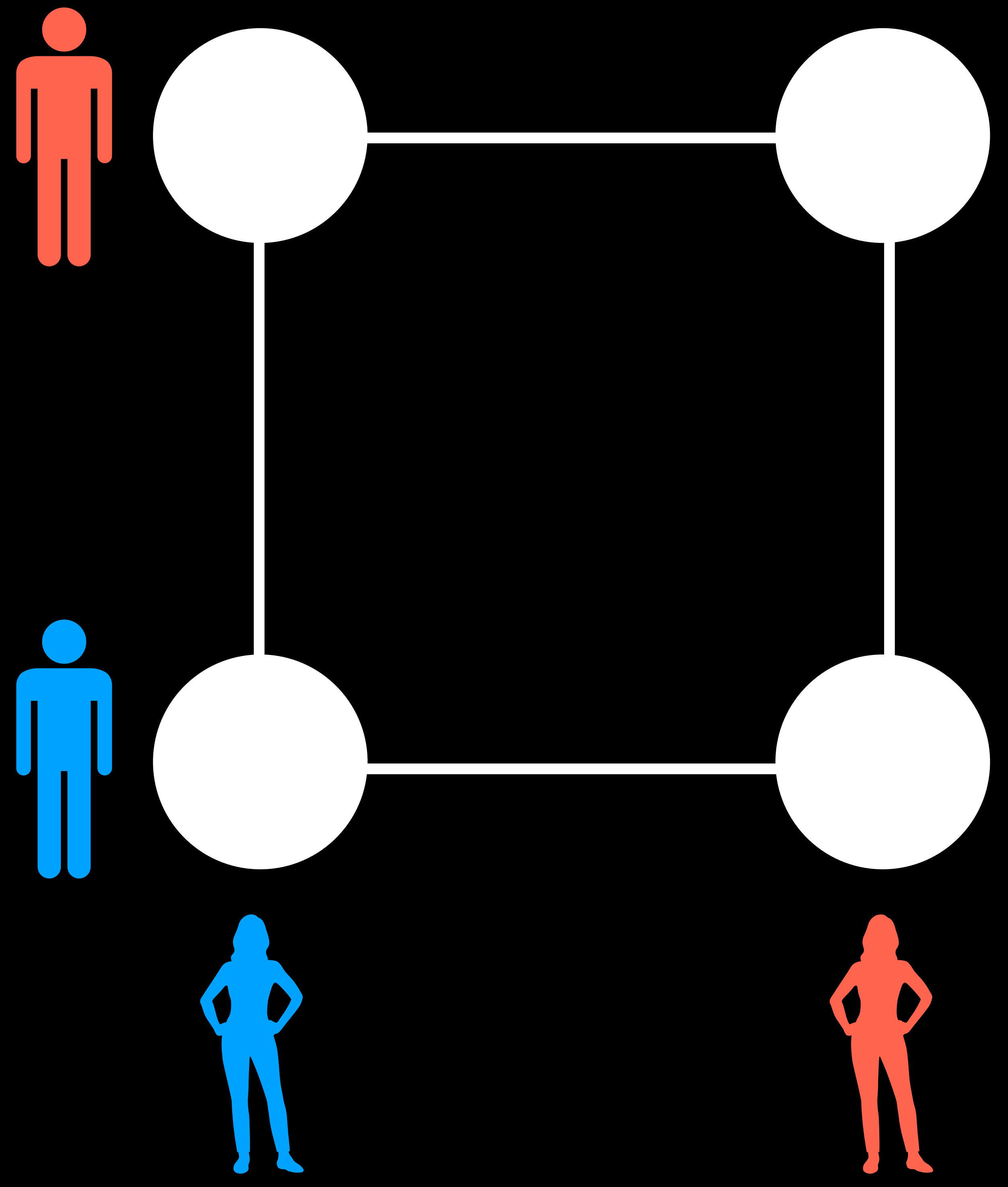
Thinking beyond the dyad with multiple strategies





