Allen's Rule, Phenotypic Plasticity, and The Nature of Evolution

by Greg Laden

Allen's Rule. One of those things you learn in graduate school along with Bergmann's Rule and Cope's Rule. It is all about body size. Cope's Rule ... which is a rule of thumb and not an absolute ... says that over time the species in a given lineage tend to be larger and larger. Bergmann's Rule says that mammals get larger in colder environments. Allen's Rule has mammals getting rounder in colder climates, by decreasing length of appendages such as limbs, tails and ears.

All three rules seem to be exemplified in human evolution. Modern humans tend to be larger and rounder in cooler environments than in tropical environments. Over time, the human lineage has gotten larger ... australopiths of the Miocene and Pliocene were smaller than Homo erectus and modern *Homo sapiens*. In comparing contemporary African modern humans and European Neanderthals, the latter are rounder and have shorter limbs, especially the distal parts of the limbs (forearms and the leg below the knees). In fact, this difference in body proportion is one of the key features that physical anthropologists use to distinguish between regular modern humans and Neanderthals when faced with that task.

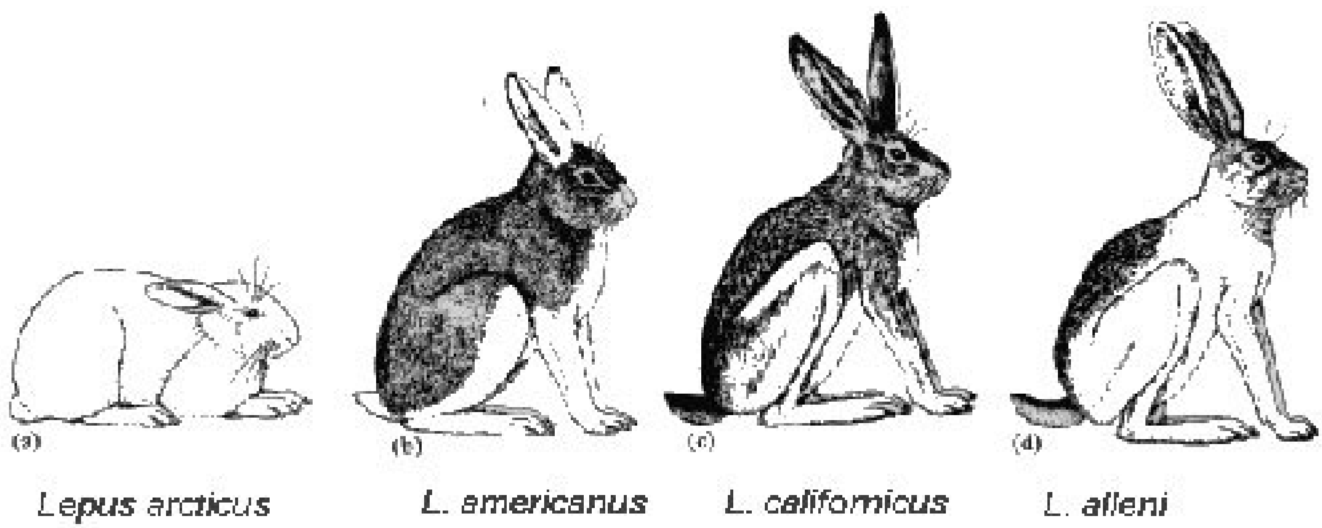

Figure 1. Bunnies demonstrating Allen's rule.

The usual assumption is that these changes in body form are selected for as a result of various environmental pressures, and that these features of body size and shape become adaptive features seen in particular populations. The body shape story is part of the Darwinian story of adaptation as well as, in some cases, the story of racial differentiation among humans or other organisms.

And of course, it is all wrong, as usual.

Well, OK, not *all* wrong, but certainly not as simple as one might think.

There is a paper just out in the *Proceedings of the National Academy of Sciences* that looks at body size proportions and Allen's rule, and that presents (and summarizes from earlier work) some interesting results. But before we look at that, let's make sure we are on the same page regarding the basic evolutionary models we are messing with here.

First, let's dispense with Cope's Rule because it really isn't too important here. The presumption is that bigger is better in enough different ways ... to avoid predators, to out compete conspecifics, whatever ... that over time there is a trend to get bigger.

Bergmann's rule -- mammals get larger in cooler environments -- is presumed to work because of the simple relationship between volume and surface area. Mammals, endothemeric creatures that they are, produce heat from their tissues (their volume) and lose it through their skin (their surface). As a a thing ... a mammal, a balloon, a color television set, whatever ... gets larger in size, the surface area goes up with a function approximated by a linear dimension squared, while the volume goes up with a function approximated by the same linear dimesion cubed. Volume grows faster than surface area, if shape is kept constant, when a thing gets bigger.

