

# Inference and Statistics in Biometry

EPSA 2019, 12.9.2019

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# Outline

1. The structure of evolutionary theory
2. The theory-world relationship, 1890–1930
  - 2.1 Early Weldon
  - 2.2 Late Weldon
  - 2.3 Why the change?
3. How to move forward?

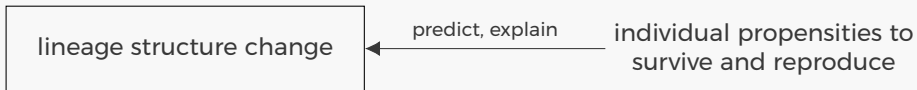
**The take-home:** The contemporary debate over the causal structure of evolution has been with us since the 1890s, and it's time to approach it from new directions!

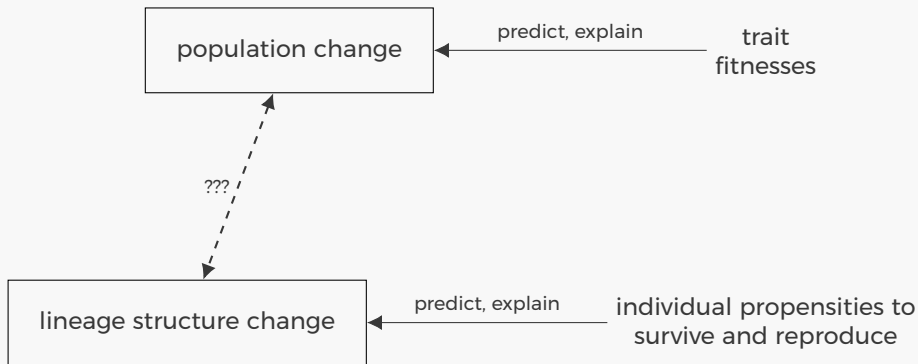
# The Structure of Evolutionary Theory

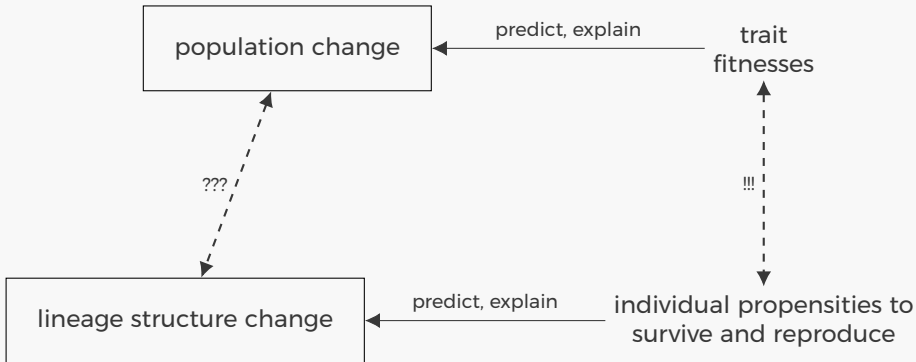
population change

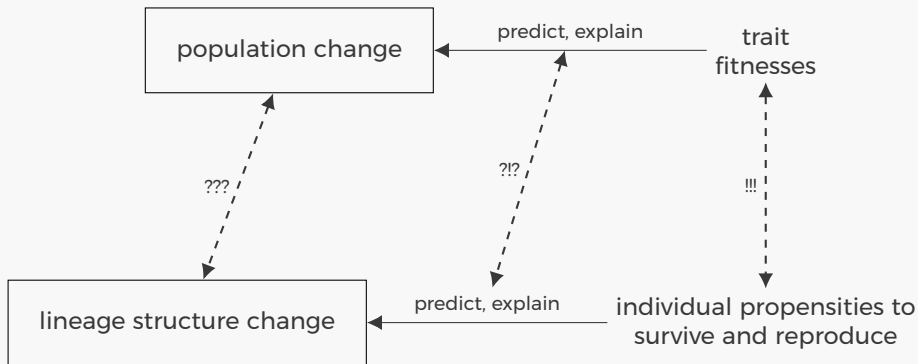
predict, explain

trait  
fitnesses

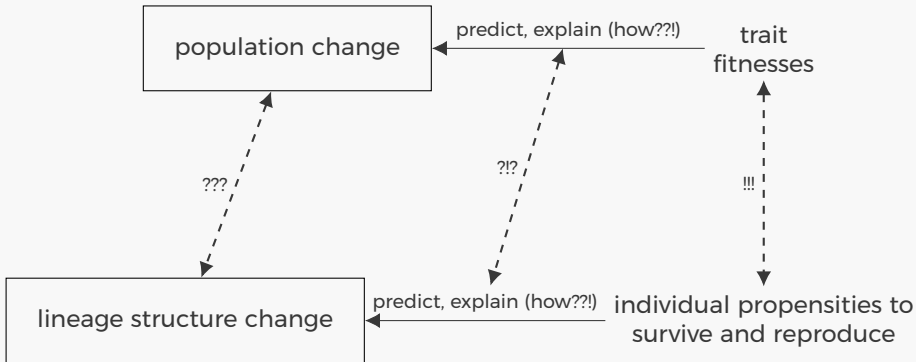








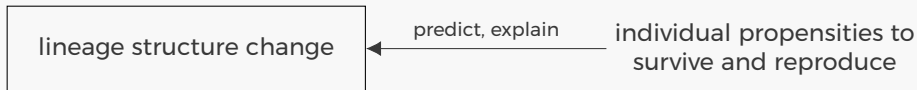


