

Sexual Selection II

The use of models (edited slides)

[pictures omitted for copyright reasons]

General References

- C. Darwin (1871) *The Descent of Man and Selection in Relation to Sex*. Republished in 1981 by Princeton University Press. (Extracts in M.Ridley (1987) *The Essential Darwin*. Unwin Hyman.)
- Andersson, M (1994) *Sexual Selection*. Princeton University Press
- Dawkins, MS (1995) *Unravelling Animal Behaviour*, 2nd edn. Chapter 6.
- Krebs, JR & Davies, NB (1993) *An introduction to Behavioural Ecology*, 3rd edn. Blackwell Scientific.
- Ridley, M (1996) *Evolution*, 2nd edn. Blackwell Science. Section 11.4. (pp 296-307)

[frontispiece omitted for
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Andersson (1994)

Why do models matter? An example:

- Idea: Fisher's runaway process
- Model: Lande's model
- Which bits
 - does the model capture?
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This slide and the three following slides show the whole treatment of Fisher's runaway process in the 1958 edition of Fisher's *Genetical Theory of Natural Selection*. The idea was first proposed by Fisher in a paper in 1915.

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and that was that. No equations, just words. An extraordinary and wonderful idea about self-reinforcement of preferences, placed within a context of other selective forces and phases of selection.

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Before Lande's model...

- O'Donald (a former student of Fisher's) had made various models that seemed to show the idea did not work, or worked partially and only in rather unusual circumstances
- Population geneticists were reluctant to accept that a verbal argument could make sense

Lande's model

- is based on Quantitative Genetics
- has a male trait 'tail length' ...
- ...and a female trait that we can think of as 'preferred tail length'
- each trait has a probability distribution in the population
- and the two traits coevolve

The mean of the male trait is

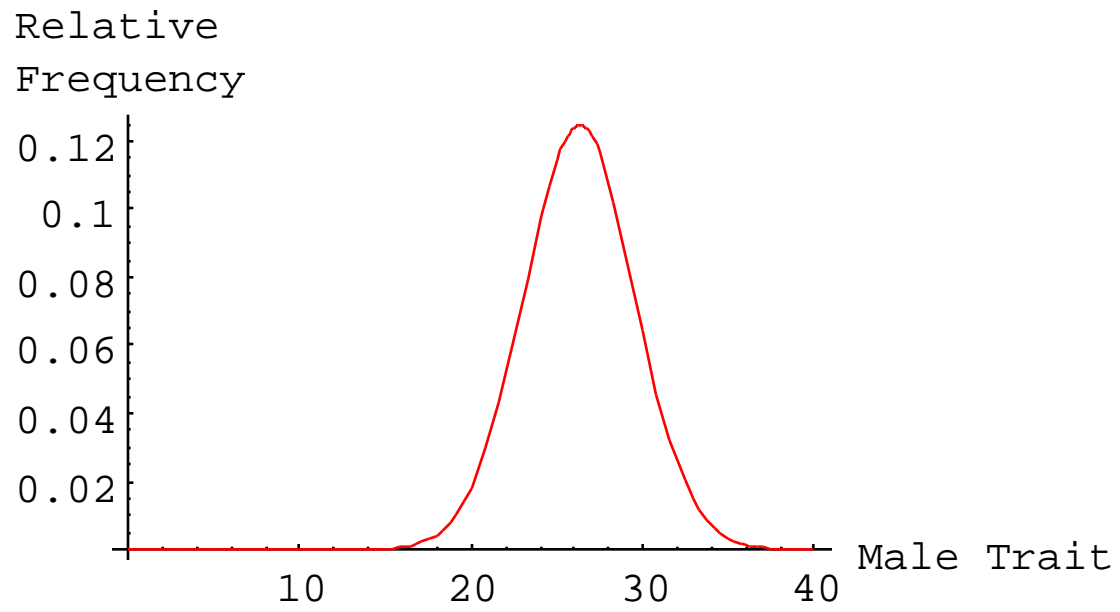
- altered by natural selection i.e. survival to breed depends on the trait
- altered by sexual selection i.e. the number of offspring of a survivor depends on the trait
- unchanging only when these two forces exactly cancel

Female preference

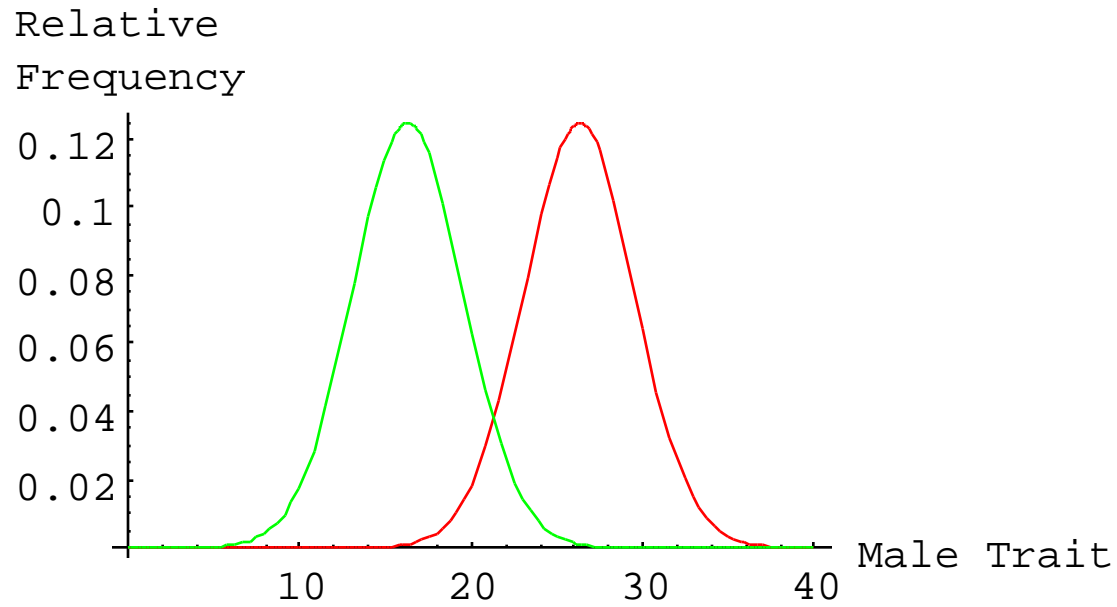
- is under no direct selection
- but genes for preferring higher trait-values are in the same bodies as genes for higher trait-values (this is called ‘linkage disequilibrium’) through assortative mating
- so if the mean male trait is increasing in value, then there is **indirect selection** for female preference

Any trait-value can be an equilibrium...

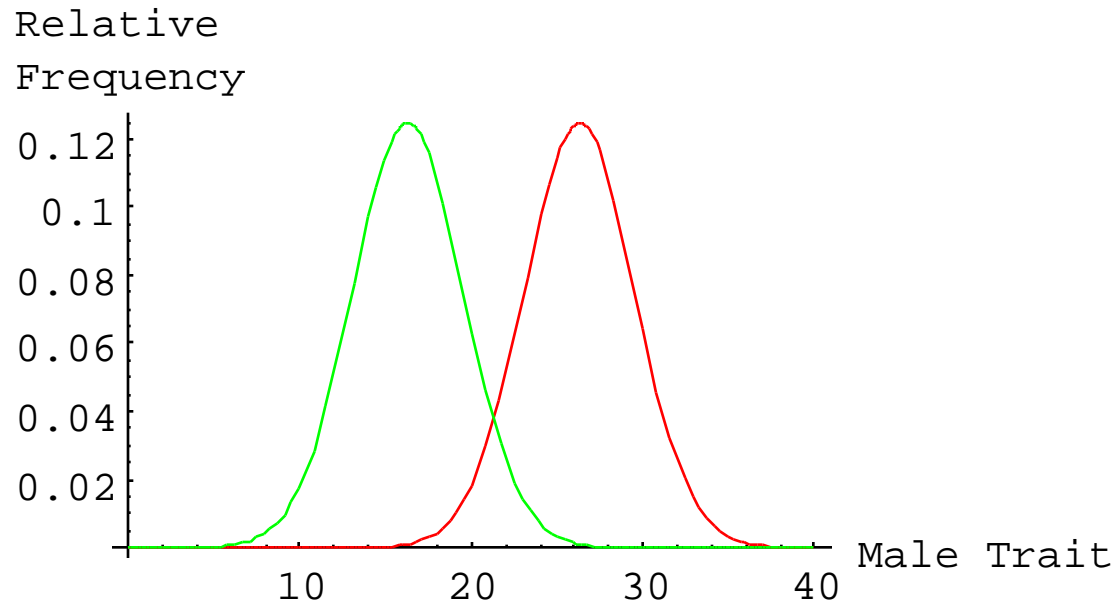
- for any trait-value, there is a certain strength of natural selection, and
- we can then find a strength of female preference that exactly balances it out
- There is then no change in male trait, or female preference
- so we have an equilibrium



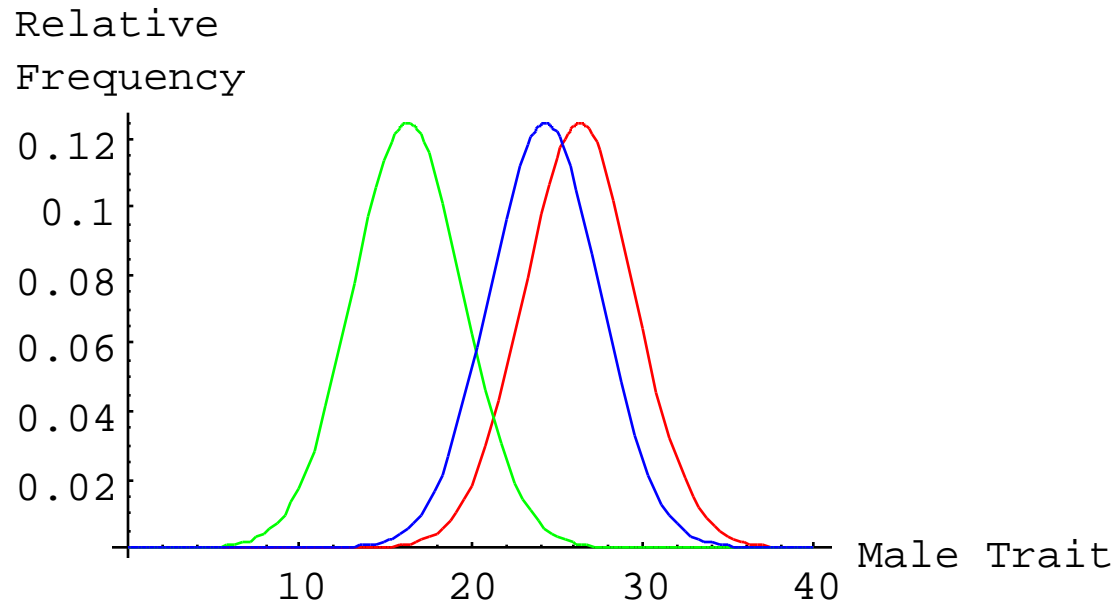
Zygotes



Zygotes, are subject to differential viability so the **Survivors** have a lower mean.