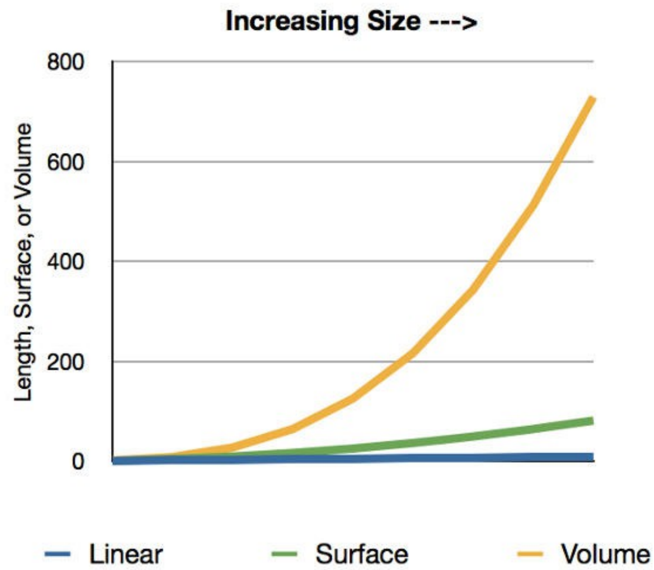

Figure 2.

So, having more heat-engine (volume, tissue) compensates for the increased loss via the surface (skin) in cold climates. Bigness is good in cool climates, and conversely, smallness is good in warm climates.

But shape need not stay constant. An object shaped like a sphere will have minimal surface area compared to volume, while an object shaped like a chopstick will have lots of surface area per volume. Getting all lean and gangly is a tropical thing to do, getting all rotund and short-limbed is an arctic thing to do. That's Allen's Rule. Shortening the limbs, tail, and in some cases, ears gets the roundosity that the cool-climate mammal benefits from.

This rule-like patterning of body size and shape has been observed within species and among related species distributed across climatically diverse geographical areas, or over time. Bergmann's rule has been observed in pack rats tracking climatic changes during the Pleistocene; Humans are said to vary in this matter, with tropical proportions being distinct from arctic proportions; rabbit species go from round short eared and short tailed forms to lanky long eared and long tailed forms, and so on.

But not all body size and shape effects that may in fact be tracking environmental clines are genetic. For instance, body size may be very much a function of diet and not genes, depending on the population.

The paper at hand examines Allen's rule in this regard. From the abstract:

> Allen's Rule documents a century-old biological observation that strong positive correlations exist among latitude, ambient temperature, and limb length in mammals. Although genetic selection for thermoregulatory adaptation is frequently presumed to be the primary basis of this phenomenon, important but frequently overlooked research has shown that appendage outgrowth is also markedly influenced by environmental temperature. Alteration of limb blood flow via vasoconstriction/vasodilation is the current default hypothesis for this growth plasticity, but here we show that tissue perfusion does not fully account for differences in extremity elongation in mice. We show that peripheral tissue temperature closely reflects housing temperature in vivo, and we demonstrate that chondrocyte proliferation and extracellular matrix volume strongly correlate with

tissue temperature in metatarsals cultured without vasculature in vitro. Taken together, these data suggest that vasomotor changes likely modulate extremity growth indirectly, via their effects on appendage temperature, rather than vascular nutrient delivery. When combined with classic evolutionary theory, especially genetic assimilation, these results provide a potentially comprehensive explanation of Allen's Rule, and may substantially impact our understanding of phenotypic variation in living and extinct mammals, including humans.

Most of that probably makes sense to the average science minded reader, but the term "genetic assimilation" may require some explanation. This is where a variant of trait...a measurable feature that look different across individuals...is found to look a certain way in a given population because of something non-genetic. Like, for instance, all people living in Canada wear warm hats in the winter. Then, over time, a genetic "answer" to the problem being addressed to the original trait happens to emerge and spread. So, at some point, a genetically determined form of hair that provides extra insulation emerges among Canadians and slowly spreads across the population, so a couple of thousand years later you see very few warm hats and mostly furry-headed people in Canada. In the more realistic situation referred to here, rabbits move into a cooler environment and adapt in a variety of ways including how their limbs end up growing (not of the adult rabbits that first moved there, but of their offspring) but later this phenotypic adaptation is augmented by genetically determined changes as selection works on whatever variation is in the population to make shorter limbs, and over time, the limb proportion of the rabbits is mostly genetic while it was originally mostly not genetic.

Figure 3.

In short, body proportions can be local non-genetic adaptations, or arise as a combination of genetic and ontogenetic causes. This paper further suggests that the non-genetic parts of the mechanism are different than previously thought.