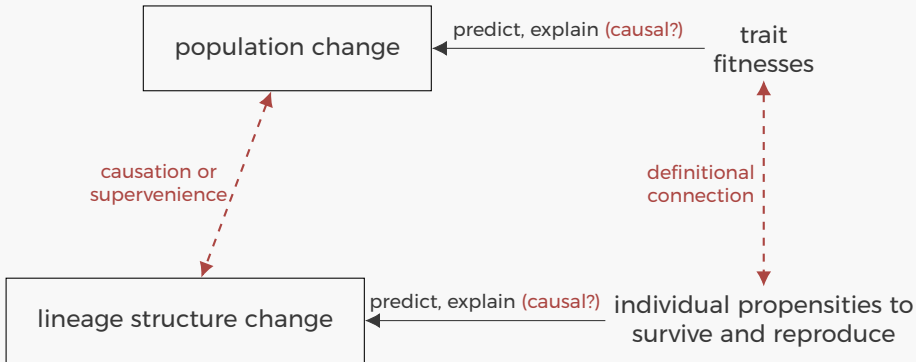




explanatory irrelevance

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# **Statistical Theories and Biological Facts**

# W.F.R. Weldon (1860–1906)



# **Early Weldon: No Connections Required!**



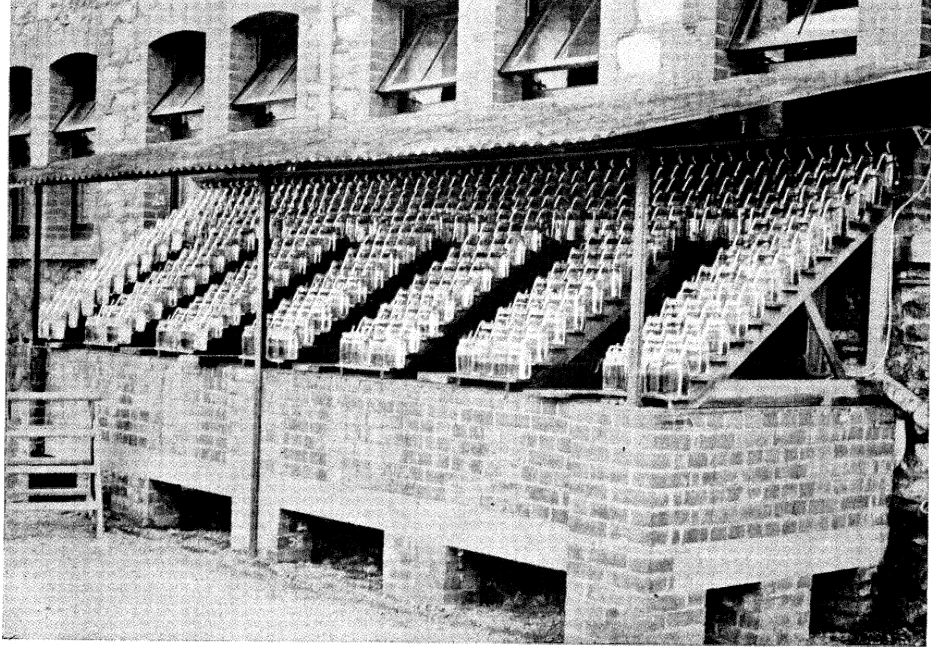
before we can properly estimate the changes at present going on in a race or species we must know accurately (*a*) the percentage of animals which exhibit a given amount of abnormality with regard to a particular character; (*b*) the degree of abnormality of other organs which accompanies a given abnormality of one; (*c*) the difference between the death rate per cent. in animals of different degrees of abnormality with respect to any organ; (*d*) the abnormality of offspring in terms of the abnormality of parents, and *vice versa*. (Weldon 1893, 329)