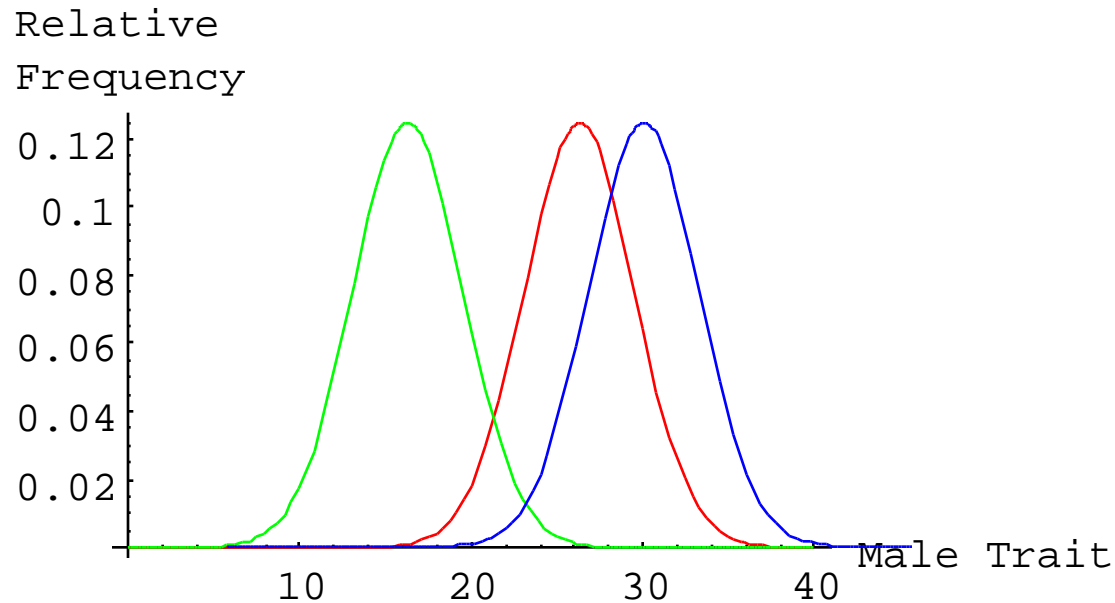


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But females mate preferentially with higher-valued males,



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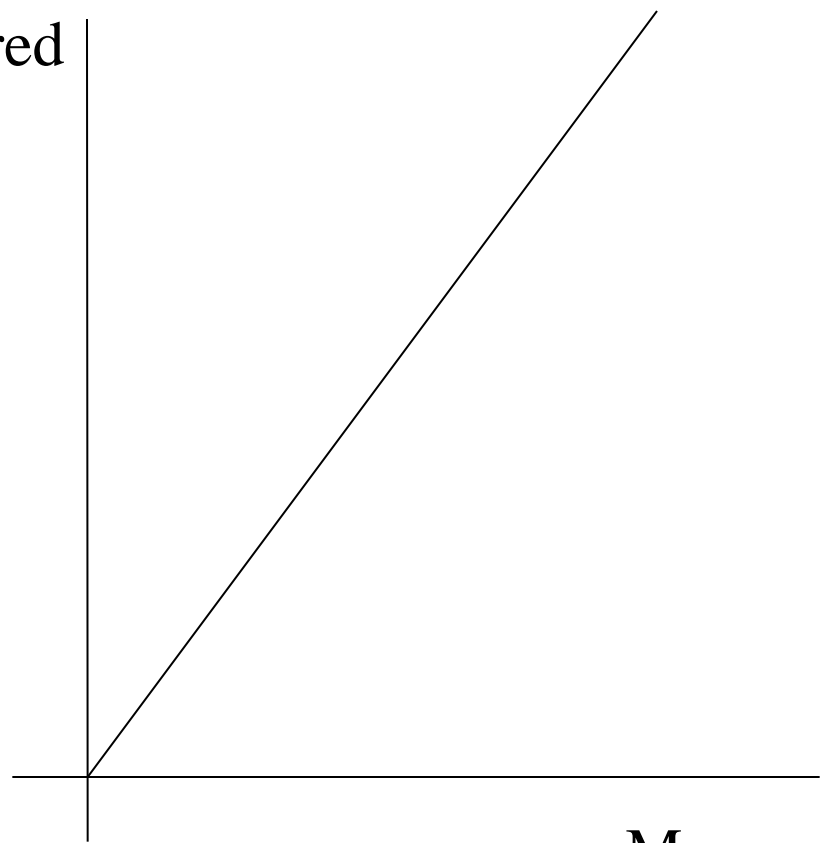
But females mate preferentially with higher-valued males, so the **Successful Gametes** have a higher mean than survivors, but in this case, not sufficiently to offset the effect of viability



Zygotes, are subject to differential viability so the **Survivors**, have a lower mean.

But females mate preferentially with higher-valued males, so the **Successful Gametes** have a higher mean than survivors, which here more than offsets the effect of viability

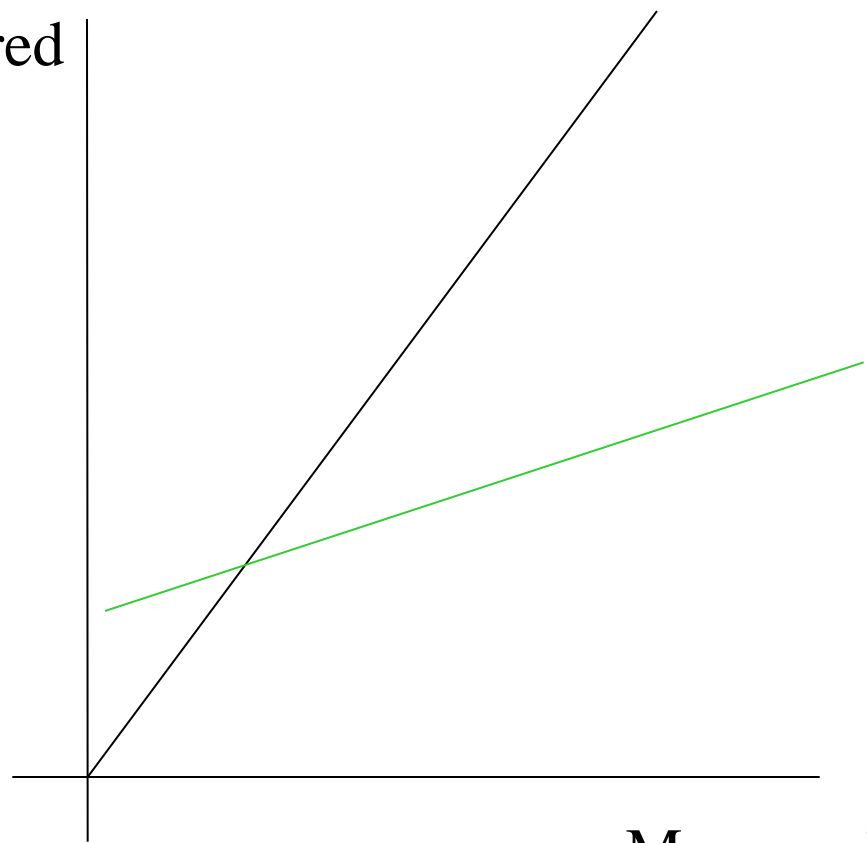
Mean preferred
trait



Line of neutral
equilibrium

Mean male trait

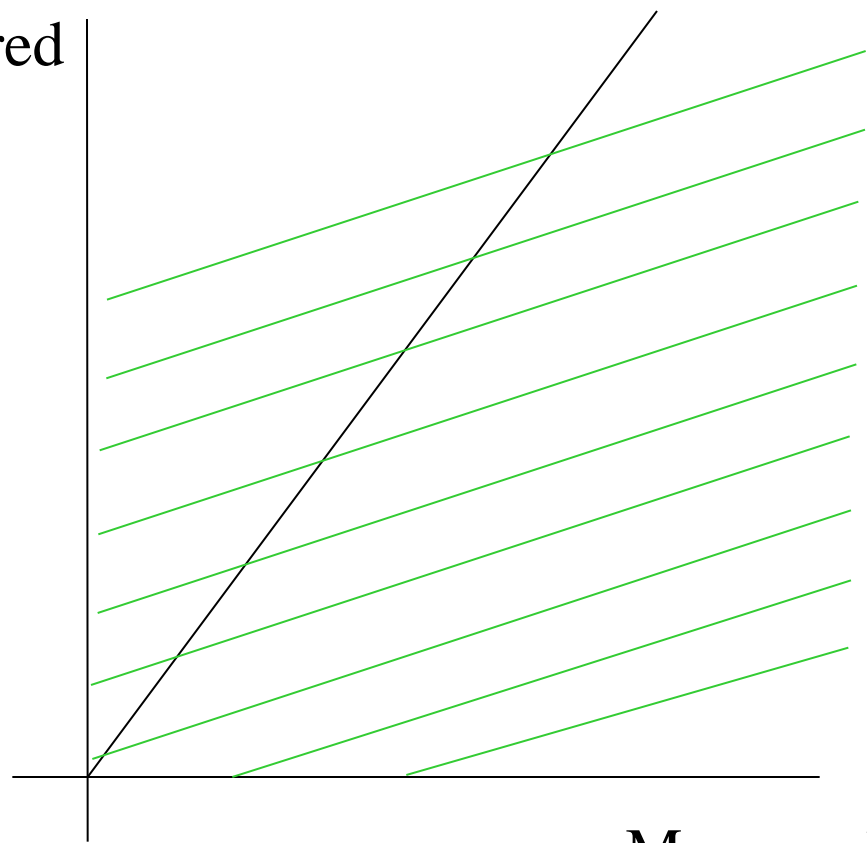
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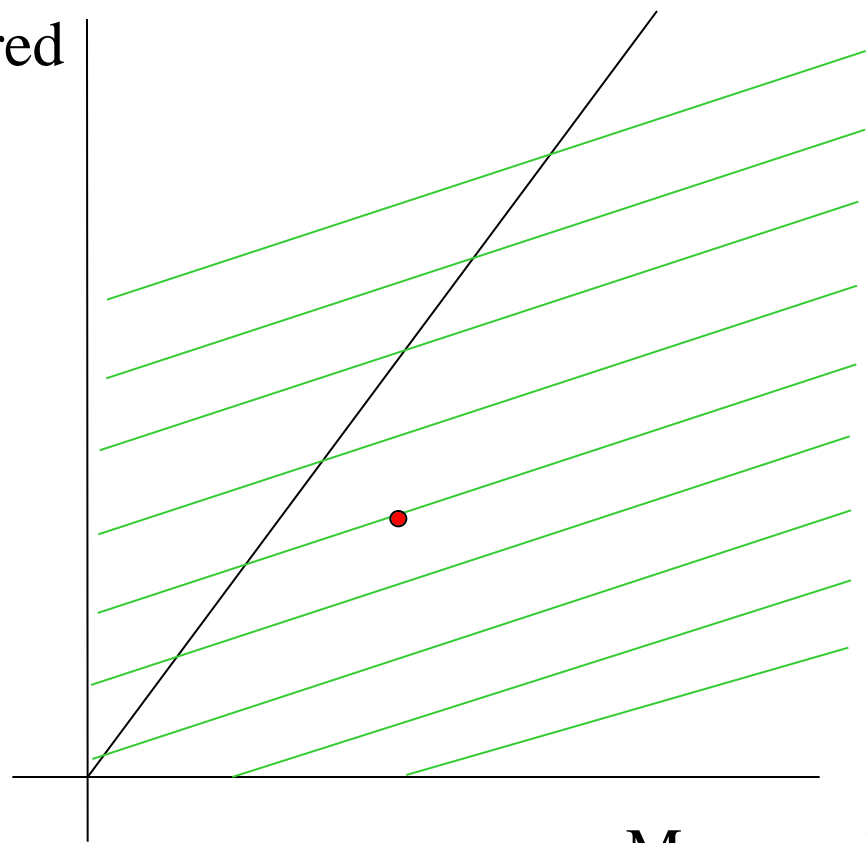