2×2

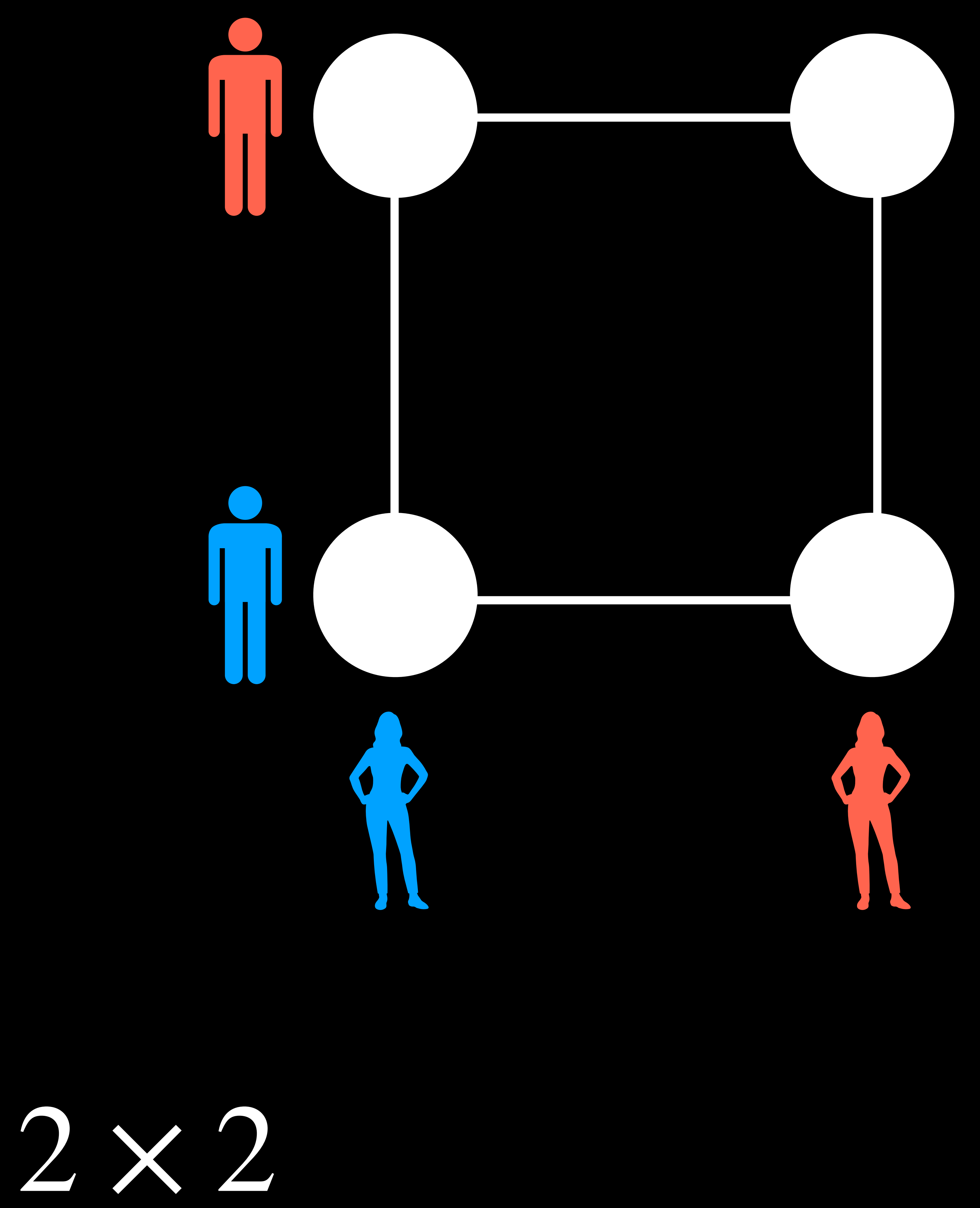


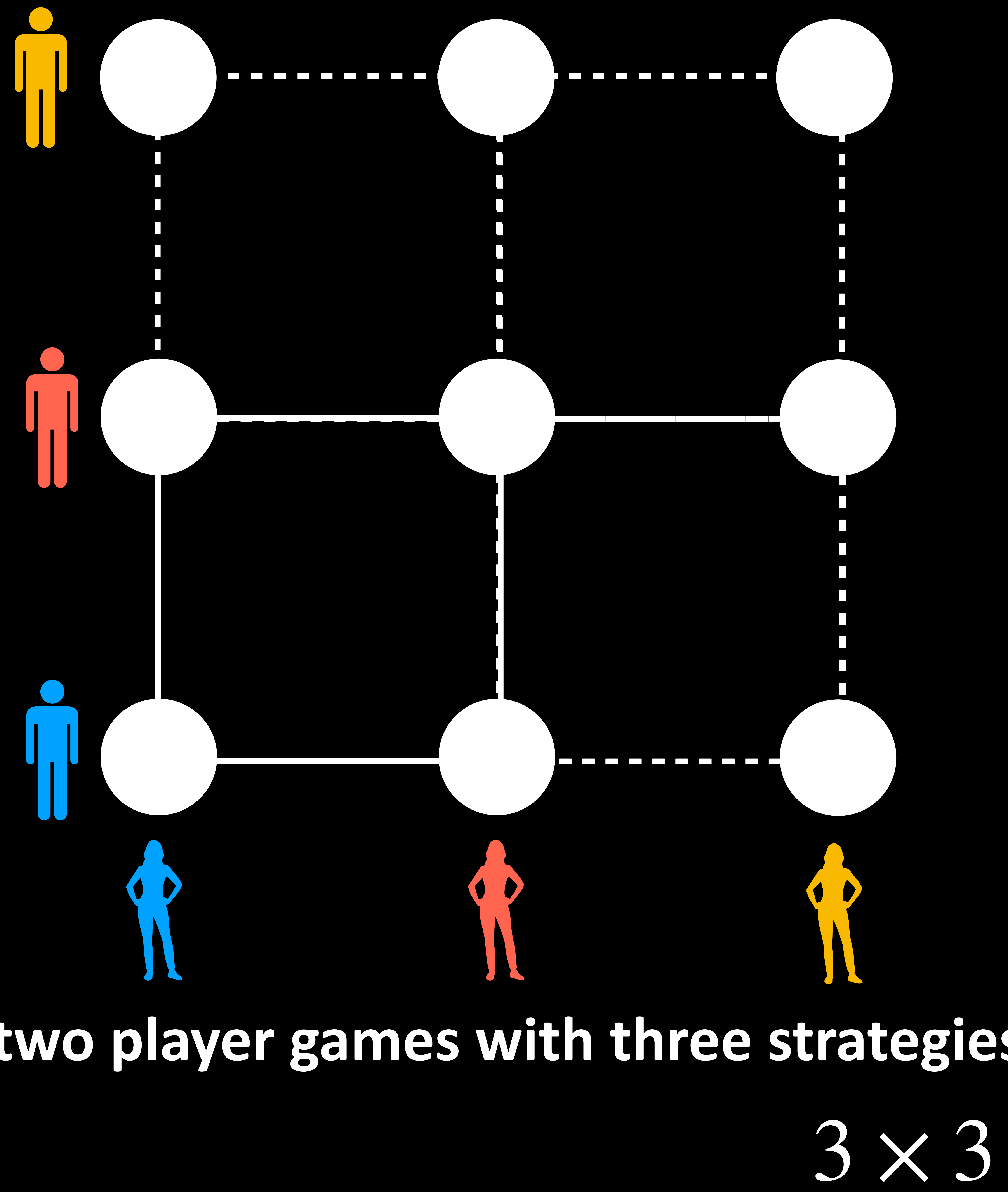


two player games with three strategies

2×2

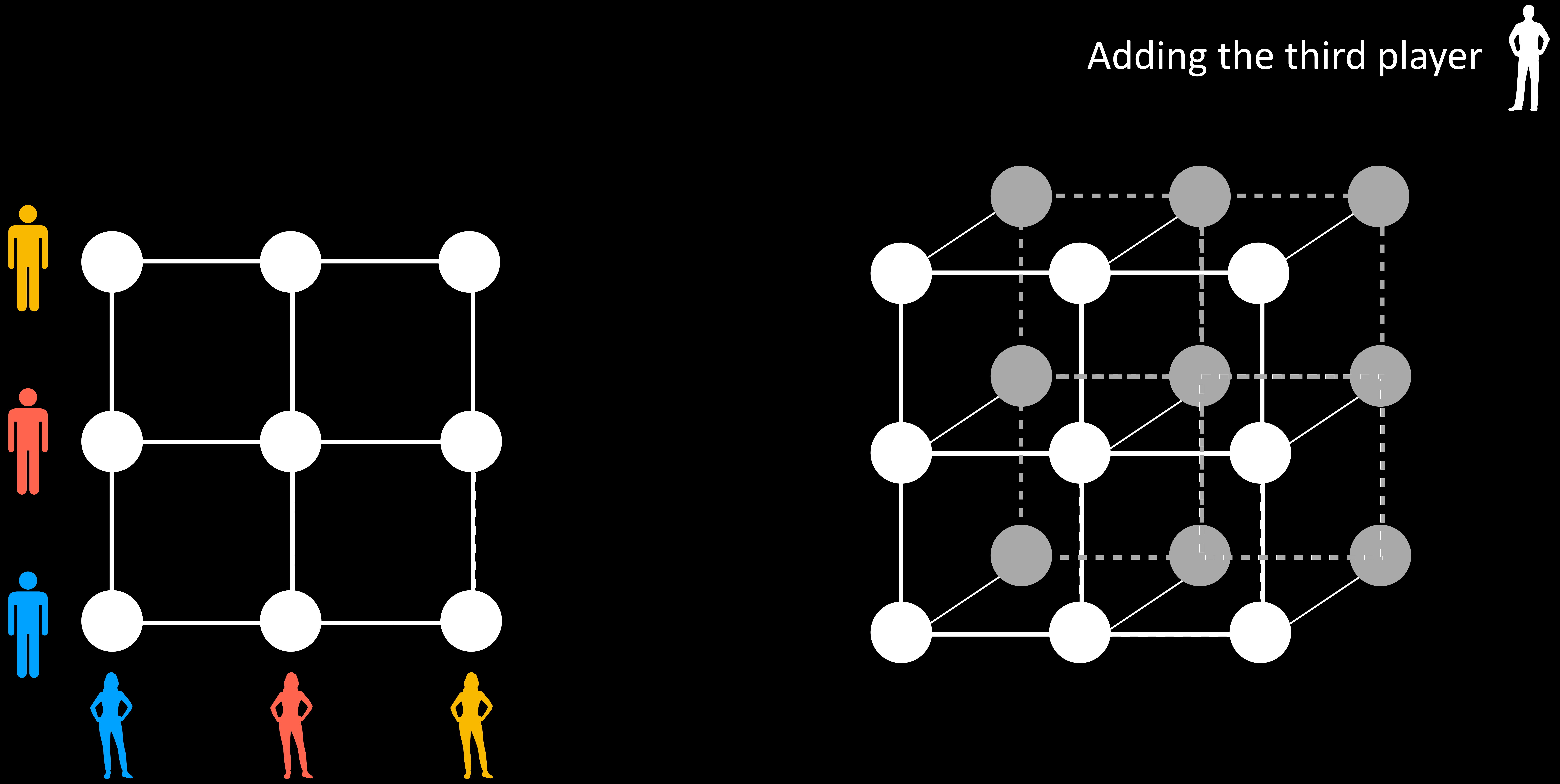
3×3





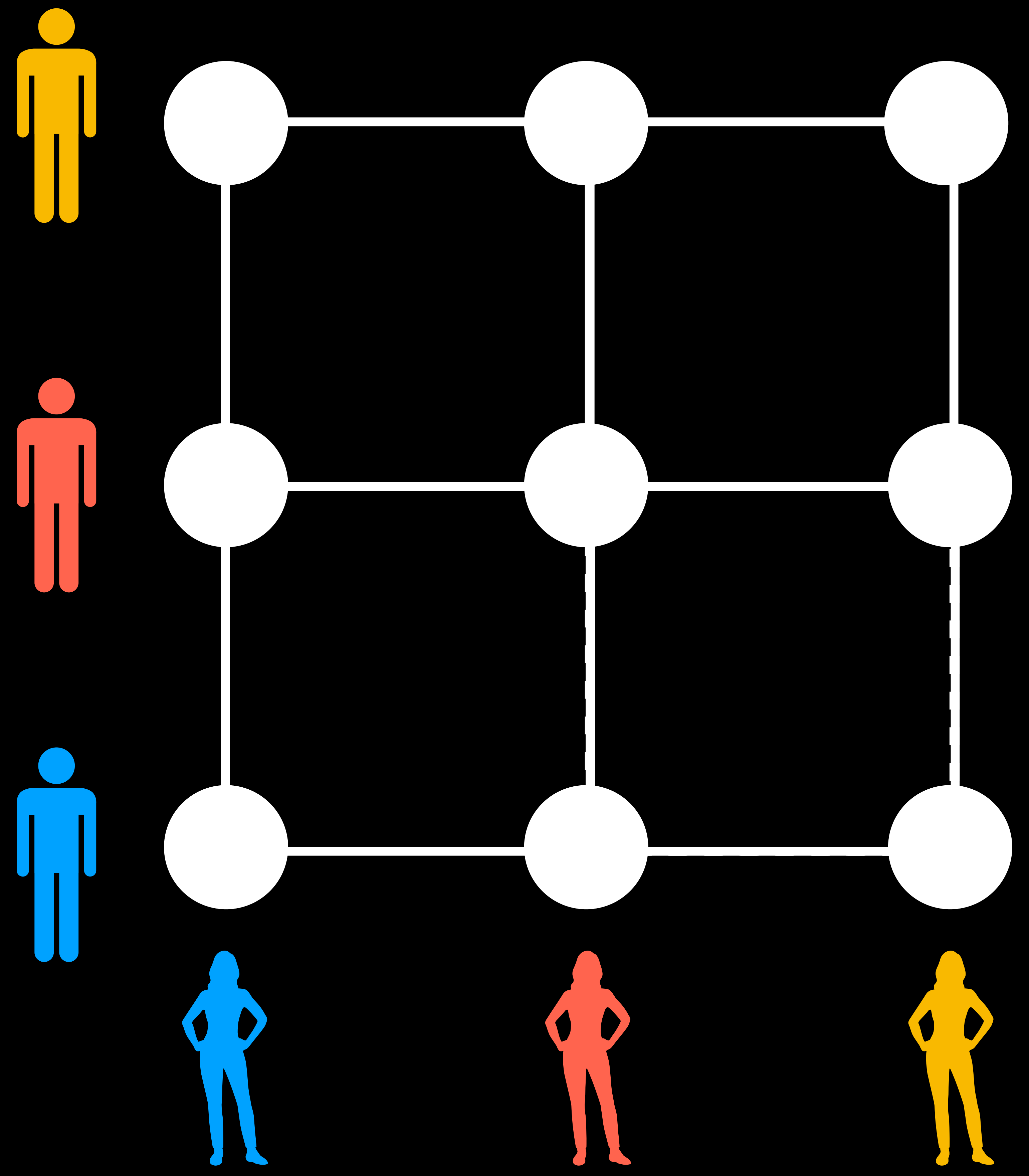
two player games with three strategies

Adding the third player

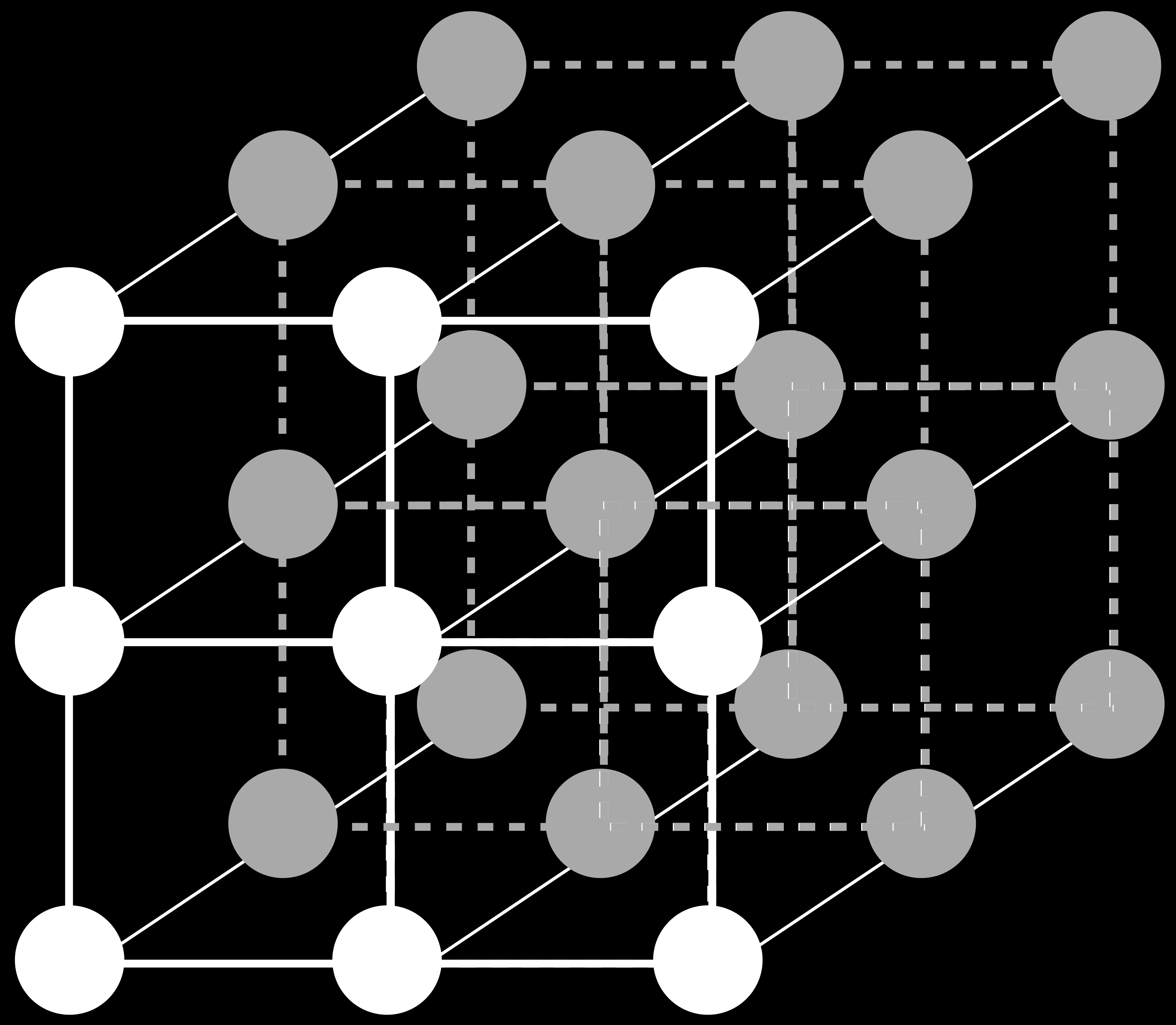


3×3

If the identity of the players matters

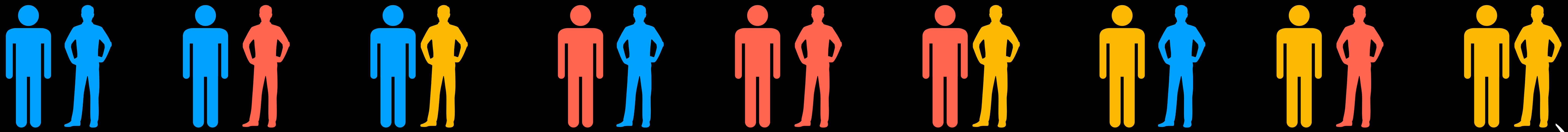


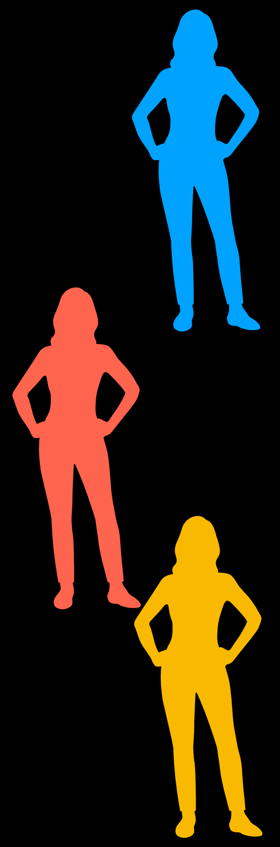
3×3



$3 \times 3 \times 3$

