

**WHY MOST BIRDS ARE SMALL
– A MACRO-ECOLOGICAL
APPROACH TO THE EVOLUTION
OF AVIAN BODY SIZE**

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Abstract

There are more small-bodied species of birds than those having large bodies. Generally, and relative to occurrence in any one place, small-bodied species also contain more individuals than large-bodied species. The same patterns have been documented for several groups of higher organisms for example, snakes, flowering plants and mammals, which suggests that there exists a general reason "why", which applies to other groups of species as well as to birds. This thesis attempts to identify this reason.

In the first place, it is possible that most species happened to become small-bodied by chance. Simulations of neutral body-size evolution indicate however that the observed bias towards small size is stronger than that accounted for by neutral evolution. Then, the most plausible explanation for why most species are small is that small-bodied species speciate faster. However, statistical analyses accounting for historical relatedness of present-day species indicate no relation between body size and the rate of speciation. Finally, instead of little by little, the dominance of small species may have arisen suddenly, when approximately 65 million years ago (presumably) a large meteorite hit the earth, causing mass extinctions. However, analysis of body sizes and genetic differences of extant species reveals that while avian species numbers were approximately halved, the catastrophe affected small and large species equally. Thus, the reason why most species are small does not seem to be due to differential rates of speciation or extinction.

Instead, the cause appears to be in the tempo and mode of evolution. It was found by analysis of extant species' body size that probably most differences in body size between species arise at the moment of speciation. Differences between small-bodied species are smaller than between large-bodied species and probably this difference also has its origin at the moment of speciation. Consequently, groups of small species stay small whereas groups of large species are more variable in body size, so that in the end most species are small.

Keywords: body size, extinction, macroevolution, punctuated equilibrium, speciation

Bokma, Folmer, Miksi suurin osa linnuista on pieniä: makro-ekologinen lähestymistapa lintujen ruumiin koon evoluutioon

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Tiivistelmä

Maailman noin 10 000 lintulajin joukossa pienikokoisia lajeja on enemmän kuin suurikokoisia. Yleensä pienikokoiset lajit ovat myös yksilömääriltään suurempia kuin samalla paikalla esiintyvät suurikokoiset lajit. Koska sama ilmiö on havaittu monissa suurissa eliöryhmissä (esim. nisäkkäät, käärmeet ja kukkakasvit), on ilmeistä, että on olemassa yhteinen syy, joka pätee niin linnuissa kuin muissakin eliöryhmissä. Tämän väitöskirjan tavoite on selvittää, mikä tämä yhteinen syy voisi olla.

Ensinnäkin on mahdollista, että suurin osa lajeista on kehittynyt pienikokoisiksi aivan sattumalta. Ruumiin koon evoluution simulaatiot kuitenkin osoittavat, että on hyvin epätodennäköistä, että neutraali evoluutio olisi johtanut pienikokoisten lajien suuriin määrään havaitussa määrin. Toinen mahdollinen selitys ilmiölle on, että pienikokoiset lajit lajiutuvat nopeammin. Tilastolliset analyysit, jotka ottavat huomioon nykyisin elävien lajien sukulaisuussuhteet, osoittavat ettei ruumiin koon ja lajiutumisen vauhdin välillä ole yhteyttä. Kolmas mahdollinen selitys pienikokoisten lajien suurelle määrällä on historiallinen. On mahdollista, että pienikokoisten lajien suhteellisen suuri määrä syntyi nopeasti noin 65 miljoonaa vuotta sitten tapahtuneen massasukupuuton seurauksena, joka fossiilaineiston perusteella kohdistui erityisesti suurikokoisiin maaeläimiin (esimerkiksi dinosauruksiin). Vertaileva analyysi nykyään elävien lintulajien ruumiin koosta ja geneettisistä eroista osoittaa, että vaikka suuri osa lintulajeista hävisi massasukupuutossa, tämä katastrofi karsi lajeja riippumatta niiden ruumiin koosta.

Näyttää siis siltä, etteivät erot lajiutumisen tai sukupuuttojen esiintymisessä selitä sitä, että suurin osa lajeista on pienikokoisia. Tämän tutkimuksen tulosten perusteella syy näyttäisi sen sijaan olevan ruumiin koon kehityksen vauhdissa ja siinä tavassa, jolla kehitys yleensä etenee. Analyysi nykyisten lajien ruumiin koosta paljasti, että suurin osa eroista lajien välillä syntyy (evolutiivissa aikataulussa) suhteellisen nopeasti lajiutumistapahtuman yhteydessä (punktualismi) eikä vähitellen pitkien aikojen kuluessa (gradualismi), kuten yleensä oletetaan. Kehityslinjojen sisällä pienikokoisten lajien väliset erot ruumiin koossa olivat pienempiä kuin isokokoisten lajien väliset erot - ja todennäköisesti myöskin tämä ero syntyy lajiutumisen yhteydessä. Tämä johtaa evoluution kuluessa tilanteeseen, että alunperin pienikokoisista lajeista kehittyneet lajit ovat myös pienikokoisia, kun taas isokokoisten lajien kehityslinjoissa on nähtävissä huomattavasti paljon enemmän vaihtelua ruumiin koossa. Näiden seurauksena eliöstöissä suurin osa lajeista lopulta on pienikokoisia.