Line of neutral equilibrium

Lines of motion

Mean male trait

Mean preferred trait

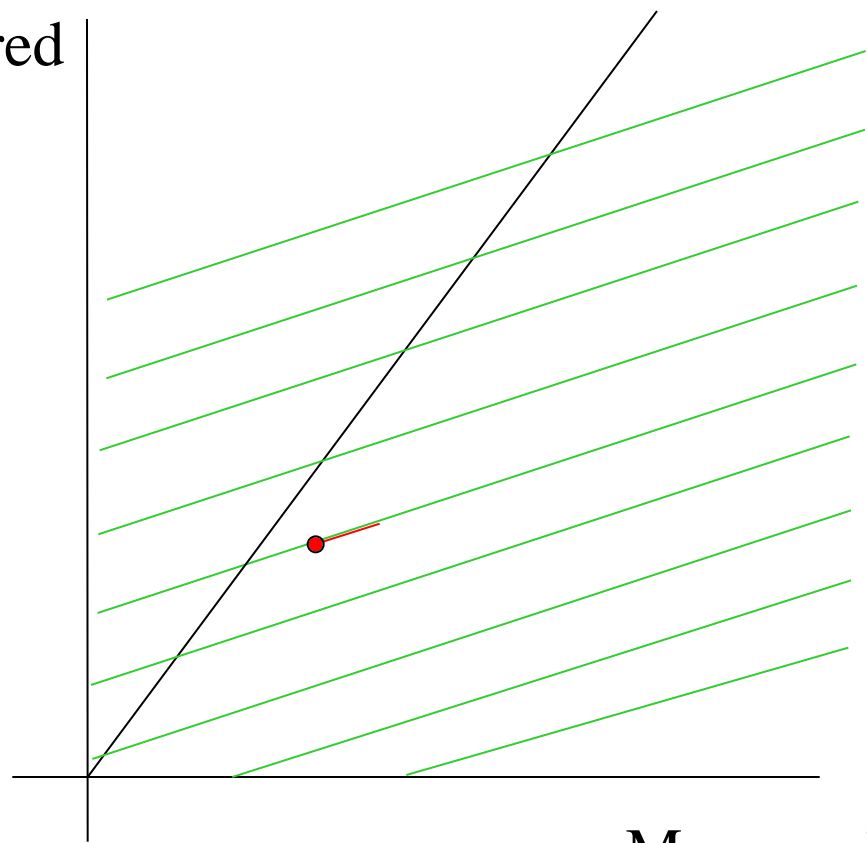


Line of neutral equilibrium

Lines of motion when genetic covariance is weak

Mean male trait

Mean preferred trait

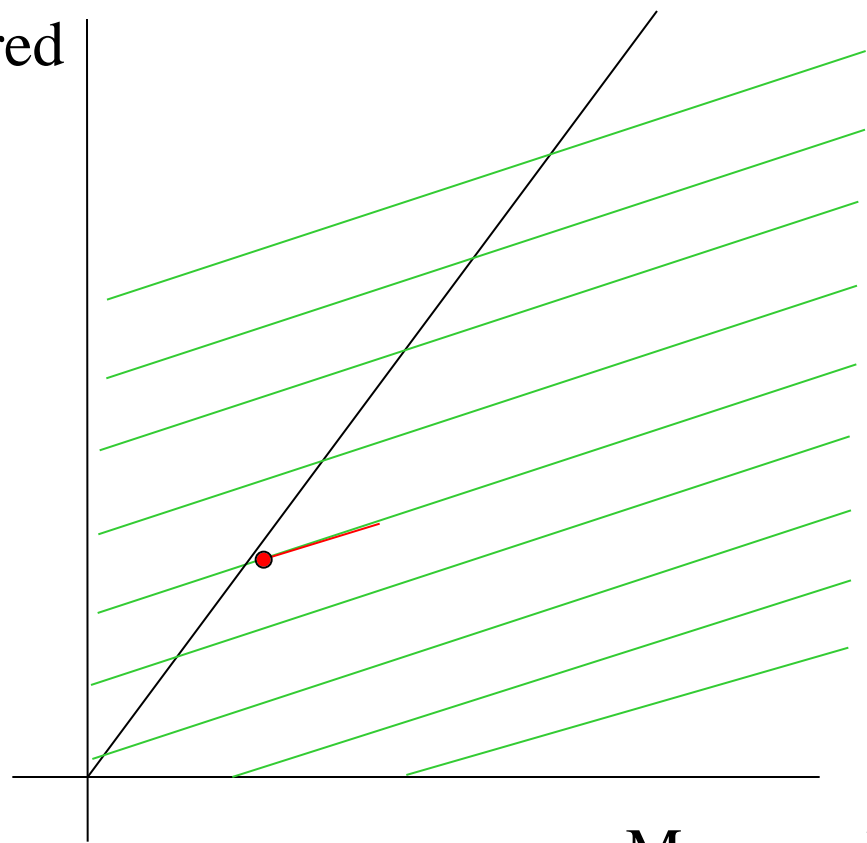


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Mean male trait

Mean preferred trait

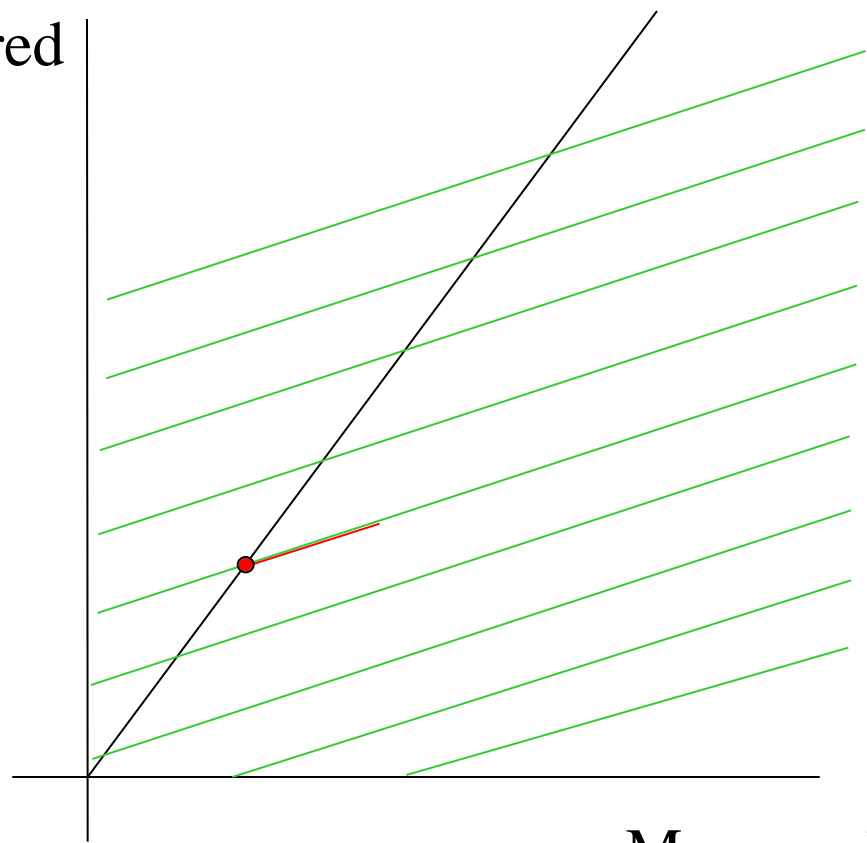


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Mean male trait

Mean preferred trait

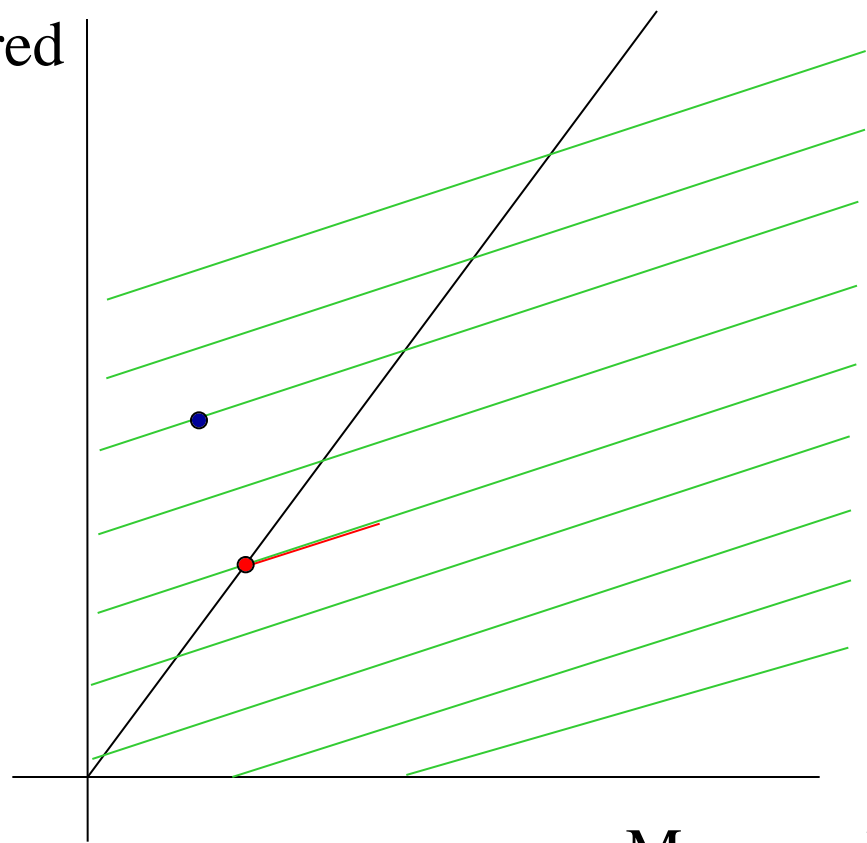


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Mean male trait

Mean preferred trait

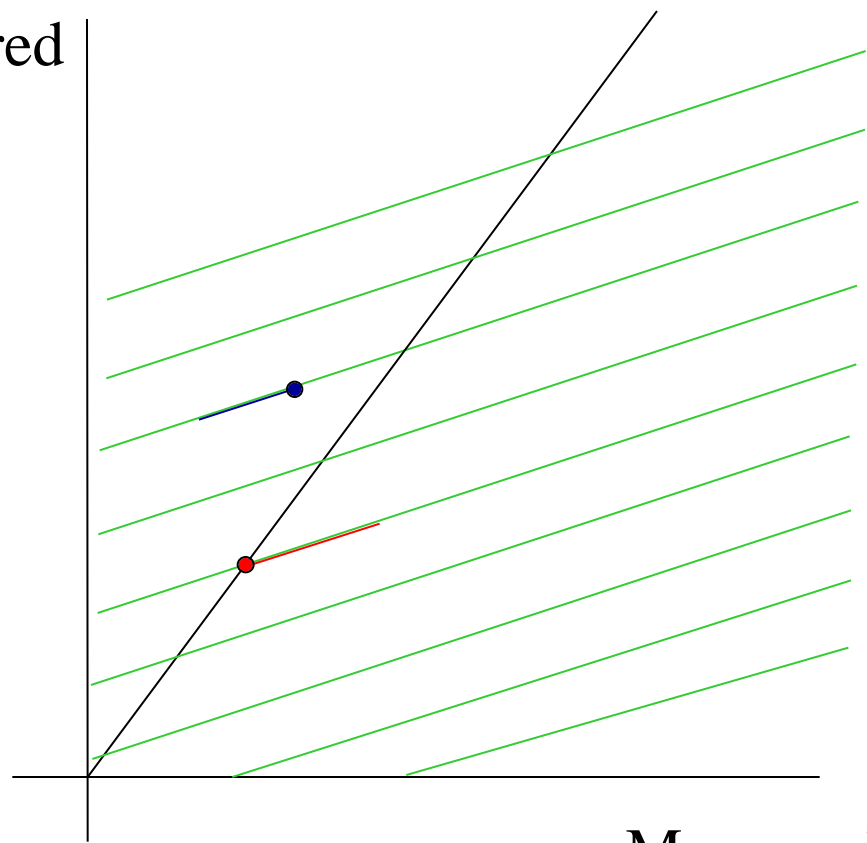


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Lines of motion when genetic covariance is weak

