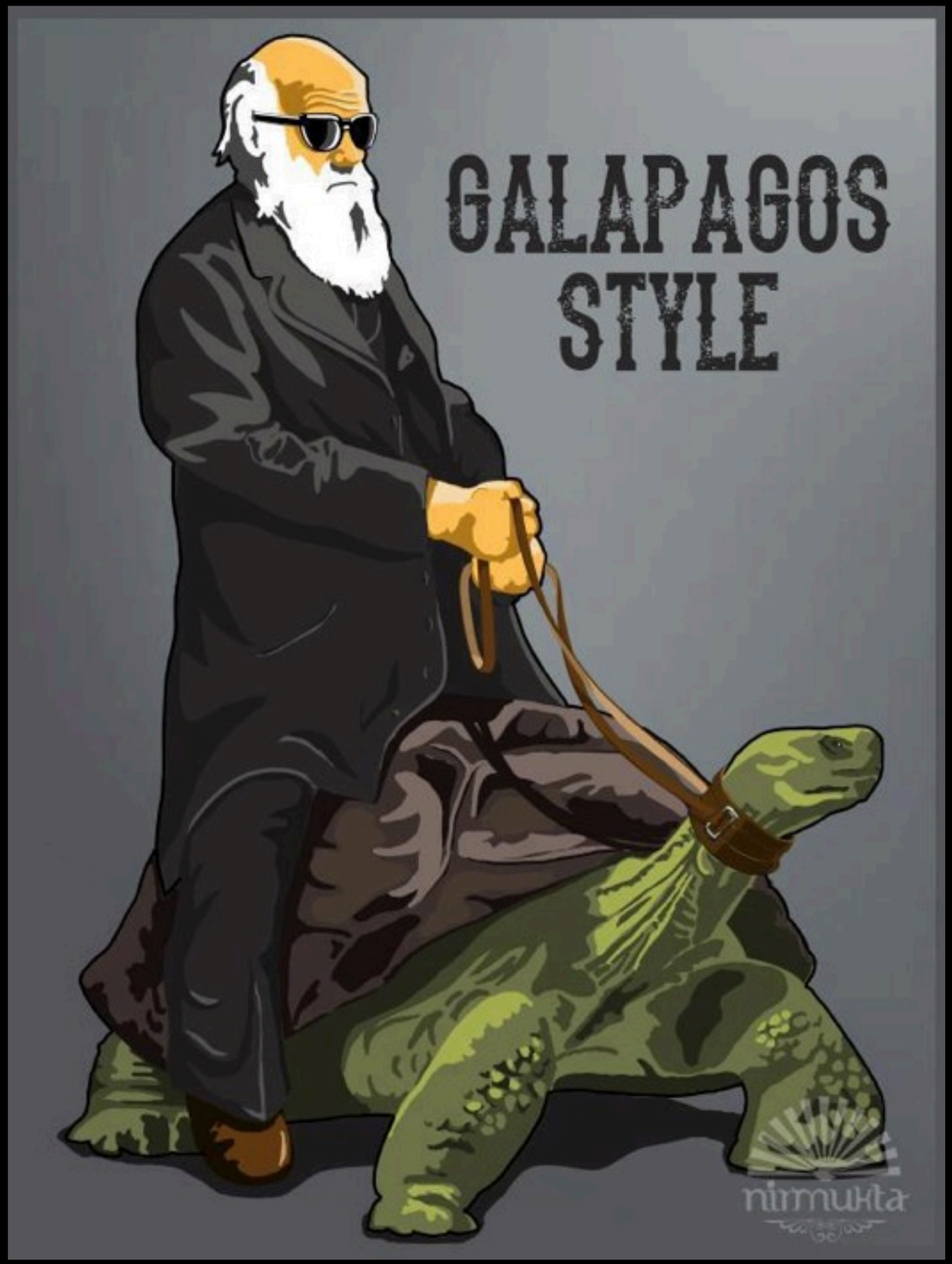

Announcements

Why Have A Social Life?

Social Continuum

Solitary

Advanced Subsocial

Parasocial

Eusocial

Social Continuum

Solitary

Advanced Subsocial

Parasocial

Eusocial

- No cooperation
- No parental care.
- Interact only to mate.

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- Same generation adults in common nest.
- Communal = nest sharing but no common brood care.
- Semisocial = cooperative brood care, reproductive castes, many reproductives.

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- Cooperative brood care.
- Reproductive division of labor.
- Overlap of generations.

Why Be Social?

Costs	Benefits
More conspicuous to predators.	Predator defense via dilution effect/mutual defense.
Disease and parasite transmission increases.	Receive assistance from others in dealing with pathogens.
Increased compeitition for food.	Improved foraging.
Energy expended in determining and holding social status.	Subordinates granted permission to stay in group.
Greater male vulnerability to cuckoldry.	Some males may cuckold others.
Greater female vulnerability to reproductive interference by others.	Opportunity to interfere with reproductive efforts of others.

Why Be Social?

- Direct benefits ...

Darwin's One Special Difficulty

- I ... will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters of sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the male and fertile females, and yet from being sterile they cannot propagate their kind.

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Altruism

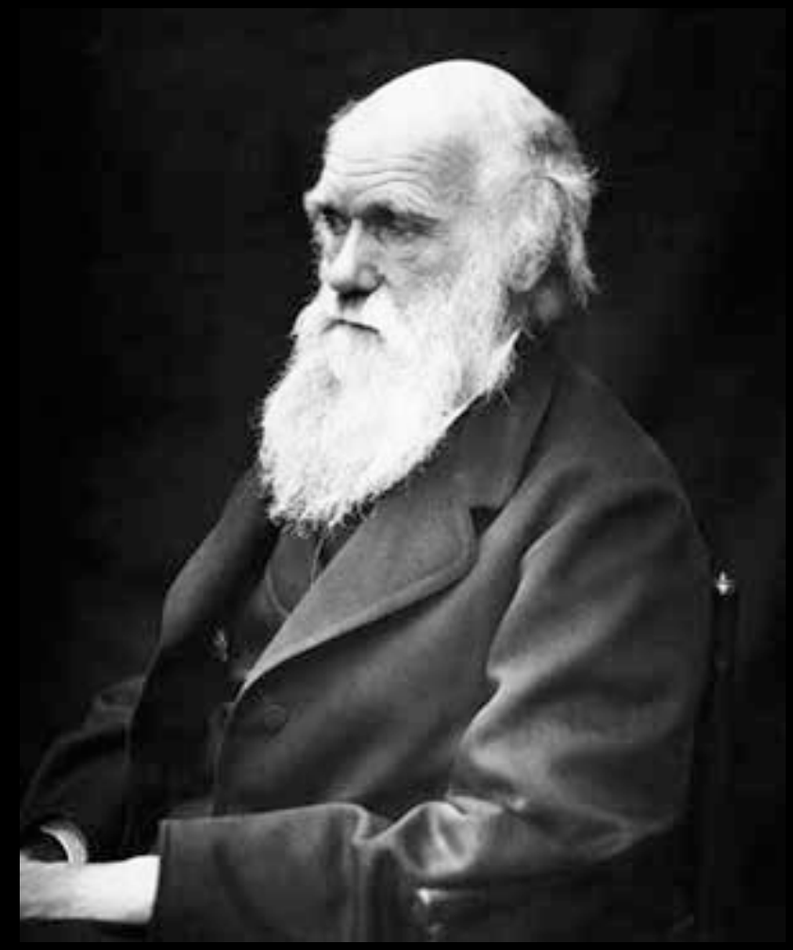
		RECIPIENT	
		+	-
ACTOR	+	Mutualism	Selfish
	-	Altruism	Spite

The Study of Social Behavior

- Founding fathers of animal behavior (e.g. Tinbergen, Lorenz, von Frisch)
  - Control and development of behavior.
- Animal ecologists (e.g. Lack, Skutch)
  - Regulation of population density.
- Population geneticists (e.g. Fisher, Haldane, Williams)
  - Operation of natural selection and the evolution of genetic systems.

Group Selection

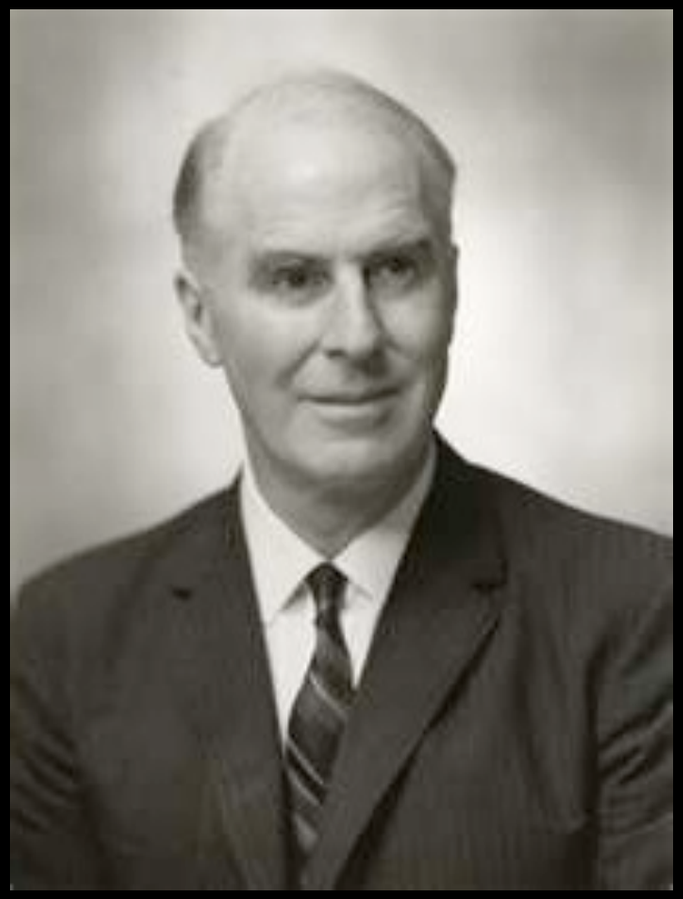
- A tribe including many members who ... sacrifice themselves for the common good would be victorious over most other tribes.



Territoriality

- Lack (1954)
  - Population dynamics in birds.
  - Territoriality regulates population density.