If the identity of the players matters





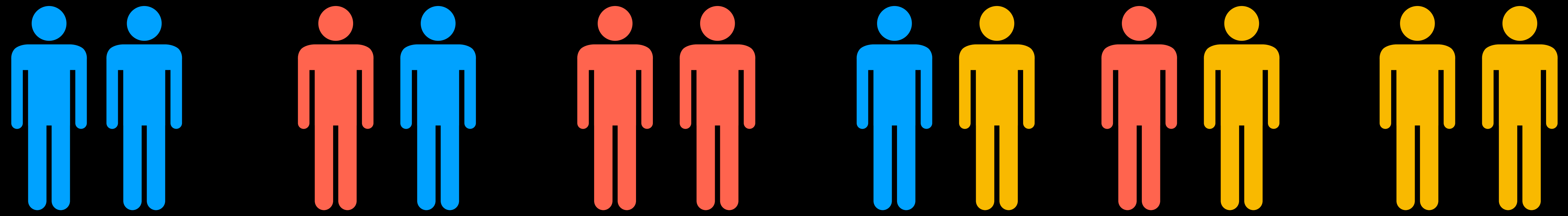
$$\begin{pmatrix} \beta_{B,B,B} & \beta_{B,B,R} & \beta_{B,B,Y} & \beta_{B,R,B} & \beta_{B,R,R} & \beta_{B,R,Y} & \beta_{B,Y,B} & \beta_{B,Y,R} & \beta_{B,Y,Y} \\ \beta_{R,B,B} & \beta_{R,B,R} & \beta_{R,B,Y} & \beta_{R,R,B} & \beta_{R,R,R} & \beta_{R,R,Y} & \beta_{R,Y,B} & \beta_{R,Y,R} & \beta_{R,Y,Y} \\ \beta_{Y,B,B} & \beta_{Y,B,R} & \beta_{Y,B,Y} & \beta_{Y,R,B} & \beta_{Y,R,R} & \beta_{Y,R,Y} & \beta_{Y,Y,B} & \beta_{Y,Y,R} & \beta_{Y,Y,Y} \end{pmatrix}$$

