The tempo and mode of evolution
a neontological reappraisal

Melanie J. Monroe
Read not to contradict nor to believe but to weigh and consider.

-Sir Francis Bacon
List of papers

This thesis is a summary and discussion of the following papers, referred to in the text by their roman numerals. Portions of this thesis have previously been published in: Monroe M.J. and Bokma F. 2010. Punctuated equilibrium in a neontological context. Theory in Bioscience 129: 103-111, and are clearly marked in the text.


II. Monroe M.J., Mattila T.M. and Bokma F. Mass extinctions do not explain skew in interspecific body size distributions. Submitted manuscript

III. Monroe M.J. and Bokma F. Does character displacement affect long-term character evolution? Submitted manuscript

IV. Monroe M.J. Does competition drive character differences between species on a macroevolutionary scale? Submitted manuscript

V. Monroe M.J. and Bokma F. Do speciation rates drive rates of body size evolution in mammals? The American Naturalist 174: 912-918

VI. Monroe M.J. and Bokma F. Punctuated Equilibrium reconciles rates of evolution in mammals and birds. Submitted manuscript

VII. Bokma F., Monroe M.J. and Merilä J. Why species fail to adapt - a reply to Dr. Hugh Falconer. Manuscript

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ABSTRACT
The theory of “punctuated equilibrium” suggests that species evolve rapidly during or immediately upon speciation, “punctuating” long periods of little or no morphological evolution. Here I confirm that body size differences within clades of birds and mammals are best explained using a model of punctuated evolution. This allows me to suggest that rates of speciation and extinction are responsible for why there are more small mammals than large, as large mammals likely speciate and go extinct at a higher rate than small mammals, and hence undergo cladogenetic change more often. Likewise, mammals appear to evolve at a higher rate than birds, because mammals, as a whole, speciate and go extinct at a higher rate than birds. Furthermore I show that mass extinctions and competition, i.e. forms of natural selection, do not seem to explain differences in body size between species on a macroevolutionary scale. Taken together, these findings not only contradict the idea that apparently different rates of evolution are due to differential selection intensities, and emphasize the importance of the speciation process in evolution, but raise the intriguing question as to what limits evolution in established species. Here I suggest that phenotypic traits, dependent on one another for development and/or function may constrain evolution by exerting stabilizing selection from within the organism, as opposed to external environmental selection, which has been the main focus of evolutionary studies thus far.

Keywords  birds, extinction, macroevolution, mammals, microevolution, punctuated equilibrium, speciation
The tempo and mode of evolution - a neontological reappraisal

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This thesis, and the chapters to which it corresponds, suggests that the majority of body mass differences among species of birds and mammals have accumulated rapidly during speciation and not gradually during their subsequent existence. Here I propose:
1. That body mass differences between species of mammals and birds are better explained using a model of punctuated evolution than as the result of continuous gradual change (Chapters V, VI).
2. That mammals diversify faster than birds because they have higher rates of speciation and extinction (Chapter VI).
3. That a gradual mode of evolution or natural selection (e.g. size selective extinctions, competition) cannot explain differences in body mass within clades of birds and mammals (Chapters I, II, III, IV).
4. That evolution is often slow because of stabilizing selection on co-adapted phenotypic traits as opposed to external, natural selection (Chapter VII).

INTRODUCTION
Evolution is not synonymous with improvement or adaptation (Cook 1908) but is a theory of change, under which species traits are passed on from generation to generation, occasionally undergoing small or large changes. These changes can affect all types of traits and processes pertaining to a population or species. Once the “new” trait has spread across the population (or species), i.e. the mean trait value and underlying genetics of the population have shifted, it is referred to as evolution (Futuyma 2005).

Evolution is subject to different processes, one of which is speciation (Coyne and Orr 2004). Speciation is a term used to describe a process in which a new species arises (Cook 1906). This process can be driven by genetic drift, i.e. the random change in frequency of gene variants (Futuyma 1997), small population sizes, i.e. where a lack of genetic inflow may give rise to fixation of traits and genes (Cook 1908; Mayr 1942), hybridization (Coyne and Orr 2004 and references therein), and selection, i.e. external forces select for traits which may (but do not have to) increase an organism's fitness (Darwin 1859). Although selection may, in some cases, drive speciation, it is especially argued to drive gradual change in the phenotype of already established species over time, the other major component of evolution (Darwin 1859). This gradual mode of evolution is often accepted by evolutionary biologists as the “default” by which evolution occurs (Mayr 1982).
Charles Darwin wasn’t the first person to formulate a coherent hypothesis of evolution (Gould 2002:187). He was, however, the first (or at least the first we are aware of) to suggest a plausible mechanism which could drive evolutionary changes, namely, natural selection (Wallace 1855; Darwin and Wallace 1858; Darwin 1859). Natural selection refers to the differential reproductive success of individuals subject to how suitable their phenotypic traits are in the environment they live in. In other words, if an individual is well suited to its environment it will survive and pass on these “traits of survival” to its offspring. The more suitable or advantageous the trait(s), relative to the majority of individuals in the population, the more offspring an individual potentially can produce, thus allowing for accumulation of “advantageous” traits over generations. Thus, over time, as the advantageous traits accumulate within the population, the mean population phenotype will slowly change and evolution will occur. If natural selection drives evolution, then it can be assumed that differences between populations and species are an environmentally driven accumulation of adaptive traits over long periods of time (Darwin 1859).

WHY ARE MOST SPECIES SMALL?
Species differ in an abundance of traits, one of which is body size. Body size strongly affects an organism’s physiology and life history (Calder 1984; Schmidt-Nielsen 1984; Ruben 1995; Dayan and Simberloff 2005). Large size is usually thought to be selectively advantageous, as, among other things, a larger organism is expected to have the upper hand in regards to predation, extended longevity, generalized food habits and resistance to small scale environmental fluctuations. Of course there are costs of being large, for example, increased developmental time, food and water requirements, lower fecundity and susceptibility to rapid environmental changes (as summarized in Hone and Benton 2005). However, if the benefits of being large outweigh the costs, then why aren’t all organisms large?