Group Selection



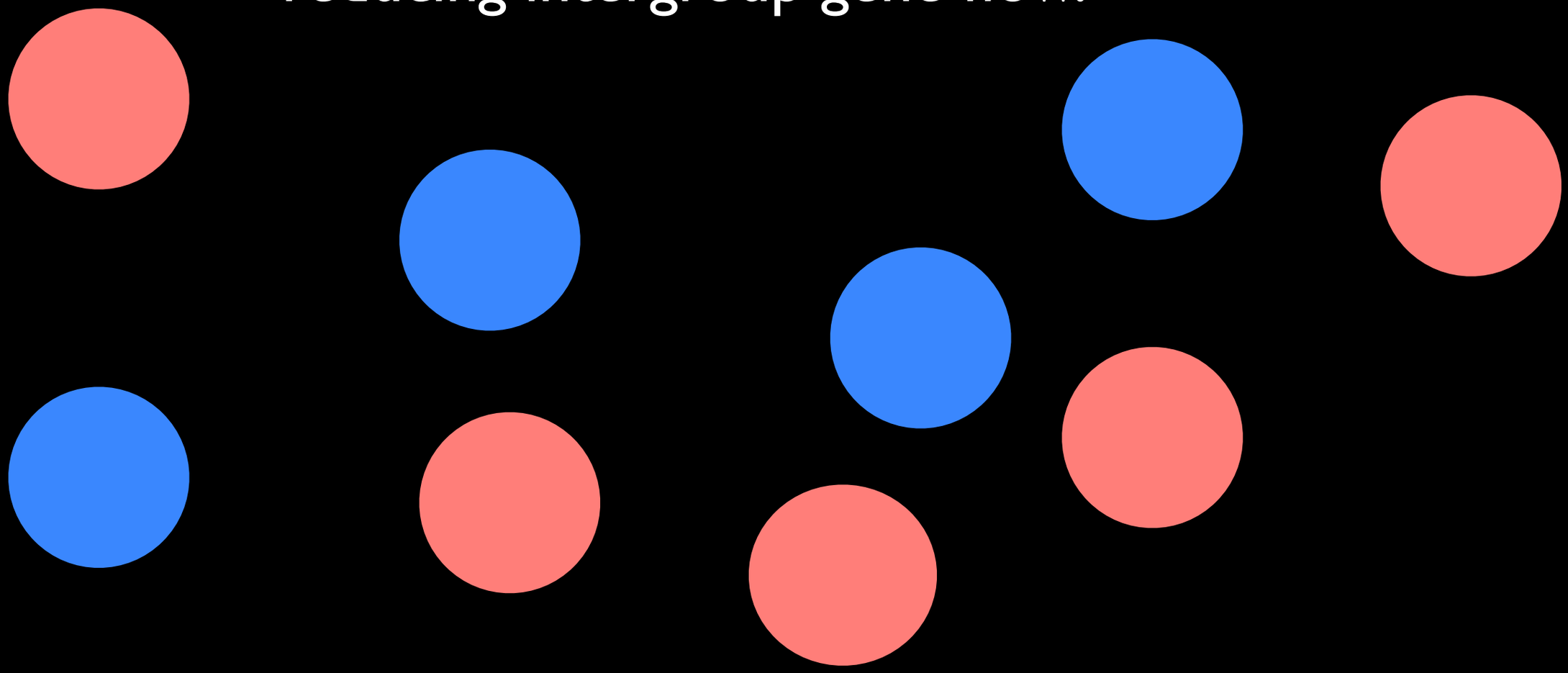
- 1962 - Wynne-Edwards
  - Populations/groups have characteristics of their own which are lacking in individuals - these can only have evolved through group selection.
  - Interests of group often conflict with those of the individual. When this is so, group selection overrides individual level selection.

Group Selection

Cooperators

Selfish

- 1962 - Wynne-Edwards
  - Groups are localized and persistent through time, reducing intergroup gene flow.



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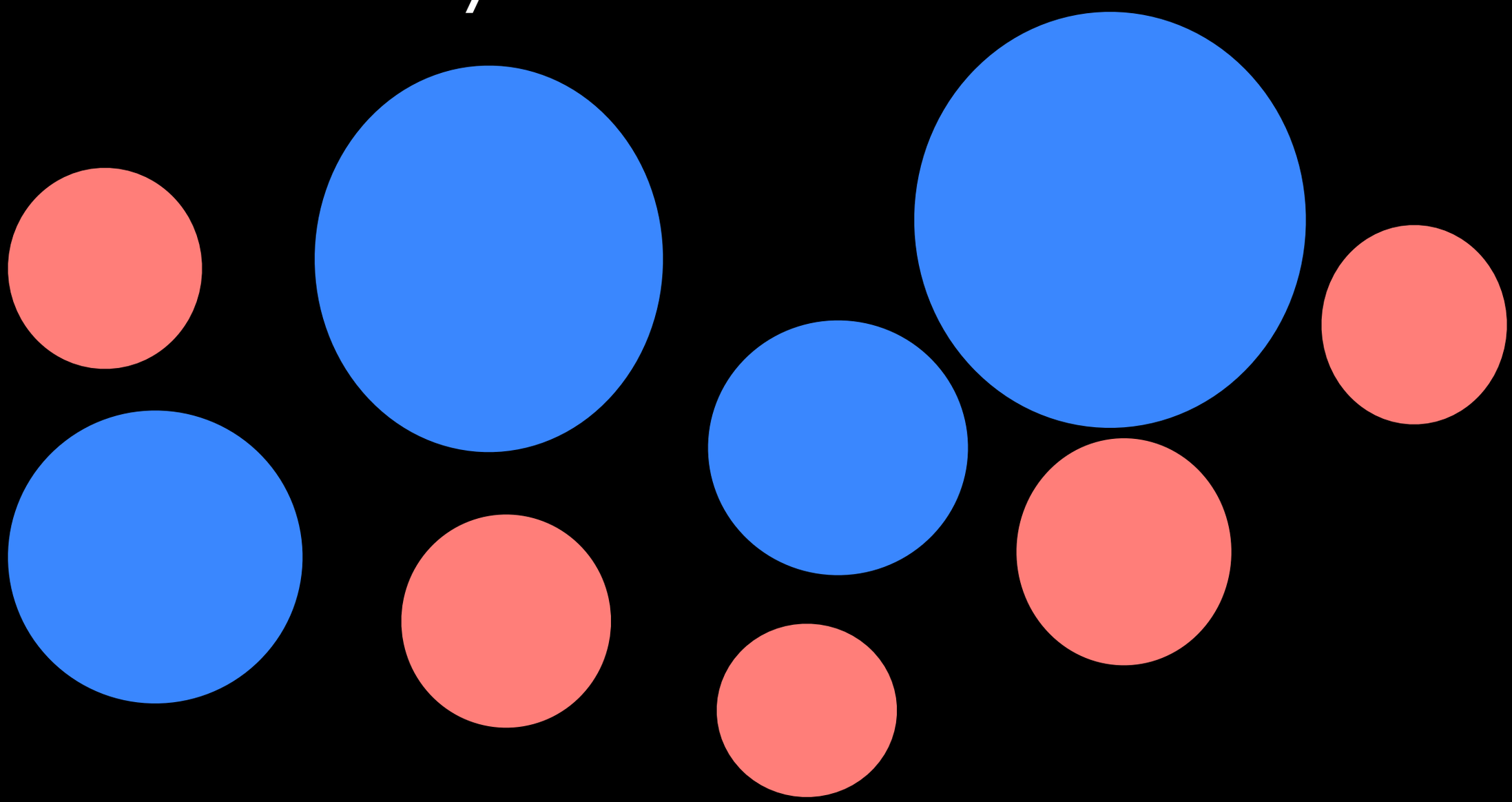

