

**GEOGRAPHIC RANGE SIZE: SPECIATION, EXTINCTION
AND WHAT HAPPENS IN-BETWEEN**

by

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ABSTRACT

I studied the impact of geographic range size on clade diversification rates. Recent studies have suggested that, although geographic range size shows phylogenetic signal, this signal may be a statistical artefact. I created two models of range size evolution to determine the expected division of range size at speciation and to model the subsequent evolution of range size in sister species. Range size "symmetry" (the degree of similarity between sister species' range sizes) was then compared to these expectations. The range size of sister species of birds both show phylogenetic signal and are more similar than expected under the model, suggesting that range size is heritable. I then show that range size has a positive relationship with diversification rate in young clades of primates, but that the relationship may become asymptotic or even negative at very large range sizes. This is the first evidence of a non-linear relationship between range size and diversification rate, and may also be evidence of a non-linear relationship between range size and speciation rate. Finally, I test the novel hypothesis that clades which can tolerate the extinction risks associated with range restriction will diversify more quickly than intolerant clades. I find that risk-tolerant primate clades do have higher diversification rates. I also find, surprisingly, that the biological correlates of extinction risk tolerance are habitat specialisation and small geographic range size. "Rare" species (i.e. those with narrow geographic distributions or small population sizes) may therefore be characterised by their tolerance of extinction risk, rather than being risk-prone as is widely thought.

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CHAPTER 1: INTRODUCTION

There are at least 19 species in the primate macaque genus and only one species in the baboon genus. Similarly, nearly half of all bird families contain fewer than 10 species, but a few bird families contain over 250 species (Owens et al. 1999). These are not exceptions, but part of a general pattern. In plants, fish, several mammal orders, invertebrates and birds, the distribution of diversity commonly shows a right skew or hollow curve shape, (in other words, the majority of higher taxa have only a few species, but one or two contain a great many species) (Dial and Marzluff 1989, Guyer and Slowinski 1993).

This may be largely because some higher taxa have had more time to increase in diversity than others (Isaac et al. 2003, McPeck and Brown 2007). However, the speed at which evolutionary lineages add new species also varies greatly (e.g. Nee et al. 1992, Purvis et al. 1995, Mooers and Heard 1997, Barraclough et al. 1998). This rate of growth of a lineage, the “diversification rate”, is made up of the number of new species added to a lineage per unit time, minus the number of species removed by extinction.

There is widespread interest among both neontologists and paleontologists as to whether these differences in diversification rate are correlated with aspects of species biology (see reviews in Barraclough et al. 1998, Isaac et al. 2005, Jablonski 2007). Particular interest has been shown in traits which can belong only to species and not to individual organisms, such as geographic range size, population density, sex ratio or age structure (reviewed in Grantham 1995, Jablonski 2007). These are particularly appealing because they are properties of the same entities whose births and death rates we are trying to explain, namely species and clades.

Geographic range size and clade diversity

Geographic range size has long been an obvious candidate as a species-level trait that should influence diversification rates. Firstly, information on range size is much more readily available than population density or population structure, both in modern and

paleontological records (e.g. Hansen 1982, Jablonski 1987, Gaston and Blackburn 2000). Secondly, both theoretical and empirical studies suggest that range size is negatively related to the probability of extinction (e.g. Stanley 1979, Hansen 1982, Jablonski 1987, 1995, McKinney 1997, Maurer and Nott 1998, Gaston and Blackburn 2000, Purvis et al. 2000a, Jablonski and Hunt 2006). More recently, there have been a number of studies on the negative correlation between a species' geographic range size and its current extinction risk, i.e. the probability of a species being listed as of conservation concern under the IUCN criteria (Purvis et al. 2000a, 2000b, Owens and Bennett 2000, Jones et al. 2003).

There has also been much theoretical interest in the relationship between range size and speciation rate. Many authors have proposed that species with larger geographic ranges will speciate more often. Large ranges are more likely to be split by barriers, offer more opportunities for adaptive divergence, and may give rise to more founder groups that migrate away from the original species range (Terborgh 1973, Endler 1977, Rosenzweig 1995, Holt 1997, Maurer and Nott 1998, Hubbell 2001). All of these processes will provide increased opportunities for reproductive isolation and therefore speciation. Other authors have proposed a negative relationship between species range size and the probability of speciation. The most commonly-proposed mechanism for this hypothesis is that high dispersal ability inhibits the reproductive isolation of populations (e.g. Hansen 1980, 1982, Jablonski 1986, 1995, Stanley 1986, Chown 1997, Gavrillets et al. 2000, Hubbell 2001, Gaston 2003), and dispersal ability and range size are often positively correlated (Hansen 1982, Juliano 1983, Jablonski 1986, 1995, Edward and Westoby 1996, Kelly 1996, Gutierrez and Menendez 1997, Dennis et al. 2000, Malmqvist 2000). The relationship between range size and speciation rate may be non-linear. For example, a hump-shaped relationship may arise because extremely large ranges are too big to be split by barriers (Rosenzweig 1995, Gaston and Chown 1999). It is also possible that the increase in opportunities for speciation with area creates a positive relationship between range size and speciation rate for most range sizes, but this is overridden by the effects of dispersal when range sizes are extremely large (Maurer and Nott 1998).

Since the relationship between range size and speciation rate is unclear, it is unclear what the hypothesis should be for the relationship between range size and diversification rate (the net difference between speciation rate and extinction rate). Nor can studies of the individual relationships between range size and speciation or extinction necessarily illuminate the relationship between range size and diversification. Speciation and extinction rates may be correlated with each other in clades (Stanley 1979, 1986) and it is therefore possible for a clade to have a high speciation rate but a low diversification rate (Chown 1997). The overall question of what drives the diversity of life requires a measure of how speciation and extinction rates balance each other out i.e. the diversification rate.

The relationship between range size and diversification rate has been difficult to address empirically, because range size is a highly labile trait (Bottjer and Jablonski 1988, Overpeck and Webb 1992, Brown 1995, FAUNMAP working group 1996, Miller 1997, Davis and Shaw 2001, Losos and Glor 2003, Lyons 2003, 2005). Diversification rate is a property of the clade, and is therefore generally compared to the range size of a clade (Gaston and Blackburn 1997, Owens et al. 1999, Cardillo et al. 2003, Jablonski and Roy 2003, Phillimore et al. 2006). Some authors have measured average clade range size (Gaston and Blackburn 1997, Cardillo et al. 2003, Jablonski and Roy 2003, Phillimore et al. 2006), and have found both negative and positive relationships between range size and diversification. Other authors have used the total range size of a clade, and have found positive or non-significant relationships with diversification (Gaston and Blackburn 1997, Owens et al. 1999). But it is questionable whether the present-day range size of a clade can be compared to diversification events that happened in the past (Gaston and Blackburn 1997, Owens et al. 1999). Speciation can cause the average range size of a clade to decline (Cardillo et al. 2003), and may cause the total area occupied by a clade to expand. Extinctions will reduce the total range size of a clade.

Chapter 3 therefore examines how a species-level trait, geographic range size, may explain differences in clade diversity. It presents a novel test, the “triplets test”, which

aims to minimise the problems of range size lability and of the impact of speciation and extinction on clade range sizes. It also presents the first (to my knowledge) test of whether the relationship between range size and clade diversity is non-linear.

Range size heritability and evolution

The enterprise of seeking correlates of speciation, extinction and diversification rates has been referred to as higher-level selection (Eldredge and Gould 1972, Stanley 1975, Grantham 1995, Okasha 2003, Jablonski 2007). This higher level of selection can be referred to as species-level selection, since it enumerates the birth and death of species, or as clade-level selection, since the metric of interest is the number of species in a clade. The effect of species-level traits on the diversification rates of clades is comparable to the effect of organismic traits on individual fitness (Eldredge and Gould 1972, Stanley 1975, Grantham 1995, Okasha 2003, Jablonski 2007). Diversification rate may therefore be interpreted as the clade-level equivalent of organismic fitness i.e. "lineage fitness".

Studies of natural selection on individual traits need to demonstrate that a trait is heritable, i.e. that it will be passed on from ancestor to descendant (Lewontin 1970). The same condition has been applied when selection on species-level traits is being studied (Webb and Gaston 2003). Heritability is important in explaining clade diversity because the creation of a large clade involves several speciation and extinction events. Range size can strongly influence diversification in a clade only if a large proportion of the clade's species share similar range sizes. If all of a clade's species have very different range sizes, then some will have positive effects on the clade's diversification and others negative effects, implying a particularly weak influence of range size overall. Similarly, if range sizes change over time, then diversification rates in a clade will be subject to varying and potentially contradictory influences from range size over the clade's lifetime.

The first study in this thesis (chapter 2) therefore seeks to establish whether range size is heritable. The heritability of range size has been highly contentious, with different methods being proposed and different conclusions reached. Jablonski (1987) argued that the range sizes of late Cretaceous molluscs exhibit heritability, since the range size of

daughter species exhibits a significant correlation with that of their most immediate known ancestor in the fossil record. Webb and Gaston (2003) found a similar correlation in the present-day range sizes of sister species of birds, but argued that correlation tests for range size heritability are unreliable and presented a new test that compares the degree of similarity between sister species to a null model. But differences in the choice of null model can cause the test to affirm or reject heritability in the same data set (Hunt et al. 2005, Webb and Gaston 2005, Waldron 2007). Analyses of variance show that most of the variation in range size occurs at the level of species within genera, suggesting that heritability cannot be strong in range size (Gaston 1998, Webb et al. 2001, Arita 1993). But at the genus level, sister clades of herbaceous plants (but not woody plants) have more similar range sizes than expected (Ricklefs and Latham 1992, Qian and Ricklefs 2004), suggesting that range size is heritable. Finally, tests of phylogenetic signal across whole phylogenies have found heritability of range size in some taxa but not others (Taylor and Gotelli 1994, Freckleton et al. 2002, Blackburn et al. 2004, Jones et al. 2005, Bohning-Gaese et al. 2006). Permutation tests, which often test phylogenetic signal on incomplete subsets of phylogenies such as sister-species pairs, have generally found that range size is heritable (Hunt et al. 2005, Waldron 2007).

Chapter 2 takes the lead of Webb and Gaston (2003) and assesses heritability of range size in the most contentious taxon (birds) using both Webb and Gaston's method and a test of phylogenetic signal. Since the results from Webb and Gaston's method differ depending on the null model chosen (Webb and Gaston 2003, 2005, Hunt et al. 2005), chapter 2 explores the choice of null model from the standpoint of the evolution of geographic range size. Chapter 2 precedes chapter 3 because it is necessary to assess the heritability of range size before proceeding to test its impact on clade diversity.