**These are all the data which are necessary, in order to determine the direction and rate of evolution; and they may be obtained without introducing any theory of the physiological function of the organs investigated.** The advantage of eliminating from the problem of evolution ideas which must often, from the nature of the case, rest chiefly upon guess-work, need hardly be insisted upon. (Weldon 1895b, 379)

# **Middle Weldon: Connections Important, Not Required**

A diminution in the frequency of abnormal frontal breadth, with increasing size of crabs, might be due either to a selective destruction of abnormal crabs during growth, or to a modification of these crabs, by which abnormal individuals lose their abnormality as they grow. In order to decide which of these imaginative hypotheses should be adopted, **I have spent a great part of the last two years in ascertaining the law of growth of crabs...** (Weldon 1896a, 413)



A "Crabbery" at Plymouth.

A complete knowledge of the processes associated with this relation between frontal breadth and death-rate is a thing of very great interest, and I believe, as firmly as Prof. Lankester, that every effort should be made to attain to it; but, desirable as it is, it is still not necessary in order to know that a crab's chance of living and breeding may be known by measuring its frontal breadth. **It is not necessary in order that the change in mean frontal breadth may be measured from generation to generation, and the direction and rate of evolution by this means ascertained.**

(Weldon 1896a, 413)

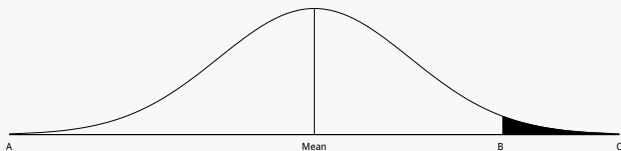
# Late Weldon: Connections Vital

I see no escape from the conclusion that we have here a case of Natural Selection acting with great rapidity **because of the rapidity with which the conditions of life are changing.** (Weldon 1898, 899-900)

These examples, chosen from many others which might have been cited, seem to me to show that it is not possible to regard dominance as a property of any character, from a simple knowledge of its presence in one of two individual parents. **The degree to which a parental character affects offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent.** (Weldon 1902, 244)



What Bateson does, and what all Mendelians do, is to take the diagram of frequency and to call a range AB one “character,” and the range BC another “character” of a Mendelian pair.



There must be a simple relation between AB, BC, and the S.D. [standard deviation] of the original system, which would make the chance that a grandchild falls within  $BC = \frac{1}{4}$ ? (Weldon to Pearson, PEARSON/11/1/22/40.7.3, 1902-06-23)

Good old Galton's stirp, in which some of the ancestral characters are latent, is still the only "machine" which will work: and **the proper line of research is an inquiry into those embryonic stimuli which make a given character evident or latent.** That is my fixed belief. (Weldon to Pearson, PEARSON/11/1/22/40.11.3, 1904-10-??)

# Why the Change?

[On Weldon's view of inheritance,] you cannot, by any amount of selection, reduce the original variability of a race beyond a certain definite amount.

[...]