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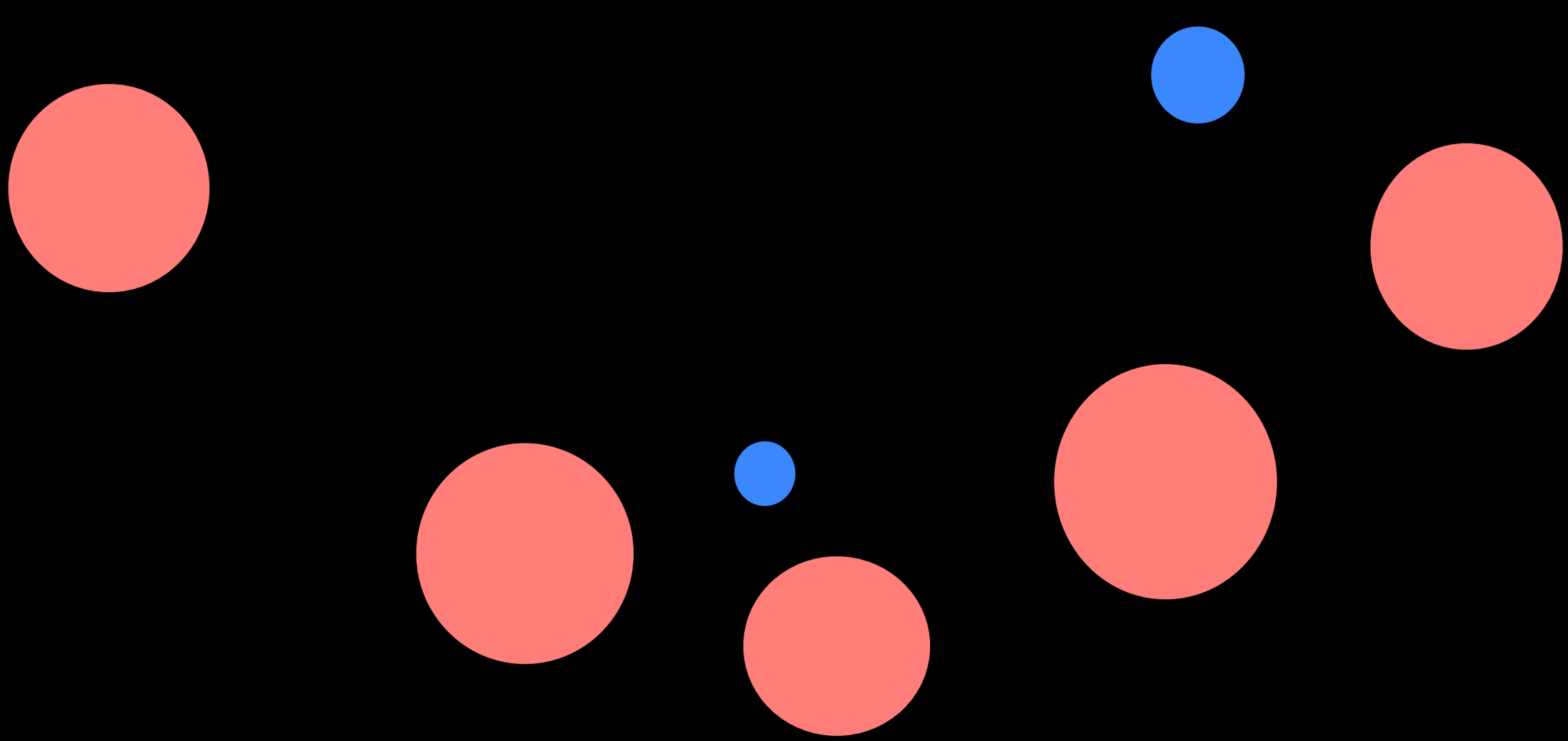
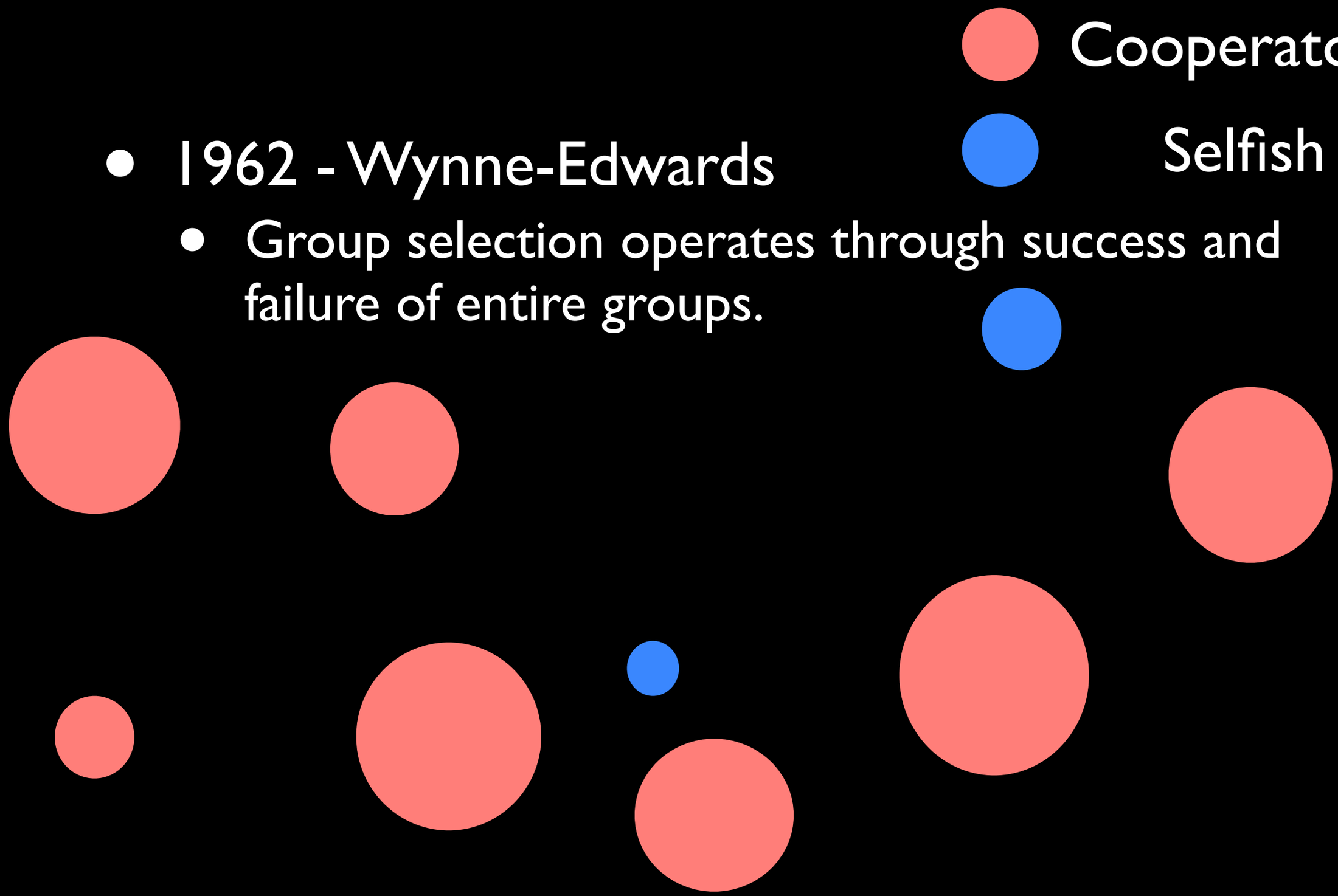


Group Selection

- 1962 - Wynne-Edwards
  - Group selection operates through success and failure of entire groups.



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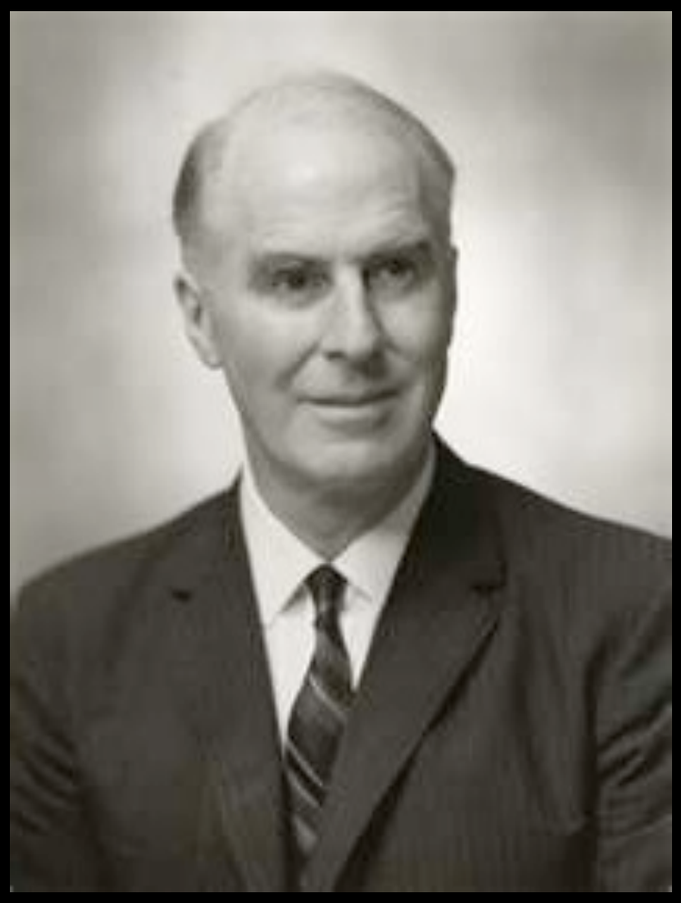
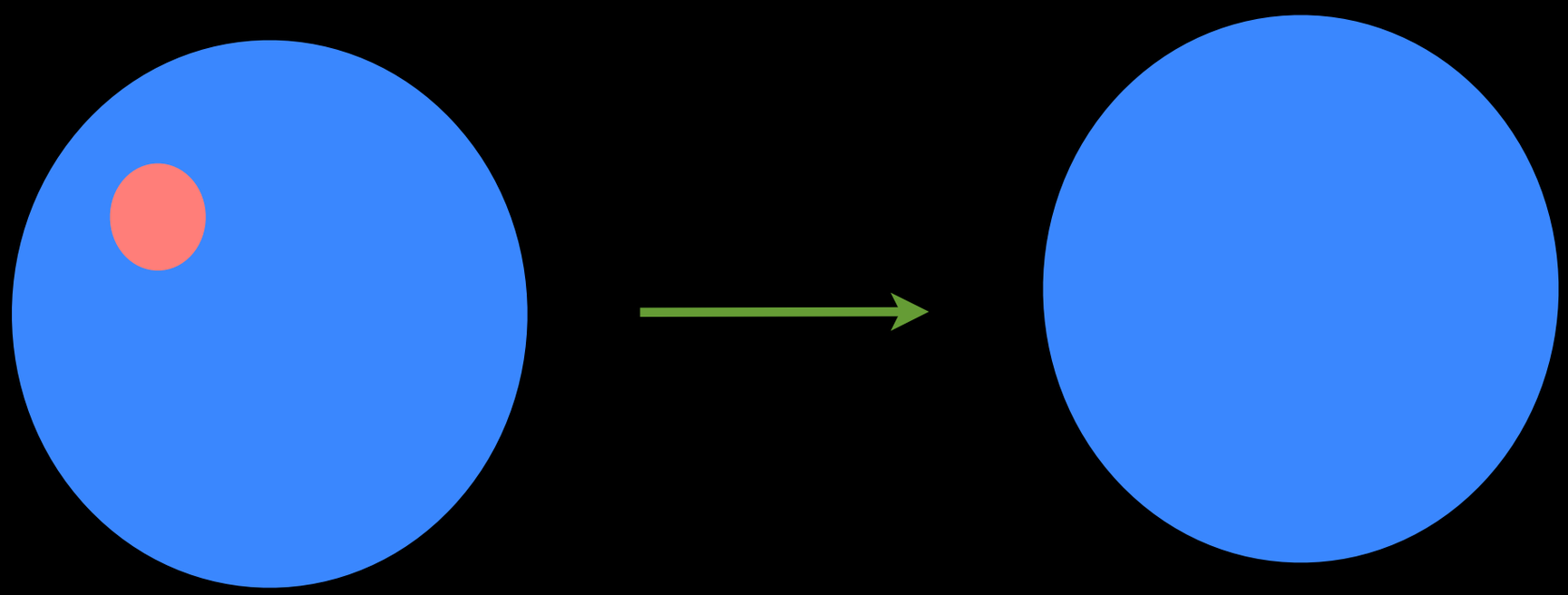


  - Interests of group often conflict with those of the individual. When this is so, group selection overrides individual level selection.
  - Group selection operates through success and failure of entire groups.
  - Groups are localized and persistent through time, reducing intergroup gene flow.

