Then and Now: Darwin and Wallace.  
(Peters, 1976; Gould and Lewontin, 1979)

I. Substitution of an advantageous mutant.

A. Darwin and Wallace both couched their arguments in terms of competition. How does this work?

B. Consider Figure 1 which assumes two varieties in a homogeneous environment.

1. Mutant assumed to have the greater per capita rate of increase for all densities.

2. Prior to introduction of mutant, population density (wild types) = N₁*.

3. After substitution, population density = N₂*.

4. At this point, wild type rate of increase negative – can’t re-invade.

Figure 1. Substitution of an advantageous mutant. N₁* and N₂* are equilibrium densities of wild type and mutant populations. a. Per capita rates of increase (birth – death rate) of mutant and wild types plotted against population size. For all densities, the mutant outperforms the original. b. Numbers of wild types and mutants vs. time.
5. Or as Wallace (W58) put it:

“The [superior] variety would now have replaced the species, of which it would be a more perfectly developed and more highly organized form. … Such a variety could not return to the original form; for that form is an inferior one, and could never compete with it for existence.” [p.58].

C. But on the same page Wallace argued that substitution requires the intervention of adverse conditions:

“Now, let some alteration of physical conditions occur in the district, … any change in fact tending to render existence more difficult to the species in question … ; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.”

D. Figure 1 predicts that the superior variety exterminates the stock from which it arose, adverse circumstances or no.
E. Under what circumstances are adverse circumstances be required?

F. Answer: When competing varieties have overlapping, but not identical ecological requirements.

1. When varieties are ecologically equivalent, one outcompetes the other (Figure 2 top).

2. When ecological requirements partly overlapping, they can co-exist (Figure 2 middle).

3. Subjecting both varieties to increasing rates of mortality ($d$) unrelated to competition drives the equilibrium density, $N_1^*$, of the inferior variety negative, in which case it goes extinct (Figure 2 bottom).

Figure 2. Competition between varieties. See text for discussion.
II. Tautology?

A. The criticism.
   1. The struggle for existence $\implies$ survival of the fittest. But who are the fittest? Apparently, those who survive.

   2. This is a tautology, \textit{i.e.}, a logical necessity and cannot, therefore, be falsified.

   3. It is not, therefore, a scientific theory.

B. Peters (1976):

   1. “The evolutionary history of an organism, its phylogeny, is limited to speculation, as opposed to experimentation ... . Further more the imperfections of the geological record make it relatively easy to explain away anomalies. The randomness of mutation couples with the unpredictability of environmental changes make prediction impractical. ...”

   2. “If phylogenetic history cannot be predicted from the theory of evolution, we must turn to those aspects of the theory which are current and so are subject to experimental analysis – the operation of natural selection on variations among organisms.”

   3. “Analysis of a number of popular ecological tenets, including natural selection, ..., reveals that they lack the predictive and operational qualities which define scientific theories. Instead they consist of the logical elaboration of certain axioms. Consequently, they must be termed tautologies.”
C. Can Fitness be Defined Independent of Who Survives?

1. For extinct species, probably not.

2. For contemporary species, relate phenotypes to fitness proxies **that can be measured**.

3. Method as follows:

   a. Equate fitness with a proxy variable, $\lambda$. An example would be number of seeds produced by an annual plant over the course of a growing season.

   b. Assume selection maximizes $\lambda$ – at least under a specifiable range of circumstances.

   c. Determine dependence, $\lambda(\varepsilon)$, of $\lambda$ on the value of some anatomical, physiological or behavioral feature, $\varepsilon$. In the plant example, $\varepsilon$ could be a set of numbers specifying the daily allocation of photosynthate to stems, leaves and flowers, *i.e.*, $\varepsilon(t) = [\varepsilon_s(t), \varepsilon_l(t), \varepsilon_f(t)]$.

   d. Determine value, $\varepsilon^*$, of $\varepsilon$ that maximizes $\lambda(\varepsilon)$.

   e. Compare $\varepsilon^*$ with the value observed.
III. Optimization in Nature.

A. Perfection of Sponges.

1. **Prediction.** Sponges should maximize distance traveled by water exiting the osculum before re-entering the pores.
   a. Maximizes waste-nutrient exchange.
   b. Implies a relationship between collar cell pressure (CCP) and osculum diameter (OD).

2. **Observation.** In 1944, Joseph Bidder made measurements consistent with calculation.

3. **Caveats.** Distance traveled by water before re-entering the sponge, a “proxy” for fitness. But,
   a. A more complete analysis would relate sponge reproduction and survival to OD and CCP.
   b. Not relevant to sponges that live in currents.