Given all of the advantages of being large, it seems strange that most species are small (Brown 1984) (fig. 1). Several suggestions as to why this may be have been proposed. Probably the most obvious was summarized by Gould in (1988): that small species have higher rates of diversification, and large species have higher rates of extinction. It has been suggested that small species diversify at a higher rate due to (i) short generation times (i.e. most small species mature at an earlier age and produce more offspring during their lifetime than do large species) (Brown 1984) (ii) the available mosaic of niches (i.e. small species may, more often, specialize on particular resources, allowing them to divide resources and space more finely) (Hutchinson and MacArthur 1959; Brown 1984:77-83) and (iii) because large species may go extinct more often as they mature later in life, produce fewer offspring and have smaller population sizes (Gaston and Blackburn 1995; Kingsolver and Pfennig 2004; Hone and Benton 2005). Another suggestion as to why there are more small species than large is Cope’s rule. Edward Drinker Cope (1887) suggested that evolutionary lineages increase in size over time, i.e.
descending lineages are, on average, larger than their predecessors. This suggests that upon origination lineages are small and become larger with each successive descendent species.

![Figure 1. Body length distribution of all known terrestrial animals (modified from May 1978).](image)

Estimates are based on crude measurements and guess work and were originally binned (histogram) such that the number of species was more accurately represented by bin height.

CHAPTER I: COPE’S RULE

Cope’s rule remains controversial (see Jablonski 1997; Alroy 1998; Kingsolver and Pfennig 2004; Hone and Benton 2005; Moen 2006; Butler and Goswami 2008; Clauset and Erwin 2008). Many fossil studies reported evidence in favour of Cope’s rule (Alroy 1998; Kingsolver and Pfennig 2004; Hone and Benton 2005; Hone et al. 2005; Hone and Benton 2007; Clauset and Erwin 2008; Hone et al. 2008). Others argue that the “rule” is a statistical artefact (Solow and Wang 2008), a passive tendency (Stanley 1973; McShea 1994; McShea 2000) or that lineages evolving to become larger are no more common than those which are becoming smaller (Gingerich 1974; Jablonski 1997). Recently we (Monroe and Bokma 2010a – Chapter I) estimated the rates of body size evolution (Bokma 2008; Mattila and Bokma 2008) from 3253 living mammal species (Smith et al. 2003) using a nearly complete molecular phylogeny (Bininda-Emonds et al. 2007, 2008) to compare whether a model with or without Cope’s rule better describes the body size distribution of present day mammals. From here on body size will always refer to log(grams). The model with Cope’s rule assumes that descendants will be larger than their ancestors, meaning that when a new species emerges it will differ from that of its ancestor by a normally distributed amount $N(d, s_v^2)$, where $N$ refers to the normal distribution, $d$ is the strength of Cope’s rule (i.e. the average difference in body size between ancestor and descendant) and $s_v^2$ the rate of cladogenetic change. Cladogenetic change refers to the phenotypic difference between an incipient species and its ancestor. If $d>0$ Cope’s rule applies whereas if $d≤0$ it does not. Our best estimate of the ancestral-descendent body size bias was $d=0.0044$, suggesting that descendants are, on average 0.4% larger than their predecessors, a negligibly small estimate. A formal model comparison strongly favours the simpler model.
without Cope’s rule. So, Cope’s rule does not seem to explain why there are relatively few large-bodied organisms when compared to the number of small bodied organisms.

CHAPTER II: SIZE SELECTIVE MASS EXTINCTIONS

Even though large body size is often suggested to be an advantage, some of the associated costs, i.e. lower fecundity and increased developmental time (Hone and Benton 2005), may render large species susceptible to major environmental changes (Diamond 1989; Gaston and Blackburn 1995; Blackburn and Gaston 1998; Alroy 2001; Stuart et al. 2004). As previously mentioned, the most obvious explanation for positively skewed body size distributions is that large species go extinct and small species speciate more frequently (Gould 1988). Small species are predicted to survive environmental perturbations for the same reasons they are predicted to speciate more often than large species, namely, due to short generation times, large population sizes (allowing for random mating and other stochastic processes), niche availability and their ability to exploit resources (Hutchinson and MacArthur 1959; Brown 1984). It could therefore be expected that if ancestral species have undergone size-selective mass extinctions that eliminated predominantly large bodied species, the majority of successors would be small. However, we show (chapter II) using simulations of body size evolution that even extremely size-selective extinction has little effect on the positive skew of body size distributions. In fact, selection against large size may skew body size distributions towards large size. This is because by decreasing the number of the largest species the upper tail of the distribution becomes relatively shorter than the lower tail.

To determine whether or not the most recent of the “big five” mass extinctions, the Cretaceous-Paleogene (K-Pg), has influenced the body size distribution of existing species, we calculated the amount of body size skewness through time using data from 6236 birds (Dunning 1993) and 3253 mammals (Smith et al. 2003). For mammals we reconstructed the ancestral phenotypes for each node (i.e. branching point) on a phylogenetic tree (Bininda-Emonds et al. 2007, 2008), and subsequently calculated a measure of skew for each node, or point in time. Unfortunately, due to a lack of an acceptable phylogenetic tree this is not an appropriate analysis for birds. Instead, using a family level phylogeny (Sibley and Ahlquist 1990) for birds we calculated the body size skew for the extant species belonging to each lineage at each branching point of the tree. Before the first branching there is only one lineage (containing all species) yielding a single skewness. At the first branching point there are two lineages, yielding two skewnesses, and at the final branching, which separates the youngest sister families, there are as many skewnesses as families. We calculated skewnesses extending back to before the K-Pg extinction which occurred approximately 65 million years ago. Body size distributions were marginally more skewed in clades which originated during the Cretaceous than were their successors that originated from the surviving lineages after the K-Pg extinction. Although these
results cannot confirm whether or not the K-Pg mass extinction was size selective, it can tell us, that this event is not responsible for the skew in the size distributions of extant birds and mammals. In fact, skewness seems to increase as the number of species in a clade increases. So, the marginally higher skew of lineages that originated during the Cretaceous seems explained by the on average greater number of species in older clades: the subclades that emerged after the K-Pg transition all contain fewer species and the fewer species there are, the less skewed their body size distributions.

Above we have eliminated two possible explanations for ubiquitous skewed distributions of body sizes: the idea that evolutionary lineages start small and evolve to larger size, i.e. Cope’s rule, and that the K-Pg mass extinction, by selecting against large bodied species, may be responsible for the current skewed size distributions. Why then, do we see such a large discrepancy in the numbers of large and small bodied organisms? At the end of chapter II we suggest that skewness increases with increasing numbers of species, i.e. species richness. If this holds true, then why, when a clade diversifies, are there more small bodied species than large ones? Probably the simplest explanation is due to the limitations of ecological niche space (Hutchinson and MacArthur 1959). As previously mentioned, the amount of geographical area that can be home to the number of small species exceeds that of large species, meaning that there is more available space and resources for small species than for large. However, the more species there are in a certain geographical area, the less area per species available. As species numbers grow so does the pressure on the shared resources, leading to competition between species (e.g. Brown and Wilson 1956; MacArthur and Levins 1967; Brown 1984).