Mean male trait

Mean preferred trait

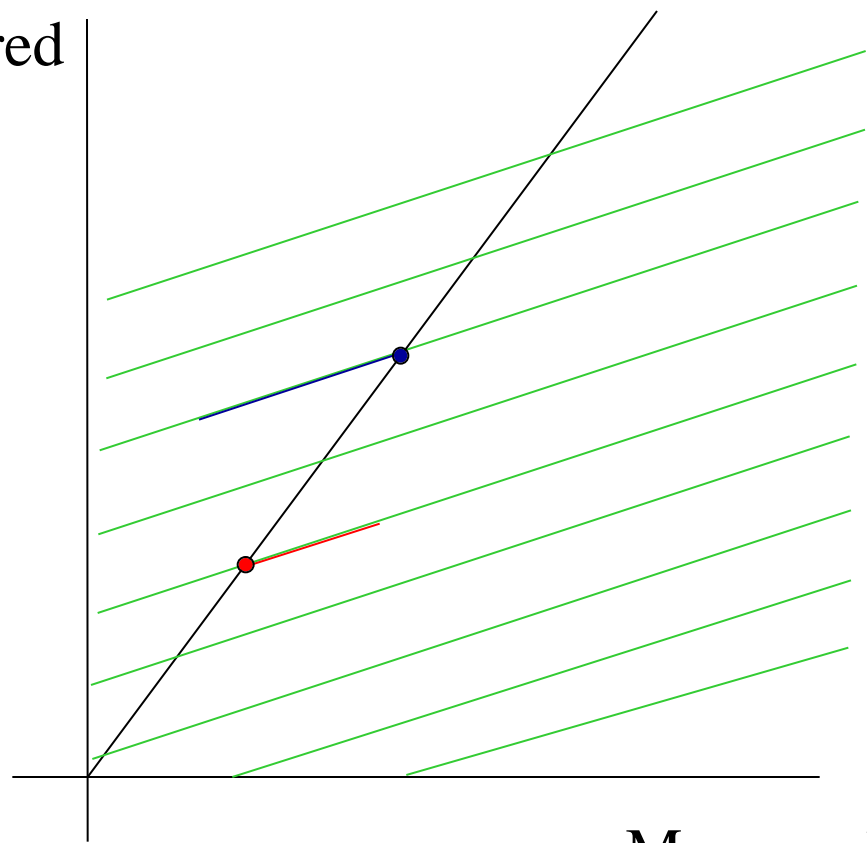


Line of neutral equilibrium

Lines of motion when genetic covariance is weak

Mean male trait

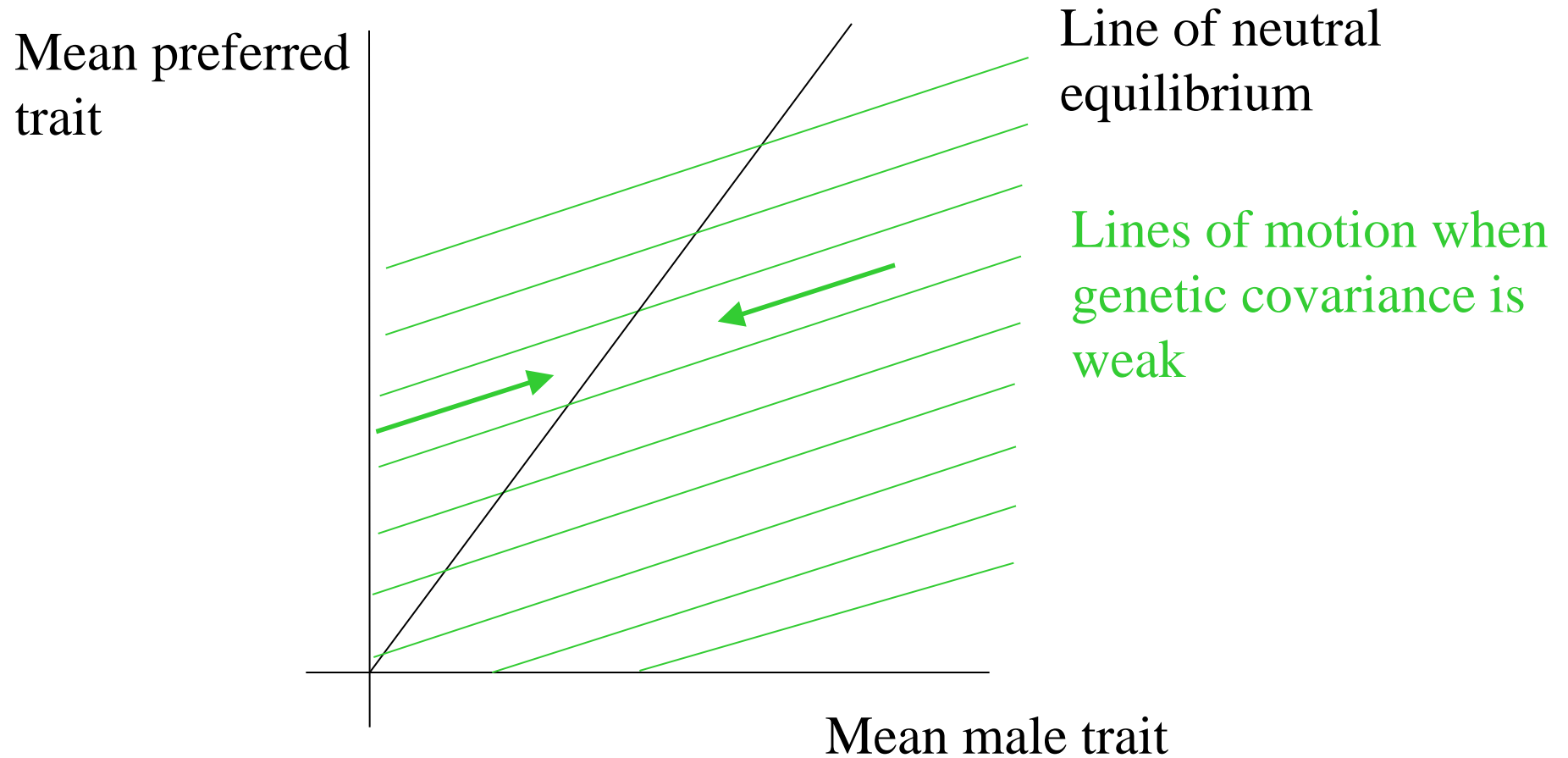
Mean preferred trait



Line of neutral equilibrium

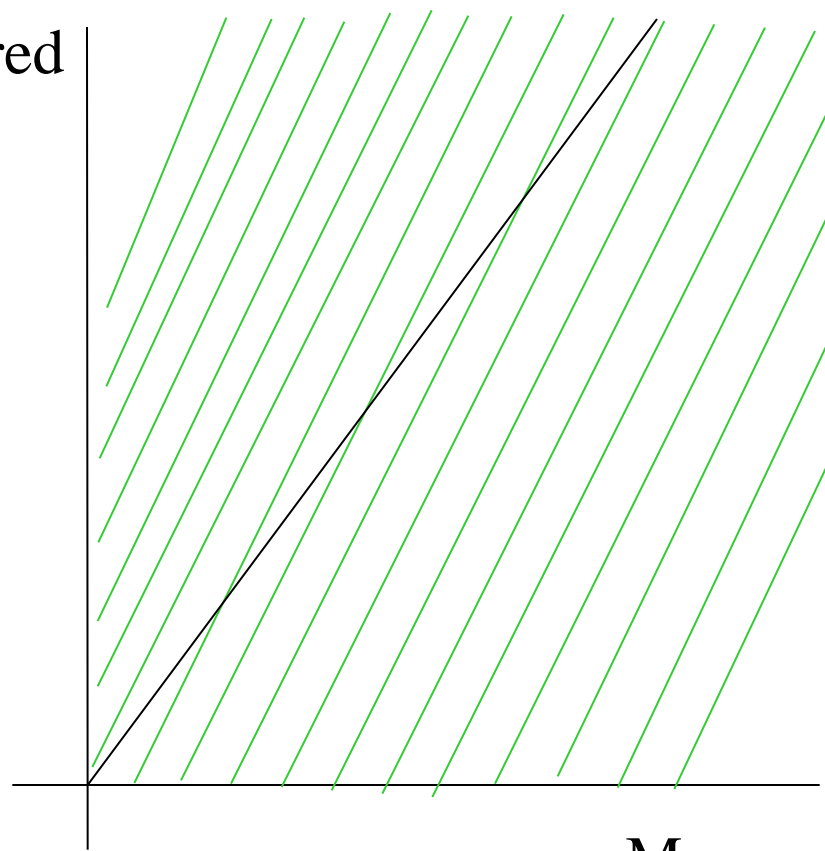
Lines of motion when genetic covariance is weak

Mean male trait



Weak genetic covariance leads to a line of stable equilibria, which is a formal version of Fisher's eventual balance between natural and sexual selection