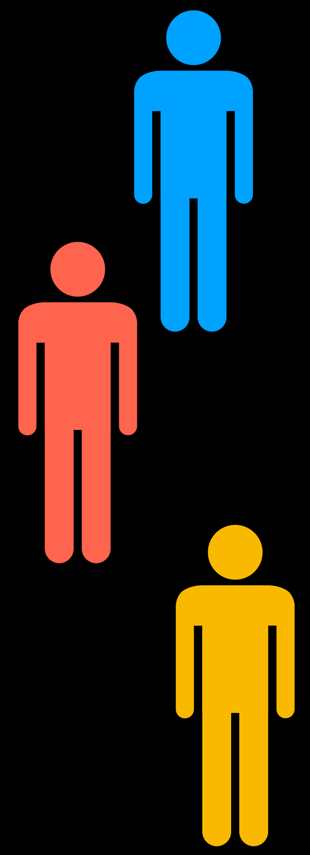
In general for a $d-$player game with n strategies we need a d dimensional tensor of size n

$$3 \times 3 \times 3$$

Assuming that the identities do not matter

1 2 1 2 2 1





$$\begin{pmatrix} a_{2,0,0} & a_{1,1,0} & a_{0,2,0} & a_{1,0,1} & a_{0,1,1} & a_{0,0,2} \\ b_{2,0,0} & b_{1,1,0} & b_{0,2,0} & b_{1,0,1} & b_{0,1,1} & b_{0,0,2} \\ c_{2,0,0} & c_{1,1,0} & c_{0,2,0} & c_{1,0,1} & c_{0,1,1} & c_{0,0,2} \end{pmatrix}$$