CHAPTER III AND IV: COEXISTENCE

Resource competition among coexisting species may lead to morphological divergence, i.e. character displacement (Brown and Wilson 1956). Character displacement suggests that competition decreases the fitness of the phenotypically most similar individuals from different populations, and, as a consequence, pushes apart their average trait values. Hence, an increase in the number of phenotypically similar species coexisting and competing for the same resources may increase rates of morphological evolution. We developed a method to test whether or not character displacement seems to be responsible for the differences we see between extant species (Chapter III). Under a null model, we expect that phenotypic evolution is unbiased and unconstrained, meaning that over evolutionary time, i.e. the length of a phylogenetic branch, a specific trait can evolve randomly. This implies that at any point in time two species may have exactly the same phenotype (fig. 2A). However, if competition influences evolution it is expected that when species become too phenotypically similar, competition will drive them apart (fig. 2B). If competition between species pushes phenotypic traits apart the traits will never be equal to one another, thus we should see phenotypic order on a
phylogenetic tree. We can then rank species trait values along the tips of a phylogenetic tree and calculate their ascending or descending order. If the species appear on the phylogenetic tree in the same order as their trait values, then a rank correlation is close to one. This would always be the case when competition has fully constrained phenotypic evolution so that no two species can have the same trait value at the same time. If, however, the correlation is low, i.e. close to zero, then competition is not responsible for the order of trait values on the tree. We tested this method using 13 phylogenies of mammalian body size. Our results did not suggest that competition affected the phenotypic differences we see between these species.

![Figure 2](image)

Figure 2. A shows unbiased evolution, i.e. species are able to invade related species phenotypic space (illustrated by trait values 3 and 4). B shows constrained evolution – when species phenotypic traits are too similar they push one another apart.

Furthermore, I conducted a study using geographical range overlap (www.iucnredlist.org see chapter IV for specifics), body masses (Smith et al. 2003) and the phylogenetic relationships (Bininda-Emonds et al. 2007, 2008) of 27 mammalian families to test whether coexistence seems to accelerate or decelerate trait evolution on a macroevolutionary scale (Chapter IV). Coexistence is supposed to lead to one of two major outcomes, character displacement (Brown and Wilson 1956), as described above or limiting similarity (Hutchinson 1961; MacArthur and Levins 1967; Abrams 1983). Limiting similarity suggests that there is a limit to how similar two coexisting species can be to one another. Thus, we would expect that the more phenotypically similar species that coexist with one another, the slower evolution will go. Simply put, similar coexisting species will “trap” one another in phenotypic space so that competition forces the species to remain similar and evolve slowly. Relaxing competition would allow species to evolve. On the contrary, if competition drives evolution through character displacement, we should expect that species coexisting with many similar species will have higher rates of evolution, thus differ more phenotypically from one another than they would if competition was relaxed.

I created an algorithm to compare triplets of species to determine the effect, if any, of character displacement or limiting similarity on a macroevolutionary time scale (refer to chapter IV). Triplets consisted of two species, B and C and an outgroup, A, all of which were phylogenetically related, but did not geographically coexist with one another (coexistence here is defined as species which overlap in their broad-scale geographical distribution). Species B always coexisted with more species than did species C. Body size differences between AB and AC were calculated and
compared to find out if species with very many coexisting species (i.e. B) seem to be more or less phenotypically similar to the outgroup. My results suggest that the number of competitors a species may be subject to has very little effect on the differences between the body masses of living mammal species. Thus, competition does not seem to accelerate or decelerate rates of phenotypic evolution.

Cope’s rule, mass extinctions and competition have thus far failed to explain why most species are small, or more generally, why there are differences between body sizes of present day species. If body size distributions are more skewed in species rich clades, and little affected by clade age itself (Chapter II), then maybe the answer lies not in processes driving (or not) phenotypic differences between species, but in the mode of evolution itself.

NOTE: The following pages 14-26 are an excerpt from: Monroe M.J. and Bokma F. 2010. Punctuated equilibrium in a neontological context. Theory in Bioscience 129: 103-111. Minor errors have been corrected from the original text and additions to the text are highlighted in blue.

**ON THE MODE OF EVOLUTION: A HISTORICAL INTRODUCTION**

Hugh Falconer (1808 – 1865) was a Scottish botanist, geologist, and palaeontologist. He studied natural history at the University of Aberdeen, where he eagerly attended the botanical classes of Prof. R. Graham, and those on geology by Prof. R. Jameson. Jameson, renown for motivating his students, also taught Charles Darwin although Darwin reportedly found the lectures boring (possibly because he was only 16 at the time). Falconer graduated in 1826, after which he continued to study medicine, and became a Medical Doctor in 1829. With his medical expertise he obtained a position as an assistant-surgeon in the Bengal establishment of the British East India Company, where he established his scientific credibility and position in India by conducting an extensive examination of the fossil bones from Ava, upper Burma. Soon thereafter, in 1832, Falconer became superintendent of the Saharanpur botanical garden, where he studied fossil mammals in the Siwalik Hills. He noticed that this fossil record showed long periods of stasis interrupted by short periods of rapid change, a pattern later to be known as “punctuated equilibrium” (Eldredge and Gould 1972).

Even though Darwin found the lectures by Jameson dull (and even neglected his medical studies so that his father decided to send him to Christ’s College, Cambridge) they introduced him to the study of geology and zoology. Interestingly, the zoology course concluded with philosophy of zoology, the first subject being “origin of the species of animals”. As is well known, after his journey on board HMS Beagle (where he became the crew’s naturalist largely due to neglected studies in Cambridge), Darwin began to slowly develop his ideas of natural selection; noting that “one
species does change into another” [in his red notebook] and made his first drawing of a tree-like phylogeny.

It is not known whether Darwin and Falconer knew each other before 1845, but Falconer probably soon obtained a copy when, sparked by Alfred Russell Wallace’s progress, Darwin finally published “On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life” in 1859. Falconer liked Darwin’s general ideas. Having returned from India to England due to poor health in 1855, he studied fossil species corresponding to those which he had discovered in India, in particular species of mastodon, rhinoceros, and elephant. Hence, he did not take up the issue of stasis and rapid change in Siwalik Hill mammals but instead confronted Darwin with a similar pattern in the European mammoth. With a letter written September 1862 he sent Darwin a manuscript describing fossil and recent species of elephant: “I am bringing out a heavy memoir on Elephants - an Omnium gatherum affair - with observations on the fossil & recent species. One section is devoted to the persistence in time of the specific characters of the mammoth. I trace him, from before the Glacial period, through it, and after it, unchangeable & unchanged, so far as the organs of digestion (teeth) & locomotion are concerned. Now the glacial period was no joke - it would have made ducks and drakes of your dear pigeons & doves.”

