Adaptive Topographies, Sewall Wright’s “Shifting-Balance” Theory and the Evolution of Horses.

I. For a two alleles at a single locus, the change in gene frequency, $\Delta p$, from one generation to the next can be written as

$$\Delta p = \frac{pq}{2W} \frac{d\bar{W}}{dp}, \quad (1)$$

where

$$\bar{W} = p^2 w_{AA} + 2pq w_{Aa} + q^2 w_{aa} \quad (2)$$

is average fitness, $w_{AA}$, etc., are genotypic fitnesses, and $q = 1 - p$.

1. Presumes H-W frequencies – hence weak selection, no linkage, constant genotypic fitnesses, etc.

2. Equation (1) implies three possible equilibria: boundary equilibria, $p = 0$; $p = 1$ and an interior equilibrium, $p^*$, defined by $d\bar{W}/dp\big|_{p=p^*} = 0$.

3. Regarding interior equilibria, it can be shown that $\bar{W}$ is a local maximum in the case of heterozygote advantage and a local minimum in the case of heterozygote inferiority. Details at [http://bill.srnarizona.edu/classes/182/Diploid.htm](http://bill.srnarizona.edu/classes/182/Diploid.htm).
4. Implications:
   a. $\bar{w}$ a potential function;
   b. Gene frequencies change under selection to maximize $\bar{w}$.

5. If $\bar{w}(p)$, i.e., the entire curve, shifts in response to changing environment, system can “jump” from one peak to the next.
   a. A population near one peak can find itself on the “shoulder” of another (Figure 1).
   b. This is Wright’s “shifting-balance” theory.
   c. Proposed as a counter to evolutionary stasis that would otherwise result if populations climbed nearest peak and stayed there.
   d. Small populations (drift) can occasion make “jumping” more likely, i.e., “sampling error” can kick a population across a valley.

6. With $n$ loci, replace Figure 1 with $n +1$ dimensional figure – $n$ gene frequencies and $\bar{w}$ (Figure 2).

\[ \text{Figure 2. Two-dimensional adaptive landscape (two loci; two alleles each). Circles are contours of equal population fitness, } \bar{w}. \]
II. Horses.

1. North America center of equid evolution (Figure 3).

2. Multiple invasions of other continents
   a. All go extinct save the last.
   b. At the same time, NA horses exterminated by Paleo-Indians.
   c. Re-introduced into NA by Europeans.

3. First horses browsers – ate leaves and twigs.

4. Grass-eating horses evolve in Miocene – period of increasing aridity, grassland expansion.

5. Grass contains silica (Figure 4) => problems for mammalian herbivores.
   a. Increases tooth wear.

6. Feedback. Grazing increases phytolyth production in grass. Contributes to vole cycles?

Figure 3. Horse evolution according to G. G. Simpson (*Tempo and Mode in Evolution*).

Figure 4. Phytoliths are accumulations of silica deposited by grasses and other plants in cell walls and elsewhere. From *The Tarkio Valley Sloth Project* [http://slothcentral.com/archives/1391](http://slothcentral.com/archives/1391).
7. Browsing and grazing horses coexist during Miocene;
a. Then browsers → extinct –
b. N.B. Writing in 1944, Simpson distinguished browsers and grazers on the basis of
tooth morphology (see below). More recently, it has
been suggested that “grazers” also ate browse.

8. Horse evolution marked by
a. Increasing body and skull size (Figure 5);
b. Hypertrophy of the central toe; reduction of side toes (Figure 6);
c. Increased tooth height – hypsodonty (Figure 7 left).
d. Concomitant deepening of the jaws (Figure 5);
e. Cusps (Figure 8) expand to form ridges – lophodonty (Figure 7 right);
f. Molarization of premolars (Figure 9);

9. a. and b. above interpretable as adaptive responses to open,
grassland habitats; remainder, adaptations to eating grass.
Figure 7. **Left.** Normal, low-crowned (a.) tooth vs. hypsodont (b.) condition. In the latter, the cusps are elevated and covered with layers of cement. **Right.** Molar teeth in ungulates. A. Simple lophodont pattern (rhinoseros); B. Advanced lophodont condition (horse); C. Selenodont pattern (ox) characteristic of artiodactyls.

Figure 8. Dentition of a primitive placental mammal showing cusps on the upper (A.) and lower (C.) molars and premolars. Occlusion of the two tooth rows shown in B.
Figure 9. Tooth evolution in horses. a. Orohippus (middle Eocene); b. Mesohippus (Oligocene); c. Miohippus (Miocene); d. Merychippus (Miocene); e. Pliohippus (Pliocene); f. Equus (Pleistocene). Note progressive increase in size, development of ridges, reduction of 1st premolar and molarization of remaining premolars. Orohippus and Mesohippus were browsers.
III. Adaptive Topographies.

1. As grazers diverge from browsers, cheek teeth become proportionately higher crowned as evidenced by ectoloph length \textit{vs.} paracone height (Figure 10).

2. Simpson interprets this shift in terms of adaptive topographies (Figure 11).

3. \textbf{Question} (10 points). Why do you think Simpson imagined (as shown in Figure 11) that the browsing adaptive peak approached the grazing peak as horses evolved? Why do you think he imagined that the peaks subsequently diverged once the grazing peak had been “colonized”, \textit{i.e.}, once true grazers had evolved?

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure10.png}
\caption{Paracone height \textit{vs.} ectoloph length of M$^3$ in fossil horses. \textit{Merychippus} and \textit{Neohipparion} are grazers.}
\end{figure}
Figure 11. Simpson’s interpretation of horse evolution in terms of adaptive topographies. As horses evolved, the browsing adaptive peak moved toward the grazing peak thereby allowing for the evolution of true grazers with proportionately higher cheek teeth.