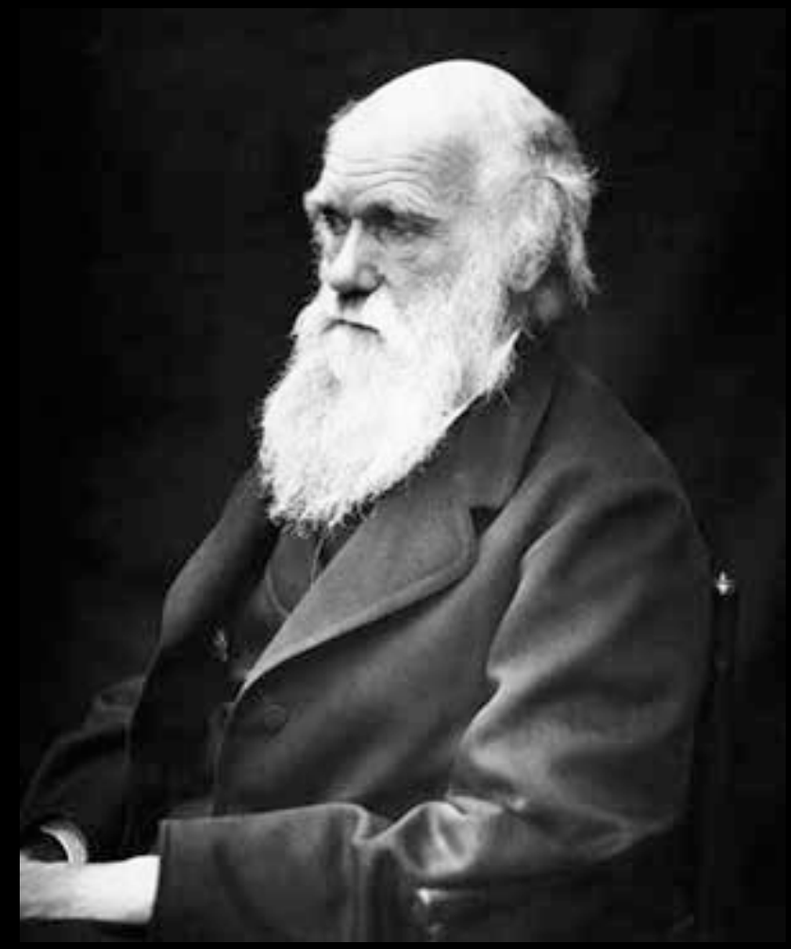
Group Selection

- How does a social trait appear and evolve in a selfish group?



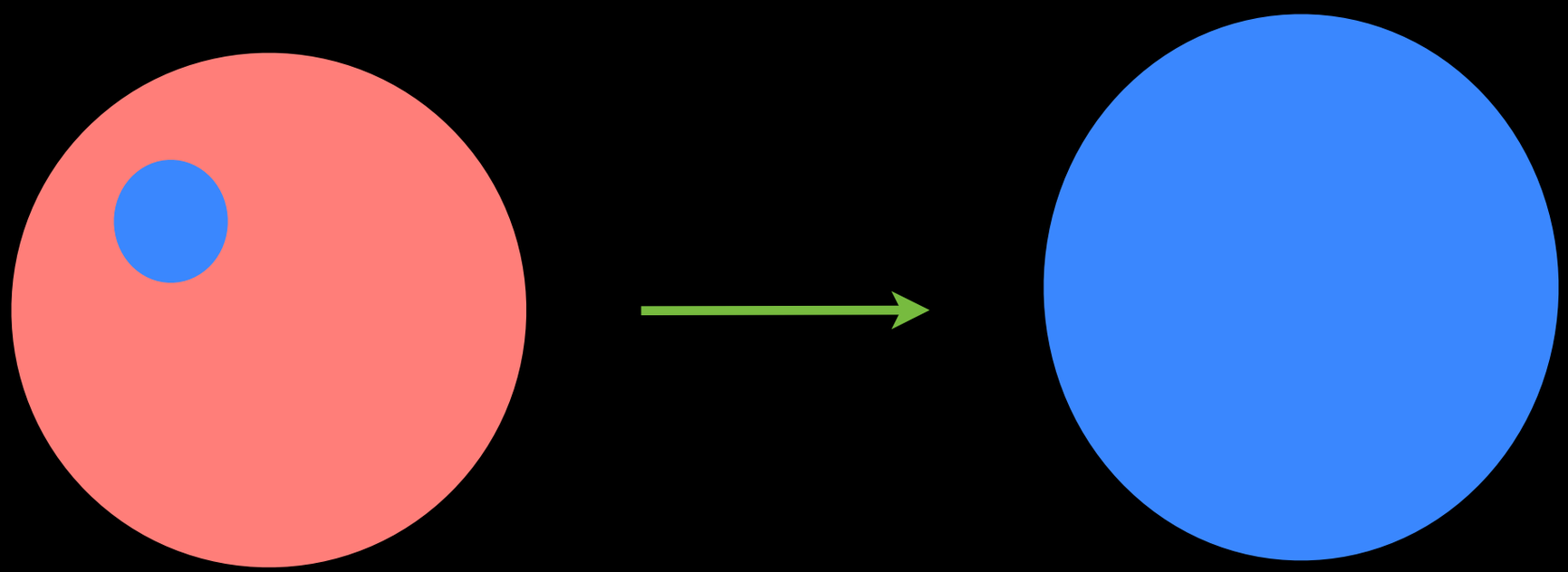
Group Selection

- He who was ready to sacrifice his life .... would often leave no offspring to inherit his noble nature.



Group Selection

- What would happen if a few selfish individuals migrated into a cooperative social group?



Group Selection

Natural Selection Requires	
Trait to be heritable.	
Variation of trait in population.	
Differential survival.	

Group Selection

Natural Selection Requires	Individuals more than groups have.
Trait to be heritable.	Correlation between traits and reproductive success.
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Group Selection

Natural Selection Requires	Individuals more than groups have.
Trait to be heritable.	Correlation between traits and reproductive success.
Variation of trait in population.	Gene variation in a trait.
Differential survival.	

Group Selection

Natural Selection Requires	Individuals more than groups have.
Trait to be heritable.	Correlation between traits and reproductive success.
Variation of trait in population.	Gene variation in a trait.
Differential survival.	Greater variation in reproductive success.

Group Selection

- Rate of natural selection depends on :

  - Strength of selection pressure
  - Generation time

  - Amount of variation existing in the population already.

Group Selection

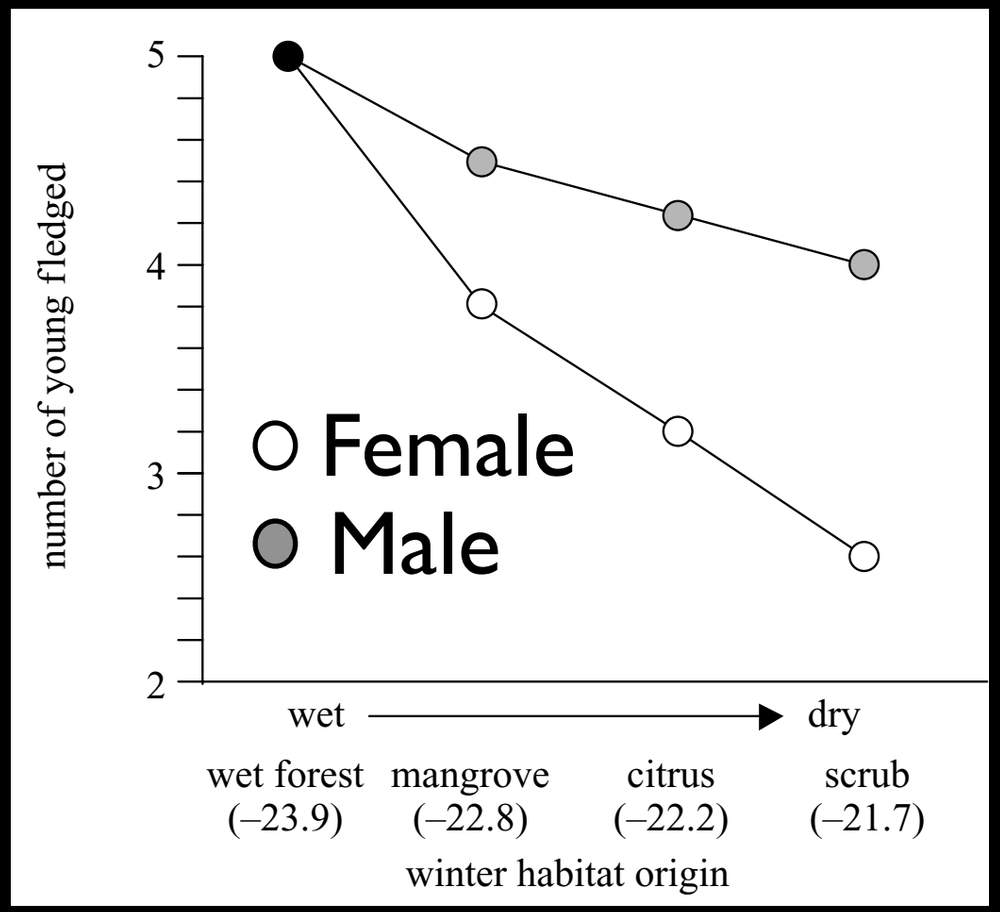
- Rate of natural selection depends on: (individual level selection)
  - Strength of selection pressure
  - Generation time
    - Shorter generation time.
    - More individuals.
    - Greater number of incidents of selection.
  - Amount of variation existing in the population already.

Group Selection

- Rate of natural selection depends on: (individual level selection)
  - Strength of selection pressure
  - Generation time
    - Shorter generation time.
    - More individuals.
    - Greater number of incidents of selection.
  - Amount of variation existing in the population already.
    - Migration.