What Falconer pointed out was, in other words, that Darwin’s theory of evolution by means of natural selection was at odds with the fossil record. Evolution by natural selection would suggest that a species like the mammoth would undergo significant changes in crucial body parts, driven by the climatic vicissitudes of several ice ages. The fossil record, however, showed stasis. Darwin replied in a letter on the first of October 1862 “You speak of these animals as having been exposed to vast range of climatal changes from before to after the Glacial period; I should have thought from analogy of sea-shells, that by migration (or local extinction when migration not possible) these animals might and would have kept under nearly the same climate” (i.e. niche/habitat tracking). Nevertheless, Darwin did add to “The Origin”: “It is a more important consideration, clearly leading to the same result, as lately insisted on by Dr. Falconer, namely, that the periods during which species have been undergoing modification, though very long as measured by years, have probably been short in comparison with the periods during which these same species remained without undergoing any change”.

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The above historical account shows many parallels to the now well-known theory of “punctuated equilibrium”, coined by Eldredge and Gould in 1972, which frames the fossil pattern of stasis and rapid change in an evolutionary biological context. However, there is an important, often neglected distinction: In the late nineteenth century, most scientists probably agreed that evolution took place, but the idea that evolution was caused by natural selection, as Darwin claimed, remained disputed. Only a minority of contemporary scientists supported Darwin’s idea of natural selection as the main mechanism behind evolution. On the contrary, by the second half of the twentieth century most evolutionary biologists “accepted as an article of faith not only that all macroevolutionary phenomena were consistent with the laws of genetics, but also that they could be explained in terms of the phenomena of geographic variation and speciation” (Mayr 1982).

It wasn’t until the early 1900’s, after the rediscovery of Gregor Mendel’s 1866 paper on heredity, that botanist Hugo De Vries misinterpreted phenotypic differences between individual primroses, and introduced the idea of rapid speciation. De Vries (1901) suggested that new species can arise over night by so-called macromutations. It was later discovered that these “mutations” actually represented polyploidization (Futuyma 1997:24; Eldredge 2000:122-124). Nevertheless, the idea of instantaneous genetic changes resulting in variation between individuals and possibly between species may have inspired geneticist Richard Goldschmidt to introduce the concept of “hopeful monsters”. Goldschmidt (1940) proposed that sudden and drastic changes, re-organizing the entire genome of an organism, may give rise to new potential species. He acknowledged that most major genetic revisions would be deleterious, and would subsequently become eradicated from the population by selection, but those few organisms that survived with these major genetic changes would be, what he termed “hopeful monsters”, able to adapt to niches radically different from those occupied by their ancestors (Futuyma 1997:24, 680-681; Eldredge 2000:135).

An example of a “hopeful monster” was the ancient Archaeopteryx, as a saltation producing a fan of tail feathers would have given it an advantage in flying that others did not share. However, these ideas of saltation, i.e. the idea that a single evolutionary step from one generation to the next can produce a new species, have been time and time again refuted. Theodosius Dobzhansky (see Eldredge 2000:126-128), Ernst Mayr (1942), and George G. Simpson (1944) along with several others (e.g. Charlesworth 1982;  

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1 Historical information in this introduction was obtained from The Friends of Falconer Museum (www.falconermuseum.co.uk) and the Darwin correspondence project (www.darwinproject.ac.uk)
Templeton 1982) disproved these ideas of saltation by explaining, for example, that feathers alone could not increase Archaeopteryx’s flight ability, but natural selection could, gradually, over time, improve skeletal and muscular structures that would be needed for flight. In addition, it has been pointed out that primordial feathers did not provide much aid in flying, and probably developed as thermoregulatory device, and became used for flight by exaptation (Gould and Vrba 1982) (i.e. a trait, like feathers, evolves for one reason (to keep the bird warm) but is used for another (e.g. flight)).

With the idea of saltation lacking support, explanations as to whether or not the pattern observed in the fossil record was plausible remained a mystery. It wasn’t until 1954 that a possible explanation of how speciation may frequently occur sparked interest. While studying speciation in island birds in New Guinea and the Pacific, Ernst Mayr (Mayr 1954) noted that most speciational changes, i.e. major trait changes resulting in novel species, took place at peripheral locations, suggesting that speciation may occur more frequently when small populations are exempt from gene flow from the main population. Eldredge (1971) revisited this idea, pointing out that most paleozoic invertebrates showed no change in species-specific characters during the duration of their stratigraphic occurrence and instead seemed to change rapidly in peripheral isolates. To describe this pattern Eldredge and Gould (1972) proposed the –now famous- theory of punctuated equilibrium. Their articles rekindled the discussion initiated by Falconer more than a century earlier, but now against a background where natural selection was widely accepted, and regarded as the default explanation for a wide range of evolutionary phenomena.

Shortly after Eldredge and Gould introduced their theory of punctuated equilibrium, Stanley (1975) published an article that would spark debate among biologists, a debate that is still going on today. In this publication, Stanley discussed two important matters: First he discussed four significant evolutionary phenomena that, he argued, could not be explained by a gradual model of evolution. These were:

i. Adaptive radiations – which produce many divergent species very quickly from a single ancestor

ii. Major environmental changes which resulted in numerous speciations and subsequently extinctions – e.g. widespread speciation when environmental conditions change, followed by widespread extinction during the next period of climatic change, but all the while retaining the ancestral genus more or less unchanged. Gradual evolution would predict that the species within the genus would change over time, meaning that the ancestral phenotype would not persist
iii. Living fossils – species which phenotypically have not changed significantly from the time, long ago according to the fossil record, when they originated. According to gradual models of evolution predicting continuous change over time, it is highly unlikely that some species would remain in a more or less static state for hundreds of millions of years.

iv. Generation time – here, Stanley argued that if evolution is the result of natural selection in subsequent generations of a population, the rate of evolution should be higher in taxa with short generation times; each generation is arguably a single instant of natural selection. This correlation between rates of evolution and generation times among fossil taxa had not been demonstrated.

The second issue Stanley discussed, and arguably the issue that sparked most debate, was the idea that if the mode of evolution followed the model of punctuated equilibrium, microevolution was “decoupled” from macroevolution. The argument went as follows: if speciation events are the major events contributing to differentiation between species, then speciation would be the process driving evolution. If speciation, like mutation, is an essentially random process (Mayr 1963), then processes such as selection acting in established species would not be, as had become widely assumed, the driving force behind macroevolution (Stanley 1975).