Asiasanat: lajiutuminen, makro-evoluutio, ruumiin koko, sukupuutto

As it net kin sa't it moat, moat it sa't it kin.

(If you cannot do it like you should, you should do it like you can.)

Âlde Fryske sizwize. / Old Frisian phrase.

For my family

Acknowledgements

The zoological museum of the University of Oulu is situated in a rather modern building. Nevertheless, the architecture retains the style found in many older museums: a large central hall covered by a high, arched roof, and –most importantly- a gallery surrounding the second floor, overlooking the museum. The hall is filled with glass boxes in which the birds and mammals of Finland are all on display, represented by at least one stuffed delegate. When I first came to Oulu as an exchange student, I happened to work in a room on that second floor. Ever since, every now and again, I have looked down on the birds from the gallery and wondered why most of them are small. I still have my room there, and I still wonder.

Fortunately, however, I did not have to wonder alone. Mikko Mönkkönen has been an inspiring supervisor and reliable mentor during all of my studies in Oulu. He came up with numerous creative ideas, and always found time to discuss or think things over, even when he obviously didn't have that time. His apparently unlimited enthusiasm for ecology and evolution has been an important drive throughout this study. I am certain he will be glad when this thesis is completed.

Because undergraduate biology courses are notoriously boring, my enthusiasm for studying the living world revived halfway through my undergraduate studies when I began doing field work at the “Herdershut” (Shepherd's hut) field station of the University of Groningen, on the island of Schiermonnikoog. I want to thank my fellow students and my supervisors: Rudi Drent, Julia Stahl, Simon Verhulst, and Leo Bruinzeel for their stimulating guidance, cooking skills, and good company.

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Myn heit en mem, omke Arend en pake en beppe hawwe my altyd stipe, ek as hja net begrepen (as net begrype koene) hwat ik die, lit stean wêrom't ik dit die. Hja hawwe altyd besyke my safolle mooglik frijhyd te jaen, en hiene dat net better dwaen kint. Finally, I owe my loving thanks to Anne and Otte for taking care of me and reminding me of the things that really matter.

Oulu, March 2004

Folmer Bokma

List of original articles

This thesis is based on the following articles, which are referred to in the text by their Roman numerals.

- I Bokma F & Mönkkönen M Body size abundance relations in patchy environments. Manuscript.
- II Bokma F (2001) Evolution of body size: limitations of an energetic definition of fitness. *Functional Ecology* 15: 696-699.
- III Bokma F (2002) A statistical test of unbiased evolution of body size in birds. *Evolution* 56: 2499-2504.
- IV Bokma F (2003) Testing for equal rates of cladogenesis in diverse taxa. *Evolution* 57: 2469-2474.
- V Bokma F Comparing ways of estimating extinction rates from molecular phylogenies. Manuscript.
- VI Bokma F Searching for bias in rates of cladogenesis. Manuscript.
- VII Bokma F Molecular evidence of avian mass extinctions at the Cretaceous-Tertiary transition. Manuscript.
- VIII Bokma F (2002) Detection of punctuated equilibrium from molecular phylogenies. *Journal of Evolutionary Biology* 15: 1048-1056.
- IX Bokma F, Mönkkönen M & Bokma J Molecular evidence of avian body size evolution by punctuated equilibrium. Manuscript.
- X Bokma F Differential rates of body size evolution in birds. *Journal of Evolutionary Biology*, in press.

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1 Observed body size distributions

1.1 Introduction

Patterns in body size have a long history of research (Elton 1927). An important reason why body size has been often researched is that every organism has a body size, which is relatively easy to measure. Moreover, the body sizes of very different organisms can be compared directly. For example, the body sizes of butterflies and whales can be measured and compared in identical units. Finally, the body size of an organism can remain well-preserved long after the organism has died: for example, fossil remains provide us with a good idea regarding the size of dinosaurs, whereas we can only guess about their colour or the way in which they behaved.

In addition to ease of measurement, there is another, more scientific reason why so much research has been done on body size. It appears that the size of an organism is closely related to a variety of characteristics (Peters 1986). To mention just a few: small-bodied organisms tend to live shorter, produce larger numbers of offspring and eat less when compared to large-bodied organisms. Thus, there is no use in comparing bill size or clutch size for two species of birds without taking into account that body size in one species is ten times greater. Body size emerges as a principle factor in much physiological, life history, evolutionary and ecological research.

It is therefore not surprising that there exists a rich history in determining the relation of all kinds of variables with body size. This thesis is largely concerned with a particular type of body size relation: that of the numbers of individuals and species. The first paper in the thesis deals with the relation between body size and different measures of the number of individuals per species. The second paper concerns the question of whether there is a simple relationship between the number of individuals belonging to species of different body size, and the numbers of species of different body size. As it appears, no such simple relationship exists and more detailed analyses of the evolution of body size are needed. Several parameters must be estimated to make such analyses possible. Papers IV - VII in this thesis present ways of estimating speciation, extinction, and mass extinction rates, and of comparing the estimates between taxa. Papers VIII and IX attempt to use these estimates to examine (or determine) tempo and mode of body size

evolution. Finally, papers III and X use all of these estimates to test models of body size evolution and to compare rates of body size evolution between groups of species, in an attempt to narrow in on a coherent explanation for why most birds are small.