Group Selection

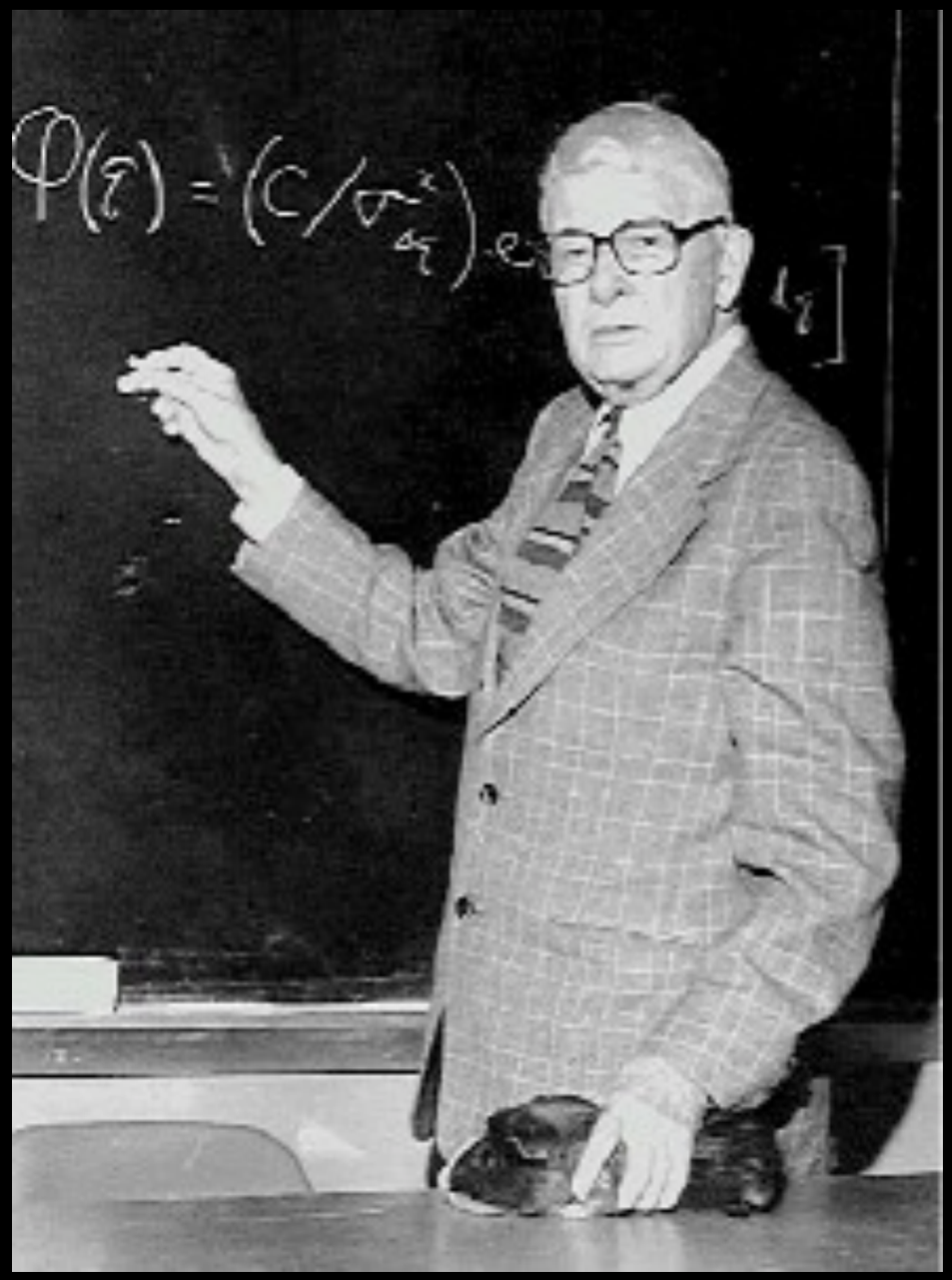
- Social behaviors that Wynne-Edwards mentions can be explained through individual level selection.



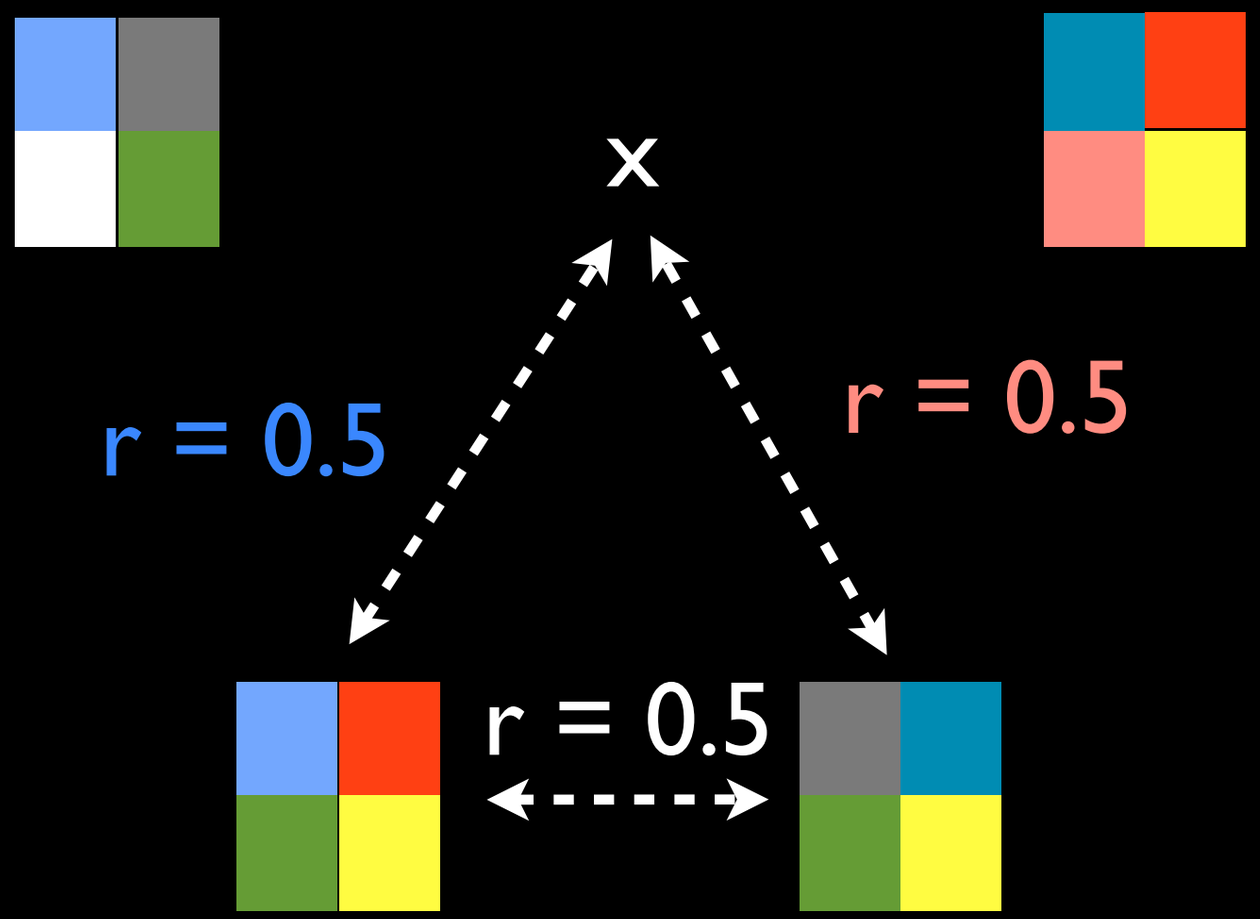
What About Altruism?

Wright

- Developed r (the measure of genetic relatedness)
- Built a group selection model of altruism.
- Never linked relatedness and altruism.



Wright



$$r = (0.5 + 0.5) / 2$$

Fisher

- Nauseous flavors as defense mechanisms.

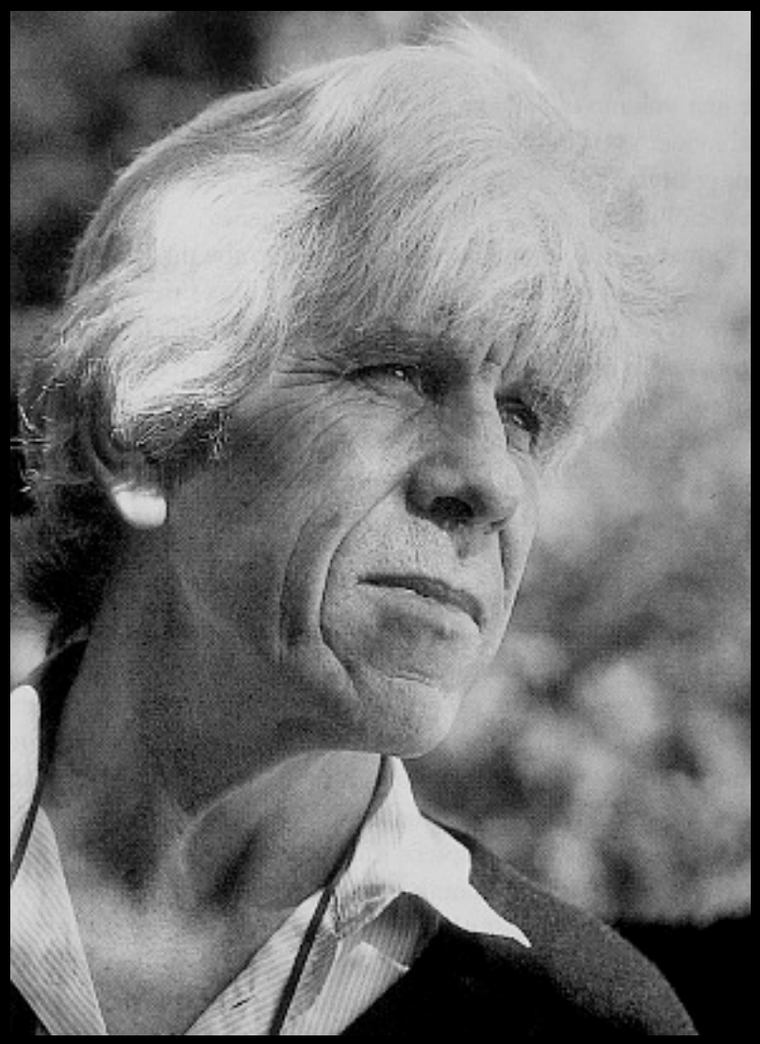
J.B.S. Haldane

- Would I lay down my life to save one brother?
- No! But I would to save two brothers or eight cousins.

J.B.S. Haldane

- Never formalized his thinking.
- Made no attempt to understand how natural selection might act to maximize rules about dispensing altruism among kin.