Because evolution by means of natural selection was (and is) the ruling paradigm in evolutionary biology, biologists met Stanley’s arguments (1975) with resistance, and articles were vigorously published in support of selection and gradual evolution. However, the question whether evolution precedes gradually over time or in bursts when new species emerge turned out surprisingly difficult to test. Studies of the fossil record were criticized for relying on fossil morphospecies: only species that are morphologically distinct can be distinguished based on fossil remains (Stebbins and Ayala 1981). In other words, the pattern of change concentrated in the emergence of novel species was attributed to the alleged habit of palaeontologists to invoke novel species only when morphology changes rapidly.

Existing species do not have this disadvantage. Generally, extant species are subjects of the biological species concept which separates species from one another on the basis of whether or not they (are able to) mate and produce viable offspring (Mayr 1995). Hence, existing species can be distinguished even when the species’ phenotypes would otherwise be too similar to tell apart. The opposite is also true, although probably rare: if phenotypes of populations within a species are very different, but the populations still mate and produce viable offspring, we can conclude that they are still the same species (examples can be found in, but are not limited to, populations
which differ, e.g. in colour or size, due to selection (sexual or natural), e.g. predation (see Reznick and Endler 2004). Unfortunately, speciation typically takes much longer than the span of human inquiry so that it is virtually impossible to study speciation in biological species from its earliest stages to completion. Consequently, evolutionary biologists continue to disagree on whether the pattern of stasis and rapid change in fossil records applies to the formation of new biological species (see Eldredge and Gould 1972).

Nevertheless, the increased interest in macroevolution from the community of evolutionary biologists and ecologists, driven mainly by the development of the field of phylogenetics, has produced a series of papers attempting to confront the theory of punctuated equilibrium with neontological evidence. Unfortunately, despite the wealth of data extant species provide and despite powerful computational methods, evolutionary biologists, unlike palaeontologists, seem to readily neglect half of the theory of punctuated equilibrium: Punctuated equilibrium is essentially studied in two parts by evolutionary biologists: The first part is stasis, which receives relatively little attention, but the attention that it does receive often corresponds to why stasis may occur as opposed to whether or not the pattern actually does occur. The other part is rapid change during speciation, which regained popularity from speciation research, but is studied mainly in respect to whether or not it occurs. Thus, while theoreticians attempted to explain stasis and discussed the role of natural selection, phylogeneticists focus on detecting the tempo and mode of character evolution, with very few studies addressing both issues. I adopt this dichotomy here, and first review studies of stasis, and then focus on the use of phylogenies as a substitute for the fossil record to investigate whether evolution is accelerated during speciation.

STASIS

Several explanations as to why species may exhibit long periods of stasis have been proposed and refuted (e.g. Hansen and Houle 2004). One of the most frequent and obvious explanations proposed is stabilizing selection (Futuyma 1987; Hansen and Houle 2004). Broadly speaking, stabilizing selection is a type of natural selection which favours the average phenotype (Ridley 2004:76-77). Futuyma (1987) criticized this explanation of stasis and questioned why stabilizing selection would favour the same phenotype over thousands or even millions of years in spite of an ever changing environment. In addition, Hansen and Houle (2004) argued that in order for stabilizing selection to explain stasis, stabilizing selection must not only be extremely common, but the selective optimum can fluctuate only within a very narrow range. They further argue that single traits, affected only by a
single selective factor, may indeed have stable optima, but state that most quantitative traits are likely to have several selective factors and any of those selective factors could be susceptible to changes in the environment.

Another explanation for stasis, proposed by Wake et al. (1983), suggests that plasticity in one set of traits would allow other traits to remain stable. For example, Lind and Johansson (2007) showed that the frog species *Rana temporaria* displayed plastically varying rates of development depending on how quickly the pool in which they live dries up. According to the theory proposed by Wake et al. (1983), this should allow other traits to remain static in these populations. Similarly, it has been suggested that plasticity allows for adaptation to different environments without changing the genetic makeup of a species. If this is true, then phenotypic traits would change in order to allow existence in different environments, but the underlying genetic variation would remain intact allowing trait fluctuation. This would likely delay evolution as trait canalization (i.e. a trait becomes “locked” so that it is consistently reproduced, often due to a lack of genetic variation) is reduced or even selected against (Pigliucci 2010 and references therein). Contrarily, however, a review by Crispo (2007) suggests that phenotypic plasticity promotes evolution by allowing initial adaptation to different environments.

A more ecological explanation for stasis is niche or habitat tracking. The idea behind niche tracking is that organisms can search for favourable living conditions instead of adapting to environmental changes, which may result in the stabilization of several selective factors (Darwin 1962; historical correspondence; Eldredge 2000). Again, Hansen and Houle (2004) criticized the idea of niche tracking by pointing out that it seems unlikely that optimal habitat preference would remain stable in an ever changing environment. Many different suggestions, more than are reviewed above (for more examples see Monroe and Bokma 2010b), of how species may remain in stasis for long periods of time throughout the fossil record have been proposed (e.g. Wake et al. 1983; Williams 1992; Eldredge 2000; Eldredge et al. 2005). At the same time, there are also many criticisms for several of these theories (e.g. Futuyma 1987; Hansen and Houle 2004) and thus, the question of why stasis occurs remains effectively unanswered. The correct explanation may be one of relative frequencies of the mechanisms already proposed, but we can only conclude that there is no consensus as to how general stasis is as an evolutionary phenomenon, let alone as to what causes it.
RAPID CHANGE
Conceptually, our understanding of rapid change in incipient species has not progressed much beyond Mayr’s (1954) ideas of speciation in peripheral populations, on which Eldredge and Gould (1972) based their theory of punctuated equilibrium. It has been shown theoretically that peripheral populations may rapidly adapt to new optima when reproductive isolation evolves as it frees those peripheral populations from the genetic load introduced by migration from more central populations in a species range (García-Ramos and Kirkpatrick 1997). Perhaps the biggest conceptual progress in this respect comes from theoretical studies of sympatric speciation, which show that selection may create barriers to gene flow even within populations, thereby facilitating or even promoting speciation while simultaneously driving rapid phenotypic change (Rundle and Nosil 2005). Hence, rapid change in incipient species is widely recognized as a possible evolutionary phenomenon. The question therefore is whether or not it is a frequent phenomenon.