1.2 Body size patterns in communities

Imagine one day going into a natural forest and somewhere, just anywhere, delimiting a few square meters on the ground, and capturing all the insects that occur there. Subsequently we would sit down with a guide to determine and identify individuals to species, and with a calliper measure the body length of each and every individual animal. Very likely we would observe (i) more species with small average body size than large size and that (ii) small-bodied species were represented by more individuals than large-bodied species. The reason why I am so convinced about the above predictions is that this kind of experiment has been done at least several tens, and probably several hundreds of times (Blackburn et al. 1990, Blackburn et al. 1993), with little variation in the outcome. Unfortunately, this is about where the general agreement ends.

It is, in fact, very interesting that relations between body size and abundance from very different locations, environmental conditions and taxonomic groups show basic similarities. This suggests that there exist common factors shaping these relations (Brown 1995). Yet, little is known regarding the influences shaping body size frequency distributions. A recent review of the proposed mechanisms appropriately concluded that: “there has been little progress towards an understanding of the mechanisms causing the relationship, focus having dwelt on debate over its form” (Blackburn & Gaston 1999).

Uncertainty about the mechanisms behind size-abundance relations stems partly from the fact that two kinds of abundance estimates are encountered in the literature. For some studies, abundance data are compiled from the literature, typically from studies on single species that report abundance for that species in suitable habitat (e.g. Damuth 1981). Other studies have derived abundance estimates from census data for many species in a single, spatially restricted landscape like a nature reserve (e.g. Siemann et al. 1996). Consensus suggests that these different types of compilations yield different shapes for the relation between body size and abundance. Literature compilations of abundance typically reveal log-linear size-abundance relations with abundance decreasing with body size. Comparatively, single-area census data typically indicate that the relation is hump-shaped, with the highest abundance for species of moderately small body size (Gregory & Blackburn 1995).

In paper I of this thesis, a single model is introduced which predicts both patterns. The idea behind it is that small-bodied animals require high-quality resources which are rare in the landscape. Large animals are not limited by resource quality but by quantity, as they require large amounts of resources so that, according to the model, species with intermediate body size reach highest population densities if measured as integrated over the landscape. If abundance is measured locally, within patches of suitable resources, the relation between body size and ecological density depends little on habitat requirements, and is predicted to be approximately a power function of body size, reflecting mainly the physiological properties of animals. In order to make quantitative rather than merely

qualitative predictions, the model requires that the exact spatial distribution of resources is known. At present such data are unavailable for suitably large geographical scales. However, the qualitative predictions are not particularly sensitive to the exact distribution of resources and so, the model may explain why most individuals are small-bodied. Yet, the model does not have any bearing on the question of why most species are small-bodied. Or does it?

1.3 Adaptive explanations

It seems possible that the distribution of body sizes of individuals in communities is largely determined by natural selection, which is then reflected in the distribution of species' body sizes. In any case, the frequency distribution of species in a higher taxon consists of the body sizes of member species in the communities. Of course, species may be distributed in different ways over communities, so that there is no straightforward correspondence between body size and the numbers of species in local communities, and the frequency distribution of species' body sizes in a taxon. Perhaps however there exists a close correlation between the distribution of body sizes of species in a taxon and the success of those species in the communities in which they (co-)exist. This idea was formulated mathematically to explain why in many groups of species there are more small-bodied than large-bodied individuals (Brown et al. 1993).

The reasoning was that what determines the success of a species is the capacity of its individuals to acquire resources from the environment and to transform those into offspring. Based on physiological relations describing the rate at which species acquire resources (metabolic rate) and the rate at which they produce offspring (e.g. egg production, lactation) a curve was derived, representing what was dubbed "reproductive power". Reproductive power, it was reasoned, measures the capacity of body size to turn resources into offspring and thus represents an "energetic definition of fitness".

It was argued that, since reproductive power represents fitness, the distribution of species body sizes should be the same shape as the reproductive power curve. Indeed the curve nicely described the relation between body size and species richness in mammals (Brown et al. 1993) and birds (Maurer 1998). The obtained reproductive power curve showed a peak at intermediate body size, and a skew towards small body sizes. It peaks at the body size that in many communities coincides with highest abundance and that which in species frequency distributions contains the most species.

However, on theoretical grounds, this theory has been shown as incorrect (Brown et al. 1996, Kozlowski 1996, Perrin 1998, Kozlowski 2002), and paper II of this thesis shows mathematically that even if this argument were correct, its predictions can not explain why, not only in birds as a whole but also in subgroups (orders, families), body size distributions are like they are.

2 Tempo and Mode of Evolution

2.1 Introduction

Before the development of molecular techniques to analyse DNA, inferences regarding rates of speciation, extinction and morphological evolution were almost exclusively the domain of paleontologists. Fossil remains –which are common in some taxa-, were often classified as different species. The average lifetimes of such species can be estimated from the ages of the layers of rock in which they are found and as such, estimates of speciation and extinction rates , as well as estimates of rates of morphological evolution can be made (Stanley 1998).