Hamilton



THE AMERICAN NATURALIST

THE EVOLUTION OF ALTRUISTIC BEHAVIOR

The Genetical Evolution of Social Behaviour. II

W. D. HAMILTON

The Galton Laboratory, University College, London, W.C.2

Kin Selection

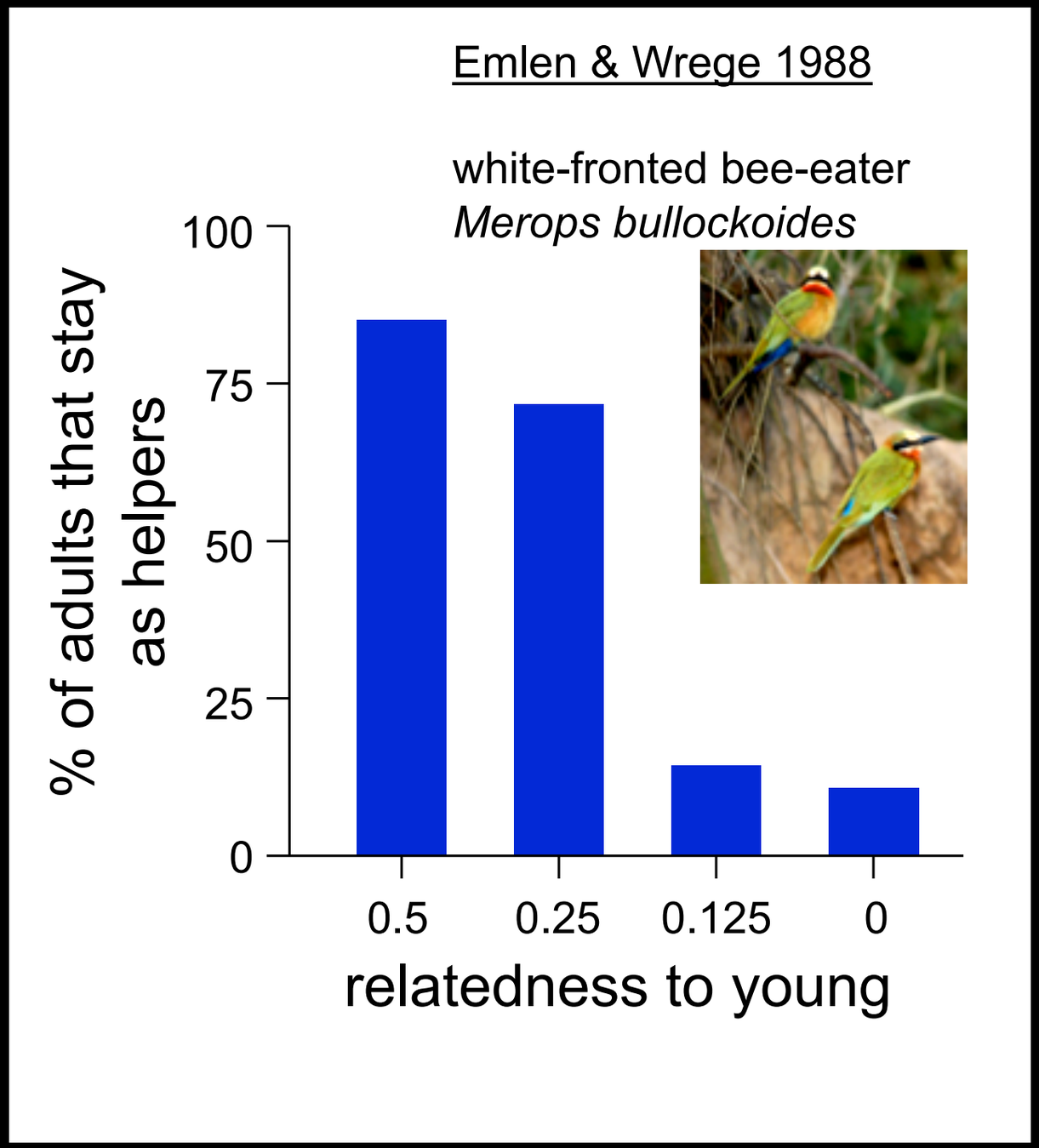
- Direct Fitness
  - Your own offspring.
- Indirect Fitness
  - Your genes in the additional offspring of a related individual that were made possible by your actions.

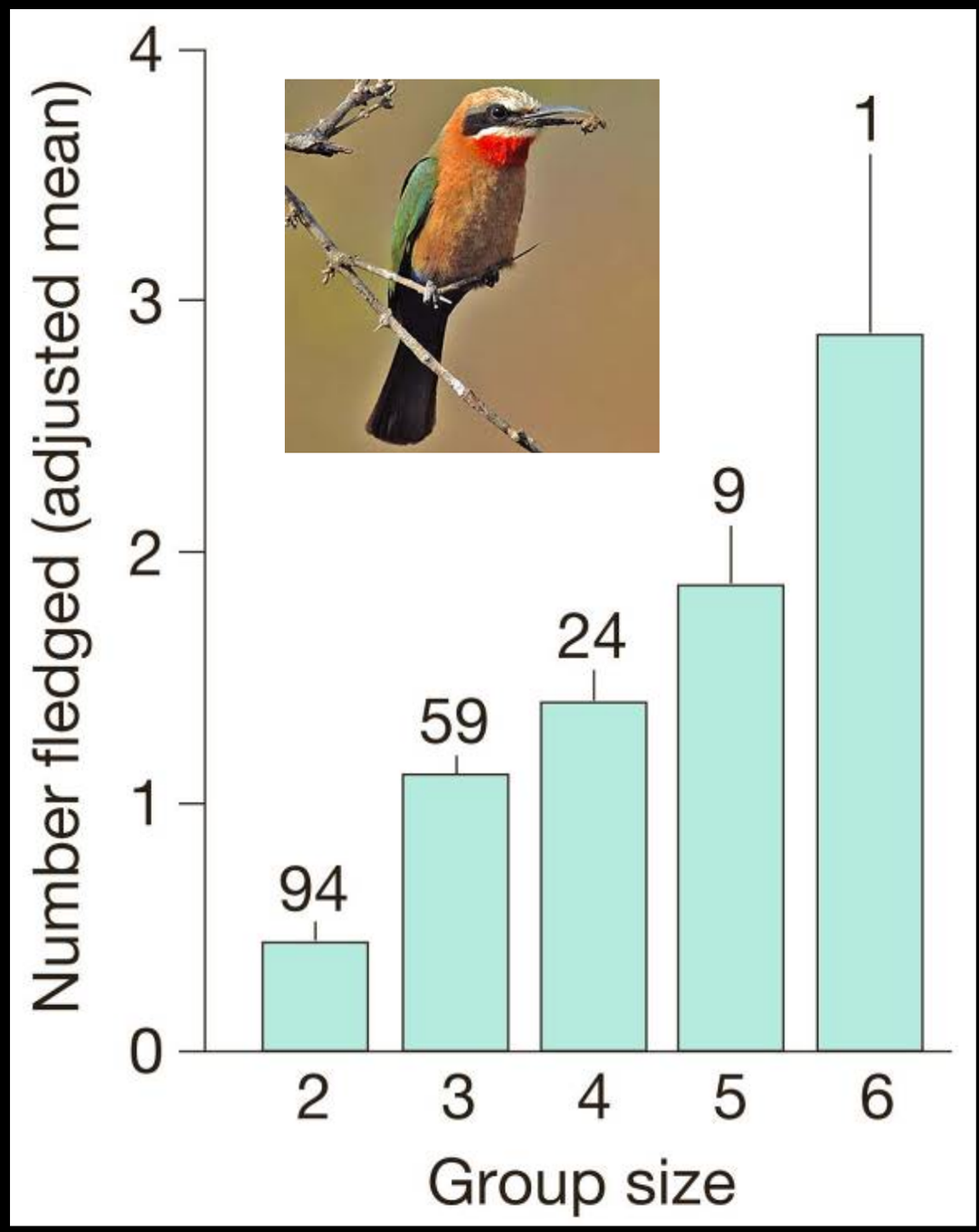
Kin Selection

- Individuals help their kin.
  - Because kin share a proportion of their genes the actor gains an indirect fitness benefit.