Very soon after the theory of punctuated equilibrium was introduced, evolutionary biologists explored the possibilities of using phylogenies of extant species to substitute for the time frame that had traditionally been provided by the fossil record. In fact, the same year that the theory of punctuated equilibrium was published, (Kohne et al. 1972) showed, by studying the rates of DNA change in primates, that rates of nucleotide sequence divergence were elevated during periods of extensive speciation relative to other periods as judged from the fossil record. Similarly, Bush et al. (1977) used rates of chromosome evolution to determine that mammals seem to speciate more frequently than other vertebrates. They further suggested that these high rates of speciation associated with high chromosomal evolution support the idea that many mammal species have diverged allopatrically, that is, allowing for increased genetic differentiation between species. Additionally, Bradshaw et al. (1995) illustrated that reproductive isolation in monkey flowers, caused by a difference in pollinators, can lead to major genetic mutations allowing for major mutations to fix more readily (see also Coyne 1995).

The same year that Stanley (1975) famously claimed that microevolution is decoupled from macroevolution, two studies (Avise and Ayala 1975; Avise et al. 1975) were published supporting gradual evolution (even though it is not sure they were published with that purpose). These studies investigated the correlation between genetic differentiation, time and the number of speciation events in species rich and poor extant phylogenetic clades. It was predicted that if evolution were gradual, genetic variation would increase over time, while if evolution were accelerated by speciation, genetic
variation would be greatest in the species-rich clades. The results from Hawaiian (Avise and Ayala 1975) and North American minnows (Avise et al. 1975) suggested that genetic differentiation was correlated to time, supporting a gradualistic model as opposed to the speciational (cladogenetic) model. These early studies were based on a principle that later studies have elaborated on: if evolution is a largely gradual process, recently diverged species should be similar as compared to species that had a common ancestor long ago. That is because species that recently shared a common ancestor have not had enough time to gradually evolve distinct phenotypes. In contrast, if evolution takes place rapidly when new species emerge, species can be phenotypically distinct even if they very recently shared a common ancestor. This principle applies to pairs of sister species as well as to clades consisting of several species. Thus, we can infer the mode of phenotypic evolution by comparing sister species pairs of different age, or by comparing phenotypic variability in clades of different age and species numbers. Recent methods employ more sophisticated algorithms, but are still based on these same premises employed by the earliest attempts to distinguish between gradual and punctuational evolution using extant species.

**NEONTOLOGICAL METHODS**

As techniques to determine nucleotide sequences became more widely available, the number of molecular phylogenies published increased dramatically, and methods were developed to compare models of gradual and punctuational evolution on molecular phylogenies. A conceptually particularly illustrative method was developed by Mooers et al. (1999). They argued that if evolution were gradual, phenotypic differences between species should be proportional to the length of the branches separating them on the phylogeny. If, on the other hand, evolution were concentrated in speciation events, branch lengths were irrelevant, as every speciation would contribute equally to phenotypic differences. Even though the above approach is illustrative due to its conceptual simplicity, it has two important drawbacks. In the first place Mooers et al.’s (1999) method, like earlier methods, compared a strictly gradual to a strictly punctuational model. It is however quite unlikely that species in nature change solely gradually over time or exclusively during speciation. A more realistic scenario is that species change both when they emerge and during their subsequent lifetime, although perhaps more quickly during emergence. The interesting question then becomes what part of interspecific phenotypic variation is due to gradual change and what part is due to punctuational
change. The second drawback is that the model assumed that extinction never occurs. Phylogenies of present-day species are pruned of extinct species because it is extremely rarely possible to obtain for example nucleotide sequence data for extinct species. However, the speciation events pruned from the phylogeny by extinction may have contributed to the phenotypic differentiation of present-day species. For example, if species C is a descendant of B and B in turn a descendant of A, then A and C would appear as sister species on a phylogeny if B went extinct. But the origin of B did contribute to the phenotypic difference between A and C. Therefore, extinction and speciation rates have to be taken into account to properly estimate how much gradual and punctuational change contribute to phenotypic evolution.

Accounting for the rate of speciation and extinction is perhaps the most demanding aspect of quantifying the relative contributions of gradual and speciational change to phenotypic evolution. In the first place, rates of speciation and extinction are generally poorly known. Assuming that these rates would be known, the number of speciation events that are pruned from the phylogeny are expected to increase with branch length. Still, the actual number of pruned speciation events will often differ by chance even between equally long sister branches, and even if the number of pruned speciation events is equal in two branches, the number of events that affected the phenotypic difference between extant species may differ. Moreover, ancient branches are expected to be pruned of more speciation events than more recent branches of the same length, as the resulting species have had a longer time to go extinct. Therefore, the challenge of partitioning the phenotypic variation among present-day species using neontological, phylogenetic approaches lies in properly accounting for extinction.

To overcome the problems associated with earlier neontological methods, Bokma (2002) used a model of evolution that incorporated gradual and speciational evolution, as well as extinction, in a statistically relatively well-understood manner. In this model, gradual evolution was described as Brownian motion over time. Named after the Scottish botanist Robert Brown who observed random movement of pollen grains submerged in water, Brownian motion is a mathematical model used to describe such random movements. When modelling Brownian motion over time, the displacement of a species’ phenotype between two points in time is normally distributed, with the variance of the distribution increasing linearly with the time span. The use of the normal distribution makes Brownian motion one of the simplest and best understood continuous-time stochastic processes and is therefore widely used as a model of phenotypic
change. Because gradual phenotypic evolution was modeled using the
normal distribution, it was decided to model also cladogenetic evolution
using this distribution: incipient species become different from their
ancestor at the moment of reproductive isolation (i.e. instantaneously) by a
normally distributed amount. Because cladogenetic change was modeled as
an instantaneous event, the variance is a constant, independent of time.
Cladogenetic change occurs always when a new species emerges, but not all
species have present-day descendants, of course. This relatively simple
model incorporates both gradual and punctuational evolution, as well as
rates of speciation and extinction, and allows for statistical evaluation of
hypothetical rates of gradual and speciational evolution.

Even with a general and relatively simple model of combined gradual-
punciational evolution it remains difficult to obtain statistical estimates of
rates of phenotypic evolution. The difficulty arises from the many unknown
parameters of the model. If evolution is assumed to be purely gradual, the
phenotypic difference between an ancestor and its direct descendant is a
function of the phenotypes of the ancestor-descendant pair, of branch
length, and of the rate of gradual evolution. The ancestral phenotypes have
to be estimated in any case, and if the phylogeny provides the branch
lengths, the rate of gradual evolution is the only additional parameter to be
estimated. If, on the other hand, it is taken into account that evolution may
be accelerated by speciation, many additional parameters have to be
estimated (the ancestral character states and the rate of gradual evolution
have to be estimated in any case). Since speciational evolution occurs in
incipient species, the number of speciation events on a branch has to be
estimated. This can be a different number for every branch of the
phylogeny. As cladogenetic evolution is assumed in incipient species it
should also be estimated which of two lineages resulting from a bifurcation
in the phylogeny was the emergent species and which was the existing
species. Finally, the numbers of speciation events depend on the rates of
speciation and extinction, which also have to be estimated. Hence even this
simple model of combined gradual-speciational evolution is parameter-rich.