The role of extinction in generating clade diversity: the challenge of restricted range size

It is difficult to assess the relative contribution of extinction to a clade's present-day diversity, because extinction often leaves little trace of its occurrence. Nevertheless, it is important to understand natural patterns of extinction, so that we can make informed

decisions about the impact of human activities on extinction risk. Geographic range size is widely believed to influence extinction risk, and a large range size is generally thought to protect species from extinction (e.g. Stanley 1979, Hansen 1982, Jablonski 1987, 1995, McKinney 1997, Maurer and Nott 1998, Gaston and Blackburn 2000, Purvis et al. 2000a, Jablonski and Hunt 2006). A large range size may also promote faster speciation, however (Terborgh 1973, Endler 1977, Rosenzweig 1995, Holt 1997, Maurer and Nott 1998, Hubbell 2001). A positive relationship between range size and clade diversity therefore yields little information on what the relative contributions of speciation and extinction were. On the other hand, if species differ in their ability to tolerate confinement to a small geographic area, this could have an impact on clade diversity that is clearly related to extinction. Species populations already restricted to small geographic areas are unlikely to split into two species. If more diverse clades contain species that have a high tolerance of range restriction, the implication is that lack of extinction has promoted higher clade diversity.

Chapter 4 therefore examines differences in species abilities to tolerate range restriction, and relates these to differences in clade diversification rates. This approach is novel, and the biological attributes which allow species to tolerate a persistent extinction threat may be very different from those typically associated with low extinction risk. Chapter 4 therefore also investigates potential biological correlates of extinction risk tolerance.

Islands are used as an example of range restriction that imposes extinction threat. Although the original theory of island biogeography implies that all species have the same probability of extinction on islands (MacArthur and Wilson 1967), subsequent research has suggested that certain species are more at risk than others on islands (Brown 1971, Diamond 1972, 1984, Faaborg 1979, Wilcox 1980, Graves and Gotelli 1983, Patterson 1984, Pimm et al. 1988, Gotelli and Graves 1990, Foufopoulos and Ives 1999, Harcourt and Schwartz 2001, Harcourt et al 2002). For example, species lists on smaller islands often form “nested subsets” of species lists on nearby larger islands (Brown 1971, Patterson 1984). In other words, some species are present on all islands in an island group, whereas other species are only present on the larger islands and have presumably

gone extinct from all of the smaller ones (Diamond 1972, 1984, Wilcox 1980, Graves and Gotelli 1983, Gotelli and Graves 1990, Harcourt and Schwartz 2001). This implies that species found only on large islands have a higher risk of extinction (Brown 1971, Diamond 1974, Faaborg 1979, Graves and Gotelli 1983, Patterson 1984, Foufopoulos and Ives 1999, Harcourt and Schwartz 2001, Harcourt et al 2002).

Because MacArthur and Wilson (1963, 1967) hypothesized that species numbers would reflect a balance between colonisation and extinction, many of these earlier studies used taxa which are able to recolonise islands after local extinction (especially birds) (Diamond 1972, 1984, Faaborg 1979, Graves and Gotelli 1983, Pimm et al. 1988). In order to study only extinction processes, colonisation needs to be eliminated, and chapter 4 therefore uses primates.

In addition, the theory of island biogeography emphasizes that the species-area curve (i.e. the fact that larger areas of land contain more species) is partly explained by sampling effects (Wilcox 1980). A number of more recent studies that have looked for biological correlates of extinction on islands have not fully taken this into account (Foufopoulos and Ives 1997, Harcourt and Schwartz 2001). Chapter 4 therefore investigates persistence on islands in a way that attempts to correct for sampling effects.

Overall, the thesis tests three aspects of geographic range size's influence on clade diversity. Only heritable traits can have an impact on "lineage fitness" (i.e. diversification rate), and chapter 2 therefore assesses the heritability of geographic range size. Chapter 3 studies the impact of geographic range size on clade diversification rates. Chapter 4 assesses whether ability to tolerate range restriction (i.e. extinction risk tolerance) has an impact on clade diversification rates.

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CHAPTER 2: NULL MODELS OF GEOGRAPHIC RANGE SIZE EVOLUTION REAFFIRM ITS HERITABILITY¹

INTRODUCTION

Studies of the determinants of geographic range size often focus on ecological factors, or on the limits to range imposed by geographic barriers such as mountains and coasts (see summaries in Brown 1995, Gaston 2003). However, a species' geographic range size is defined in the first instance by the fraction of the ancestor's range that it receives at the moment of reproductive isolation. Range size (and indeed extinction) at other moments in a species' lifetime are the product of changes made to that original fraction (Gaston and Blackburn 1997, Price et al. 1997, Gaston 1998). The process of inheritance and the degree of heritability (defined as a pattern of similarity between relatives) are therefore potentially important influences on present-day species distributions.

Species-level heritability is also crucial for studies of species sorting or "clade selection" (Eldredge and Gould 1972, Stanley 1975, Jablonski 1987, 2000, Grantham 1995, Okasha 2003, Webb and Gaston 2003). Species-level traits that influence the chances of extinction and speciation might be able to explain differences in diversification rates between clades (for reviews see Barraclough et al. 1998, Isaac et al. 2005), so long as such traits are heritable (Lewontin 1970). Range size is widely postulated to have such effects (Jablonski 1987, Rosenzweig 1995, Gaston and Blackburn 1997, McKinney 1997, Gaston 1998, Gaston and Chown 1999, Purvis et al. 2000, Cardillo et al. 2003) and so its heritability is of considerable interest.

A debate over whether a species' geographic range is indeed heritable has simmered and recently re-erupted in the literature (Hunt et al. 2005, Webb and Gaston 2005). Jablonski (1987) presented evidence that the range sizes of late Cretaceous molluscs exhibit heritability, since the range size of daughter species exhibits a significant correlation

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(both product moment and Spearman's rank) with that of their most immediate known ancestor in the fossil record. Webb and Gaston (2003) found that the present-day range sizes of sister species of birds also exhibit a significant correlation.

However, Webb and Gaston (2003) argued that correlation provides an unreliable test of range size heritability, because range size distributions are highly right-skewed, and this can affect the validity of even non-parametric correlation. They created a new approach to measuring heritability, comprised of comparing the "symmetry" between the ranges of sister species to a null model (where symmetry is defined as the smaller range size divided by the larger one). This null model draws pairs of range sizes at random from a uniform distribution (Hunt et al. 2005, Webb and Gaston 2005). Sister species of birds were no more symmetrical in their present-day range sizes than the null model predicted (in fact, they were significantly less symmetrical than expected). The authors therefore argued that range size is not heritable. However, Hunt et al. (2005) showed that if such a model takes random draws from a right-skewed distribution (such as is typical of range sizes), instead of a uniform one, then heritability is reaffirmed.

More recent tests of range size heritability have used Pagel's lambda (Pagel 1999, Freckleton et al. 2002) and Moran's I (Gittleman and Kot 1990). These tests ask whether the distance between species on a phylogenetic tree is related to the distance between their trait values. They found a weak phylogenetic signal in the range sizes of mammals, suckers (fish) and parrots, although results for individual mammalian orders were mixed (Freckleton et al. 2002, Blackburn et al. 2004, Jones et al. 2005). There was no signal in the ranges of sunfish or in the British ranges of Lepidoptera (Freckleton et al. 2002). Table 1 summarizes the diverse methods used to assess phylogenetic signal in range size.

Different concepts of heritability

The disagreements over whether range size is heritable, and over the validity of the many different methods used, arise from two different concepts of "heritability" in a species-level trait. The first I will refer to as "phylogenetic signal" (Blomberg et al. 2003). A signal occurs if closely related species are more similar in their character values than are more distantly related species. Correlation and regression tests (Jablonski 1987, Ricklefs

and Latham 1992, Webb et al. 2001, Qian and Ricklefs 2004), permutation tests (Taylor and Gotelli 1994, Hunt et al. 2005, Bohning-Gaese et al. 2006) and whole-tree tests such as Moran's I (Gittleman and Kot 1990, Blackburn et al. 2004, Jones et al. 2005) and Pagel's lambda (Pagel 1999, Freckleton et al. 2002, Jones et al. 2005) all measure phylogenetic signal.

The second concept proposes an expectation for the similarity between sister species based on a null model. A trait is classed as heritable if the similarity between sisters exceeds this null expectation (Webb and Gaston 2003). I will refer to the approach as the "general null expectation" or GNE test for heritability, since model and expectation are designed to be generalizable to all taxa and all traits (Webb and Gaston 2005). The GNE test differs from phylogenetic signal tests because it does not involve any comparison between the trait values for sister species and those of other species in the phylogeny.

Range size heritability tests require an evolutionary model

Phylogenetic signal tests are based on the premise that similarity (and symmetry) between two species decays with time since their common ancestor. GNE tests have not, to date, made explicit their underlying model of change in symmetry (Webb and Gaston 2003, 2005). However, a situation whereby sister species' symmetry changed after speciation would affect the interpretation of heritability tests. An explicit model of the evolution of range size symmetry, starting at speciation and then describing a trajectory through time, is therefore crucial if tests of heritability are to be properly applied (Jones et al. 2005).

Barracough and Vogler (2000) generated an expectation for range size symmetry by simulating vicariant speciation in rectangular ranges and then allowing range size to change by random drift. Their expectation applies to the total range encompassed by sister clades rather than to the ranges of sister species and so is difficult to apply to Webb and Gaston's (2003) approach. In addition, Barracough and Vogler's (2000) model used a one-dimensional broken stick distribution (MacArthur 1957) to divide two-dimensional ranges and did not allow extinction when range size dwindled to nothing, neither of which is biologically realistic.

Taxon	Heritability test category	Result	Source
Molluscs (fossil)	Phylogenetic signal (correlation and regression between ancestor and descendant)	Heritable $r_s = 0.65$ (for gastropods)	Jablonski (1987)
Birds	Phylogenetic signal (correlation)	Heritable $r_s = 0.26$	Webb and Gaston (2003)
Anseriform birds	Phylogenetic signal (correlation)	Not heritable $r_s = 0.18$	Webb et al. (2001)
Cyprinellid fish	Phylogenetic signal (correlation)	Heritable $r_s = -0.35$	Taylor and Gotelli (1994)
Genera of herbaceous plants	Phylogenetic signal (correlation)	Heritable $r_s = 0.53$	Qian and Ricklefs (2004)
Genera of woody plants	Phylogenetic signal (correlation)	Not heritable $r_s = 0.18$	Qian and Ricklefs (2004)
Molluscs (fossil) and birds	Phylogenetic signal (permutation)	Heritable	Hunt et al. (2005), reanalyzing Jablonski (1987) and Webb and Gaston (2003)
Parrots (Psittaciformes)	Phylogenetic signal (Moran's I and Pagel's λ)	Heritable below the level of tribe $\lambda = 0.16$, $I = 0.28$	Blackburn et al. (2004)
Lepidoptera (UK range only)	Phylogenetic signal (Pagel's λ)	Not heritable $\lambda = 0.64$	Freckleton et al. (2002), reanalyzing Dennis et al. (2000)
Sunfish	Phylogenetic signal (Pagel's λ)	Not heritable $\lambda = 0.0$	Freckleton et al. (2002), reanalyzing Pyron (1999)
Suckers	Phylogenetic signal (Pagel's λ)	Heritable $\lambda = 0.66$	Freckleton et al. (2002), reanalyzing Pyron (1999)
Australian marsupials	Phylogenetic signal (Pagel's λ)	Heritable $\lambda = 0.53$	Freckleton et al. (2002), reanalyzing Johnson (1998)
Mammals	Phylogenetic signal (Moran's I)	Heritable overall, and for some orders $I = 0.32$ overall	Jones et al. (2005)
Primates	Phylogenetic signal (Moran's I and Pagel's λ)	Heritable $\lambda = 0.33$, $I = 0.49$	Jones et al. (2005)
Carnivores	Phylogenetic signal (Moran's I and Pagel's λ)	Heritable $\lambda = 0.36$, $I = 0.14$	Jones et al. (2005)
Genus <i>Sylvia</i> (birds)	Phylogenetic signal (multiple regression with permutation for significance testing)	Not heritable	Bohning-Gaese et al. (2006)

Table 2.1: Methods used to assess phylogenetic signal in range size and their outcomes. For correlational studies, the Spearman's rank correlation coefficient r_s is reported, since range size does not meet the assumptions of parametric statistics. For studies using Pagel's lambda, the lambda statistic is reported. Lambda varies from 0 to 1, where 0 means no phylogenetic signal and 1 means that variation in the trait is perfectly correlated with phylogeny. Studies using Moran's I give a summary of the I statistic. I values range from -1 to +1, where positive values indicate that at a particular taxonomic level, closely related taxa are more similar than expected by chance and negative values indicate more dissimilarity than expected. I values are reported here only for species within genera. Complete I statistics can be found in the sources referred to.