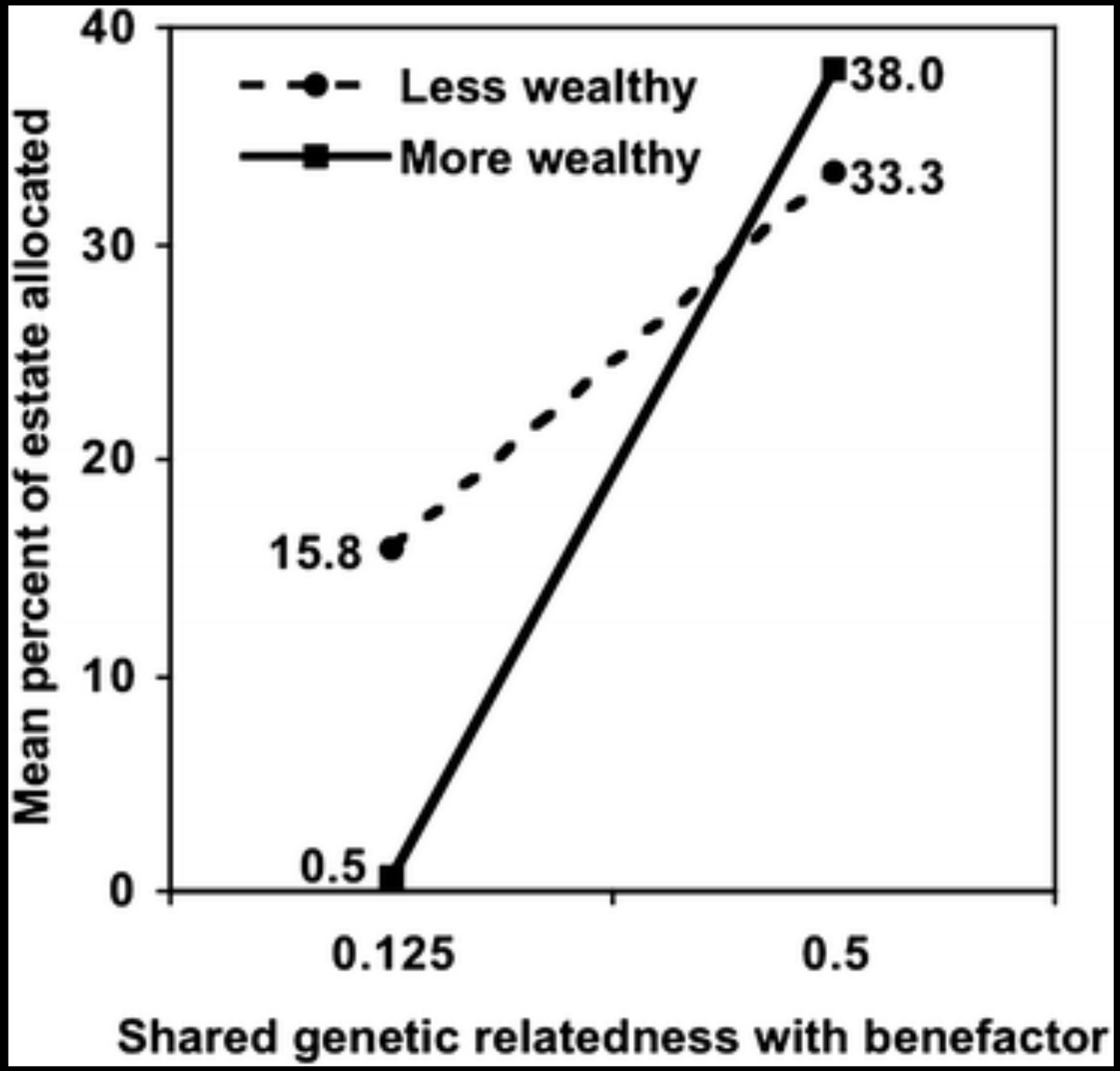
$$rB - C > 0$$

Kin Selection





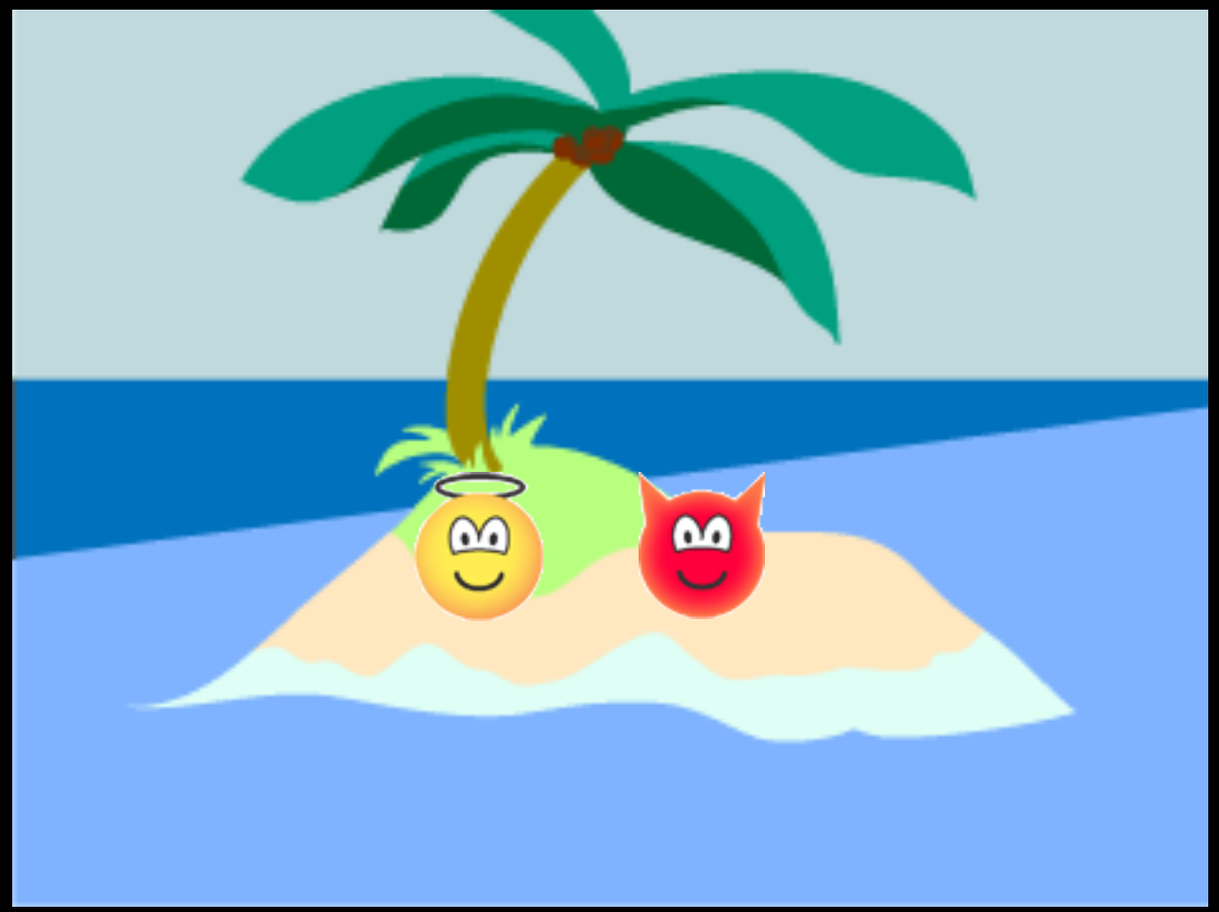
Kin Selection



Kin Selection

- Individuals in eusocial societies are no more related than those in simpler societies.
- Importance of indirect fitness benefits has often been overestimated.
- Importance of direct fitness benefits has often been underestimated.

Multi-Level Selection



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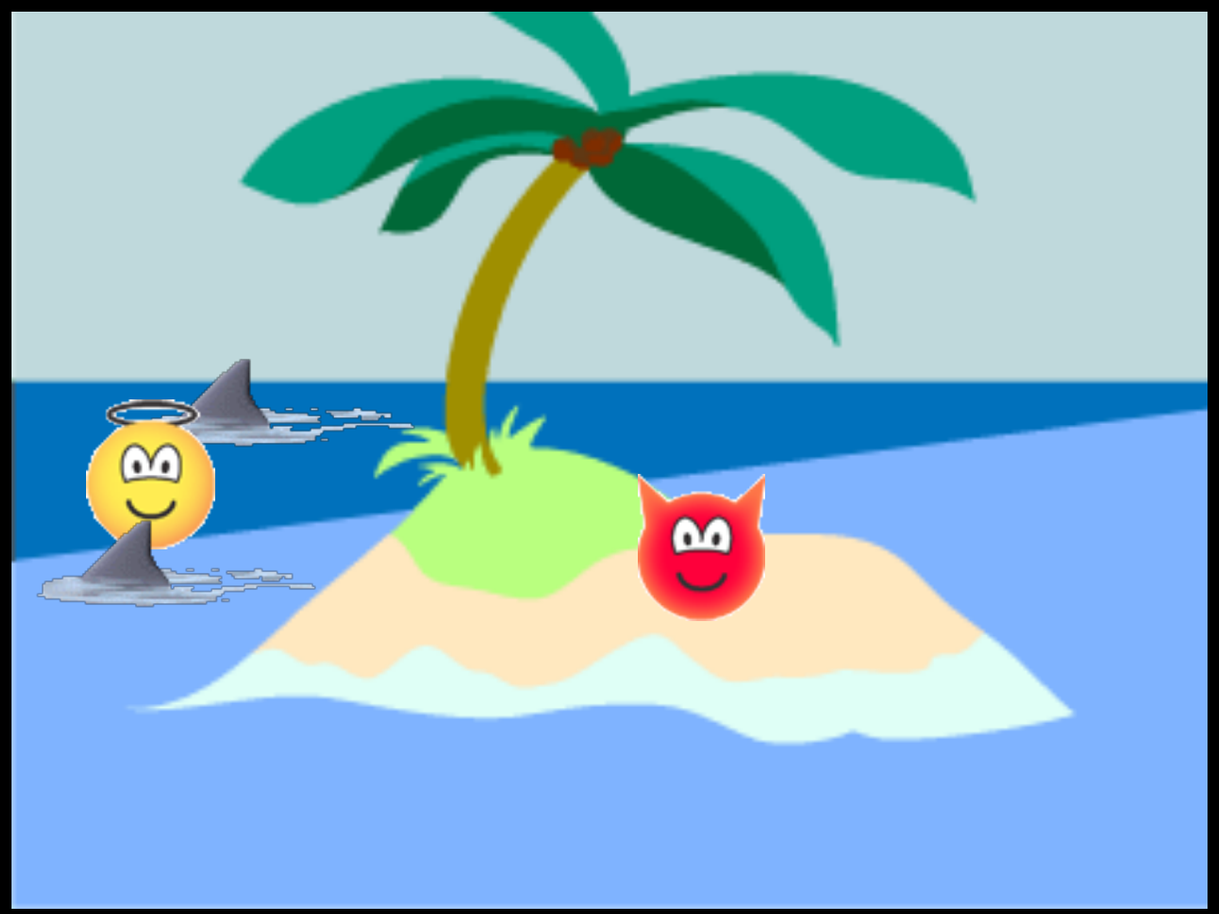

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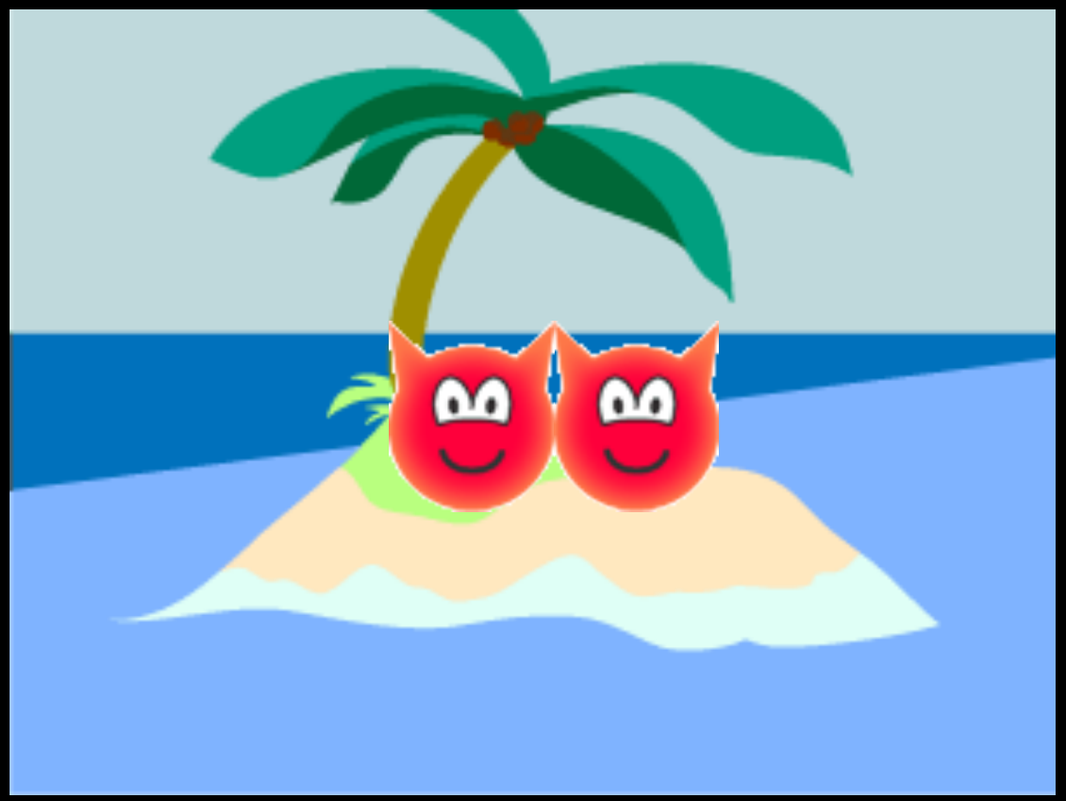