Assuming that identity does not matter

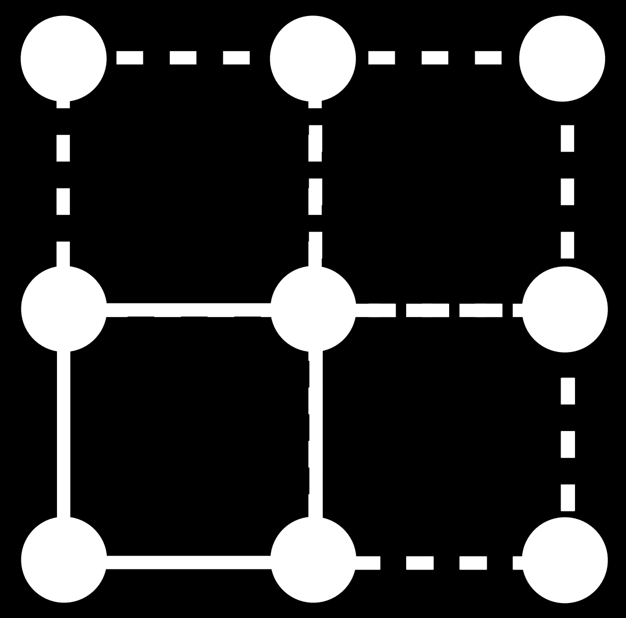
$$a_{(\#ofB,\#ofR,\#ofY)}$$

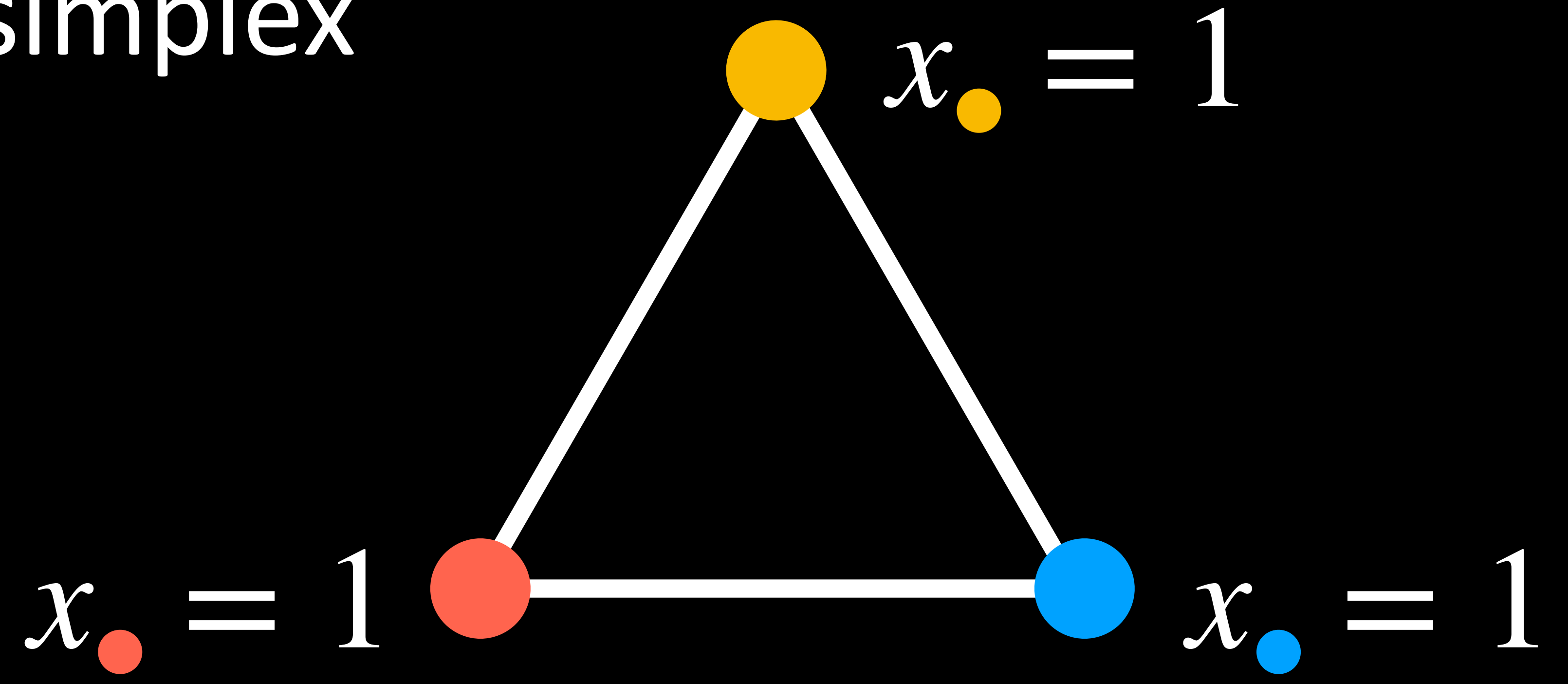
$$3 \times 3 \times 3$$

Adding a new strategy to the game

Increases the size of the payoff matrix but not the dimensions

Increases the dimensions of the simplex

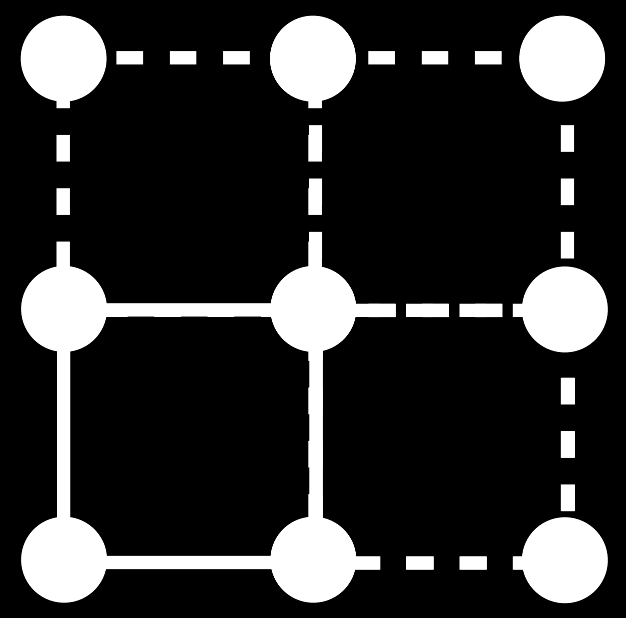


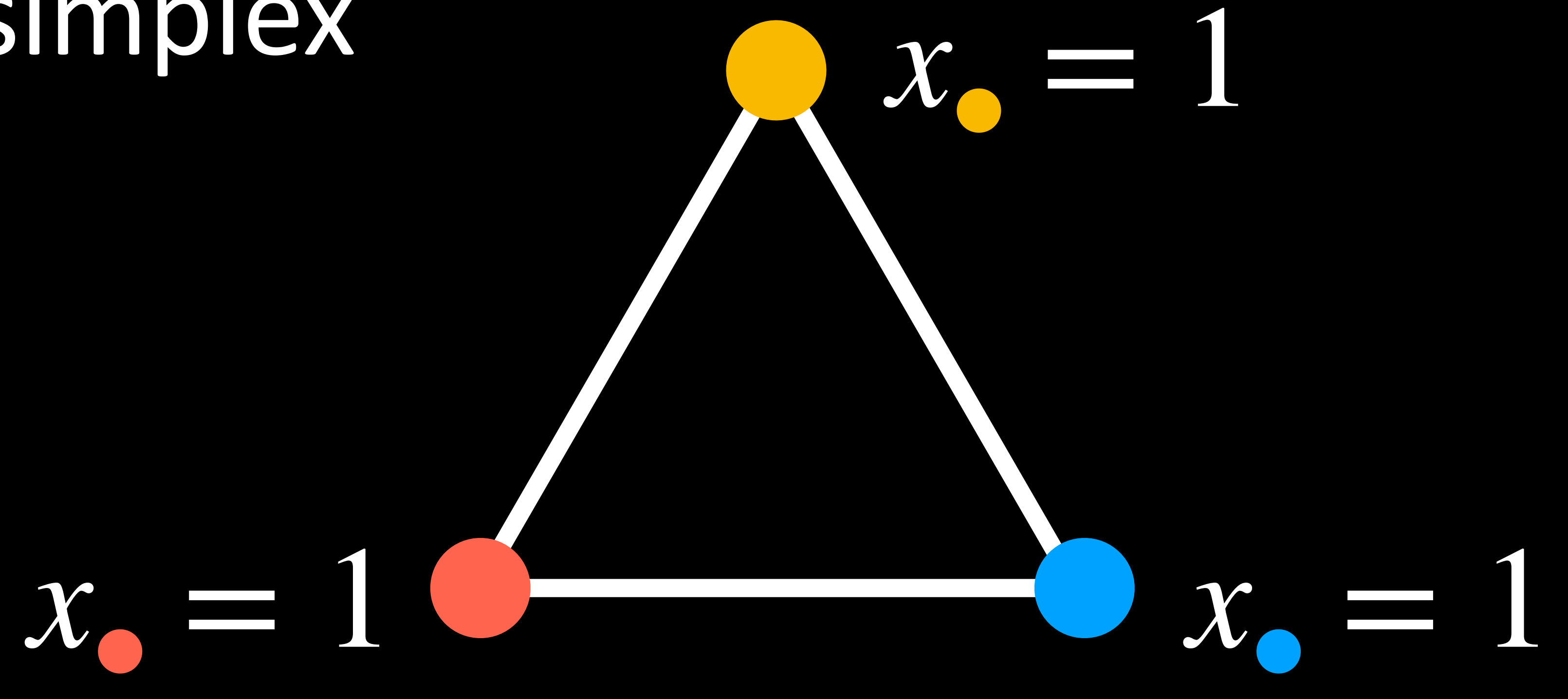


Adding a new strategy to the game

Increases the size of the payoff matrix but not the dimensions

Increases the dimensions of the simplex

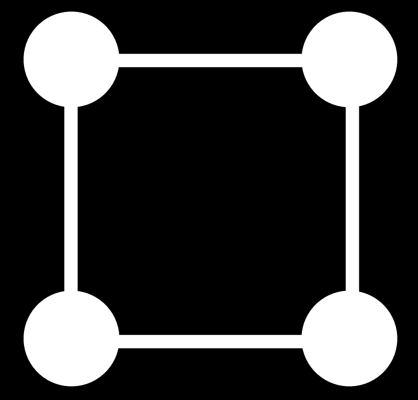


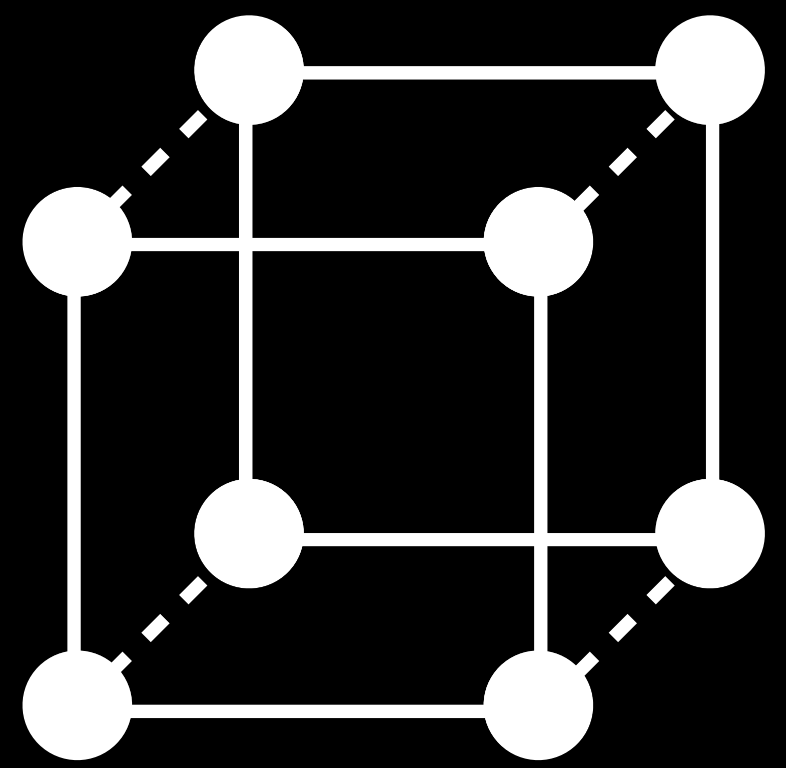


Adding a new player to the game

Increases the dimensionality of the payoff matrix

Preserves the dimensionality of the simplex

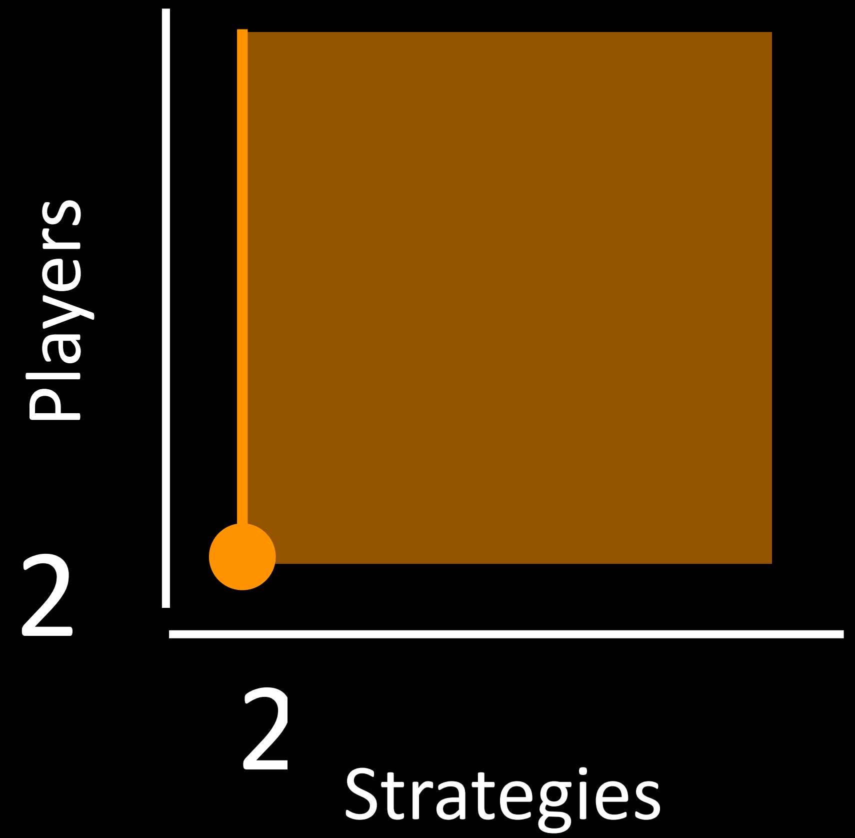




Lecture 1

Introduction to MEGs

Connection to PopGen



Neat… but what can we do with this?

Genotypes and their fitnesses

AA	Aa	aa
α	β	γ

	A A	A a	a a
A A	$\begin{vmatrix} AA & AA \\ AA & AA \end{vmatrix}$	$\begin{vmatrix} AA & Aa \\ AA & Aa \end{vmatrix}$	$\begin{vmatrix} Aa & Aa \\ Aa & Aa \end{vmatrix}$
A a		$\begin{vmatrix} AA & Aa \\ Aa & aa \end{vmatrix}$	$\begin{vmatrix} Aa & Aa \\ aa & aa \end{vmatrix}$
a a			$\begin{vmatrix} aa & aa \\ aa & aa \end{vmatrix}$

Happens half the time

Sexes switch rows/columns

Let us look at this slightly differently,

- each allele (say A) is with its (one other) partner in an individual
- The individual will interact with another individual with two alleles
- Hence besides the focal allele there are 3 other alleles $\boxed{A}$ A,a,a

$$\underset{A}{\boxed{A}}^{\,a\ \ a} \ \beta \qquad \underset{a}{\boxed{A}}^{\,A\ \ a} \ (\alpha+\beta)/2 \qquad \underset{a}{\boxed{A}}^{\,A\ \ a} \ (\alpha+\beta)/2$$

In the offspring, the A allele appears with what fitness