Mean preferred trait

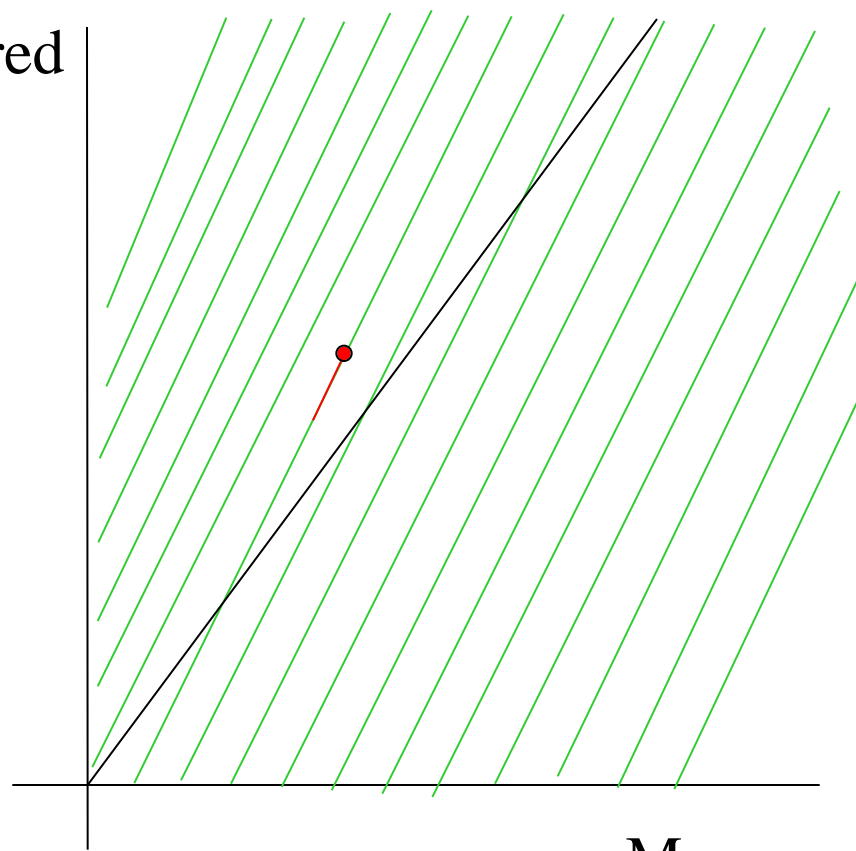


Line of neutral equilibrium

Lines of motion with strong genetic covariance

Mean male trait

Mean preferred trait

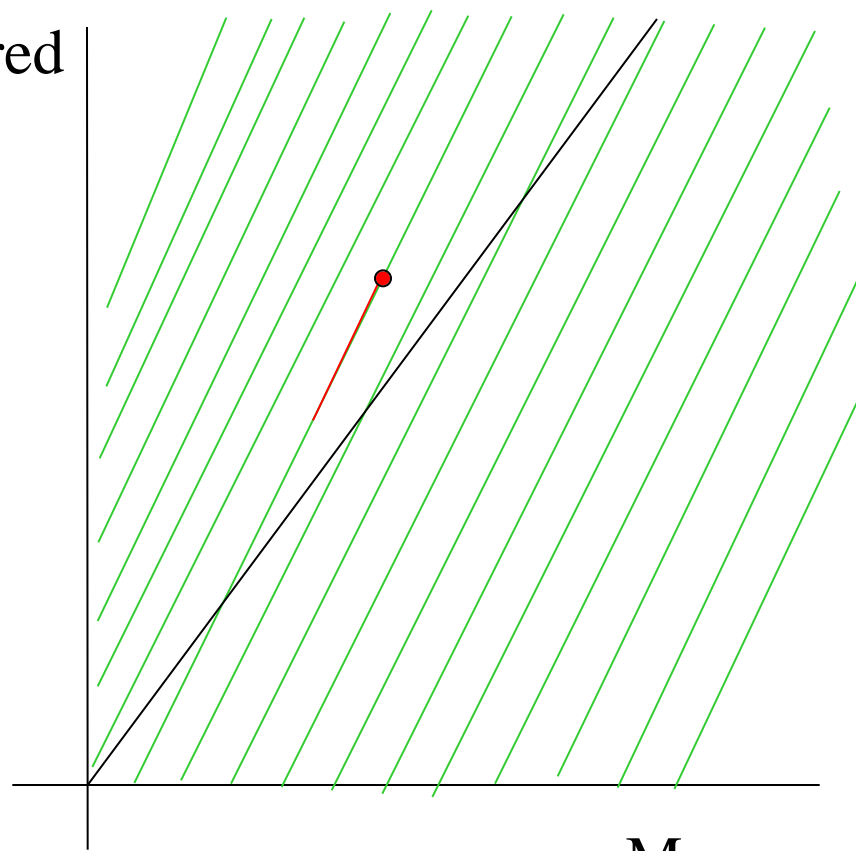


Line of neutral equilibrium

Lines of motion with strong genetic covariance

Mean male trait

Mean preferred trait

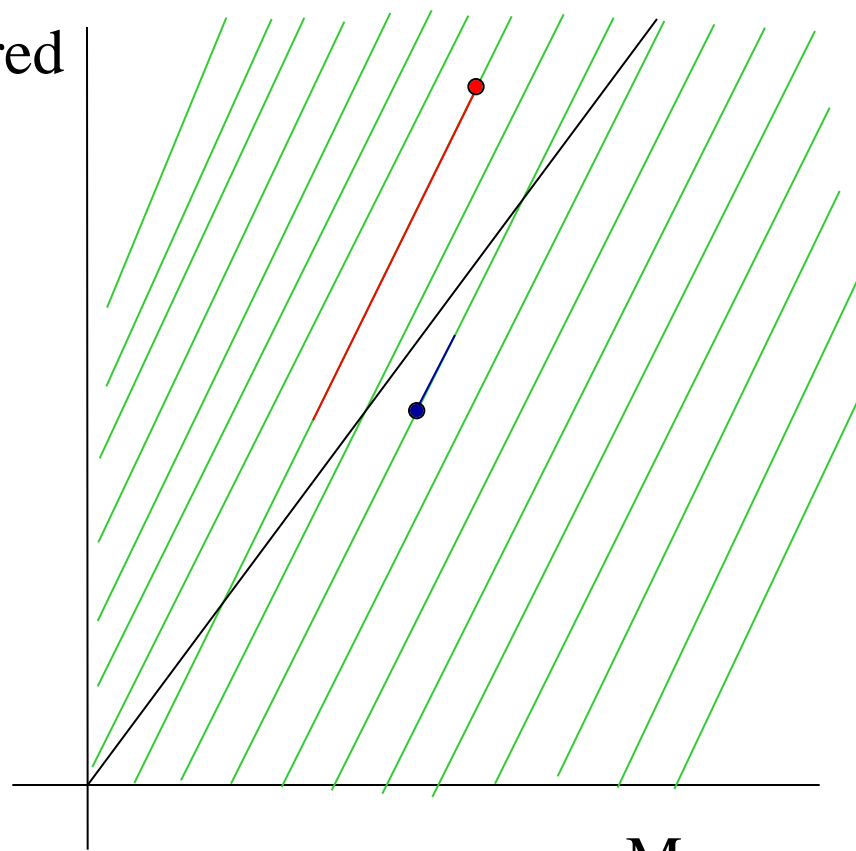


Line of neutral equilibrium

Lines of motion with strong genetic covariance

Mean male trait

Mean preferred trait

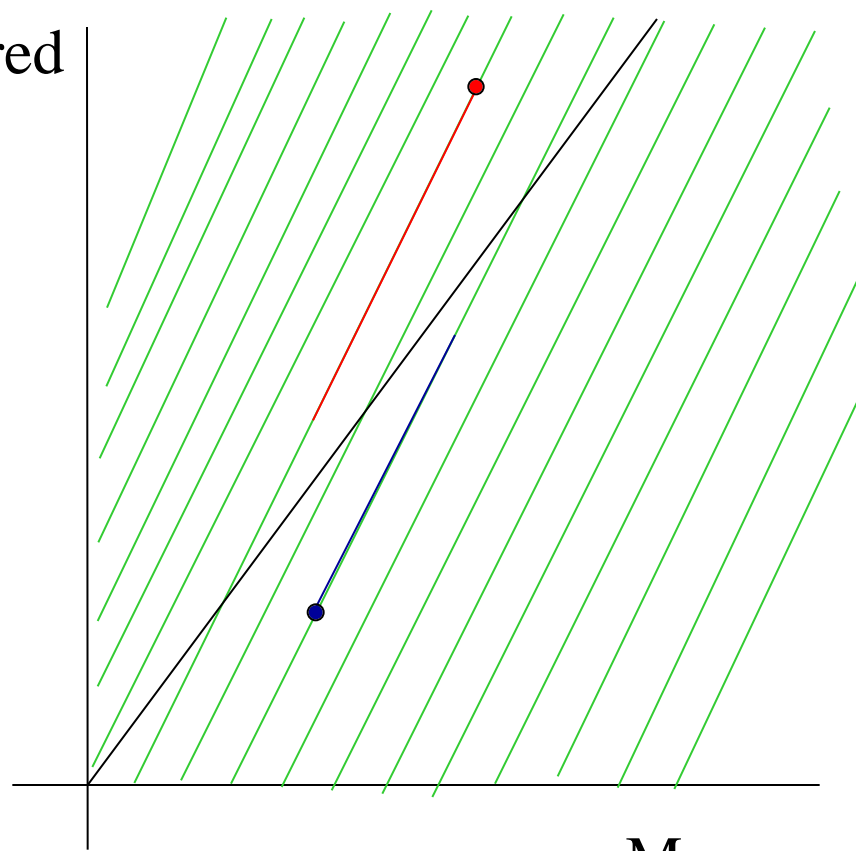


Line of neutral equilibrium