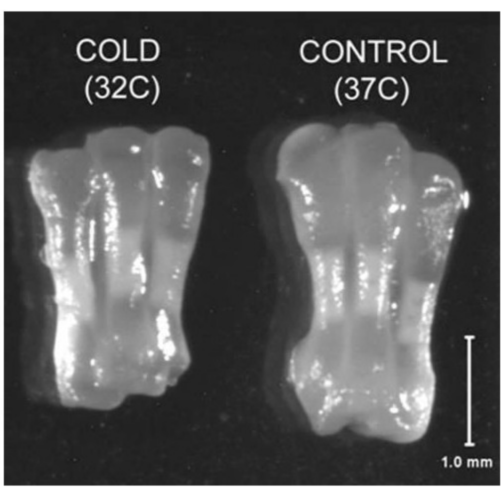

Figure 4.

The photograph in Figure 3 demonstrates the effect of environment on limb proportion. The researchers grew mice in very different temperatures, and low and behold, the mice grew up with different proportioned limbs. From the original paper's figure caption: *Temperature effects on femur length. Representative femora from mice housed at cold (7 degees C) and warm (27 degrees C) temperatures from weaning age to adulthood showing the effect of ambient temperature on extremity size. The underlying cause of such effects is not immediately obvious because homeotherms maintain tightly regulated internal body temperatures independent of their external environment.*

The same effect is seen when little mouse bones are grown in vivo. Have a close look at Figure

4. Notice the difference between the size *and shape* of the bone grown in cold vs. control (not cold) conditions, in this case, in a container in the lab, and not in the actual mouse.

Figure 5 is a graph showing the in vivo effects of cold, control, and warm grown metatarsals over two and four days. The colder the setting, the shorter the bone.

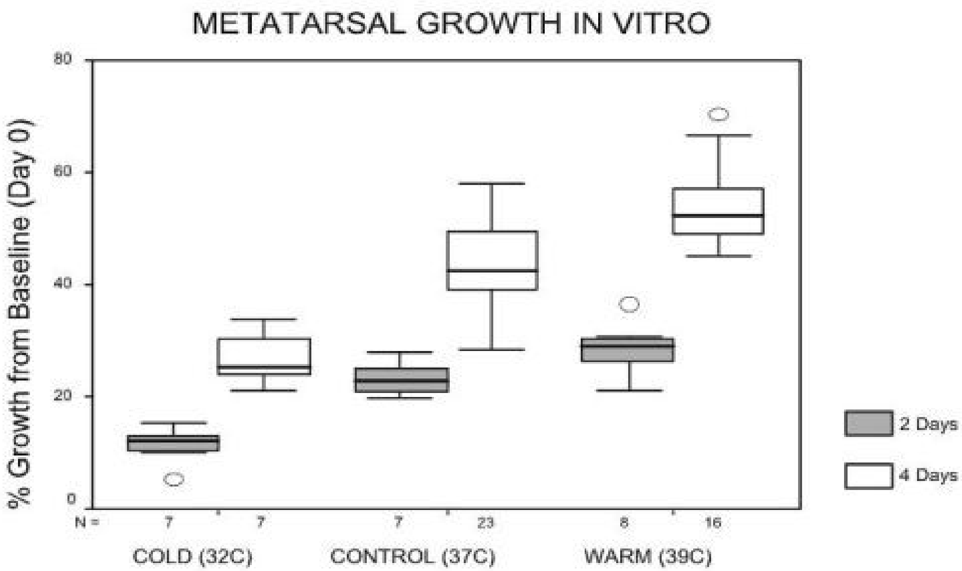

Illustration 1: Figure 5

From the paper’s conclusion:

> From an evolutionary perspective, Allen’s ”extremity size rule” may not actually reflect a functional genotypic adaptation in some or even many homeotherms (9, 10), but may instead be partially or wholly dependent on environmental temperature; that is, a secondary growth response to ”facultative extremity heterothermy” in mammals that maintain constant core body temperatures.

One would assume that significant differences in limb proportions between species that follow Allen’s rule are genetic, even if there is a phenotypic effect. I know of no widespread reports that tropical animals kept in temperate zoos or temperate or arctic animals raised in zoos in warmer climes show major body proportion shifts. On the other hand, since zoos can buffer the environment, especially for baby animals, and no one has looked for this specifically, I’m not taking any bets.

Within species … across clines or subspecies … this raises very significant (and addressable) questions regarding adaptation in the genetic vs. the ontogenetic realms. If Allen’s rule is primarily an ontogenetic effect in some species, one can still consider the possibility that it is adaptive, but the nature of adaptation becomes somewhat more nuanced. Which is appropriate, because adaptation is probably never as straight forward as the textbook version of it towards whic we tend to gravitate.

M. A. Serrat, D. King, C. O. Lovejoy (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth *Proceedings of the National Academy of Sciences* DOI:10.1073/pnas.0803319105