Now, assuming random pairing and mating, and correcting for the combinatorics

	a a		A a		A a
A A	β	A a	$(\alpha+\beta)/2$	A a	$(\alpha+\beta)/2$

$$a_1 = \beta + (\alpha+\beta)/2 + (\alpha+\beta)/2$$

A

Aaa

a_1

Now, assuming random pairing and mating, and correcting for the combinatorics

	a	a		A	a		A	a
A	β		A	$(\alpha+\beta)/2$		A	$(\alpha+\beta)/2$	
A			a			a		

$$a_1 = \frac{\beta + (\alpha+\beta)/2 + (\alpha+\beta)/2}{3} = \frac{\alpha + 2\beta}{3}$$

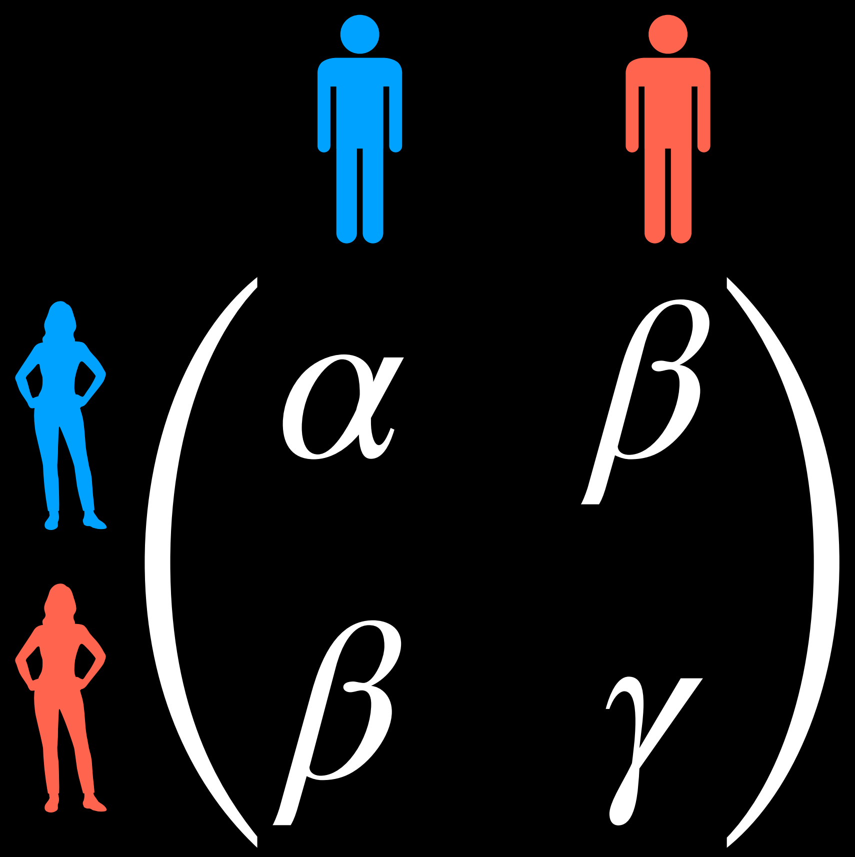
	AAA	AAa	Aaa	aaa
A	a_3	a_2	a_1	a_0
a	b_3	b_2	b_1	b_0

	AAA	AAa	Aaa	aaa
A	α	$\frac{2\alpha+\beta}{3}$	$\frac{\alpha+2\beta}{3}$	β
a	β	$\frac{2\beta+\gamma}{3}$	$\frac{\beta+2\gamma}{3}$	γ

Thats a 4- player game with 2-strategies!

	AAA	AAa	Aaa	aaa
A	α	$\frac{2\alpha+\beta}{3}$	$\frac{\alpha+2\beta}{3}$	β
a	β	$\frac{2\beta+\gamma}{3}$	$\frac{\beta+2\gamma}{3}$	γ

$$\pi_A = \alpha x + \beta(1-x)$$
$$\pi_a = \beta x + \gamma(1-x)$$



$$\begin{pmatrix} \alpha & \beta \\ \beta & \gamma \end{pmatrix}$$

$$\dot{x} = x(\pi_A - \bar{\pi})$$

Great so we can reduce a diploid selection model to a two player game

So what?

Asexual Population Consider that there are many genetic types in the population, and that each reproduces its own type exactly. The model is also appropriate for a Y-chromosome factor (if only males are considered), for an X-chromosomal factor in either sex in an attached-X stock, or cytoplasmic inheritance transmitted through one sex.

Assume that the genotypes $A_1, A_2, A_3, \ldots$ have fitnesses $w_1, w_2, w_3, \ldots$ and are present in the population in frequencies $p_1, p_2, p_3, \ldots$. Then the proportion of A_i genotypes next generation will be

$$p_i' = \frac{p_i w_i}{p_1 w_1 + p_2 w_2 + \cdots} = \frac{p_i w_i}{\bar{w}},$$

where $\bar{w} = \sum p_i w_i$ is the average fitness.