Accordingly, in every generation of [a population under heavy stabilizing selection,] the variability has to be reduced, though the mean is no longer changed, by a selective destruction. (Weldon 1905f, f. 24, 27)

[W]hile astronomers, chemists, and physicists have by great and successful efforts reduced the limits of uncertainty concerning the results of their observations until for many purposes they can neglect the discrepancies between the results of individual experiments, and treat their experience as uniform, biologists have not yet gone so far, and they are still forced to base such general statements as they can make on the characters of long series of observations. (Weldon 1906, 96)

# How to Move Forward?

Some biologists: firmly invested in  
explanatory irrelevance

Others: firmly invested in discovering links  
between levels, causal and definitional  
relationships between properties

An important issue from the very earliest days of “statisticalized” evolution, entirely independent from the classic biometry-Mendelism debate

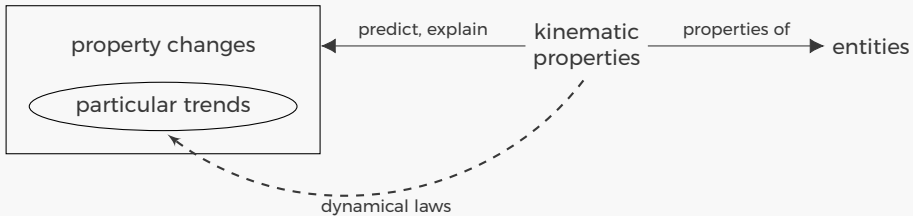


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**Stop.** Tackle the problem from other directions!  
(Especially the metaphysics of science and analogies with other sciences.)

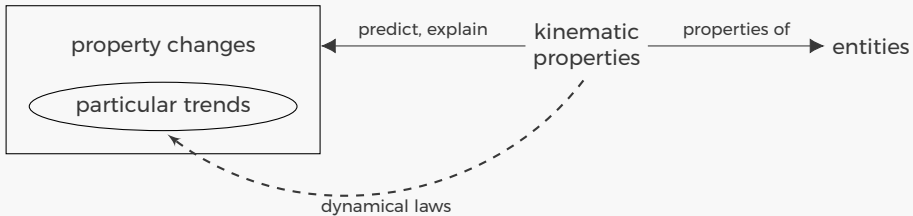
1. This is in no way a distinctively biological (or philosophy-of-biological) problem!

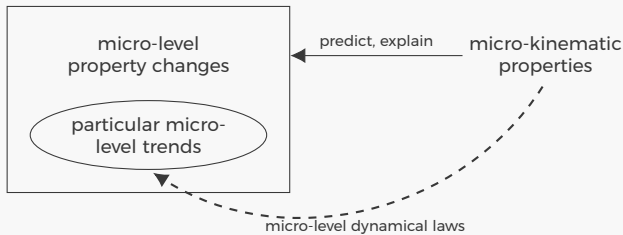
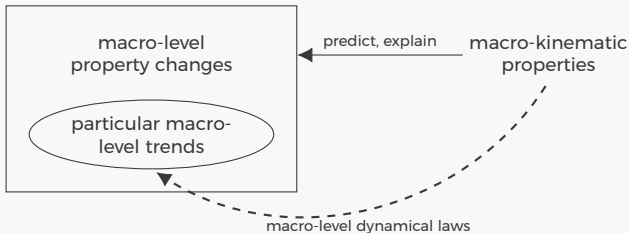


1. This is in no way a distinctively biological (or philosophy-of-biological) problem!
2. Attempts to resolve it using biological data or cases date back to the 1890s, and have been generally unfruitful.

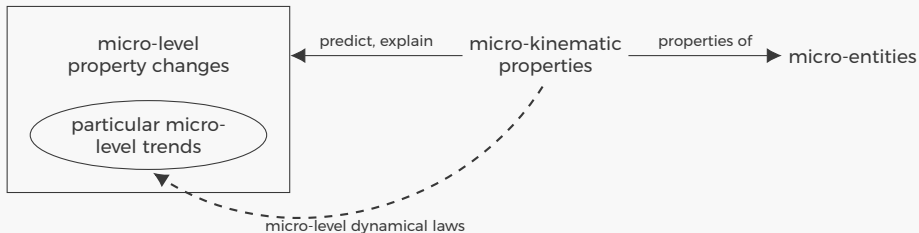
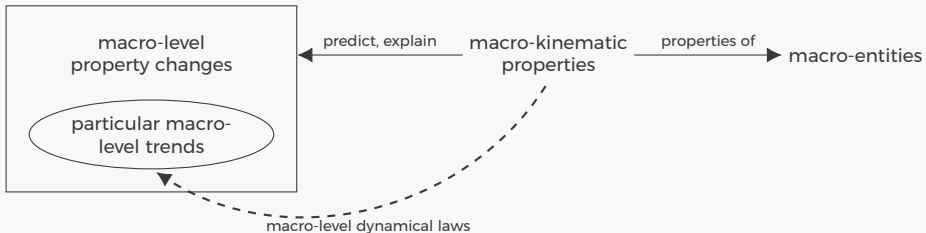
# Questions?