Here, I model range size symmetry of sister species pairs two-dimensionally, first at the moment of speciation, and then over a period of evolution. I use results from the models to produce a general null expectation (GNE) test of heritability. I then apply the GNE test to the range sizes of sister species of North American birds. I also apply a test for phylogenetic signal to the bird data, and compare the outcomes of the two tests. Finally, I discuss how results may vary with the test used, and which biological questions are best addressed by each approach.

METHODS

Ranges of North American Birds

In order to minimize the effects of available land area on species ranges, I selected from Weir and Schluter (in press) 65 sister species pairs of birds whose breeding ranges were predominantly limited to continental North America. All species had >99% of their breeding ranges north of the Mexico/Guatemala border except for *Sayornis nigricans* (76%) and *Sturnella magna* (81%). I used only the North American range of the mallard *Anas platyrhynchos* on the grounds that it is effectively independent of its Old World range. Excluding these three species did not alter the conclusions of the study.

Breeding range maps were taken from Birds of North America (Poole et al. 1992) or from Ridgely et al. (2005) where phylogeny had changed with respect to Poole et al. (1992). Source maps were converted to equal-area using the Arcview 3.2 extension ImageWarp (MacVay 2000), then digitized. Range areas were calculated using Arcview utilities. There are two ways of measuring range size: "area of occupancy" sums the individual areas where a species is actually found, whereas "extent of occurrence" measures the total area of a single polygon drawn around the species' most extreme geographic limits (Gaston 1991, 1994). The range maps used here measure area of occupancy, albeit at a coarse resolution.

The range size of a species is constrained by the land area of the region in which it occurs (Letcher and Harvey 1994). For example, Mexican species could well have a small range size compared to United States species, simply because the continent narrows at lower latitudes. I therefore also measured range as a percentage of the total land area available within the species' latitudinal limits on that continent. This method probably overestimates the relative size of smaller ranges, because the assumption that a species could potentially occupy the same percent of its latitudinal band irrespective of continent width might be unrealistic. For brevity, it will be referred to in this paper as "percent of latitudinal band".

I also measured the ratio between the maximum latitudinal and longitudinal extent for each species as an approximate indicator of range shape. Latitudinal and longitudinal limits were measured in Microsoft Encarta to the nearest half degree and then transformed to kilometer values using the haversine method (Sinnott 1984).

Finally, I calculated the symmetry between sister species, where "symmetry" means the area of the smaller range value divided by that of the larger range in each pair.

Phylogenetic Signal

To test for phylogenetic signal, I used a randomization test on range size symmetry (Maddison and Slatkin 1991, Blomberg et al. 2003, Hunt et al. 2005). This test repeatedly shuffles the range size values whilst keeping the phylogeny constant, and then asks how often the average symmetry of sister species in the original arrangement exceeds the average symmetry of species pairs when values have been so shuffled. If sister species are more symmetrical (i.e. more similar to each other) than random pairs 95% of the time, then the data are judged to have a significant phylogenetic signal. I repeated this test for the bird data with range size expressed as arcsine-transformed percent of latitudinal band.

To quantify the strength of the phylogenetic signal, I used the intraclass correlation for the sister species pairs (Snedecor and Cochran 1967). This measures the proportion of

total variance that is between species pairs to give an estimate of heritability on a scale from 0 to 1, where 0 indicates no heritability.

Modeling the Inheritance of Geographic Range Size at Speciation

I simulated the inheritance of range size at the moment of divergence under vicariant modes of speciation. Moment of range splitting will be referred to as “moment of speciation” from this point on, although speciation occurs some time after the splitting of a species’ range into two. I will refer to speciation that occurs when a species range is split into two parts as “range-splitting speciation”, and to that occurring when a founder population migrates to a new area as “founder dispersal speciation”. This is to avoid the confusions that can arise with the terms “peripheral isolate” and “vicariant” speciation, since peripheral isolates may be the result either of microvicariance (i.e. highly asymmetrical range splits) or of founder dispersal (Brooks and McLennan 1991).

To model range-splitting speciation, I took rectangular shapes of varying long side:short side ratios and randomly split them in two 100,000 times. Empirical long side:short side ratios (where sides lengths are represented by latitudinal and longitudinal extent) are typically between 1 and 10 in North American bird ranges, and so this range of values was explored. Rectangles were split by picking a random point on the periphery and then drawing a chord at a random angle across the shape. The resulting frequency distribution of symmetries will be referred to as a “broken tile distribution” (model A1). Not all the barriers that arise in nature will split ranges in two, because shorter barriers are not always able to span whole geographic ranges (Gaston 1998, but see Rosenzweig 1995). I therefore varied barrier length in model A1 whilst keeping other parameters constant, and discarded simulations in which the barrier was not long enough to cause a split.

For comparison with Anderson and Evelyn (1978) and Barraclough and Vogler (2000), I also used MacArthur’s (1957) broken stick model. This repeatedly breaks a one-dimensional stick at a single random point along its length, therefore treating range size as a one-dimensional number. Results from this process (model A2) will be referred to as a broken stick distribution (MacArthur 1957).

As a special case of range-splitting speciation (model A3), I also modeled a situation in which the sub-ranges of two populations contract and become isolated from each other, as may occur when climate change causes a formerly continuous range to fragment (Diamond and Hamilton 1980). This will be referred to as “range contraction speciation”. It was simulated by randomly taking two (x,y) coordinate points within the ancestral range and drawing independent, non-overlapping circles of random radius about these points (within the limits of the ancestral range). Random numbers in all simulations were drawn from a uniform distribution, with one exception: in model A3, to reflect the right-skewed distribution of range sizes (Gaston 1998, Hunt et al. 2005), I added an extra simulation which drew the radii at random from a lognormal distribution.

Unlike range-splitting speciation, founder-dispersal speciation envisages the rare migration of a breeding population to a novel area, followed by divergence and reproductive isolation (Mayr 1963, Chesson and Zink 1994). I did not model range symmetry for founder dispersal at the precise moment of speciation, but simply observe that it is likely to be very low. Founder populations which travel away from the ancestral range are unlikely to represent more than a small percentage of the total species population in that first moment of migration.

All of the above models assume that speciation is allopatric or parapatric, a largely safe assumption in birds (Barracough and Vogler 2000, Coyne and Price 2000).

Modelling the subsequent evolution of range size symmetry

The above simulations generate an expectation at the moment of speciation, but do not tell us how this may evolve towards an expectation in the present day. To model the post-speciation evolution of range sizes (model B), I took 250 (the computing memory limit) of the range pairs resulting from model A1 (broken tile) and applied a random drift process to them (following Barracough and Vogler 2000). Range sizes either multiplied or divided by 1.01 at each timestep. Ranges which fell to zero (defined computationally as <0.001) were declared extinct. At each timestep, average symmetry of all pairs which had lost neither of the two sisters to extinction was calculated.

The size of the North American continent would set an upper limit to range growth (bird ranges are a median one-sixth of the continental area). But since opinions differ widely on which range sizes account for the majority of speciation events (Mayr 1963, Terborgh 1973, Jablonski 1986, Rosenzweig 1995, Holt 1997, Maurer and Nott 1998, Gaston and Chown 1999, Hubbell 2001, Jablonski and Roy 2003), the definition of an appropriate frequency distribution of post-speciation growth limits for North American bird ranges would be contentious. Fortunately, the qualitative results of the model remained unchanged under a wide variety of growth limit distributions.

To assess how long the model should run for, I applied the drift process to the actual bird ranges to see how long it took for phylogenetic signal to disappear (as measured by the permutation test described above). 30,000 timesteps proved sufficient. All models were run a minimum of five times to check robustness of the conclusions.

Comparison of models and bird data

Since the bird range size symmetry data does not meet the assumptions of parametric statistics, I generated 95% confidence intervals for its mean symmetry by bootstrapping the data 100,000 times and calculating the mean for each bootstrap replicate. This process generates a frequency distribution of the bootstrapped means, and the 95% confidence interval of the mean then spans the 2.5% percentile and the 97.5% percentile of this distribution (Manly 1997). In addition to comparing the mean symmetry of the models and the data, I used Kolmogorov-Smirnov goodness of fit tests to compare their distributions of symmetry (Sokal and Rohlf 1995). Simulations were carried out using Visual Basic (Microsoft Corporation 1997). Statistical analysis was carried out using S-Plus 6.0 (Insightful 2000).

RESULTS

Phylogenetic Signal and Intraclass correlation

The randomization test shows that symmetry in the range sizes of bird species pairs is higher than in a random reordering of the data more than 99 percent of the time ($p < 0.01$, log-transformed data). North American species pairs therefore show a phylogenetic signal. The intraclass correlation is 0.15 for log-transformed ranges.

Null Expectations for Range Symmetry at the moment of speciation

Expected symmetry between the range sizes of sister species is low under a variety of speciation scenarios (Table 2.2). For the broken tile model (A1), biologically realistic parameter sets give an expectation between 0.2 and 0.3. North American bird ranges have an average long side:short side ratio of 1.6, and inputting this value produces an expected symmetry of 0.26 at speciation. When barrier length is constrained rather than being infinite, expected symmetry is reduced (Table 2.2). The model's maximum expected symmetry is 0.39, but this only occurs when the long side:short side ratio is approximately 100,000.

Model	Long side:short side ratio of the rectangle		
	1	1.6	10
(A1) Broken tile	0.21	0.26	0.36
	(0.19, 0.07)	(0.20, 0.04)	(0.32, 0.01)
(A2) Broken stick	0.39	NA	NA
(A3) Range-contraction	0.25	0.25	0.25
			(0.28 if using a uniform distribution)

Table 2.2: Expectations for the mean symmetry (small/large ratio) between sister species' range sizes at the moment of speciation. Numbers in parentheses for model A1 show the effects of limiting maximum barrier length to 1.2 times and 1 times the rectangle's shorter side respectively. In the case of model A2, the long side:short side ratio is not relevant since the model breaks a one-dimensional line. Results for model A3 are the same for lognormal and uniform distribution of range size radii, except where shown (see text).