The change in the proportion of A_i in one generation is

$$\Delta p_i = \frac{p_i w_i}{\bar{w}} - p_i = \frac{p_i(w_i - \bar{w})}{\bar{w}}. \qquad 5.2.1$$

The quantity $w_i - \bar{w}$ is the *average excess* in fitness of the genotype A_i. For only two alleles, this formula is conveniently written as

$$\Delta p_1 = \frac{p_1 p_2 (w_1 - w_2)}{\bar{w}} = \frac{s p_1 p_2}{\bar{w}}, \qquad 5.2.2$$

where s, the selection coefficient, is $w_1 - w_2$ and $p_1 + p_2 = 1$.

Notice that selection is most rapid when the two types are nearly equal in frequency and becomes slower when one is much more common than the other. For example, if w_1 is 1.1 and w_2 is .9, the frequency of A_1 will increase from .50 to .55 in one generation, but if the frequency is 0.10, it will only change to .1195 in one generation.

Diploid Sexual Population We now let w_{ij} stand for the average fitness of the genotype $A_i A_j$. As before we let P_{ii} be the frequency of the homozygous genotype $A_i A_i$ and $2P_{ij}$ the frequency of the heterozygote $A_i A_j$. Then the frequency of the gene A_i is (from equation 2.1.2)

$$p_i = \sum_j P_{ij}.$$

Next generation the proportion of A_i genes will be

$$p_i' = \frac{\sum_j P_{ij} w_{ij}}{\bar{w}} = \frac{p_i w_i}{\bar{w}}, \qquad 5.2.3$$

where

$$\bar{w} = \sum_i \sum_j P_{ij} w_{ij} = \sum_i p_i w_i \qquad 5.2.4$$

and

$$w_i = \frac{\sum_j P_{ij} w_{ij}}{p_i}. \qquad 5.2.5$$

Hence,

$$\Delta p_i = \frac{p_i(w_i - \bar{w})}{\bar{w}}. \qquad 5.2.6$$

The formula is the same as that for asexual selection, but w_i now has a more complex meaning. In this equation w_i is the average fitness of the A_i allele; more specifically, it is the average fitness of all genotypes containing A_i, weighted by the frequency of the genotype and by the number of A_i alleles (1 or 2). Then $\bar{w}$, the average fitness of the population, can be expressed in either of two ways: (1) the average of all the genotypes in the population, and (2) the average fitness of all the genes at this locus. These correspond to the two expressions given in 5.2.4.

Equation 5.2.6 shows that the rate of change of the gene frequency is proportional to:

(1) The gene frequency, p_i. Thus a very rare gene will change slowly, regardless of how strongly it is selected.
(2) The average excess in fitness of the A_i allele over the population average. If the excess, $w_i - \bar{w}$, is positive, the allele will increase; if negative, it will decrease. If this is large the frequency of A_i will change rapidly; if small, slowly.

Notice also that the gene frequency change will be slow when the allele becomes very common ($p_i \to 1$). In this case, w_i and $\bar{w}$ are not very different, since most of the population contains the A_i gene. This point can be brought out by rewriting 5.2.6 in another way:

$$\Delta p_i = \frac{p_i(1 - p_i)(w_i - w_x)}{\bar{w}}, \qquad 5.2.7$$

where w_x is the average fitness of all alleles other than A_i. This shows clearly that Δp_i approaches 0 as p_i gets near to either 0 or 1.

If the population is in random-mating proportions we can write 5.2.7 in still another way, often used by Wright (e.g., 1949). With random mating $P_{ij} = p_i p_j$ and

$$w_i = \frac{\sum_i \sum_j p_i p_j w_{ij}}{p_i} = \sum_j p_j w_{ij}, \qquad 5.2.8$$

$$\Delta p_i = \frac{p_i(w_i - \bar{w})}{\bar{w}}$$

The selection equation from population genetics!

Crow, James F., and Motoo Kimura. *An Introduction to Population Genetics Theory*. 1970

Then why the four player shenanigans?

Medea dynamics

the Medea element plays its role in half the cases of $++\times+M$ and $+M\times+M$, as half the times, the $+M$ will be a female and the fitness of the ++ offspring will be $1-t$.

		♀		
		$++$	$+M$	MM
	$++$	$\sim$	!	$\sim$
♂	$+M$	$\sim$	!	$\sim$
	MM	$\sim$	$\sim$	$\sim$

$\sim$ Unaffected offspring

! ++ die with probability t

	MMM	$MM+$	$M++$	$+++$
M	ν	$\frac{\omega+2\nu}{3}$	$\frac{2\omega+\nu}{3}$	ω
$+$	ω	$\frac{2\omega+1-t}{3}$	$\frac{2+\omega-t}{3}$	1

$$\pi_M = \nu x + \omega(1-x)$$
$$\pi_+ = \omega x + (1-xt)(1-x).$$

Multiplayer Evolutionary Games provide a natural means of including non-linearities in interaction structures

Today

Population Genetics

$$\dot{x} = x(1-x)(f_{\color{blue}\bullet} - f_{\color{red}\bullet})$$

Replicator equation

(In the multiplayer context)

Tuesday

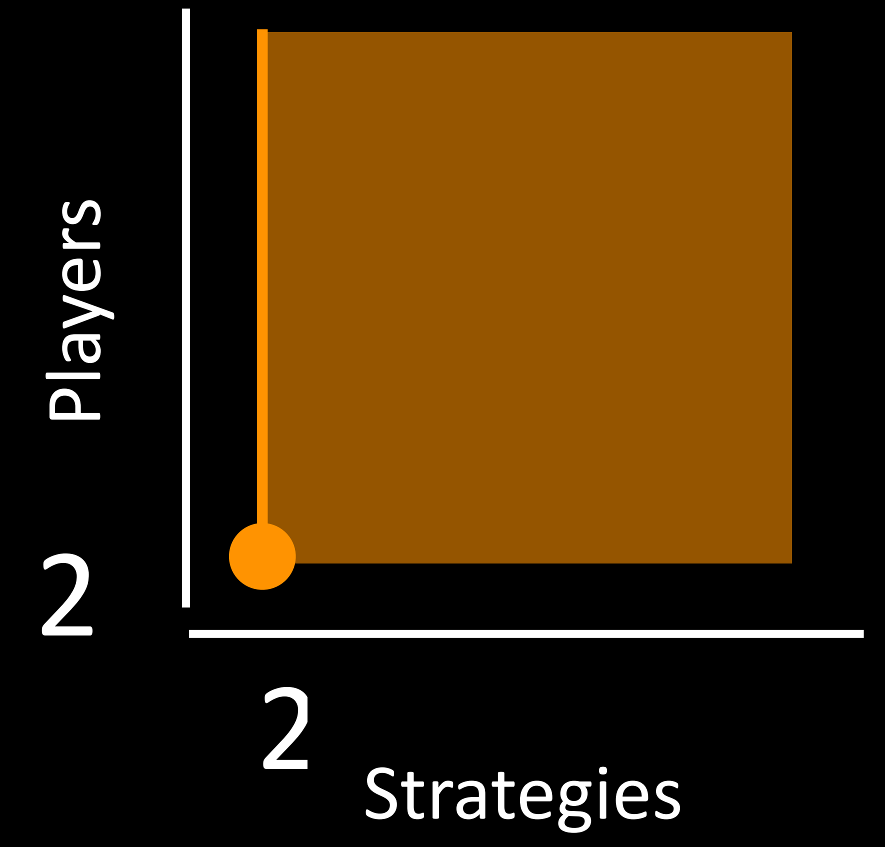
Population Dynamics/ Social Evolution

Wednesday

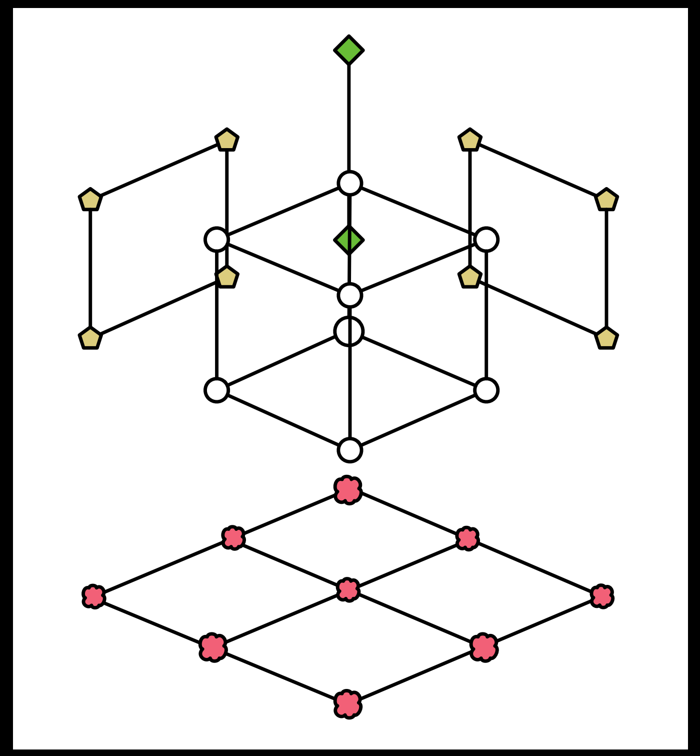
Theoretical Ecology/ Sociocultural dynamics