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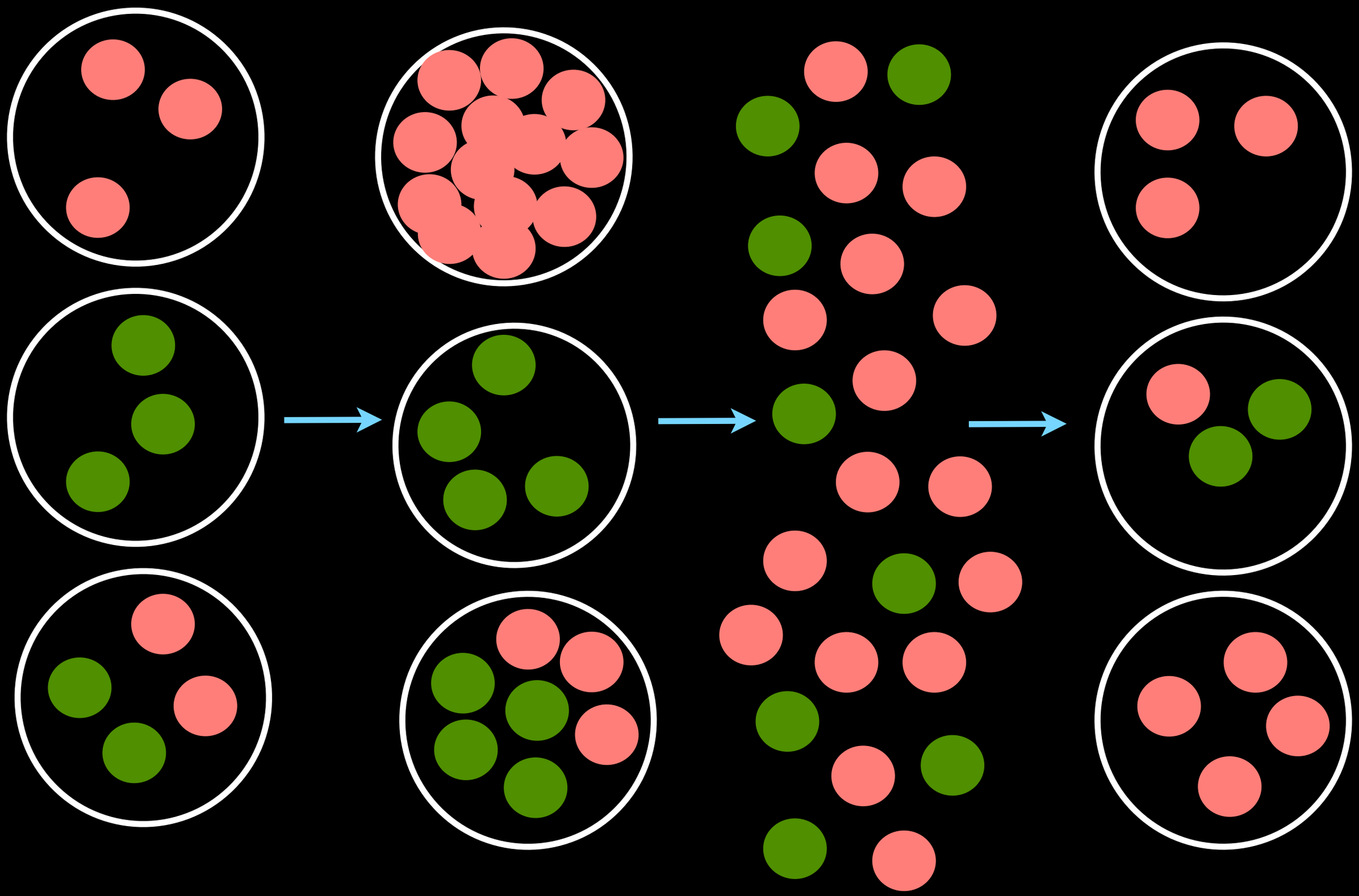

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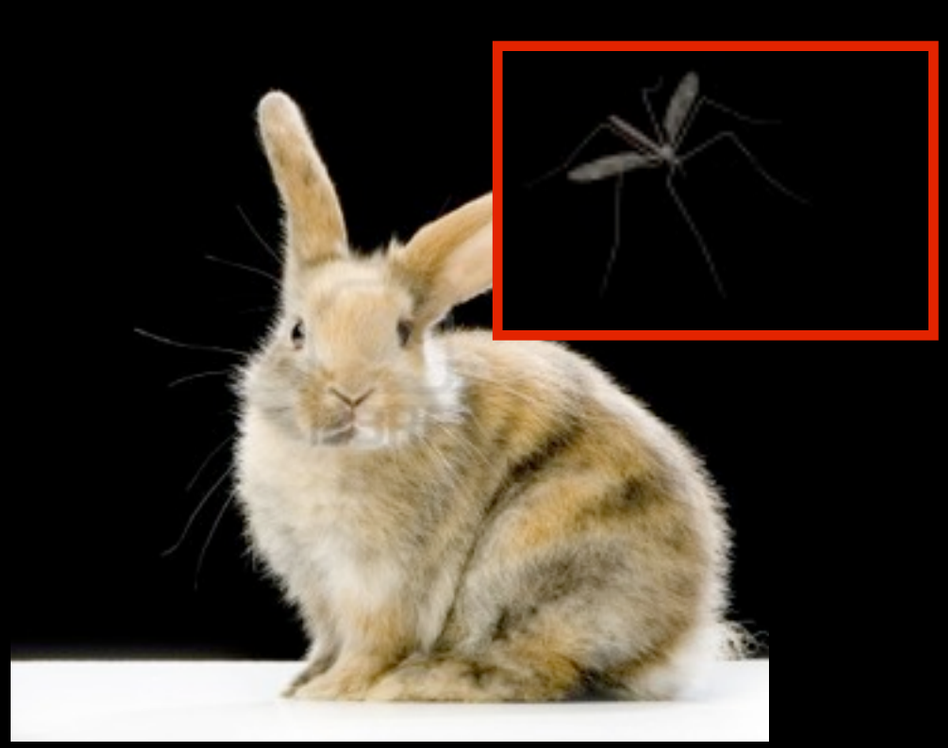

Multi-Level Selection

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So What Is Going On?

There is nothing wrong with inclusive fitness

Kevin R. Foster[1], Tom Wenseleers[2], Francis L.W. Ratnieks[3] and David C. Queller[4]

The evolution of eusociality

Martin A. Nowak[1], Corina E. Tarnita[1] & Edward O. Wilson[2]

Eusociality, in which some individuals reduce their own lifetime reproductive potential to raise the offspring of others, underlies the most advanced forms of social organization and the ecologically dominant role of social insects and humans. For the past four decades kin selection theory, based on the concept of inclusive fitness, has been the major theoretical attempt to explain the evolution of eusociality. Here we show the limitations of this approach. We argue that standard natural selection theory in the context of precise models of population structure represents a simpler and superior approach, allows the evaluation of multiple competing hypotheses, and provides an exact framework for interpreting empirical observations.

Inclusive fitness theory and eusociality

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466,** 1057–1062 (2010)

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Inclusive fitness theor

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466,** 105

Patrick Abbot[1], Jun Abe[2], John Alcock[3], Samuel Alizon[4], Joao A. C. Alpedrinha[5], Malte Andersson[6], Jean-Baptiste Andre[7], Minus van Baalen[7], Francois Balloux[8], Sigal Balshine[9], Nick Barton[10], Leo W. Beukeboom[11], Jay M. Biernaskie[5], Trine Bilde[12], Gerald Borgia[13], Michael Breed[14], Sam Brown[5], Redouan Bshary[15], Angus Buckling[5], Nancy T. Burley[16], Max N. Burton-Chellew[5], Michael A. Cant[17], Michel Chapuisat[18], Eric L. Charnov[19], Tim Clutton-Brock[20], Andrew Cockburn[21], Blaine J. Cole[22], Nick Colegrave[23], Leda Cosmides[24], Iain D. Couzin[25], Jerry A. Coyne[26], Scott Creel[27], Bernard Crespi[28], Robert L. Curry[29], Sasha R. X. Dall[17], Troy Day[30], Janis L. Dickinson[31], Lee Alan Dugatkin[32], Claire El Mouden[5], Stephen T. Emlen[33], Jay Evans[34], Regis Ferriere[35], Jeremy Field[36], Susanne Foitzik[37], Kevin Foster[5], William A. Foster[20], Charles W. Fox[38], Juergen Gadau[39], Sylvain Gandon[40], Andy Gardner[5], Michael G. Gardner[41], Thomas Getty[42], Michael A. D. Goodisman[43], Alan Grafen[5], Rick Grosberg[44], Christina M. Grozinger[45], Pierre-Henri Gouyon[46], Darryl Gwynne[47], Paul H. Harvey[5], Ben J. Hatchwell[48], Jürgen Heinze[49], Heikki Helantera[50], Ken R. Helms[51], Kim Hill[52], Natalie Jiricny[5], Rufus A. Johnstone[20], Alex Kacelnik[5], E. Toby Kiers[53], Hanna Kokko[21], Jan Komdeur[54], Judith Korb[55], Daniel Kronauer[56], Rolf Kümmerli[57], Laurent Lehmann[15], Timothy A. Linksvayer[58], Sébastien Lion[59], Bruce Lyon[60], James A. R. Marshall[61], Richard McElreath[62], Yannis Michalakis[4], Richard E. Michod[63], Douglas Mock[64], Thibaud Monnin[7], Robert Montgomerie[65], Allen J. Moore[17], Ulrich G. Mueller[66], Ronald Noë[67], Samir Okasha[68], Pekka Pamilo[69], Geoff A. Parker[70], Jes S. Pedersen[58], Ido Pen[71], David Pfennig[72], David C. Queller[73], Daniel J. Rankin[74], Sarah E. Reece[23], Hudson K. Reeve[33], Max Reuter[75], Gilbert Roberts[76], Simon K. A. Robson[77], Denis Roze[78], Francois Rousset[79], Olav Rueppell[80], Joel L. Sachs[81], Lorenzo Santorelli[5], Paul Schmid-Hempel[82], Michael P. Schwarz[41], Tom Scott-Phillips[83], Janet Shellmann-Sherman[33], Paul W. Sherman[33], David M. Shuker[84], Jeff Smith[73], Joseph C. Spagna[85], Beverly Strassmann[86], Andrew V. Suarez[87], Liselotte Sundström[50], Michael Taborsky[88], Peter Taylor[30], Graham Thompson[89], John Tooby[90], Neil D. Tsutsui[91], Kazuki Tsuji[92], Stefano Turillazzi[93], Francisco Úbeda[94], Edward L. Vargo[95], Bernard Voelkl[96], Tom Wenseleers[97], Stuart A. West[5], Mary Jane West-Eberhard[98], David F. Westneat[99], Diane C. Wiernasz[22], Geoff Wild[100], Richard Wrangham[101], Andrew J. Young[17], David W. Zeh[102], Jeanne A. Zeh[102] & Andrew Zink[103]

eusociality

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Take Home Messages

- Social groups are costly and beneficial.
- Social groups formation due to both:
  - Direct benefits.
  - Indirect benefits.
- Both group and individual levels of selection may be important in the evolution of social groups.