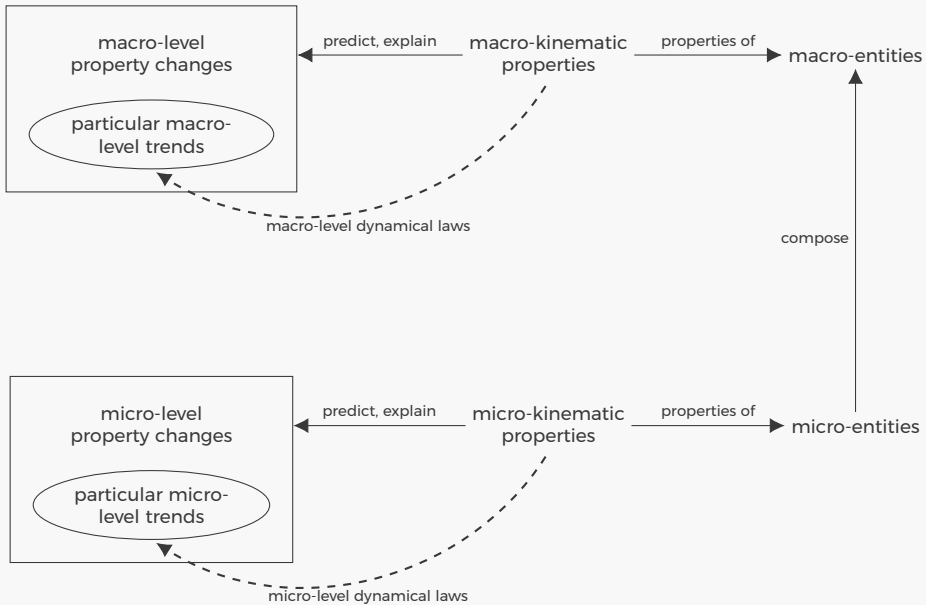
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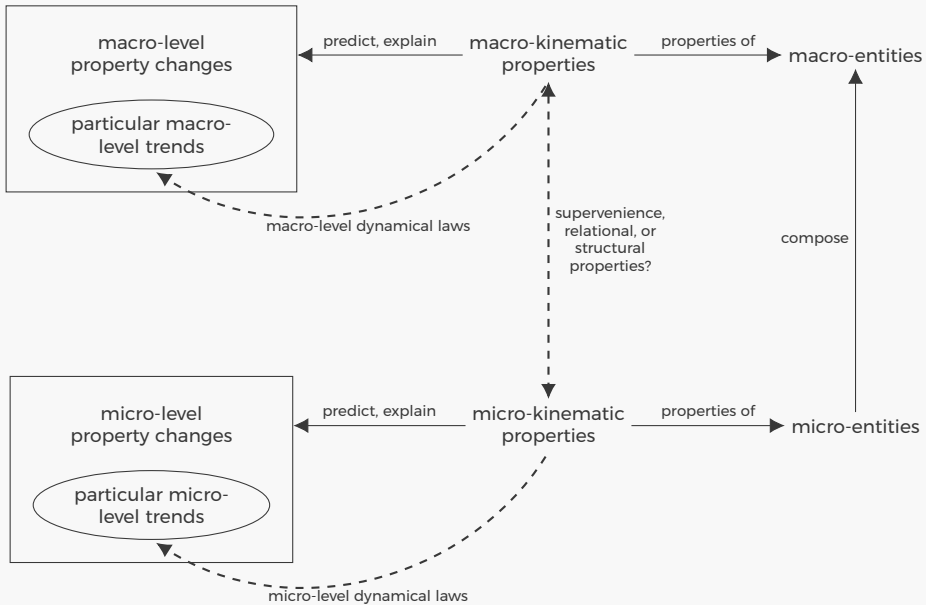