The broken stick model (A2) has an expected symmetry of 0.39. This result is unsurprising, since it is the same as that for a very long, thin rectangle in model A1. The range-contraction model (A3) has an expectation of 0.25 -0.28 for biologically realistic long side:short side ratios, and this changes little whether the ratios of the contracted range sizes are drawn from a uniform or a right-skewed distribution (Table 2.2). The frequency distribution of symmetries for moment-of-speciation models has a hollow curve shape in all models, with the lowest symmetry being the modal class (figure 2.1).

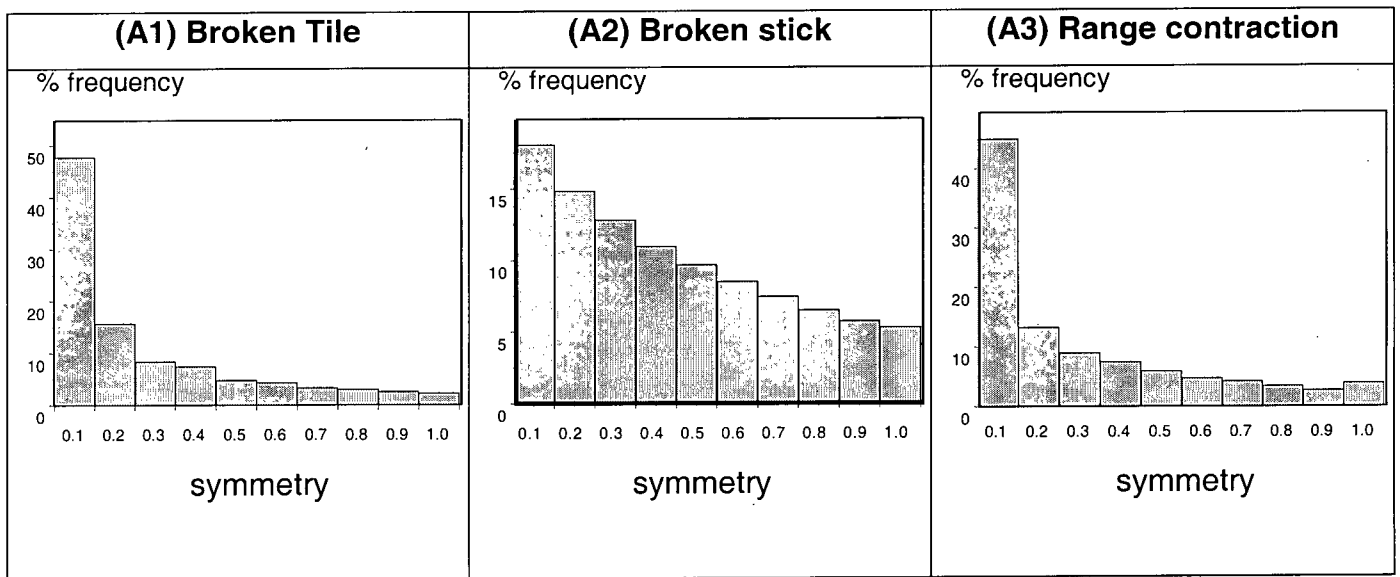


Figure 2.1: Expected frequency distributions of symmetry between sister species range sizes at the moment of speciation. Models A1 and A3 show results for a longside:shortside ratio of 1. The model A3 figure used a uniform distribution of radii to model range size; a lognormal distribution yielded very similar results (see text).

Null Expectations for Range Symmetry after a period of evolution

In ten runs of model B (post-speciational random drift), average symmetry for the 250 lineages (minus extinctions) lay between 0.2 and 0.3 in over 95% of timesteps, and never exceeded 0.32. A representative time sequence is shown in figure 2.2. The distribution of symmetries at the end of 30,000 timesteps was strongly right-skewed in all ten runs (not shown), similar to that for the broken tile model.

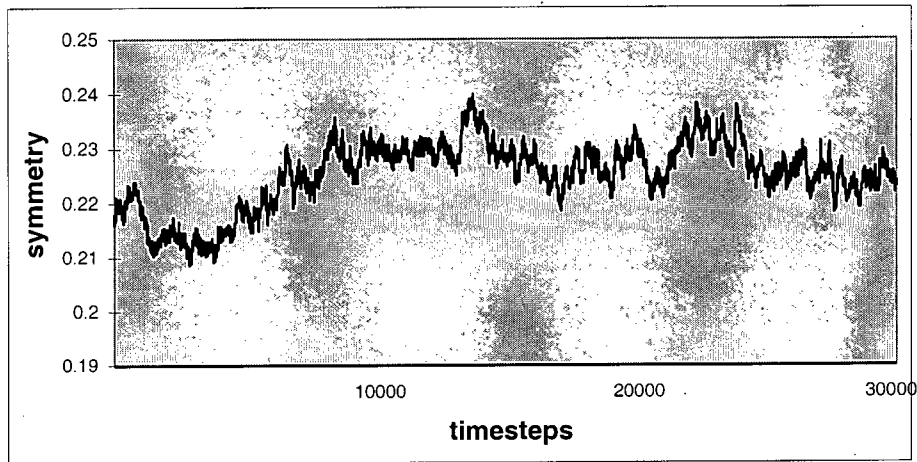


Figure 2.2: A typical trajectory of range symmetry evolution using a model of random drift. The line shows the average of smaller range/larger range for 250 sister species pairs.

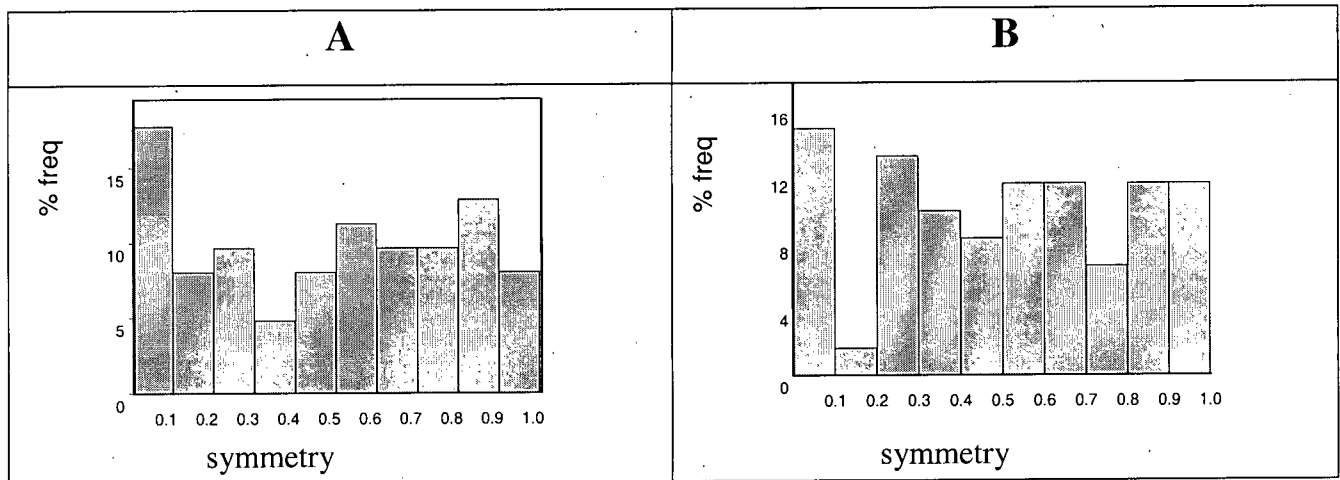


Figure 2.3: Symmetry of range sizes in North American sister species of birds. A: symmetry based on raw range sizes; B: symmetry based on range sizes expressed as the percentage of the land area between the northern and southern latitudinal limits of the species occupied by that species.

Sister species symmetry in North American birds

The mean symmetry for the range sizes of North American bird sister species is 0.48 (95% CI 0.41-0.56), or 0.55 (95% CI 0.47-0.62) when measured as percent latitudinal band (appendix 2.1). The distributions of symmetries are shown in figure 2.3.

Kolmogorov-Smirnov tests indicate that these frequency distributions fit none the general null expectations ($p < 0.05$ in all cases). Empirical distributions have a much greater proportion of high symmetries than expected under the models.

DISCUSSION

There is a phylogenetic component to the range size of North American birds. Sister species of birds also display greater symmetry between their range sizes than expected under null models.

Phylogenetic Signal

The finding of phylogenetic signal in North American bird ranges is in agreement with the majority of comparable studies in other taxa (see Table 2.1). A few studies have found negative results - for certain mammalian orders (Jones et al. 2005), for sunfish (Freckleton et al. 2002, in a re-analysis of Pyron 1999), and for 26 warblers of the avian genus *Sylvia* (Bohning-Gaese et al. 2006). It is interesting that positive results have been found in large clades such as marsupials, mammals and North American birds, whereas negative results in general come from tests of individual orders or of even lower taxonomic levels.

The strength of phylogenetic signal, measured by intraclass correlation, is low for North American bird ranges. Other studies have also found that the phylogenetic signal in range size is weak, comparable in strength to the signal for an ecologically labile trait such as diet (summary in Freckleton et al. 2002). Even so, heritability of range size is weaker in birds than in other taxa. Correlation coefficients are relatively low in this and other avian range size studies (Webb et al. 2001, Webb and Gaston 2003) compared to those for other taxa (see Table 2.1). Similarly, the one study to use Pagel's lambda on birds (parrots, Blackburn et al. 2004) found one of the lowest lambda values for geographic range size of all the taxa studied to date. Low estimates of phylogenetic signal in birds are also consistent with the results of studies that partition the variance in range size among taxonomic levels (Gaston and Blackburn 1997, Cotgreave and Pagel 1997, Webb and Gaston 2000, Webb et al. 2001).

A phylogenetic signal for range size probably arises because ancestor range size is passed on to descendants at speciation, although not as simply as occurs with a trait such as body size. Small ancestral ranges are likely to give rise to two small descendant ranges.

Similarly, large-ranged ancestors will give rise to at least one large-ranged daughter. The second daughter may sometimes have a small range, either because of an asymmetrical vicariance event (Gaston and Chown 1999), or because of range changes after speciation.

The General Null Expectation Test

Models of vicariance suggest that average range size symmetry between North American avian sister species is expected to be 0.26 or less at speciation - potentially much less if speciation occurs by the dispersal of a founder population, or if many of the barriers that arise are relatively short compared to range size. Following speciation, the maximum mean symmetry achieved during the process of random drift is 0.32. Since it is unlikely that all species pairs reach the maximum simultaneously, a conservative realistic expectation would be 0.3 or less.

The symmetry in the bird data, at 0.48, is appreciably higher than the null expectations in any model. North American bird range sizes therefore show heritability under the general null expectation test, as well as under the phylogenetic signal test. Whilst there is no statistical measure of the strength of this form of heritability, present-day ranges appear to be about twice as symmetrical as they would have been at speciation. They are also some 50% more symmetrical than expected after a period of evolution.