The procedure to estimate speciation and extinction rates from fossil remains isn't exactly as straightforward as the above description might suggest. Differences in the fossilizing capacity of different rock layers, and more generally the uncertainty about the completeness of the fossil record need to be taken into account. These problems however can be controlled statistically, so that they do not necessarily bias rate estimates but merely widen the confidence limits around them.

A more important limitation of using fossil data to make macro-evolutionary inferences is that fossils reveal little more than the morphology of ancient species. Other important differences that may set species apart – like the coloration or behaviour of dinosaurs - are badly preserved. There are many present examples in nature of “morphologically cryptic” species: i.e., species that are morphologically indistinguishable, and would certainly not be seen (or viewed) as separate species if encountered as fossils. In some cases, such species may not even be close relatives. In *Anolis* lizards of the Caribbean, for example, there exist strikingly similar ecomorphs on different islands, that appear to be more closely related to morphologically more distinct species than to each other (Losos et al. 1998). This is a more serious limitation of deriving macro-evolutionary inferences from fossils, since it appears impossible to correct. However, this is also an interesting reason to explore the possibilities of using extant species in testing hypotheses regarding the tempo and mode of evolution.

2.2 Molecular extinction rate estimates

Nowadays, extant species can be used to estimate both speciation and extinction rates (Nee et al. 1994a). This may appear counterintuitive, since extinct species can no longer be observed except perhaps as fossils. Indeed, the estimation procedure is quite complex in theory as well as in practice. In principle, the possibility exists since the DNA of extant species can be used to estimate their time since divergence, and more recent species have had less opportunity in time of going extinct than old species, even if at any moment, all species – whether old or young - are equally likely to go extinct.

The DNA of species continuously change during time. And consequently, species gradually become genetically different. It is not precisely known how genetic divergence takes place, but in general, we may expect that species that started diversifying recently are genetically more similar than ones those having separated long ago. Unfortunately, it appears that some parts of the genome change more rapidly than others, and that identical parts evolve at different rates in different species (Bleiweiss 1998, Yoder & Yang 2000). Also, it appears that between somewhat more distantly related species, differences are often caused by larger parts of the genome having been relocated in their entirety, rather than by small, single-point mutations (Levine & Tjian 2003). Nevertheless, it is theoretically possible to compare suitable parts of the genomes of a group of species and, by turning reasoning around, estimate which species in the group are closely related and which are distantly related based on their genetic differences. In that way, historical relations between species can be determined and drawn usually in the form of a tree, a molecular phylogeny. A molecular phylogeny is a graph of the estimated historical relationships between species. It is not necessarily the correct hypothesis. It is therefore important to keep in mind that all of the phylogenetic analyses presented herein are at best as good as the phylogeny on which they are based.

2.2.1 *Estimates from branching times*

Several ways have been developed to estimate extinction rates from molecular phylogenies. The first approach was initiated by Nee and colleagues (Nee et al. 1992) who used plots of the number of lineages in a molecular phylogeny against time to study rates of diversification in birds. If the diversification process is a pure speciation process (that is, without extinction) the plot forms a straight line (i.e., after suitable axis transformation), but if species can go extinct the plot becomes curved. As time approaches the present, the slope of the plot asymptotically approaches the net rate of speciation, as species have not had the time to go extinct. The curvature of the plot provides information about the extinction rate.

That property of reconstructed lineage-through-time plots was subsequently employed to estimate the speciation and extinction rates (Kubo & Iwasa 1995). It was determined, for the special case in which speciation and extinction rates are constant through time, how the ratio of the number of present lineages to the number of lineages at some time before present changes, depending on the speciation and extinction probabilities. This

function was subsequently used to find the rates of speciation and extinction that best fit the lineages-through-time series.

The above approach yields estimates of speciation and extinction rates, but it remained rather complicated to test hypotheses regarding the estimated parameters, for example whether the extinction rate exceeds zero (Kubo & Iwasa 1995). That problem was largely overcome with a new way to estimate speciation and extinction rates by maximum likelihood (Nee et al. 1994a, Nee et al. 1994b). Maximum likelihood estimation is a more general estimation technique, with the advantage of a much broader range of statistical applications. The likelihood approach employed the same data: the times of origination of lineages in the reconstructed phylogeny. The distribution of the intervals between those times depends on the rates of speciation and extinction (Nee et al. 1994a) (which also creates the curvature of lineage-through-time plots).