Lecture 1

Introduction to MEGs



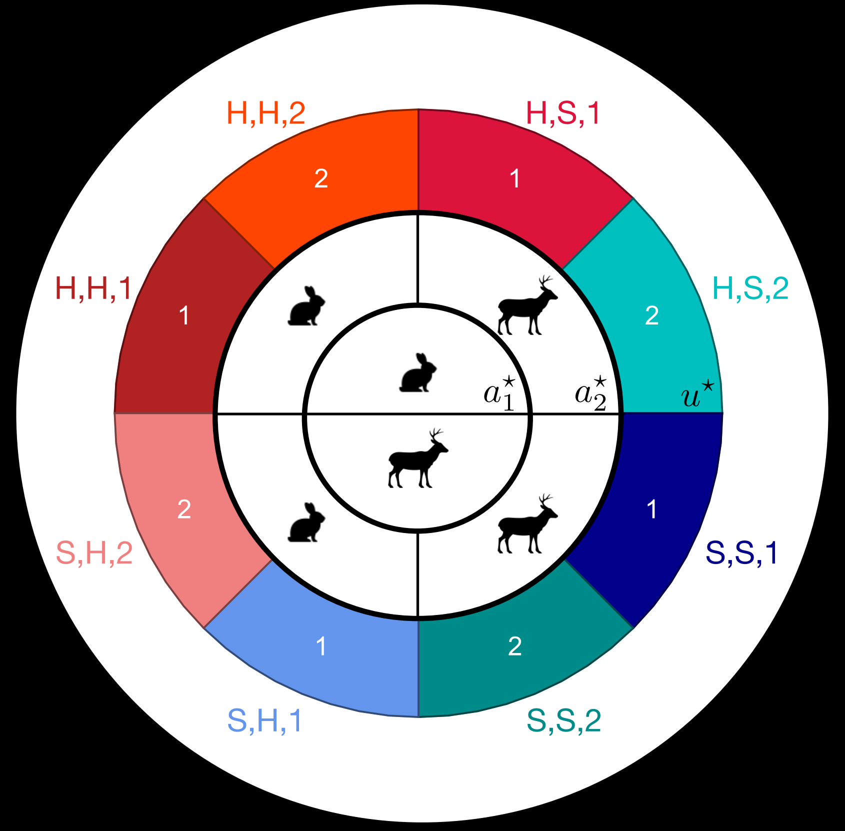
Connection to PopGen



Lecture 3

Higher-order interactions

Collective beliefs and trust



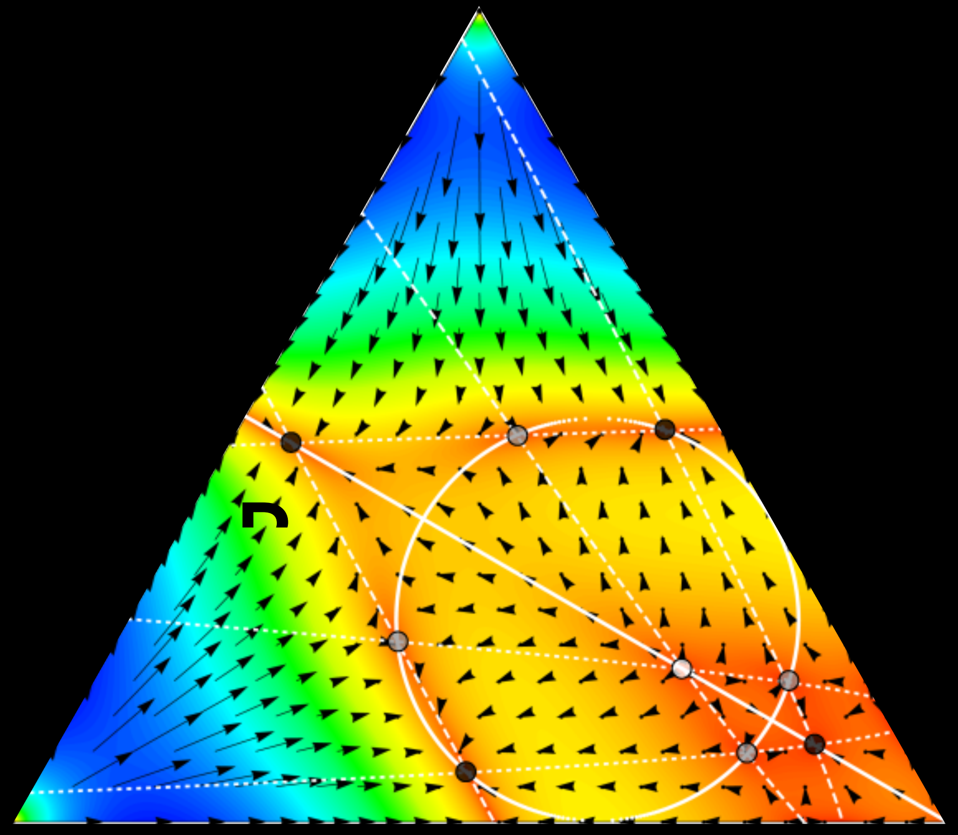
Lecture 2

If .. .when & how of MEGs in the long run

(If time permits)

MEGs in mutualism and

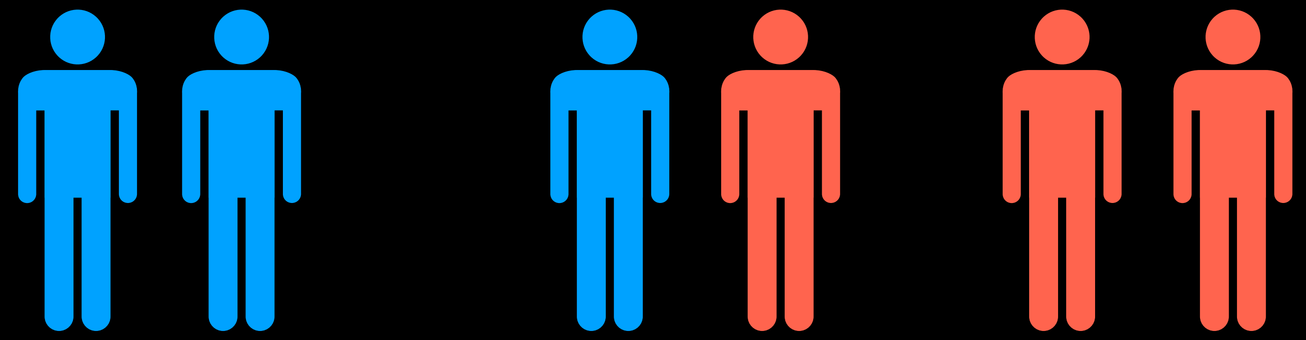
Eco-evolutionary dynamics

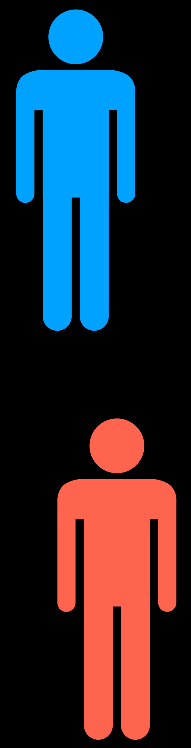


As this is a school… there is some homework

Exercise - Too many cooks!

Lets say you want to bake a cake. For each chef, baking costs c leading to a delicious cake b . Two chefs can bake the cake perfectly but three diminish the quality.





$$\begin{pmatrix} \frac{b}{2} - c & b - c & -c \\ b & 0 & 0 \end{pmatrix}$$

Assuming c = 1; test for different values of b.
How does the replicator dynamics look like?