Lines of motion with strong genetic covariance

Mean male trait

Mean preferred trait

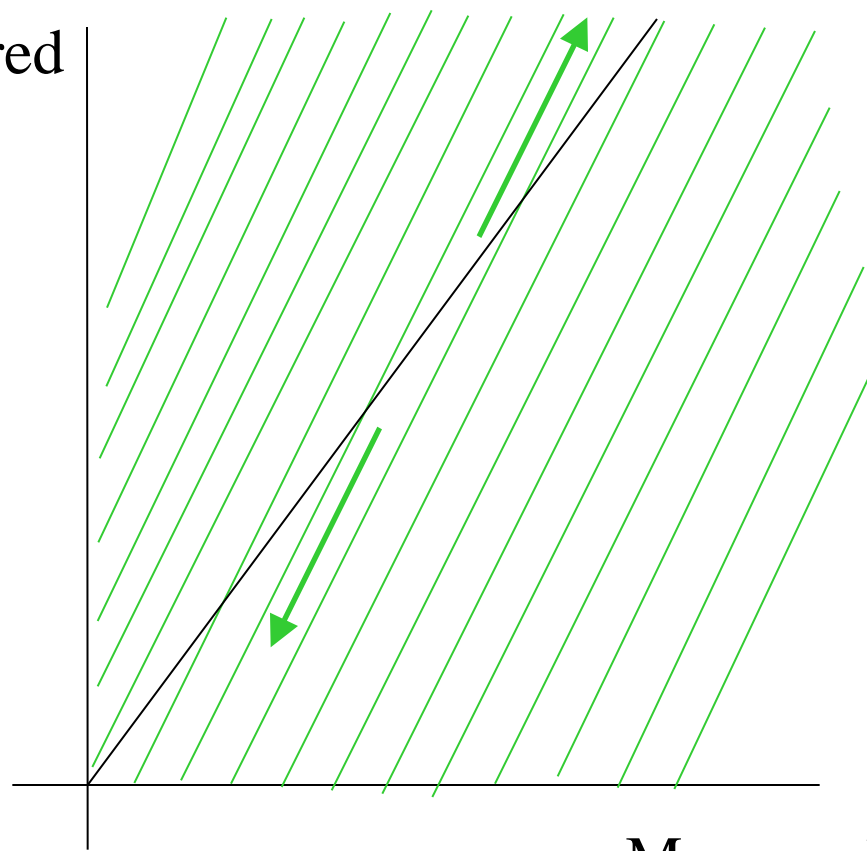


Line of neutral equilibrium

Lines of motion with strong genetic covariance

Mean male trait

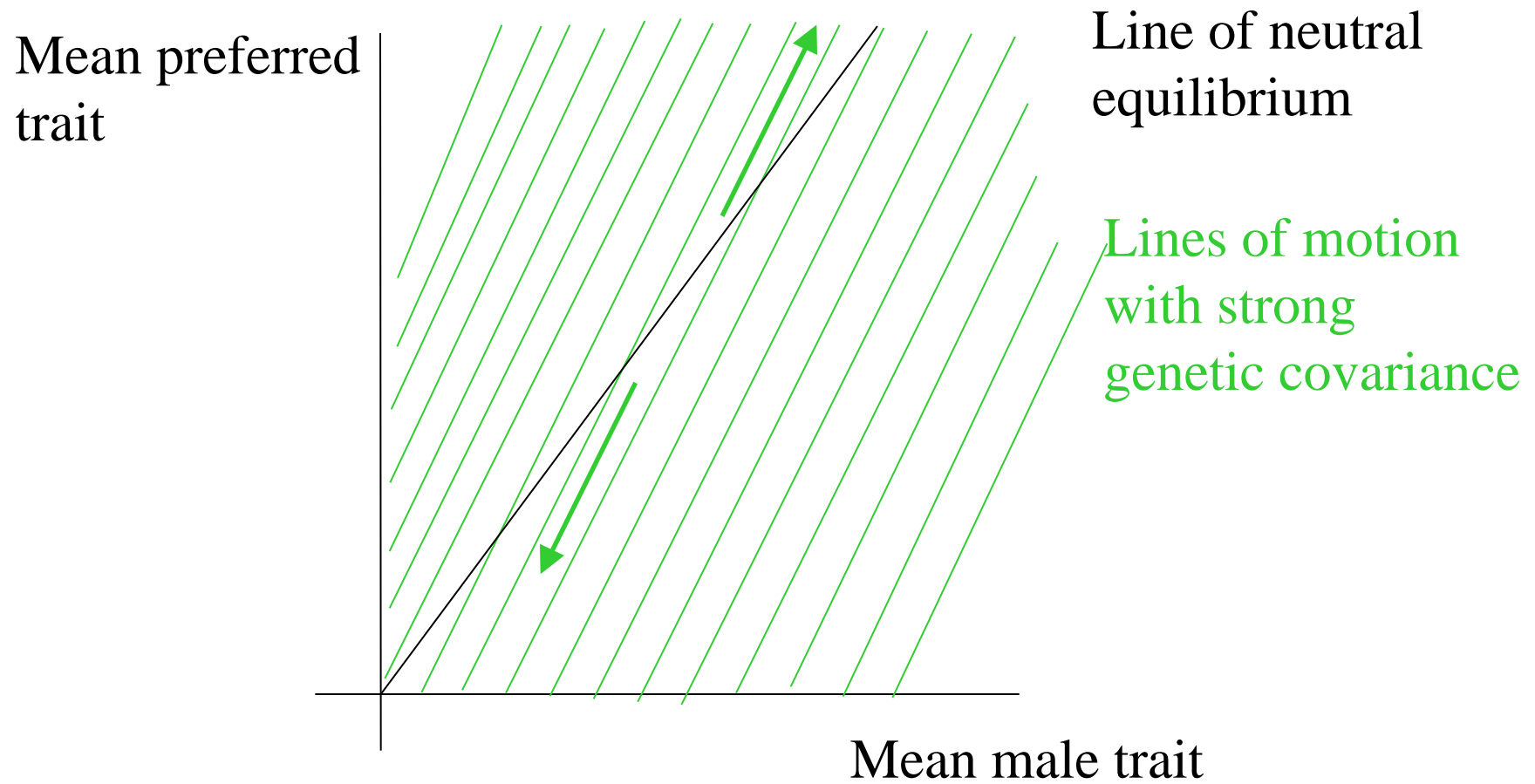
Mean preferred trait



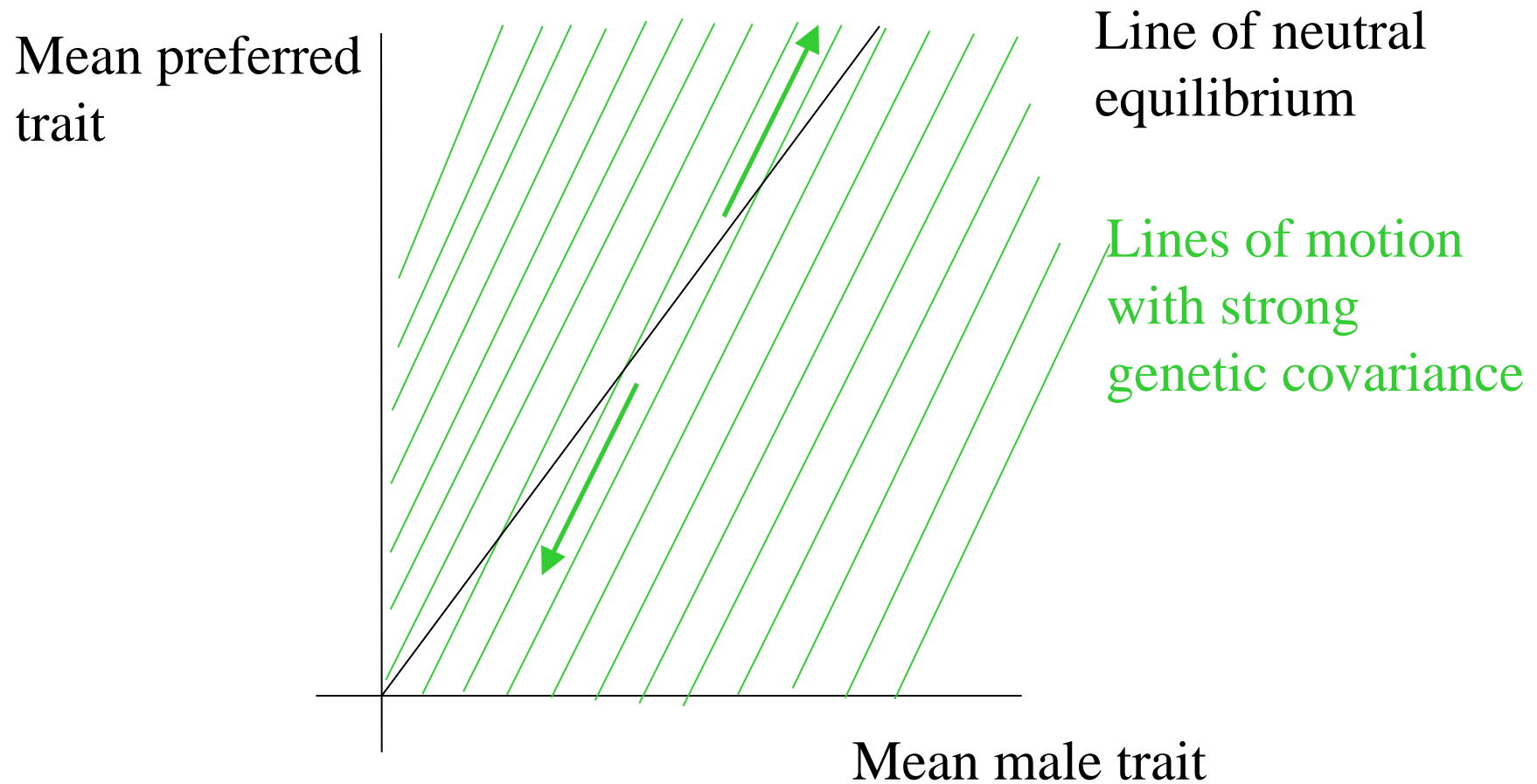
Line of neutral equilibrium

Lines of motion with strong genetic covariance

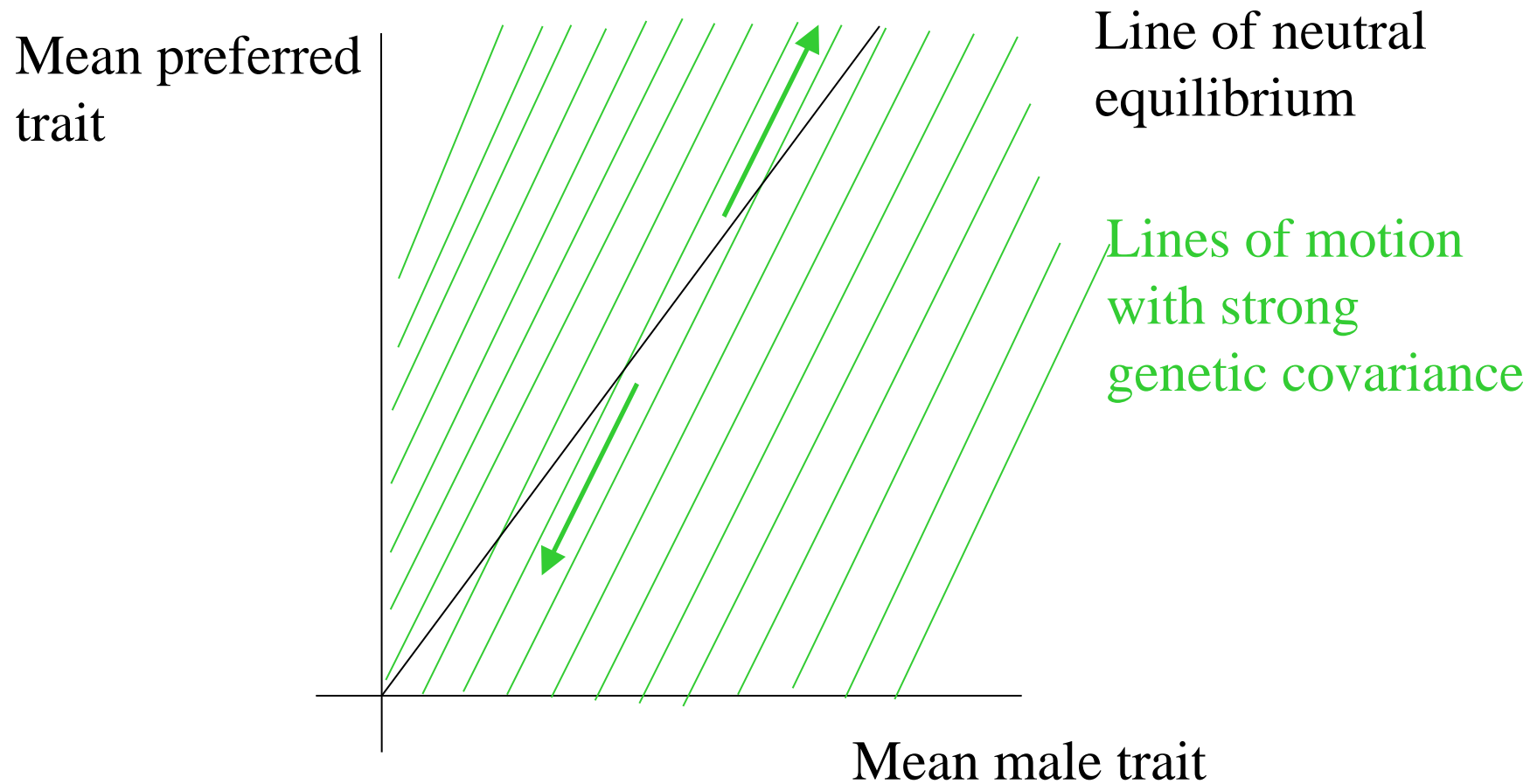
Mean male trait



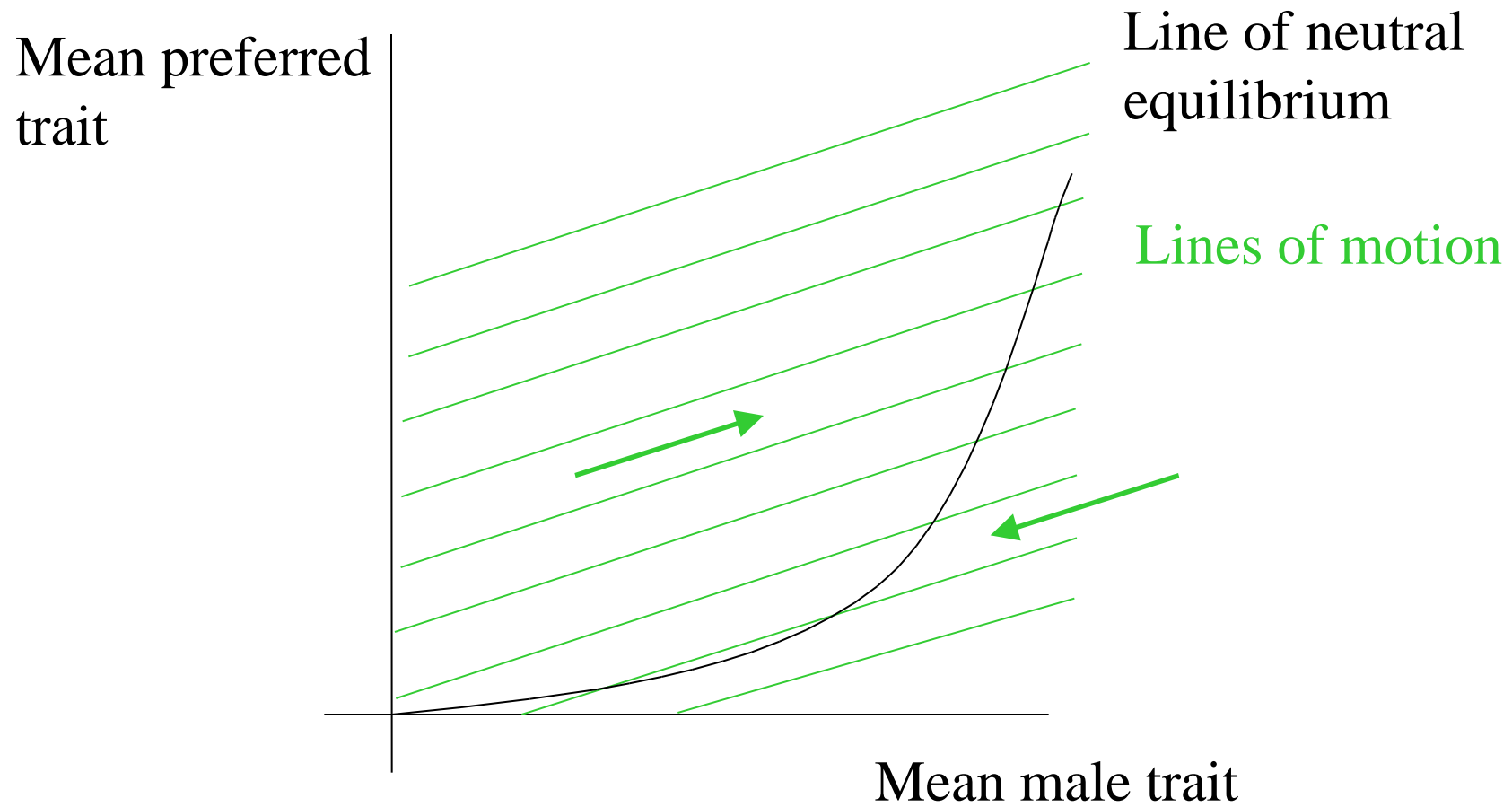
Strong genetic covariance leads to a line of unstable equilibria