2.2.2 Estimates from the distribution of species over taxa

All previous methods use information about the extinction rate contained in the branching points of the phylogeny. They work best with complete phylogenies since complete phylogenies contain most branching points. Most phylogenies however are incomplete, lacking some extant species. Sometimes it is known which species are missing from the phylogeny, yet their closest relatives can be identified with reasonable certainty. Such might, for example, be the case with mammals, for which phylogenies at higher taxonomic levels exist (Blomberg & Garland 2002), and for which we know fairly well how many species those higher taxa contain. Another, well-known example is Sibley and Ahlquist's molecular phylogeny of birds (Sibley & Ahlquist 1990, Sibley & Monroe 1990). The estimation procedure outlined in paper IV in this thesis was designed especially for this type of phylogenetic information. It does not rely on branching times, but on the distribution of species over higher taxa of different age. The distribution of species over taxa depends on a combination of the speciation rate, the extinction rate, and the age of the taxa (Bailey 1964). The interplay between these three factors makes it possible to estimate speciation and extinction rates from a set of taxa with different ages.

If the extinction rate is small relative to the speciation rate, most taxa contain few species. If the extinction rate is large relative to the speciation rate, taxa with very large numbers of species become more common. Application of the estimation procedure to lineages of birds suggests that extinction rates have been very close to speciation rates (IV), since several avian families contain substantial proportions of the total number of species. Such a distribution however, may result from processes other than high extinction rates and as such needs further investigation.

2.3 Testing hypotheses about speciation and extinction rates

2.3.1 *Constancy over time*

Molecular phylogenies can be used to gain additional inferences regarding the rates of speciation and extinction than just an estimation of their magnitude (Purvis 1996, Pagel 1997, Pagel 1999). Several of the estimation procedures mentioned above assume that speciation and extinction probabilities have been equal in all species at all times. It is possible to test whether this assumption is correct based on the same data that were used to estimate speciation and extinction rates.

A first test to estimate whether net rates of speciation have been equal during the evolution of birds was designed by Nee and his co-workers. They fitted a constant-rate and a decreasing-rate model to the branching times in Sibley and Ahlquist's (Sibley & Ahlquist 1990) molecular phylogeny of birds and found that the decreasing rate model provided a better fit (Nee et al. 1992). Kubo and Iwasa elaborated on this analysis using the same data, and showed that not only a decreasing speciation rate, but also an increasing extinction rate and any combination of the two can yield indistinguishable branching patterns in the phylogeny (Kubo & Iwasa 1995). Also the likelihood approach to estimate speciation and extinction rates has been extended to detect changes in rates of cladogenesis (Nee et al. 1994a).

2.3.2 *Mass extinctions*

In addition to testing whether rates of speciation or extinction change gradually over time, it is also possible to test whether any mass extinctions have taken place. This is especially interesting in the case of birds, because birds have a sporadic fossil record, so that relatively little is known about avian evolutionary history (Nee et al. 1992, Padian & Chiappe 1998, Chiappe & Dyke 2002).

Kubo and Iwasa (Kubo & Iwasa 1995) extended their analysis of lineages-through-time data to test for explosive radiation and mass extinction. They had to conclude however, that while explosive branching imparts clear marks on branching times, mass extinctions are particularly hard to detect in this way. The same was found by Harvey and colleagues who analysed the effects of different kinds of mass extinctions on branching time patterns (Harvey et al. 1994): mass extinction was detected with reasonable accuracy only when about 80% of species went extinct, which is a very high percentage (Benton 1995).

Paper VII of this thesis introduces a related procedure. It does not look at the entire time scale of the phylogeny for the traces of mass extinctions, but estimates the fraction of species that went extinct at a certain moment in history. This test allows estimation of the fraction of bird species that went extinct at the end of the Cretaceous. At that time – approximately 65 million years ago – presumably the impact of a large meteorite (Beerling et al. 2002) wiped out large numbers of species (Benton 1995) including

dinosaurs. Birds (also dinosaurs, in a sense) survived the catastrophe, but it remains unknown how many species perished. The fossil record is too scarce to allow quantitative estimates (Padian & Chiappe 1998), and although many Cretaceous fossils have been recently discovered, no primitive avian species are known to have survived into the Tertiary (Chiappe & Dyke 2002) which suggests the toll has been rather heavy. The presented estimation procedure uses the distribution of species over families instead of origination times. If mass extinctions have affected avian species 65 million years ago, taxa older than that should show reduced species numbers as compared to younger taxa. The test puts the fraction of species that slipped through the bottleneck at over 75%, a perhaps unrealistically high percentage.

If a large fraction of avian species went extinct at the Cretaceous-Tertiary transition, this may markedly affect the distribution of species' body sizes, especially if large-bodied species were affected more than small-bodied ones (Janzen 1995). Paper VII of this thesis also presents an analysis of whether this was the case. At all branching points in the family level phylogenetic tree, the skewness of species average body sizes was calculated for all lineages existing in the tree at that point in time. Thus, skewness was calculated for the same species at all points in time, although the species became increasingly subdivided. This test shows that grouping species before and after the mass extinction yields comparable skewnesses, which suggests that the Cretaceous-Tertiary mass extinctions are not the reason why most bird species are small.