More recently, Bokma (2008) developed a Bayesian algorithm to
simultaneously estimate all the parameters of the combined gradual-
speciational model, using Markov Chain Monte Carlo (MCMC) to sample
from the posterior distribution. This Bayesian approach yields estimates of
all parameters: the rates of speciation and extinction estimated from the
branching times of the phylogeny (Nee et al. 1994; Bokma 2003), the
numbers of speciation events contributing the phenotypic evolution of the
extant species for every branch, which lineage was the novel species at
every observed split, ancestral phenotypes, as well as the rates of gradual
and speciational phenotypic evolution. The advantage of using MCMC sampling is that it not only provides point estimates, but rather the entire posterior distribution of parameters is obtained. In addition, the dependency of parameter values on one another can be investigated from the joint posterior distributions. For example, if the extinction rate is low, it is unlikely that branches are pruned of many speciation events, and as observed phenotypic differences are ascribed to fewer speciation events, the estimated rate of cladogenetic evolution per speciation event will be higher. Moreover, the Bayesian structure of the algorithms allows for missing data and for the use of prior information. Prior information can be particularly useful, since, for example, the phenotypes of species are often only estimated. For example, if we compare limb lengths of five individuals to those of five other individuals from the same populations, we will observe a difference. Similarly we will observe a difference between the average phenotypes of individuals sampled from different species even if the true mean phenotypes of the species are exactly equal. Prior information may also be available for other parameters: one may, for example, have prior knowledge about rates of speciation and extinction. These features make the algorithm the most sophisticated so far to investigate the mode of character evolution on molecular phylogenies.

CHAPTER V: EVIDENCE IN SUPPORT OF RAPID CHANGE

Given the intensity of the punctuated equilibrium debate and considering the discussion went on for over three decades, surprisingly few studies have attempted to use empirical neontological data to investigate the mode of character evolution, most effort having been invested in development of methods. Mooers et al. (1999) applied their method to a phylogeny of cranes (Gruinae) and found that a model with freely varying rates of phenotypic evolution fit far better than either a purely gradual or purely speciational. Mattila and Bokma (2008) investigated evolution of body mass on a near complete phylogeny of mammals, and found that rapid change during speciation is responsible for a significant part, very approximately half, of interspecific phenotypic variation. More recently we used the same method (Bokma 2008; Mattila and Bokma 2008) to corroborate these results (Monroe and Bokma 2009 - Chapter V). We estimated rates of body size evolution using average body masses of over 3000 mammal species (Smith et al. 2003) to calculate the difference between ancestor-descendent species pairs in relation to the branch length (i.e. time) separating them. These estimates showed that, contrary to popular belief (i.e. Gould 1988), large mammals evolved at a higher rate than small mammals. In contrast, rates of body size evolution in recent (>5 million years old) sister species appeared independent of their average body mass. We argue that this pattern stems from accelerated evolution
upon speciation: it has been shown (Liow et al. 2008) that large mammals speciate and go extinct more often than small mammals. If evolution is concentrated in speciation events, this will increase the rate of evolution in large-bodied mammals, but not so in recent sister species that have not had the time to undergo series of speciation and extinction events. In addition we suggested (Monroe and Bokma 2009) that this result is not only applicable to mammals, but to birds as well. Bokma (2004) ran a similar analysis using 6000 of the approximately 9500 bird species and found that large-bodied groups seem to diversify at a higher rate than small-bodied groups. We suggest that lineages of large birds do not evolve at higher rates than small birds, but that these lineages speciate and go extinct more often than small-bodied ones, so that a group of such lineages accumulates variance at a higher rate. Thus, we argue that also in birds there is evidence for punctuated equilibrium, even though the fossil record of the group is notoriously sporadic.


In a related study (Bokma et al. submitted), we used a method of approximate Bayesian computation (Marjoram et al. 2003) to directly test whether or not body mass variation in birds seems to be the product of speciation events as opposed to purely gradual evolution over time. Approximate Bayesian computation is a method which allows the user to estimate unknown variables through a process of simulations and is used when likelihood estimates are not available, in our case due to a lack of phylogenetic data. We simulated phylogenies of avian families (Sibley and Ahlquist 1990; Sibley and Monroe 1990) matching the known number of species and approximate divergence age. On these simulated phylogenies we simulated body size evolution with different rates of anagenetic and cladogenetic change. We then compared variances of simulated body sizes to variances of observed average species body masses (Dunning 1993). Each simulation was subject to rejection based on how similar the variances of simulated body masses were to the observed variances; only rates of evolution that yielded simulated variances similar to observed variances are deemed realistic (Marjoram et al. 2003). Our simulations suggest that models including both gradual and rapid evolution are more likely to account for the body mass variation between bird species, speciation accounting for approximately 61% and gradual change accounting for 39% of the body mass variation.

Body size variance may be greater in species rich clades, not only because of cladogenetic change but also because some process accelerates both the rate of speciation and the rate of gradual evolution. Therefore, we used 10 complete avian species level phylogenies compiled by McPeek and Brown (2007) which we
analyzed using Bokma’s 2008 method. Eight of the 10 phylogenies supported a model of combined gradual and speciational evolution as opposed to a purely gradual model. This further supports the idea that body size differences in birds are best explained by speciation (Bokma et al. submitted).

CHAPTER VI: EXPLAINING DIFFERENCES IN RATES OF EVOLUTION

In chapter VI we investigate whether speciation and extinction rates can explain the differences in rates of evolution between birds and mammals. Birds and mammals share many characteristics: Both dominate higher trophic levels. Both originated during the late Jurassic, while most extant diversity originated during the Paleogene. Also physiologically both groups share many common characteristics, the most obvious being homeothermy, which has resulted in similar life history characteristics (Ruben 1995). However, even with all of these similarities, rates of evolution in mammals have been suggested to be extremely high in comparison to other taxa, including birds (Simpson 1944; Bush et al. 1977; Stanley and Harrison 1999; Nabholz et al. 2008, 2009). The high rates of evolution in mammals is poorly understood. It has, for example, been attributed to high metabolic rates (Martin and Palumbi 1993), even though birds have even higher metabolic rates than mammals, yet seem to have lower rates of evolution (Mindell et al. 1996; Stanley and Harrison 1999; Nabholz et al. 2008, 2009).