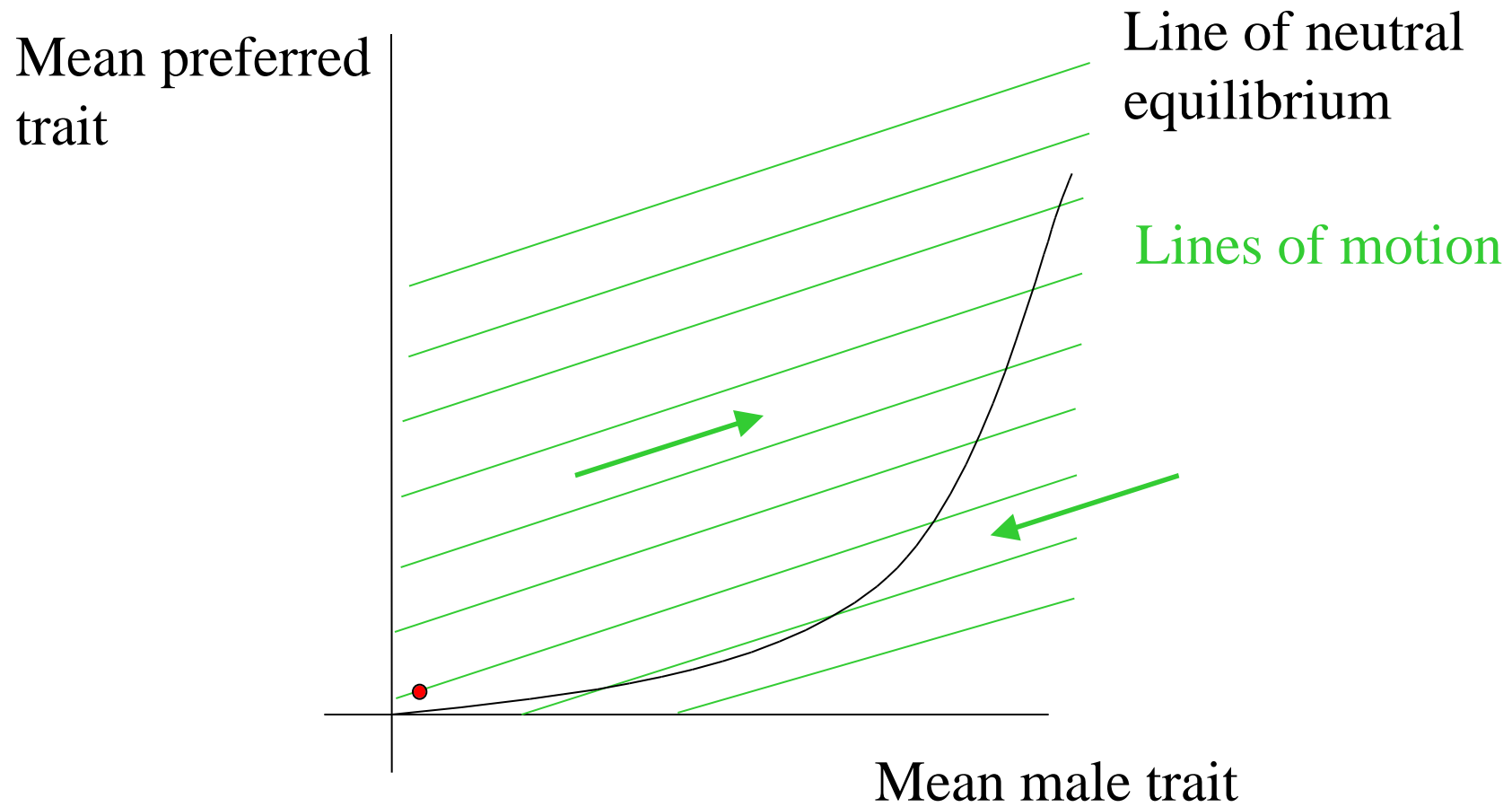
Strong genetic covariance leads to a line of unstable equilibria which is a formal version of Fisher's runaway process



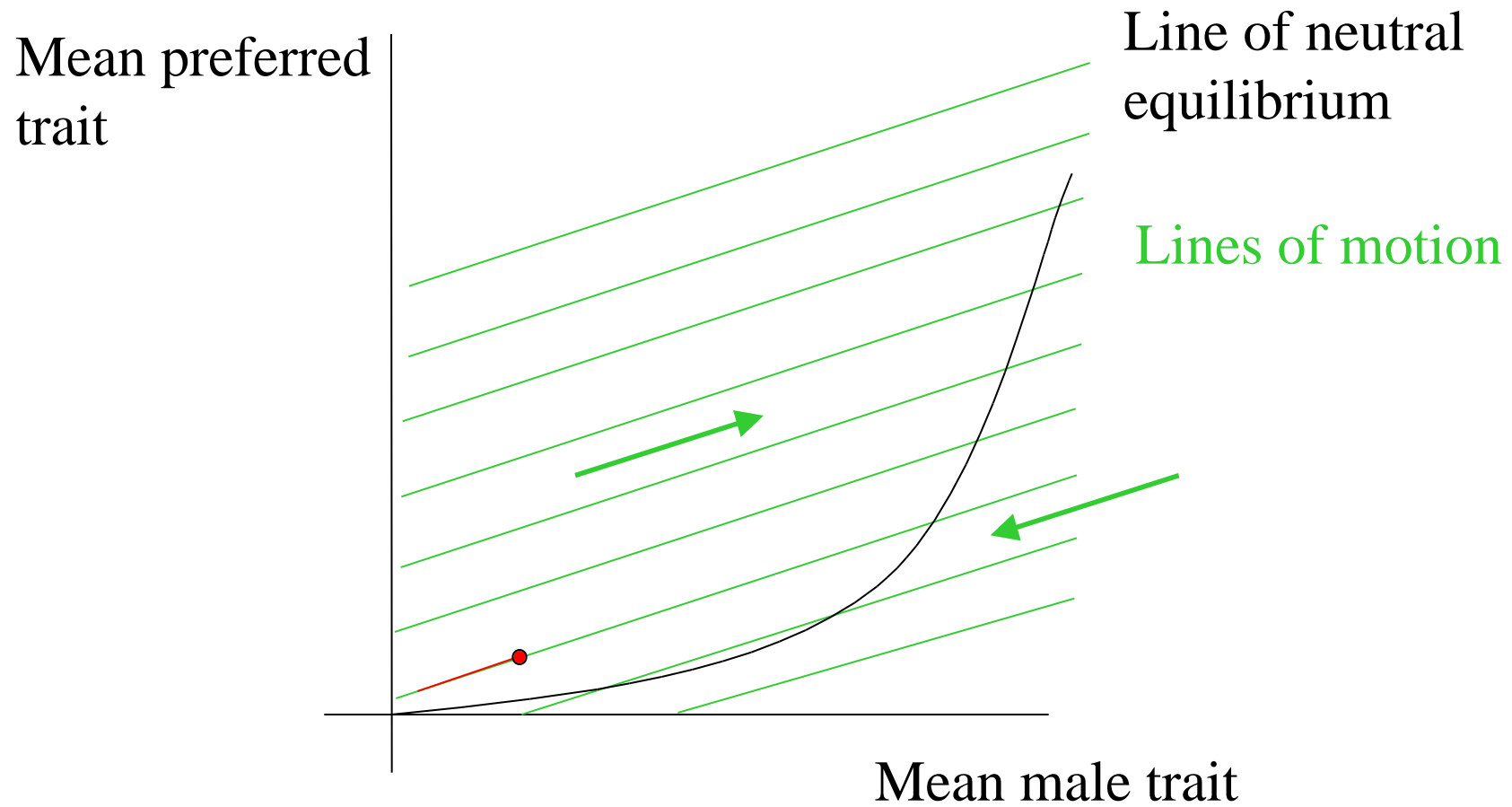
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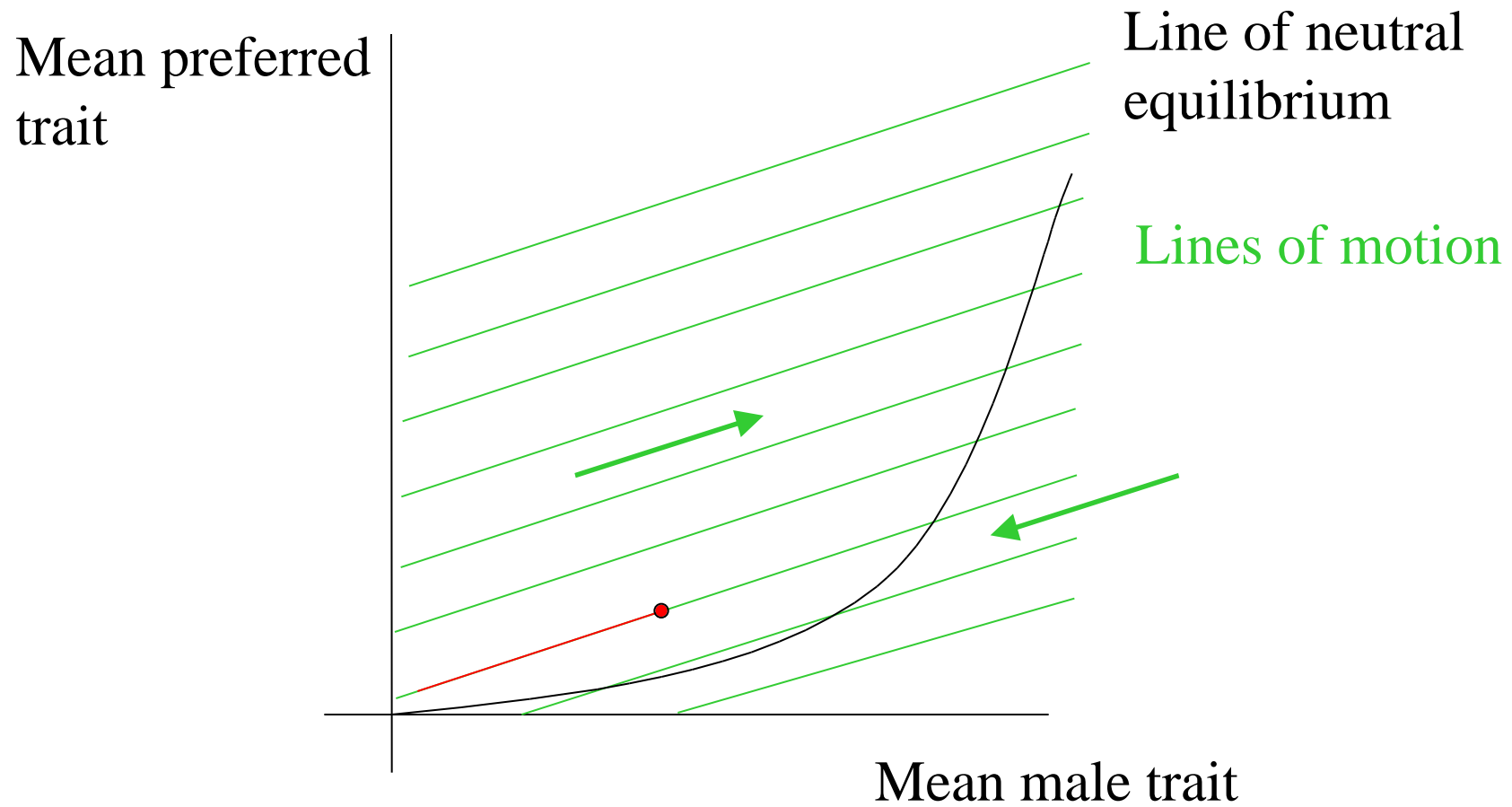
To get both the runaway and the eventual stability, we need to bend the line