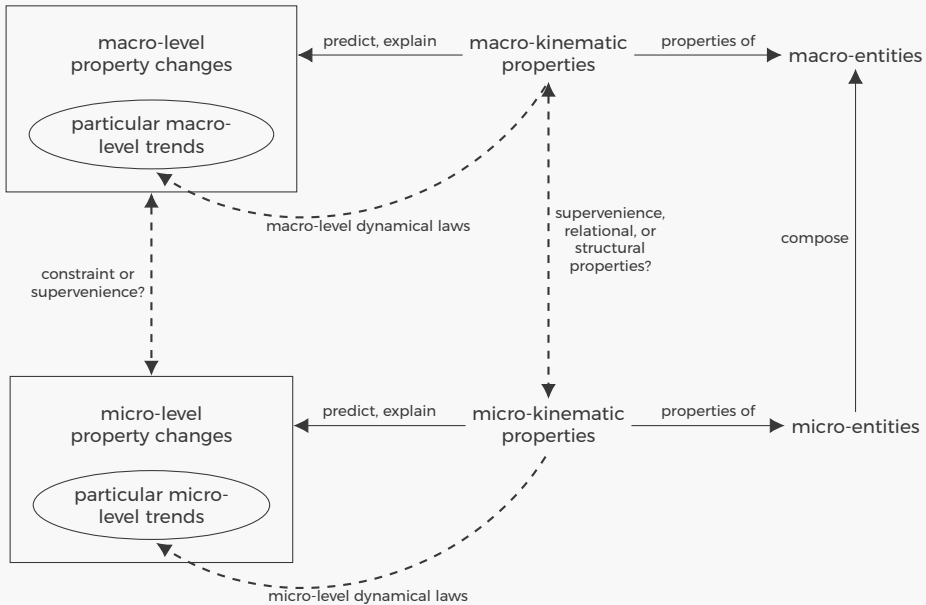


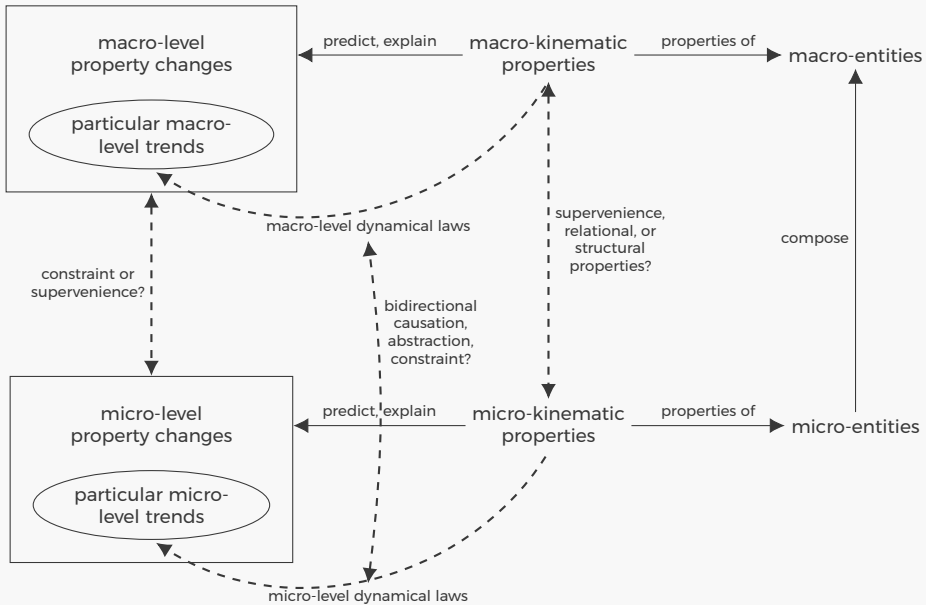












# R.A. Fisher

In these cases [of traits arising from multiple factors] we can confidently fall back upon statistical methods, and recognise that **if a complete analysis is unattainable it is also unnecessary to practical progress.** [...] A number of points of general interest are shown **to flow from purely statistical premises.** (Fisher 1922, 415)

# Sewall Wright

It should be emphasized, however, that [Fisher's] conclusion rests to a large extent on the low frequency of even heterozygous mutants, to be expected where mutation is balanced by adverse selection of a higher order. [...] **It seems unlikely that similar conditions would occur in nature except in special cases.** [...] [In the absence of these,] probably most geneticists would hold that dominance in general has **some immediate physiological explanation.** (Wright 1929, 277)