The only comparable study to use a general null expectation approach found no heritability in bird ranges (Webb and Gaston 2003), even though their empirical symmetry value, at 0.45, is similar to that found here (Webb and Gaston 2005). Their expectation for symmetry was 0.5, which they achieved by taking random draws from a uniform distribution of range sizes (Hunt et al. 2005, Webb and Gaston 2005). The model used in the present study simulates an explicit evolutionary process of range splitting and random drift for range size, and this process leads to a right-skewed distribution of range sizes similar to that found in nature (Gaston 1998). Webb and Gaston's model does not emerge from an evolutionary process, and so it is unclear what the biological rationale is for using a uniform distribution (Hunt et al. 2005).

Possible mechanisms for greater-than-expected symmetry in range size

The results of this study suggest an unusual evolutionary process, in which resemblances between related species evolve over time rather than being immediately present at speciation. Random vicariance events and founder dispersal events initially create high asymmetry, but biological processes such as non-random extinctions and niche conservatism may lead to post-speciational changes in range size symmetry.

For example, if a species requires a certain minimum range size to avoid extinction, and the original vicariance event leaves one of the daughters with a range size below that critical threshold, then the “runt” species will become extinct. Repetition of this process would progressively remove extreme asymmetries from the dataset and so increase average symmetry of those sister pairs which persist over time. (The effect would be increased if runt species die out on closely-related branches of the phylogeny. The surviving species, all of which have larger ranges, will be classified as sisters and their symmetry will be high).

Sister species might also grow to resemble each other more over time because range size is influenced by other, heritable aspects of species biology. For example, Brown and Maurer (1987, see also Brown 1995) postulated that range size may be a function of species' ecological breadths. If ecological breadth is phylogenetically conserved (Ricklefs and Latham 1992, Price et al. 1997, Peterson et al. 1999, Wiens and Donoghue 2004, Wiens and Graham 2005), then sister species ranges will evolve to become more similar than they were at the moment of speciation.

A non-random, unusually symmetrical pattern of range barriers at speciation could also account for high symmetry today, abolishing the need to invoke post-speciational increases in symmetry. For example, Pleistocene ice sheets central to the North American continent may have caused the unusually symmetrical east-west divisions of some ranges seen today (Mengel 1964, 1970). It is beyond the scope of this study to establish the geography of speciation of each species pair. Nevertheless, the orientation and location of present-day contact boundaries are highly varied for the sister species studied, with a large number of pairs that are not split into clear east and west sisters

(many indeed have a northern and southern sister). Recent biogeographical studies have also suggested that a variety of geographic events at several different times may underlie speciation in North American birds (Bermingham et al. 1992, Klicka and Zink 1997, 1999). It therefore seems unlikely that non-random vicariance alone explains greater-than-expected symmetry.

Finally, rectangles may be an inaccurate representation of species ranges. But simulations using ellipses produced lower expectations of average symmetry than rectangles (0.16 and 0.18 for longside:shortside ratios of 1.6 and 10 respectively), because of the increased probability of a barrier shaving off a very thin slice from a range edge. The same seems likely to be true of irregular polygons; further work using much more complex models is required to confirm this.

Implications for comparative biology and evolutionary modeling

Large, post-speciational changes in range size are consistent with fossil evidence (mostly from periods of extensive climate change in the Pleistocene) that range size is highly dynamic (Overpeck and Webb 1992, FAUNMAP working group 1996, Davis and Shaw 2001, Lyons 2003, 2005; see also Brown 1995 and Losos and Glor 2003 for a neontological view) and argue against Zink et al.'s (2000) suggestion that ranges of North American birds are stable over a million years.

At the same time, phylogenetic signal in range size implies that sister-species similarities are not erased over time, no matter how labile the individual ranges are. Demonstrations of niche conservatism, including long-term similarity between the niches of sister species of birds (Price et al. 1997, Peterson et al. 1999, but see Rice et al. 2003) support this. Relatives' range sizes may therefore co-vary in response to environmental change.

Modern comparative methods (e.g. Felsenstein 1985, Harvey and Pagel 1991, Pagel 1999, Freckleton et al. 2002) depend on the assumed evolutionary model that symmetry will be near unity at speciation, and then decline with time according to a random walk process. But the models presented here suggest that range size does not behave in this way, since sister species are expected initially to be very dissimilar, and then perhaps to

become more similar over time. Some comparative methods may therefore produce erroneous results if applied to range size.

An expectation of symmetry has also been used to study the process of speciation itself. Barraclough and Vogler (2000), seeking to distinguish sympatric from allopatric speciation, simulated range splitting by using MacArthur's (1957) one-dimensional broken stick model. Anderson and Evensen (1978) used the same model to test for randomness in vicariance. But this study suggests that range symmetry at diversification in more realistic models of range-splitting is only half that expected under the broken stick model (and indeed clarifies that the broken stick symmetry expectation is 0.39). Models of speciation should use two-dimensional simulations of range division rather than one-dimensional ones.

Various authors (e.g. Lynch 1989, Chesson and Zink 1994) have also sought to distinguish peripheral-isolate from vicariant speciation on the basis of current range symmetries, but again without using any evolutionary model to define their null expectation of symmetry. Lynch suggested that speciation had probably occurred by founder dispersal ("peripheral isolates") if sister species ranges displayed a symmetry of five percent or less. Chesson and Zink (1994) take issue with the five percent rule, but apply the same test with different threshold criteria.

This study suggests a fundamental problem with this approach. The simplest broken tile model predicts that range-splitting (i.e. vicariant) speciation will lead to a 5% ratio of range sizes 35% of the time. After evolution by random drift, this falls to 22% of the time. If low range size symmetry is so typical of 'vicariant' speciation, it will not be informative of founder-dispersal events.

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CHAPTER 3: GEOGRAPHIC RANGE SIZE HAS A NON-LINEAR EFFECT ON NET SPECIATION RATES IN PRIMATES¹

INTRODUCTION

Evolutionary lineages differ substantially and non-randomly in their diversification rates (the net difference between their speciation and extinction rates) (Nee et al. 1992, Guyer and Slowinski 1993, Purvis et al. 1995, Maurer and Nott 1998, Owens et al. 1999, Katzourakis et al. 2001, Ricklefs 2003). This has generated widespread interest in species-level characteristics that might influence diversification, much of it focused on speciation (for reviews see Barraclough et al. 1998, Isaac et al. 2005, Jablonski 2007). Geographic range size is a promising candidate species trait, because it is thought to affect the probability of both speciation and extinction (for summaries see McKinney 1997, Purvis et al. 2000, Jablonski and Roy 2003).

Extinction rate is widely found to decline as range size increases (Stanley 1979, Hansen 1982, Jablonski 1987, 1995, McKinney 1997, Maurer and Nott 1998, Gaston and Blackburn 2000, Purvis et al. 2000, Jablonski and Hunt 2006). However, there is no clear theoretical prediction about the relationship between range size and diversification, because contradictory hypotheses exist regarding the speciation component, variously arguing that speciation rate is a positive, a negative or a hump-shaped function of range size (e.g. Terborgh 1973, Vermeij 1987, Rosenzweig 1995, Chown 1997, Holt 1997, Maurer and Nott 1998, Gaston 1998, Gaston and Chown 1999, Maurer 1999, Gavrillets et al. 2000, Hubbell 2001, Jablonski and Roy 2003). The expected shape of the relationship between range size and diversity among clades is similarly unclear.

Empirical tests have not clarified the picture. Positive, negative and non-significant linear relationships have all been found between average (rather than total) clade range size and diversity, with no clear majority verdict emerging (Gaston and Blackburn 1997, Cardillo et al. 2003, Jablonski and Roy 2003, Phillimore et al. 2006). Diversification rate

¹ A version of this chapter has been submitted for publication.

has no relationship to either the total or average range size of avian tribes (Gaston and Blackburn 1997). Yet the diversity of avian tribes and families is positively related to total taxon range size (Gaston and Blackburn 1997, Owens et al. 1999). No study that I am aware of has explored the possibility of non-linear effects, in spite of the non-linear theories about speciation and range size.

The generally-used method in studies to date compares higher-level sister taxa (e.g. families), and asks whether the one with the bigger range in the present day is also the more diverse (or whether it diversified more quickly than its sister at a moment in the distant past) (e.g. Gaston and Blackburn 1997, Owens et al. 1999, Cardillo et al. 2003). The reliability of these studies' conclusions is strongly affected by two factors. Firstly, range size varies considerably between species in the same genus (Gaston 1998, Webb and Gaston 2001) and generally has low heritability (for a summary, see Waldron 2007). Higher-taxon range size therefore gives a very diffuse picture of how range size affects the probabilities of speciation and extinction in individual species. Indeed, genus range has no relation with species range in bivalves (Jablonski 2005).

Secondly, relative clade range sizes may have changed over history (Gaston and Blackburn 1997, Owens et al. 1999). The fact that an entire family has a larger range size today does not necessarily imply that a single species within that family had a relatively larger range in the past, when speciation or extinction events actually occurred. Clade range sizes fluctuate in the fossil record (Bottjer and Jablonski 1988, Miller 1997, Davis and Shaw 2001); and must indeed be altered by the processes of speciation and extinction themselves. Total clade range size will be reduced by extinction. It may also be increased by speciation, since the addition of new species can allow a clade to expand into previously unexploited areas. The older and more diverse a clade, the more likely it is that its current range size will be uninformative about past diversification events.

In this study, I use relatively young clades of primates, which have not yet experienced much speciation and extinction, to explore the relationship between diversification and range size. Firstly, I studied "triplets" from the primate phylogeny, i.e. monophyletic groups of three species from the tips of the tree. Each triplet (figure 3.1) provides a

comparison between a pair of sister lineages, one of which experienced only one extant speciation event (lineage A) and the other no surviving speciation events (lineage B). Secondly, I compare diversity and range size in all extant primate clades less than one million and two million years of age, and show that the relationship is non-linear.

In addition, I show that the magnitude of the differences between sister-clade range sizes diminishes dramatically over 8 million years in the triplets. This implies that the information provided by current range sizes on past diversification rates decays rapidly with time.

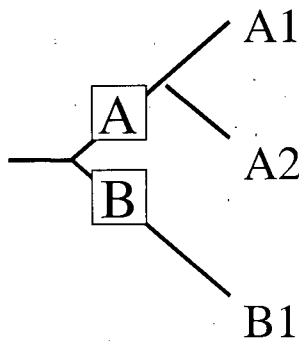


Figure 3.1: a species triplet. Lineage (B) has no extant speciation events, and its sister lineage (A) has one extant speciation event. Correlates of net speciation probability can then be assessed at the minimum possible remove from the original sister pair A and B.

METHODS

Range and phylogeny data

Range sizes of all primates were calculated by digitizing published range maps onto a continent-specific, equal-area projection in ArcGIS 9 (ESRI), and by using ArcGIS utilities to measure the extent of species distributional areas. For phylogenetic relationships between the primates and dates of divergence, I used the supertree of Vos and Mooers (2006), with updates from more recent literature (detailed in Appendix 3.1).