2.3.3 Differences between lineages

Another somewhat related question is whether different lineages that exist at the same moment have equal probabilities of speciation. Several tests have been designed for this purpose. Owens and colleagues tested whether the distribution of species over higher taxa conforms to a geometric distribution (Owens et al. 1999), thereby neglecting that higher taxa are not equally old. Purvis and co-workers estimated speciation and extinction rates from complete phylogenies of several primate taxa and compared the obtained likelihoods (Purvis & Webster 1999). Even though their statistical procedure was not entirely correct, the differences in rate estimates were so large that their conclusion that rates have been significantly different probably remains (Purvis, pers. comm.). Magallon and Sanderson used fossil estimates of the ages of flowering plant taxa in combination with very high and low extinction rates to test for unexpectedly species rich or poor taxa (Magallon & Sanderson 2001) and also found that such exceptionally poor and rich taxa exist. Finally, Mayhew (2002) compared the species richness of sister taxa of hexapods, and also found evidence that rates of speciation and/or extinction have not been equal across taxa.

What all previous tests have in common is that they compare closely related taxa. If there are differences in speciation and extinction rates between taxa, however, they are presumably larger between distantly related taxa. The test described in paper IV of this thesis was designed to exploit this distinction. It estimates the rates of speciation and extinction from the distribution of species over higher taxa in several groups (birds, insects, flowering plants, and primates). These maximum-likelihood estimates were

compared statistically with each other, which revealed that there are significant differences between groups of species in either speciation or extinction rates.

If speciation and extinction rates are equal across taxa and over time, it is impossible to predict from its location on the tree the number of species of a higher taxon. But even if rates are not universal, it may still be so that species richness of higher taxa is randomly located on the phylogenetic tree. Paper VI of this thesis presents an analysis of this hypothesis. The procedure tests whether closely related taxa are more equivalent to one another in species richness than those more distantly related. This appears not to be the case: distantly related taxa are even slightly more similar in species richness than closely related ones. Thus, even though there appear to be differences between taxa in rates of speciation and extinction, they cannot be traced on the phylogenetic tree (Ricklefs 2003).

2.4 Estimating rates of morphological evolution

Species presently seen in nature are often different from each other, and differences between higher taxa are generally larger than between species. Where do those differences come from? Darwin suggested that they are due to natural selection. In his perspective, species during their lifetime slowly change under the influence of natural selection. Given enough time, the differences accumulate to the point where species can be considered separate genera, or still higher taxa. This view appears to have been adopted without much critical thinking by many geneticists and evolutionary biologists, even though in his time Darwin was apparently virtually alone in this belief (Mayr 1982).

In 1972, Eldredge and Gould emphasized in an influential book chapter that the fossil record does not support the idea of Darwin and that of most geneticists at the time (Gould & Eldredge 1993). Species according to the fossil record did not change gradually over time, but appear suddenly different, showing little change during their subsequent lifetime (Stanley 1998). Eldredge and Gould's interpretation of the fossil record has been often disputed (Gould & Eldredge 1993). It has been suggested that the completeness of the fossil record is insufficient, and that fossil remains are assigned to different species only if clearly different (Stebbins & Ayala 1981). At present, it is acknowledged that it is not impossible that new species rapidly become different. Still, however, it remains unknown why species change so little during their existence (Maynard Smith 1983, Seaborg 1999).

2.4.1 Molecular estimates

Using a phylogeny and phenotypes of extant species, papers VIII and IX of this thesis present ways to estimate how much morphological change in species can be attributed to speciation and how much can be attributed to gradual change. This approach is quantitative and overcomes the limitations of the fossil record. The principle of the test is simple: if species change slowly over time, then species that recently shared a common ancestor are virtually identical. If, on the other hand, species are suddenly different, even a young pair of sister species would already be quite distinct morphologically. Molecular

phylogenies identify the time since species last shared a common ancestor, but not the number of speciations that separates species, because extinct species don't appear in the tree. This, however, can be taken into account statistically, since speciation and extinction rates can also be estimated from phylogenies (IV).

A quite similar procedure can be applied to taxa. If change in body size is largely gradual, old taxa show wide interspecific variance even if they contain few species, while young taxa always show little variation even if they contain many species. On the other hand, if species become suddenly different, a young but species rich taxon already shows extensive body size variation. It is possible to quantify these predictions by computer simulations, to estimate which mode of evolution best agrees with the observations (IX). The estimates indicate that body size divergence is largely cladogenetic, supporting Eldredge and Gould's theory (Eldredge & Gould 1972, Gould & Eldredge 1993). Interestingly, the estimated difference between newly originated species is approximately similar to the difference observed in extant subspecies. These estimates, however, are conditional on a critical assumption: that rates of morphological evolution are equal in all taxa.

2.4.2 Differential rates of morphological evolution

Finally, we must consider the possibility that the rates of morphological evolution differ between taxa. For example, the rate at which body size evolves may not have been equal in all groups of avian species. Especially if there is a relation between body size itself and the evolutionary variability of body size, for instance if large species are more variable in body size, then species may get "trapped" in having a smaller body size, so that most species become small. Large species would become small more rapidly than small species would become large. This idea is addressed in paper X of this thesis.

In order to test whether the rate of body size divergence has been constant across taxa , one has to consider and take into account the fact that taxa of different age and species richness are expected to show, in extent, different body size variation. The comparisons between families and between genera of birds circumvent these problems and show that, indeed, families of small body size show less interspecific variation in body size than large-bodied families of similar age and species richness (X). Finally, this appears to be an important reason why most species are small.