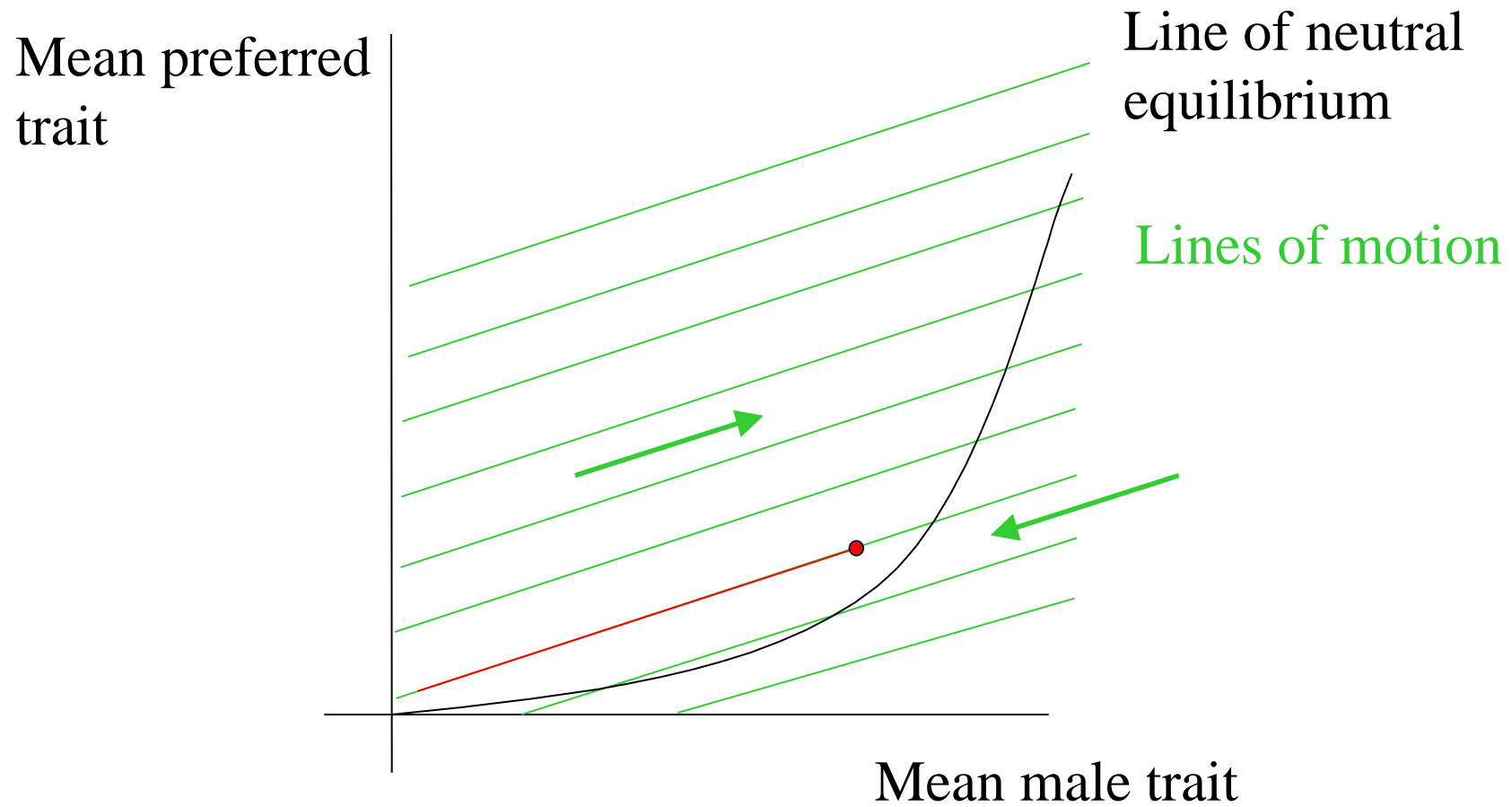
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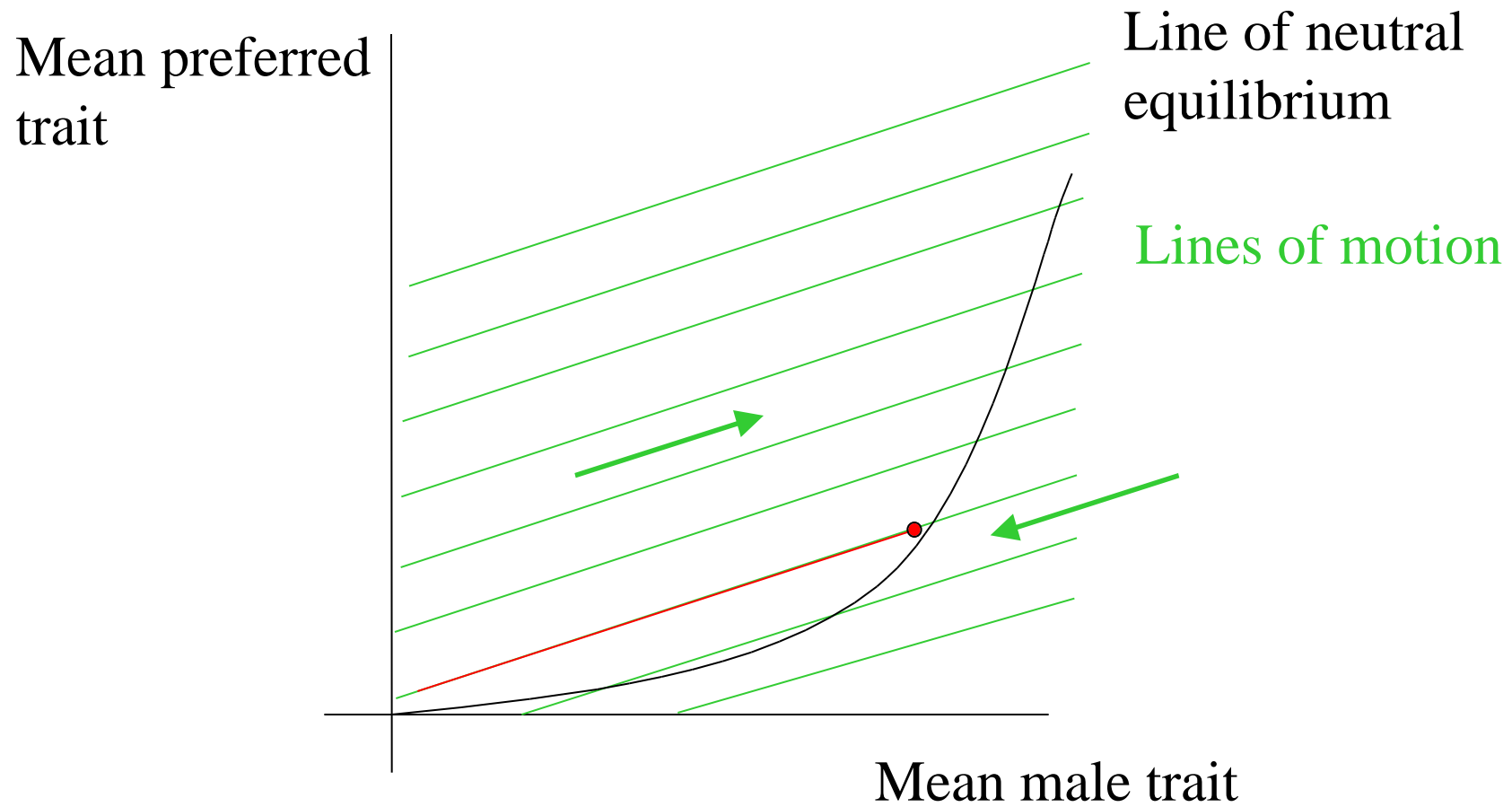
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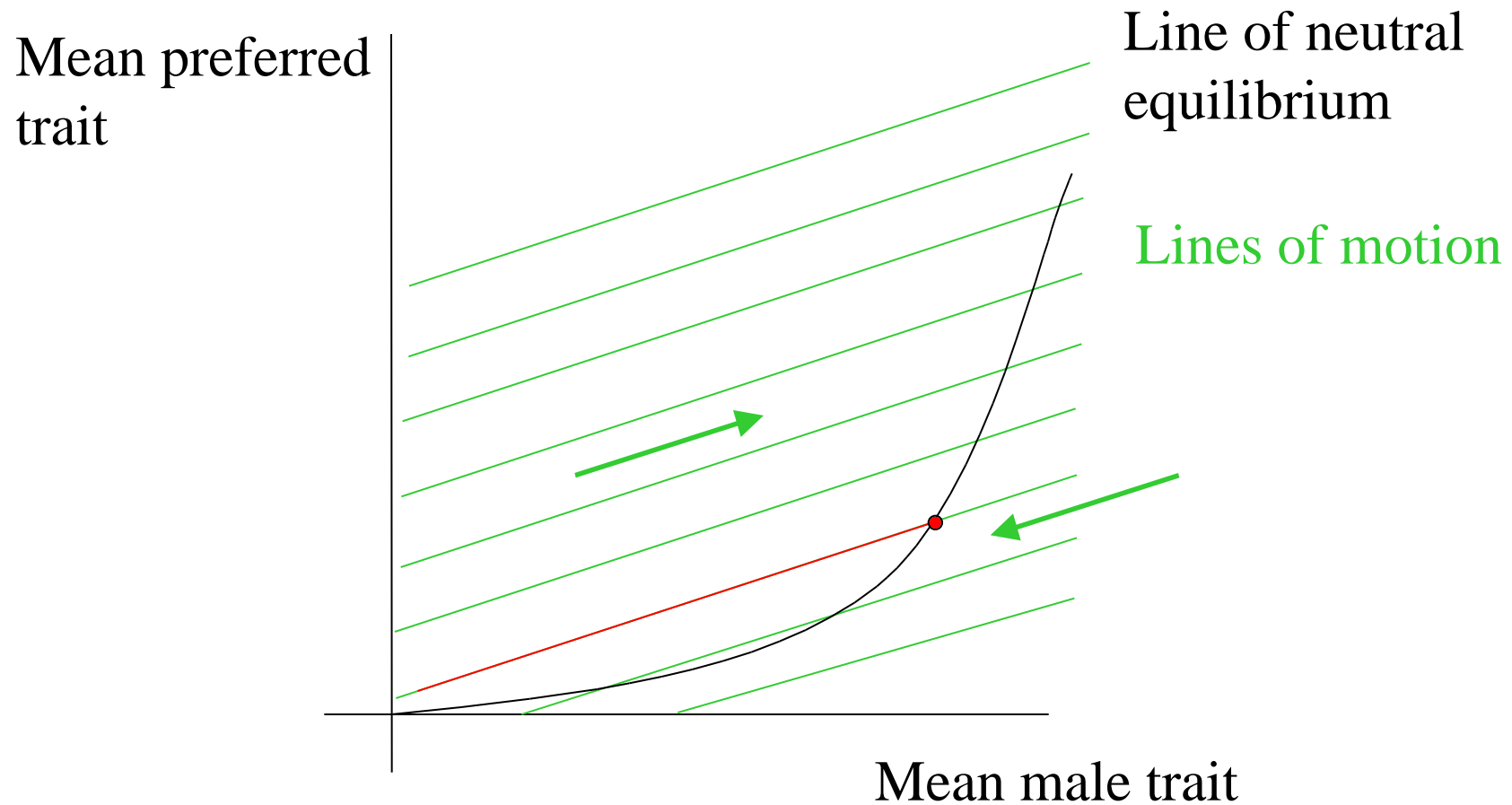
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To get both the runaway and the eventual stability, we need to bend the line, which is an informal extension of the model.

Making the model

- takes all the biology out of it...
- ... but, despite what you may first think, this is a good idea! Because...
- it shows the argument is complete in itself

Why do models matter? An example:

- Idea: Fisher's runaway process
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The model captures

- runaway (i.e. exponential motion)
- balance between natural and sexual selection
- (though formally only in different versions of the model - the extension to both is informal)
- the crucial role of genetic covariance

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The model does not capture

- the evolution of choosiness in Fisher's "first phase"
- Fisher's "cutting away at the roots of the process" by reduced male survival

The model's narrow effects:

- to persuade biologists that Fisher's idea was right (in the sense of internally consistent)
- and so to make the study of sexual selection more respectable
- to put linkage disequilibrium centre-stage in thought about sexual selection
- to make explicit the crucial assumption that female choice was costless

The model omits, as Fisher did,

- the costs of choice
- the possibility of disentangling the observed trait and the naturally selected trait
- (which lead on to handicap models)

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If we compare a model to facts, we will want to

- ask if its assumptions are true
- measure its parameters
- check if its predictions are true
- value a model by how closely it represents reality
- judge a model as a picture of reality

‘Pictures of reality’ are useful when

- Designing a nuclear power station
- Designing a vaccination program
- Eradicating BSE

If we model an idea, we will want to

- ask if the model contains all the essential ingredients of the idea
- ask if the model misrepresents the idea
- check that the model is internally consistent
- look for unthought of implications
- value a model by how closely it represents the idea

‘Articulations of ideas’ are useful for

- asking if an idea makes sense
- looking for implications of the idea
- looking for how the idea links to others

How does the model mislead?

- Many biologists believed that linkage disequilibrium was the essence of sexual selection (as argued by Steven Arnold)
- (whereas I think a single-locus model of Fisherian self-reinforcing preferences would work)
- The handicap models show this to be wrong

What does the model do?

- Focusses the biological community on a particular idea
- Provides one interpretation and validates it, against previous failed or negative models (O'Donald)
- Lifts the debate from the verbal to the mathematical
- Creates two classes of biologists
 - “in the know” vs “not in the know”
 - exegesis
 - ‘know thine enemy’

Two other formal ideas

- Hamilton/Zuk
- Handicaps & Signalling
 - Zahavi
 - Grafen (see Chapter 1 of Third Edition of Behavioural Ecology edited by Krebs & Davies for references and exposition)

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- is the subject of empirical and theoretical studies that inform and inspire each other

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and is a LOT more fun than statistics!