The triplets test

I took all 26 monophyletic triplets of species at the tips of the primate phylogeny (figure 3.1). Monophyletic triplets arise from two sister species, A and B. A had produced one surviving descendant in addition to itself and so its young modern lineage has two species (A1 and A2). B has produced no descendants and so its modern lineage has only one species (B1). The hypothesis is that if faster diversification is associated with larger range size, then A has a larger range than B. This hypothesis generates testable predictions about the range sizes of the modern-day species A1, A2 and B1. (The possible confounding effects of invisible extinction, range size changes and reverse causality are addressed in the Discussion.) The precise prediction depends on the mode of speciation assumed.

Vicariant speciation scenario

If the range of ancestor A was larger and split in two by vicariance, the prediction in the present is that the non-overlapping total range size of A1 + A2 will be greater than the range size of B1 (i.e. $(A1 + A2)/B1$ will be greater than one.) I counted how often the observed ratio exceeded 1.0 in the triplets ("successes"). I declared ratios which differed by 2% or less to be ties, since the digitization measurement error is approximately 2% (Waldron, unpublished data).

Ratios close to 1 may be uninformative, since even small changes in that ratio might reverse the results in individual triplets. I therefore repeated the test with more conservative criteria, requiring $(A1 + A2)/B1$ to be >2 or <0.5 for inclusion.

A null model is then required to see how many successes would be expected at random in the present day (two ranges added together will often be larger than one). A random expectation also represents a situation where range sizes have changed so much that modern lineages retain no signal of their past range sizes. In this and subsequent scenarios, I derived the null expectation by randomly drawing the range sizes of A1, A2 and B1 from the dataset 100,000 times with replacement. Unless otherwise specified, I compared the observed frequency of positive associations with the mean expected

frequency using a one-tailed binomial test (H_0 : number of observed positive associations $>$ expected). In the vicariant scenario, the randomization recorded the number of times that the sum of two random range sizes was greater than the size of a third random range. Null expectation tests for conservative-criteria observations used the same criteria in the randomizations.

Founder-dispersal speciation scenario (and sympatric speciation)

Founder-dispersal speciation occurs when a founder population migrates to a previously unoccupied area and becomes reproductively isolated (Mayr 1963, Templeton 1980, Carson and Templeton 1984). If one assumes that the smaller range of the pair (defined as A2) represents a migrant that exists outside of the original range of A, then the hypothesis predicts that A1 on its own should have a bigger range than B1. I counted how often the ratio $A1/B1 > 1$ in the triplets, and compared this with randomized triplets. I also applied the more conservative set of tests (i.e. excluding ratios that lay between 0.5 and 2). This scenario is labelled as founder-dispersal speciation [larger]. Sympatric speciation generates the same prediction as this scenario, since the larger member of the pair gave rise to the smaller in both cases.

It is widely taken for granted that in founder dispersal, the larger sister species range (the ancestor) gave rise to the smaller (the daughter) (Lynch 1989, Brooks and McLennan 1991, Barraclough and Vogler 2000). However, the current study tests the hypothesis that it is indeed wide-ranging species that tend to speciate more often than narrowly-distributed ones. To avoid circularity of argument, I therefore randomized whether A1 or A2 was assumed to be the ancestor, and asked in what percentage of the triplets its range was greater than that of B1. I repeated this test 100,000 times, generating frequency distributions for the observed values under both conservative and non-conservative criteria. There are significantly more positive associations than expected if the null expectation lies below the 5th percentile of the observed distribution (Manley 1996). This scenario is labelled as founder-dispersal speciation [random].

Decay in the range/diversification association over time

To investigate the rate at which information on relative range sizes decays over time, I regressed the ratio (lineage A range size/ lineage B range size) against the age of the node at which A and B diverged. Node age was ln-transformed to linearise the regression relationship. Cases where, for example, one sister evolves on an island and the other on the mainland may greatly bias the magnitude of the difference between their range sizes. I therefore included only triplets in which all three species occupy the same landmass ($n=23$). For the founder dispersal scenario I repeated the regression, but using the ratio (largest of {A1,A2}/B1) as the dependent variable.

Non-linearity in the relationship

To investigate the shape of the relationship between range size and diversification rate, I took all extant primate lineages that were separate at one million years ago, and recorded the diversity of the clade that had arisen from each of them in the present day. I regressed clade diversification rate (defined as ln number of species divided by time (Isaac et al. 2003) against clade range size. Clade range size was defined as the sum of the non-overlapping ranges of the clade's members. In other words, vicariant speciation was assumed.

I tested for non-linearity in the relationship firstly by fitting a cubic spline with no prior assumption about the relationship shape (using the method in Schluter 1988), and secondly by seeing whether the addition of a quadratic term to the regression model generated a significant improvement in model fit. Previous theoretical discussions (Rosenzweig 1995, Gaston and Chown 1999) do not make it clear whether non-linearity in the relationship between geographic range size and speciation rate is expected with range size on a raw scale or on a log scale, and a similar ambiguity must therefore be applied to the relationship between range size and diversification rate. Range size is commonly log-transformed to normalise its distribution (Gaston 1998) and because of a perception that a strongly right-skewed explanatory variable will distort the results of regression (Webb and Gaston 2003). However, performing a logarithmic transformation will linearize a non-linear relationship and I therefore used raw range data. To test for statistically significant non-linearity, I generated a null expectation for the quadratic

regression coefficient by regressing clade diversification rate on randomized clade range sizes 1,000 times and recording the regression coefficients. Significant non-linearity is demonstrated if the observed quadratic coefficient lies below the 2.5th percentile or above the 97.5th percentile of the distribution of expected coefficients, and significance testing will not be distorted by skew in the data distribution (Manly 1997). Clade ranges were randomized by drawing a random species range size for each member of the clade, and then summing these.

The results of cross-species regression analyses will be distorted by relatedness between species, if this leads to non-independence of the errors (Grafen 1989). I therefore tested whether the regression errors from the best-fitting model (the quadratic) were independent of phylogeny, using Abouheif's (1999) phylogenetic independence (PI) program.

Only 8% of the one-million-year old clades had more than one species, with the maximum diversity being 4 species. Since this low degree of variation may make it difficult to detect patterns, I repeated the above analyses for two-million-year-old clades, where 17% had more than one species, and maximum diversity was 5 species.

I repeated all of the above analyses using generalized linear models with Poisson errors (Venables and Ripley 2002). All statistical testing apart from the phylogenetic independence test was performed in R (R Core Development Team 2005). A list of triplets, range sizes and sources, along with details of updates made to the primate phylogeny, is available in Appendix 3.

RESULTS

The triplets test

The percentage of triplets in which range size was positively associated with diversity was significantly greater than expected for all cases, irrespective of the mode of speciation assumed (Table 3.1). There were no ties in the vicariant speciation results, and one tie (*Lepilemur*) for founder-dispersal.

Decline in the ratio with time since diversification

The ratio between sister-clade range sizes declines with the time since the clades diverged. Linear regression slopes were significant for both vicariant and founder-dispersal scenarios (F test, $p < 0.02$ and $p < 0.03$ respectively, figure 3.2).

MODEL						
	Vicariant speciation	Vicariant speciation - Conservative test	Founder-dispersal [larger]	Founder-dispersal [larger] - Conservative test	Founder-dispersal [random]	Founder-dispersal [random] - Conservative test
Observed positive associations	26/26	19/19	23/25	19/19	16/25	NA
Observed %	100	100	92	100	64 (52)	76 (62.5)
Expected %	70	74	67	70	50	50
p-value	$p < 0.001$	$p = 0.003$	$p = 0.004$	$p = 0.001$	$p = 0.02$	$p < 0.001$

Table 3.1: The frequency with which triplets show a positive range size/diversity relationship, compared to the null expectations for those frequencies. Last two columns: mean observed values from 100,000 randomizations, with 5th percentile shown in-brackets; the “NA” refers to the fact that each randomization produces a different number of trials under conservative criteria (see Methods for details).

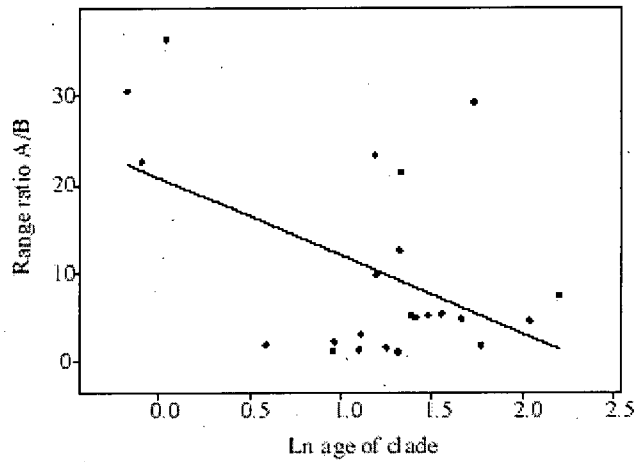


Figure 3.2: Change in the ratio between sister clade range sizes as a function of node age. The solid line represents a statistically significant linear regression model. The ratio (largest of {A1, A2}/B) declines very similarly over time (not shown).

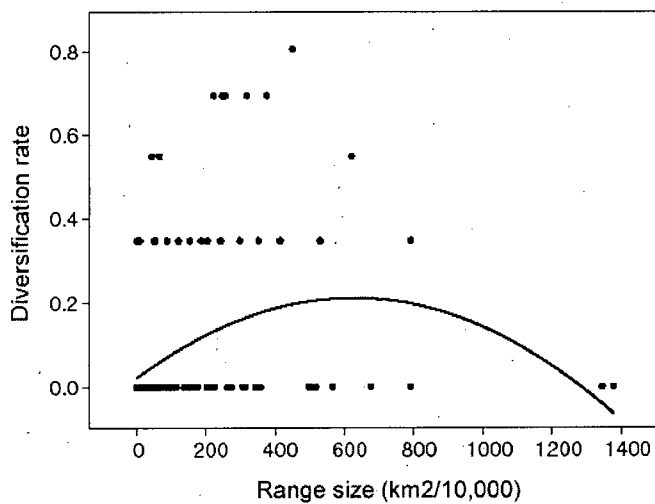


Figure 3.3: Diversification rate in two-million-year-old primate clades as a function of total clade range size. The solid line represents a fitted quadratic model, but should be taken to indicate only that the function curve is convex, which may or may not indicate a decrease in diversity at large range sizes. The removal of the two outliers on the far right does not alter the qualitative conclusions. The plot for one-million-year-old clades is almost identical, except that the fitted curve has a lower maximum value.

Non-linearity in the relationship

For the observed data, a quadratic term significantly improved model fit ($p < 0.01$ for both one and two myrs). The quadratic coefficient was negative in both cases. It was significantly more negative than the null expectation in two-million-year-old clades (observed coefficient = -0.48 , $p = 0.005$, two-tailed test), but marginally not significant in one-million-year-old clades (observed coefficient = -0.06 , $p = 0.06$, all coefficients times 10^{-6}). The leverage exerted by two largest range sizes may influence the shape of the curve (see figure 3.3), but surprisingly, their removal strengthened the results stated above: with outliers removed, the non-linearity is significant for both two-million-year and one-million-year datasets (observed quadratic coefficients = -0.95×10^{-6} and -0.93×10^{-6} respectively; $p = 0.001$ and $p < 0.0001$ respectively). The errors from the quadratic model were independent of phylogeny (Abouheif's test for serial independence, $p = 0.24$ for 1 myr, $p = 0.26$ for 2 myrs), indicating that the interspecific comparison did not require methods that correct for phylogeny (Gittleman et al. 1996, Abouheif 1999).