There are approximately twice as many extant bird species as there are mammal species, but mammalian body mass is much more variable, its distribution spanning more than twice that of birds. Under a purely gradual model of evolution, rates of anagenetic change would therefore need to be much higher in mammals than in birds, which is probably why so many scientists before us have suggested that mammals evolve at a higher rate than do birds (Simpson 1944; Van Valen 1974; Bush et al. 1977; Nabholz et al. 2008, 2009; Stanley and Harrison 1999). Using approximate Bayesian computation (Marjoram et al. 2003), we confirmed that speciation and extinction rates are higher in mammals (Darwin 1859:700) (turnover rate of approximately 0.8) than in birds (turnover rate of approximately 0.35), and that this can explain why mammals appear to evolve at a higher rate than birds. Speciation events account for large changes in phenotypes, and as these changes take place in mammals more frequently than in birds, mammals appear to evolve at a higher rate. It is only under a model combining both speciational and gradual change that we can reasonably estimate the approximate rates by which evolution occurs in birds and mammals. It is under this model that we can explain that mammals and birds evolve at approximately the same rate, but that turnover rates in birds and mammals differ, so that mammals undergo rapid, cladogenetic evolution more frequently. However the question as to why mammals speciate and go extinct at a higher rate than birds remains unanswered.
CHAPTER VII: WHY IS EVOLUTION SO SLOW?

Charles Darwin (1859) originally suggested that evolution is a gradual process driven by natural selection, in particular, adaptation to the environment. However, if species differences accumulate mainly upon speciation (i.e. cladogenetic change), as we show above (Chapter V, VI), then the idea that small adaptations accumulated over time drive evolution is less likely (Stanley 1975, 1998).

Fitness, however, is not determined exclusively by the environment. Fitness may be to a substantial degree be an inherent property, largely independent from the environment. Form and function of traits may benefit from interactions with other traits, which would increase the fitness of the organism. Consequently, selection may act co-adapting and canalizing traits, which is achieved with regulatory networks. Co-adapted complexes of traits would cause stabilizing selection on one another, so that each trait, through the complex as a whole, is maintained. Changes in a trait that is part of a co-adapted complex will not be beneficial without simultaneous changes in the other traits. For example, any mutation affecting body temperature in homeotherms would be strongly selected against because of many other processes within the organism that are dependent for their development or function on a specific temperature. Consequently, any mutation affecting temperature would result in decreased fitness, irrespective of the natural environment in which the organism finds itself. Temperature is of course an extreme example of stasis, but the same principle should apply, to a lesser extent, to other traits.

Some traits, however, are not important for the development and processes of multiple traits and may readily change in response to external natural selection. For example, when the peppered moth, originally recorded to have light colour, was exposed to the soot darkened trees of the British industrial revolution, those with light colour were easy targets for predators, whereas a darker variant was better camouflaged. Because predators were not able to see the dark variant as well, dark moths survived and were able to pass on their dark colour to their offspring. However, post industrialization, when the trees regained their lighter colour, moths with the light phenotype had the selective advantage over the dark phenotypes (Kettlewell 1959). This is a famous and clear cut case of external natural selection in the wild. Trait complexes, however, pertaining to the form and function of the moth, whether adhering to wing or body development should have been unaffected by the “adaptation” such that the organism would survive.

Thus, we propose that fitness is to some extent an internal property of the organism and that selection stabilizes complexes of traits so that evolution occurs less frequently or at a lower rate than one would expect if regarding fitness as determined solely by the environment. Why rapid evolution sometimes occurs is still unknown. Whether it be due to a lack of gene flow (in small populations), hybridization, genetic drift, or natural selection (Coyne and Orr 2004 and references therein) we can only speculate. We propose that scientific efforts need to re-focus on stasis. In discovering which traits are static, which interactions make them static,
and to what degree they are static, we may also shed light on when and for what reasons species change.

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SAMMANFATTNING (Swedish summary)

AUTHOR CONTRIBUTIONS
NOTE: Authors are referred to by their initials

Part of the thesis: Monroe M.J. and Bokma F. Punctuated Equilibrium in a neontological context. Theory in Bioscience 129: 103-111
This is a review paper which was mostly written by MJM.

Chapter I: Monroe M.J. and Bokma F. 2010. Little Evidence for Cope’s rule from Bayesian phylogenetic analysis of extant mammals. Journal of Evolutionary Biology 17: 933-940
This paper resulted from a rejected comment on a paper in Science. The method we used here was a slight modification of a paper FB wrote with TMM (T.M. Mattila)
earlier. MJM wrote most of the unpublished comment, after which we wrote this published paper together.

**Chapter II:** Monroe M.J., Mattila T.M. and Bokma F. Little effect of selective mass extinctions on body size distributions of present-day species. *Submitted manuscript*
This paper shows that mass extinctions are not the reason why most species are small-bodied. MJM and TMM collected data, FB analyzed them, and MJM and TMM wrote most of the manuscript.

**Chapter III:** Monroe M.J. and Bokma F. Does character displacement affect long-term evolution of characters? *Submitted manuscript*
This paper presents a novel phylogenetic method. We developed and (after initial rejection) modified this, and applied it to empirical data. FB did most methodology, MJM most analyses. The paper was discussed and written together.

**Chapter IV:** Monroe M.J. Does competition drive character differences between species on a macroevolutionary scale? *Submitted manuscript*
This paper tests for an effect of coexistence on trait evolution by exhaustive comparisons of triplets of coexisting and non-coexisting species. MJM wrote, analyzed and developed the method for the paper, FB helped with programming.

**Chapter V:** Monroe M.J. and Bokma F. 2009. Do speciation rates drive rates of body size evolution in mammals? *The American Naturalist* 174: 912-918
MJM and FB planned and did the analyses, extensively discussed comments on previous versions. MJM wrote a large part of the paper.

**Chapter VI:** Monroe M.J. and Bokma F. Punctuated Equilibrium reconciles rates of evolution in mammals and birds. *Submitted manuscript*
MJM collected most of the data, participated in planning of the analyses, and did much of the writing. FB designed the method and contributed to the writing.

**Chapter VII:** Bokma F., Monroe M.J. and Merilä J. Why species fail to adapt - a reply to Dr. Hugh Falconer. *Manuscript*
We planned on a perspective summarizing our findings for a long time. Finally FB started writing after a meeting with JM. FB wrote the majority of the paper, MJM contributed with extensive comments, discussions and text. JM has contributed with comments and text.
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