B. Optimality Theory.

1. Bidder’s study representative of studies seeking to demonstrate optimal design in nature.

2. Others:
   a. Schedules of reproduction and mortality.
   b. Mating preferences and behavior.
C. Why are there perennials? Most famous question in life history evolution due to Lamont Cole (1954).

1. Cole equated fitness with yearly rates of multiplication of competing clones, i.e., annuals vs. perennials.

2. Calculated \( \lambda_a > \lambda_p \iff b_a > b_p + p \) , where \( b_a \) and \( b_p \) are numbers of seeds set by annuals and perennials and \( p \) is year to year survival among perennials.

3. Max value of \( p \) is 1.0. Hence it would seem that annuals ought always to win – i.e., a plant abandoning the perennial habit ought to save enough energy for > 1 seed.

4. In fact, not all seeds survive. Correct criterion is \( \lambda_a > \lambda_p \iff b_a > b_p + p/c \) , where \( c \) is seed survival.

5. Predictions:
   a. Perennial habit selected for in environments where the ratio, \( p/c \), is large.
   b. Annual habit when \( p/c \) is small.

D. Difficulties (Gould and Lewontin, 1979).

1. Atomizing individuals inappropriate –
   a. Correlated characters – limits ability of Darwin’s demon to pick and choose.
   b. Physiological / genetic / developmental constraints.

2. Past environments may differ from present.
IV. The Giraffe’s Neck.

A. Traditional hypothesis: Long neck allows individuals to eat leaves high in the canopy.

1. Sometimes, trees are in fact clipped bare up to the maximum height giraffe’s can reach.

   “Groves of African acacia trees (I have seen this phenomenon in the field) are often denuded below a sharp line representing the reach of local giraffes.” – [Gould (1996) “The Tallest Tale.”]

2. Anatomy of the skull permits maximum extension of the head.

3. 18" tongue extends reach.

4. Related hypothesis: Evolution of long neck driven by competition with other, smaller herbivores.

Giraffe feeding on acacia leaves with head fully extended. Below this level, the tree has been stripped.

Male giraffe skull in section. The enlarged occipital condyle (OC) permits backwards rotation of the head so as to bring the anterior-posterior axis of the skull in line with the neck, thereby permitting maximum extension of the head. From Owen (1866).
B. But –

1. Giraffes often forage low down (Simmons and Scheepers, 1996).

2. Males use their necks to fight with each other. Their necks are larger and more heavily muscled than those of females.

C. New Hypothesis:

1. Long necks in males evolved in response to sexual selection – males contesting for females.

2. Females “dragged along” to a lesser extent.

D. These hypotheses **not** mutually exclusive.

1. Prominent air sinuses in the frontal and parietal bones of the skull observed in other species in which males contest by bashing heads.
3. Neck length / head mass vs. body mass in males and females indicates only head mass increases more rapidly in males.

[Graph showing neck length and head mass plotted against body mass for male and female giraffes. Only head mass is proportionately larger in males. From Mitchell, G. *et al.* 2009. *J. Zool.* 278: 281–286.]

E. Giraffes descended from forest dwelling, okapi-like ancestor.

1. Moving out onto the Savannah may have selected for larger body size: 200-250 kg → 1600 / 1000 (males / females).

2. Being tall allows animals to
   a. Forage over a larger area;
   b. Browse higher up in the foliage;
   c. Watch for predators from afar;
   d. Run faster when danger threatens – have been clocked at 35 mph.

The ancestor of savanna-dwelling giraffes resembled the much smaller okapi that lives in forests.
F. What really needs to be determined is what kind of an animal you get when you “scale up” an okapi.

G. Requires an understanding of allometric growth in giraffids.
H. Allometry.

A. Growth of different parts of an animal correlated, but parts grow at different rates.

B. If, on a log-log plot, one often observes a linear relation, say between $x$ and $y$, e.g., antler size and body size,

1. One says that there is an *allometric* relation.

2. Changes in relative proportions of the two organs explicable solely in terms of different sizes of one.

3. Gould showed that *Megaloceros*, fits such a relationship for cervids. Hence, nothing special about the size of its antlers.

4. Says nothing about selective pressures. In the case of *Megaloceros*, selection could have been for large bodies, large antlers or both.

Allometry in the “Irish elk” (top) *Megaloceros giganteus*. According to this, the animal’s extraordinarily large antlers are entirely explicable in terms of correlated growth (bottom) and large body size. From Gould (1974).