Removal of the two largest range values (figure 3.3) did not alter the qualitative results, and so the non-linear term is not solely driven by these two values. Results using a generalized linear model with Poisson errors gave qualitatively similar results in all cases.

Clade diversity is therefore a convexly increasing function of range size in primates, (figure 3.3). The negative quadratic term indicates two possibilities: either that the rate of increase in diversity slows down at large range sizes (perhaps trending towards an asymptote); or that diversity actually decreases at large range sizes. Because so few species have very large range sizes, it is unlikely that statistical testing would be able to reliably distinguish between these two possibilities. Indeed, attempts to fit a spline were unable to resolve the precise shape of the curve, since the fitted splines were extremely sensitive to the lambda parameter used.

DISCUSSION

Clade diversity increases with increasing range size for the great majority of young primate clades. The increase is non-linear, indicating either that diversity actually decreases for very widespread clades, or that it decelerates towards an asymptote at very large range sizes (figure 3.3). Since the clades studied are young and mostly contain only one or two species, it is reasonable to assert that figure 3.3 also describes the qualitative relationship between a species' range size and its probability of diversifying (at least over the next few million years).

Higher-level selection and range size

If we are interested in the processes that cause some clades to leave more descendants than others, then clades descended from widespread ancestors clearly demonstrate a faster rate of diversification in the short term. The question of whether this effect could also produce differences in the size of higher taxa requires further modelling. Each vicariant speciation event will reduce the probability of further speciation and also increase extinction risk, because it splits species ranges into two smaller parts. The rate of diversification will therefore go down as speciation events build up, counterbalancing the original influence of the widespread ancestor. (Although the daughters could theoretically recover the ancestral range size over time (Gaston and Blackburn 1997), this would imply both that range size heritability is strong and that sympatry is common, and neither of these conditions holds (Barraclough and Vogler 2000, Jones et al 2005, Waldron 2007).

Range size and speciation rates

The net difference between births and deaths is the appropriate measure of lineage fitness (where fitness has the special meaning of diversification rate for clade-level selection), and does not require knowledge of the underlying rates of speciation and extinction. However, given the many competing hypotheses about range size's influence on

speciation rates, it is interesting to ask whether diversification rate pattern can cast light on the speciation debate.

A positive relationship between range size and speciation probability is predicted if one focuses on the initial probability of two populations within a species becoming isolated from each other. Vicariance barriers, migrant groups and incidents of local adaptive divergence will all arise more frequently in bigger areas, respectively increasing the probabilities of vicariant, founder-dispersal and parapatric speciation (Terborgh 1973, Endler 1977, Rosenzweig 1995, Holt 1997, Maurer and Nott 1998, Hubbell 2001).

A negative relationship is predicted if one focuses instead on the probability of those newly-separated populations re-establishing gene flow, because widespread species are generally good dispersers with broad environmental tolerances and so will easily break own temporary isolation of demes (Hansen 1980, 1982, Jablonski 1986, Stanley 1986, Chown 1997, Gavrillets et al. 2000, Hubbell 2001, Gaston 2003).

Non-linear functions can be predicted if competing influences have different strengths at different range sizes (e.g. a hump shape arises if a generally positive function based on area is overridden at very large range sizes by dispersal (Maurer and Nott 1998)). A hump shape can be hypothesized for areal effect alone, on the grounds that very large ranges are too big to be split by realistic-length barriers (Rosenzweig 1995, Gaston and Chown 1999). Dispersal alone could also predict a hump shape if very low dispersal fails to generate new founder species, or if it restricts range growth.

Is the hump-shaped diversification function the first evidence for a hump-shaped speciation function? This depends on how extinction is believed to counterbalance speciation for any given range size. The decrease (or asymptote) in diversity at very large range sizes (figure 3.3) almost certainly indicates that speciation rate is decreasing at very large range sizes- the alternative is a sudden increase in extinction probability for the largest range sizes, and this seems highly unlikely. What is less certain, is whether this decrease in speciation probability at large range sizes implies that speciation probability decreases smoothly over all range sizes (i.e. a simple negative function), or

whether speciation probabilities are positive at smaller range sizes (i.e. a hump-shaped speciation function).

If the speciation function is negative, then the positive association between range size and diversification in the triplets must be caused by differential extinction. This seems unlikely, since diversification in young clades should reflect speciation more than pure extinction (median age for the triplets is 3.6 million years). In addition, if small ranges speciate rapidly and large ranges speciate slowly (Chown 1997), there should be several observable triplets where the large A has not yet speciated, and the small B has speciated but has not yet suffered an extinction. Such triplets occurred never or rarely under the most realistic speciation scenarios (Range A > Range B 100% of the time under vicariance and conservative founder-dispersal scenarios, Table 3.1), if speciation is defined as the production of new evolutionary units which persist long enough to be recognised.

This study therefore provides evidence that speciation is a hump-shaped function of range size and not a negative function. But fossil studies which convincingly tease out range size's effect on speciation from its effect on species longevity are needed (Wagner and Erwin 1995).

Confounding factors: reverse causality and extinction

Small range size will also be a consequence of fragmentation followed by speciation. Jablonski and Roy (2003) found that speciation rates were negatively correlated with average genus range size in fossil molluscs, and present this as the first clear empirical evidence that smaller ranges have a higher probability of speciating. But a more compelling explanation for the mollusc pattern is that each speciation event causes average range size in a genus to go down e.g. because of range subdivision by vicariance (Cardillo et al. 2003, Phillimore et al. 2006).

Could reverse causality confound the relationships deduced here between range size and diversification, as it does in the fossil molluscs? I used total rather than average clade range sizes in the vicariant scenario, to account for the impact of range division at

speciation. Nevertheless, even the total range size of a clade can increase as a result of speciation, for example if the isolation of one population frees it from maladaptive gene flow and allows it to adapt to previously unavailable environments (Garcia-Ramos and Kirkpatrick 1997). Genera indeed expand their ranges as they diversify in the fossil record (Miller 1997). I would, however, suggest that causality flows both ways, since A1 on its own is still an average 11.3 times larger than B1. For non-linearity, it is harder to see how a downturn in diversity at very large range sizes could be a consequence of speciation.

On the other hand, studies which compare higher taxa will be significantly impacted by processes which change clade range size as the clade diversifies. This may explain why Blackburn and Gaston (1997) found no significant relationship between diversification rate and range size. They compared the rate of cladogenesis at the root of avian tribes with the total and average range size of the entire tribe. But the relative range sizes of sister tribes may be very poor predictors of the relative range sizes of the ancestral species at the tribes' roots. The decay in the variation between sister clade range sizes over 8 million years (figure 3.2) also suggests that studies using higher taxa may fail to detect patterns related to range size.

Extinction

In young triplets, it is reasonable to assume that diversification does not reflect extensive extinction. It is theoretically possible that numerous unseen extinctions obscure any connection between the past and the present ranges of A and B, in a way not controlled for by the randomizations. The worst-case scenario is that lineage B was in fact larger than lineage A during most of history, and is only smaller today because of the extinction of one or more wide-ranging B species (B2).

However, a putatively extinct species B2 would often need to be ten or twenty times larger than its surviving sister B1 in order for B to become bigger than A in the past (see the magnitude of the differences between A and B in figure 3.2). Extinctions repeatedly biased towards the death of a larger sister contradict observed fossil patterns (Stanley 1979, Hansen 1982, Jablonski 1987, 1995, McKinney 1997, Gaston and Blackburn 2000,

Purvis et al. 2000, Jablonski and Hunt 2006) and so are highly improbable. The triplets approach therefore seems robust to a variety of possible changes in clade range size over history.

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CHAPTER 4: TOLERATION OF RANGE RESTRICTION AFFECTS THE DIVERSITY OF PRIMATE LINEAGES.

INTRODUCTION

The diversity of species today is the result of the counterbalancing forces of speciation and extinction. Clades of the same age can have very different numbers of species from each other, and this implies differences in their diversification rates (the net difference between speciation and extinction rates) (Nee et al. 1992, Guyer and Slowinski 1993, Purvis et al. 1996, Maurer and Nott 1998, Owens et al. 1999, Katzourakis et al. 2001, Ricklefs 2003). Diversification rate differences are often influenced by species' biological traits (e.g. Owens et al. 1999, Phillimore et al. 2006).

However, it is difficult to know what the relative contributions of speciation and extinction have been to a clade's diversity, because extinction often leaves no trace of its occurrence. It is difficult to determine whether a particular biological trait has its main impact on speciation or extinction for the same reason. As a result, neontological studies of clade diversity have focused heavily on differences in speciation rate, and on identifying traits which should influence speciation (for reviews see Barraclough et al. 1998, Isaac et al. 2005, Jablonski 2007).

A large body of theory exists on which traits should correlate with extinction risk. Generally, small populations are regarded as extinction-prone (Lande 1993, Lawton 1994). Traits that imply small population size in a species, such as limited geographic distribution, limited niche breadth, high trophic level and a large body size, are therefore thought to impose a high extinction risk (reviewed in McKinney 1997, Purvis et al. 2000). These theoretical predictions concur with the results of paleontological studies; for example, fossil species with large range sizes are often observed to persist for a long time (Stanley 1979, Jablonski 1987, 1995, Jablonski and Hunt 2006).

Low abundance and small geographic range also feature heavily in conservation biologists' decision to list a species as threatened with extinction today (Mace and Kershaw 1997, IUCN 2000). Low abundance (density) and small geographic range are often correlated both with each other (for reviews see Hanski 1982, Gaston 1996, Gaston 2003) and may both may be correlated with niche breadth (Brown 1984, but see Gaston 2003). Species showing one or more of these three attributes are often referred to as "rare" (Rabinowitz 1986, Gaston 1994), and rare species have generally been regarded as extinction-prone (Pimm et al. 1988, Lawton 1993, 1994, Caughley and Gunn 1996, Mace and Kershaw 1997, Harcourt 2006).

The traditional view is therefore, that clades with low-risk attributes such as large population or range size should avoid extinction and therefore be more diverse (e.g. Jablonski 1987, Cardillo et al. 2003). But these clades are in the minority; the majority of species have small range sizes, low abundance, and often both (Gaston 1998, Blackburn and Gaston 2000). Furthermore, even widespread species today may have passed through a period of range restriction and therefore low abundance. Several models of speciation predict that newly-created species will often have small range and population sizes (Mayr 1963, Templeton 1980, Carson and Templeton 1984, Waldron 2007), and this is supported by data in the fossil record (Vrba and DeGusta 2004). Climate change may also temporarily restrict species ranges, for example by fragmentation or by restricting species to refugia (Haffer 1997, Bonaccorso et al. 2006).