3 Directions for future research

The papers in this thesis provide answers to some questions concerning the macroevolution of avian body size. In broad scope, it is shown that body sizes of present day species agree with the expectations of neutral evolution. In details however they differ. This suggests, nevertheless, that evolutionary diversification can largely be described as an effectively random process.

In addition, it was shown that rates of speciation differ between higher taxa, affecting speciation and extinction rates. Nevertheless, high speciation rates appear to take place randomly on phylogenetic trees.

Third, it appeared that species acquire their morphological differences suddenly, instead of gradually over time. Further study is needed to take into account that the rate of body size evolution appears to differ between taxa. Especially interesting questions are (i) whether morphological evolution can drive speciation, to result in a correlation between species richness of taxa and morphological variance, and (ii) what are the relative roles of natural selection and other processes in determining the rate of evolution.

Fourth, it was shown that even though birds probably experienced mass extinctions some 65 million years ago, the extinctions were not body size-selective.

Finally, it has been demonstrated that small-bodied groups of species diversify morphologically at a lower rate than large-bodied groups.

The answers are incomplete however and several open questions remain. Is macroevolution random in essence, or is it deterministic, but so that the outcome of the deterministic process is identical to that of a random process? What determines speciation and extinction rates if the process is idiosyncratic? Why is skewness of body sizes distributions higher in species rich taxa? What happens to the genotype of species during speciation, and why do small-bodied species evolve at lower rates than large-bodied species?

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Appendix on logarithmic body sizes

Throughout this thesis, body size is measured on a logarithmic scale. This is common practice for such studies (as well as in much physiological work): often interspecific distributions of body size are approximately lognormal, even though the intraspecific distribution for many species seems normal. Exactly how this difference is brought about is not often considered, although macroevolutionary models of quantitative trait evolution should explicitly account for this difference if they are (to be) based on biological theory. Here, particular attention is paid to Brownian motion, a general model of quantitative trait evolution. This model is, if not adopted solely for its mathematically relatively well-understood behaviour, ultimately based on the intraspecific distribution of phenotypes. Consequently, the model cannot be applied to a logarithmic scale without justification. That justification is given here: it is shown that Brownian motion approaches the same process on a logarithmic scale under certain conditions.

The term “Brownian motion” was coined after the botanist Robert Brown who, in 1827, observed that the motion of submerged pollen grains was in random directions, as was later discovered to be due to the joint effect of collisions with molecules of the liquid. Similarly, the changes or “motion” of species average phenotypes over time can be assumed to result from the joint effects of stochastic population genetic processes like drift, mutation and selection on the average phenotype of a species. Thus, essentially this model of phenotypic evolution is not just mathematically convenient but connected in a plausible or, at least tractable, way to biological theory.

Two prominent examples of body size frequency distributions that are approximately normal on a logarithmic scale are those of birds and mammals, which are known in considerable detail. Within those major taxa, the body size distributions of lower and therefore younger taxa (orders, families) are approximately log-normal as well (though with smaller variance), which suggests that the distribution is, at least to some extent, shaped by a process that preserves the log-normality of the pattern over time. Perhaps based on such empirical observations, it is often assumed that body size evolution is approximately like Brownian motion on a logarithmic scale.

The statistical behaviour of the Brownian motion process has been extensively studied, and consequently it came as no surprise that the process describes observed body size distributions well for analytical purposes, and appropriately mimics observed

distributions for simulation purposes. However, while the assumption of Brownian motion on a logarithmic scale may be justified as a modelling convention, it does not provide a reasonable conjecture of the actual process of evolution. In the first place, evolution may not be unconstrained in phenotypic space as Brownian motion assumes. In fact, some researchers have criticised its assumptions and prefer to model long-term phenotypic evolution as (for example) an Ornstein-Uhlenbeck process, in which the phenotype is attracted to a certain value, reflecting the idea of stabilising selection. Here however, I will not consider whether Ornstein-Uhlenbeck types of processes are any better or more objective in describing phenotypic macroevolution than Brownian motion.

If body size evolves following Brownian motion on a logarithmic scale, the average phenotype of a species m_n is a function of the species ancient body size m_o :

$$m_n = m_o + a_1 + a_2 + \dots + a_n$$

where a are normally distributed random numbers with zero mean, which symbolize the change the average phenotype undergoes during a time interval t . This time interval may, for example, be thought of as a generation. The variance of the normal distribution from which the a are drawn s_a^2 is related to t as

$$s_a^2 = s_{ag}^2 * t$$

where s_{ag}^2 is a constant: for example a per-generation variance.

The distribution of the average phenotype of a species is more complicated if body size evolves following Brownian motion on a standard scale. The change in a species average body size is normally distributed, so that:

$$m_1 = m_o + b_1$$

where b is a normally distributed random variable with zero mean. It is reasonable to assume that the standard deviation of b is proportional to m_o , as the standard deviation of individual body size within a species is proportional to body size. This means that species of different body size are equally likely to change for example 10% in body size. Thus, we can rewrite

$$m_1 = m_o + c_1 * m_o$$

where c is a normal random variate with zero mean and standard deviation independent of body size. Hence we can write:

$$m_1 = m_o * d_1 \quad \text{and}$$

$$m_n = m_o * d_1 * d_2 * \dots * d_n$$

where the d are normal random numbers with mean 1 and variance independent of m . The variance of d is s_d^2 and increases over time as $s_d^2 = s_{dg}^2 * t$, where s_{dg}^2 is a constant, for example per generation variance.

For the case of Brownian motion on a logarithmic scale, it is straightforward to proceed from the probability density function of a to the probability density function of the sum of n a , making use of the following theorem: If x_1, x_2, \dots , and x_n are independent random variables with the moment generating functions $M_{x_1}(t), M_{x_2}(t), \dots, M_{x_n}(t)$, and $y = x_1 + x_2 + \dots + x_n$, then

$$M_y(t) = \prod_{i=1}^n M_{x_i}(t)$$

Since a are assumed to be identically distributed the evaluation is particularly simple since it reduces to

$$M_y(t) = \{M_a(t)\}^n.$$

Thus, it can be shown that the sum of a fixed number of normally distributed random variates with mean zero and variance s_{ag}^2 is itself normally distributed with mean zero and variance $n s_{ag}^2$. (Although it does not follow directly from the above, in a set of phylogenetically related species (a taxon) the interspecific distribution of body sizes will also be approximately lognormal at any point in time if the change in the average phenotype over time is lognormal.)

It is not as straightforward, however, to find the probability density function of the product z of the random variables d . But it is possible to come closer to a solution by writing the product as the exponent of the sum of logarithms:

$$z = \prod_i^n d_i = \exp \sum_i^n \ln d_i$$

Thus it may be possible to arrive at the p.d.f. of z in general as follows:

1. from the $\phi(d_i)$, determine the $\phi(\ln d_i)$
2. from the $\phi(\ln d_i)$, determine $\phi \sum \ln d_i$
3. from $\phi \sum \ln d_i$, determine $\phi(z)$

$\phi(\ln d_i)$ can be found making use of the following theorem: If the probability density of x is given by $f(x)$ and the function given by $y = h(x)$ is differentiable and either increasing or decreasing for all values within the range of x for which $f(x) \neq 0$, then the probability density of y is given by:

$$g(y) = f(x) \left| \frac{dx}{dy} \right|, \quad \frac{dy}{dx} \neq 0$$

It will be noted that the function h is $h := y = \ln d$, which is increasing for all values within the range of d . If we treat $m_n - m_o$ as a sum of changes instead of a product by taking logarithms:

$$\ln m_n - \ln m_o = + \ln d_1 + \ln d_2 + \dots + \ln d_n$$

we must determine the distribution of $\ln d$. (It is emphasized that $\ln d$ is not lognormally distributed: if $\ln x$ is normally distributed then x is lognormally distributed, but observe that in the present case x is normally distributed.) This distribution is found by application of the above formula:

$$\phi(q) = \frac{e^q}{\sigma \sqrt{2\pi}} \exp \left(-\frac{1}{2} \frac{(e^q - 1)^2}{\sigma^2} \right)$$

where $q = \ln d$.

Unfortunately the author found himself unable to determine the moment generating function of the above distribution, so that no exact equation is presented here for the distribution of the product of z . Fortunately however, the particular properties of this equation render such unnecessary. It is namely observed that this probability density function of $\ln d$ where d is a normal random variate with mean 1 is almost identical the the normal distribution with mean zero and the same standard deviation, provided that the standard deviation is small.

Lognormal distributions of body size are documented for birds and mammals, which have generation times of one or a few years, while time to extinction of avian and mammalian species, for example, is in the order of magnitude of a million years. Thus, the time step over which the average phenotype changes (a few years) is orders of magnitudes smaller than the time giving rise to differences between species, in which case the Central Limit Theorem predicts that differences between Brownian motion on standard and lognormal scales will be virtually absent. In other words, Brownian motion of the average phenotype of a species on a standard scale, as predicted by population genetic models, would manifest itself as Brownian motion on a logarithmic scale when observed over long periods of time.

Brownian motion on a logarithmic scale is a particularly good approximation of Brownian motion if the standard deviation of change per unit time is small. If the standard deviation is large, the Central Limit Theorem still predicts Brownian motion is still as a decent descriptor. To illustrate the implications, let us consider the evolutionary an evolutionary quite ridiculous model, though quite ridiculous, in which character change per generation u is uniformly distributed 0 and $1m$, so that

$$m_n = m_o + \prod_{i=1}^n v_i$$

The p.d.f. of v is uniform so that the distribution of $\ln v$ is exponential. It can be shown that the sum of n exponential random numbers is gamma-distributed with parameters $\alpha = n$ and $\beta = 1$. For large n , the gamma ($n,1$) distribution converges to the normal distribution, which shows that even a biologically unrealistic model of trait evolution behaves as logarithmic scale Brownian motion if:

- changes to the average phenotype are independent of each other
- changes are distributed symmetrically around the average phenotype
- the variance of changes is directly proportional to the average phenotype

As far as I know there is no evidence against any of these conditions.