What may be more important, therefore, is the degree to which species are able to persist in spite of small population and range sizes. I shall refer to this as "risk tolerance", and to the traditional view as "risk avoidance". Avoidance means that a species almost never encounters extinction risk, while tolerance means that it is able to survive risk.

Clades that are risk-tolerant should have higher diversification rates because they have lower extinction rates. As a measure of risk-tolerance, I use persistence of primates on small, near-shore landbridge islands that were cut off from the mainland by rising sea levels approximately 10,000 years ago (Rohling et al. 1998, Harcourt and Schwartz

2001). These islands presumably contained the same fauna as the adjacent mainland prior to separation, and so any differences today can be ascribed to extinction on the island (Diamond 1974, Wilcox 1980, Harcourt and Schwartz 2001). Species which survived are classed as risk-tolerant.

I then assess whether two-million-year-old clades that contain risk-tolerant species have diversified faster than clades that contain risk-intolerant species. I also examine several possible biological predictors of risk-tolerance. These may be very different from the traits associated with risk avoidance. For example, species with large range sizes today may have rarely been at risk, whereas narrowly distributed species have faced relatively constant extinction risk throughout their history. It is therefore possible that narrowly-distributed species will show higher risk tolerance than widespread species.

In a world where human pressures are driving most species into smaller areas, the distinction between risk-avoiding traits and risk-tolerant ones is crucial. Risk-tolerance should be an important part of the puzzle in deciding which species are at risk from habitat reduction or in small protected areas. Red List criteria currently assess mostly whether species are simply avoiding risk e.g. by sustaining large populations or range sizes (IUCN 2000). But avoiding risk altogether will be an increasingly improbable luxury as the human footprint grows. We urgently need to know how species will respond to and tolerate risk.

METHODS

I used species persistence on near-shore landbridge islands to assess whether primate clades were tolerant or intolerant of extinction risk. These islands were connected to the nearby mainland coast up until approximately 10,000 years ago, when they were isolated by rising sea levels (Rohling et al. 1998). Insularization presents a risk of extinction since it isolates a small population in a restricted area. Primate species found on the mainland coast directly opposite an island are referred to as “candidate species”, i.e. they

are assumed to have been on the island at the time of insularization (following the methods of Diamond 1972, 1974, Wilcox 1980, Graves and Gotelli 1983, Gotelli and Graves 1990, Harcourt and Schwartz 2001). Candidate species which still persist on the islands today are defined as “risk-tolerant”. Those absent today from the islands are assumed to have gone extinct and are defined as “risk-intolerant”.

Using published distribution maps and accounts (see appendix 4.1), I searched for landbridge islands which are separated from the mainland by a small (max. 166km) water gap. I was only interested in islands where primates were demonstrably present at the time of separation. I therefore included only islands that today contain non-water crossing primate species, and which are near a mainland coast on which primates also exist. The species *Macaca fascicularis* was excluded because of its extensive water-crossing ability (Abegg and Thierry 2002).

The larger an island, the less extinction risk it represents and the more species will survive on it (MacArthur and Wilson 1963). In order to focus on islands which provide substantive information on risk-tolerance, I set an arbitrary upper limit to island size of 5000km², equivalent to one quarter of one percent of the average range size for the candidate species (the smallest candidate species range size is 8,200km²). I set a lower limit of 10km², since only one primate species (*Nycticebus coucang*) has survived on islands below this size. These search criteria produced a list of 36 near-shore landbridge islands with 53 candidate species (appendix 4.2). The mean island size is approximately 850km² (the smallest known primate range size is 820 km²). The very large islands of Borneo (757,770 km²), Sumatra (472,780 km²), Sulawesi (179,370 km²) and Madagascar (587,713 km²) were treated as continental mainlands for the purposes of this study.

Extinction risk tolerance and diversification rates

I then measured separately the diversification rates of clades which contain only risk-tolerant species and of clades which contain only risk-intolerant species. I defined the clades as monophyletic groups of two million years of age in the phylogeny of Mooers and Vos (2006), since this is the earliest date at which risk-tolerant species always belong

to different clades from risk-intolerant species. Clade diversification rates were calculated as half the natural logarithm of its diversity (Isaac et al. 2003). This produced 49 “candidate clades”. Candidate clades were represented by a single species in 45 out of 49 cases, and by two species in the other 4/49 cases.

Some clades were candidates for more than one island. In such cases, I classed presence on >50% islands as risk-tolerance. For the island of Trinidad, I excluded the *Cebus* species, since the mainland *Cebus albifrons* population is disjunct from the Trinidadian one by over 1,000km, whereas the candidate species *C. olivaceus* is absent from Trinidad.

Since the pre-separation islands were small areas of land, a number of sampling artefacts could affect the robustness of the assumption that every candidate species was present on the island at the moment of its separation. First, it is possible that the habitat or niche required by a species was not present on the island and so neither was the species. Second, since the distribution of individuals of a species is rarely homogeneous across the landscape (Blackburn and Gaston 2000), species whose populations are at low density or are patchily distributed may by chance have not been present as rising sea levels cut off the island.

I therefore verified where possible that a candidate species’ habitat requirements were present on the island. Where detailed information was not available, I judged that a habitat requirement was fulfilled on an island if at least one primate species associated with that habitat was present on the island. In addition, I compared the population density and degree of habitat and diet specialisation of tolerant and intolerant species. I took from the literature the mean population density of each candidate species, and counted how many out of a possible nine habitats and six diet categories a candidate species was recorded as using (see appendix 4.1 for sources). I also created a binary variable for habitat specialisation, where candidate species were categorised as specialists if they use two or fewer habitats and non-specialists otherwise (all clades use primary lowland rainforest and only one is specialised on that habitat). I compared the density,

degree of habitat and diet specialisation and proportion of specialists to non-specialists between risk-tolerant and risk-intolerant candidate species. Density was ln-transformed, and counts of habitats and diets were incremented by 0.5 then square-root transformed in order to normalize distributions.

Low population density and high degrees of specialisation are often regarded as potential correlates of risk intolerance (Brown 1971, Diamond 1974, Case 1975, Harcourt and Schwartz 2001). If candidate species with low densities and narrow habitat use are not found on landbridge islands, this could indicate either a sampling effect, or that low-density and specialist species are risk-intolerant. If, on the other hand, density and niche breadth do not positively correlate with island presence, the implication is that absence from islands is not a sampling artefact.

Biological correlates of extinction risk-tolerance

To identify correlates of risk tolerance at the species level, I compared risk-tolerant and risk-intolerant candidate species in a number of other traits in addition to density and niche breadth. These traits were geographic range size, female body mass, reproductive rate (births per year), and the composite variable biomass per km² (= female body mass multiplied by average population density). Biomass, body mass, reproductive rate and geographic range size were all ln-transformed in order to normalize data distributions prior to regression analysis. I assessed trait values of candidate species rather than of entire candidate clades, since it is the species values that explain presence/absence on the islands.

I also performed a multiple regression of presence/absence on all candidate species variables, using a generalized linear model with a binomial error structure (Venables and Ripley 2002) and carried out subtraction of terms to define a minimum adequate model for biological correlates explaining island survival.

Risk tolerance in one or two members of a clade implies risk-tolerance in the whole clade only if tolerance is phylogenetically correlated. A similar argument applies to traits

associated with risk tolerance. I therefore tested for phylogenetic signal in all variables using Abouheif's test for serial independence (TFSI) for continuous variables, and his Runs Test for the binary variables tolerant/intolerant and specialist/non-specialist (Abouheif 1999).

Statistical analysis

Statistical tests using species values as data points may misrepresent their degrees of freedom if the phylogenetic relatedness between species values is not taken into account (Harvey and Pagel 1991). Since phylogenetic signal existed in all variables (see Results), I carried out phylogenetically corrected tests. Tolerance/intolerance was compared to both diversification rate and to potential biological correlates using Grafen's phylogenetic GLS regression (Grafen 1989), which is equivalent to a phylogenetically-corrected T-test when a binary x variable is used. Comparisons of proportions (i.e. a phylogenetically-corrected contingency test) were carried out using Pagel's method for discrete variables (Pagel 1994). All islands were pooled for the analysis.

Non-phylogenetically corrected statistics were performed in R (R Core Development Team 2005). Grafen's phylogenetic regression was also implemented in R using the APE package (Paradis and Strimmer 2004). Pagel's method was implemented in the program Discrete (Pagel 1994).

Details of all variables, data sources, islands and candidates can be found in appendices 4.1 and 4.2.

RESULTS

Extinction risk tolerance and diversification rates

Clades whose species survive on landbridge islands have significantly higher diversification rates than clades whose species went extinct on those islands (phylogenetic regression, $t = 4.56$, $p < 0.001$; figure 4.1). Indeed, only 1/21 (5%) of the clades absent from the islands have diversified at all in the last 2 million years, compared

to 12/28 (43%) of the clades that survived. Risk-tolerance is therefore strongly correlated with diversification rate. Risk tolerance also shows a phylogenetic signal (TFSI test, $p = 0.026$).

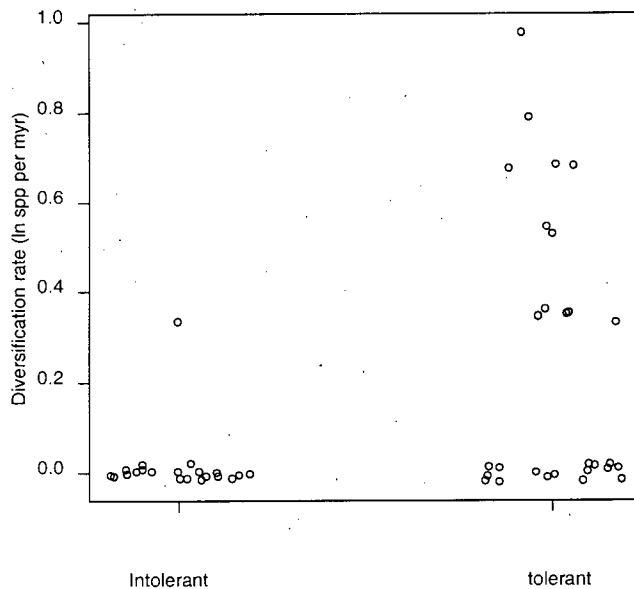


Figure 4.1: Difference in diversification rates between risk-tolerant and risk-intolerant clades. Data points are slightly offset from each other to make overlapping points visible.

Biological correlates of extinction risk-tolerance

Tolerant and intolerant primate species differed in two traits (Table 4.1). Risk-tolerant species had smaller average range sizes than intolerant species; and risk-tolerant species showed greater habitat specialisation than intolerant species (figure 4.2). All the traits investigated as potential correlates of species' risk-tolerance were correlated with phylogeny (Table 4.1). In the non-phylogenetic multiple regression model, specialism alone was the minimum adequate model explaining survival after stepwise removal of terms ($p=0.011$).

Species' presence on landbridge islands is therefore not explained by a sampling effect. Population density was not associated with presence on islands, and the observed

relationship with habitat specialisation points in the opposite direction from that expected under a sampling effect: specialists, not generalists are more often associated with presence on islands.

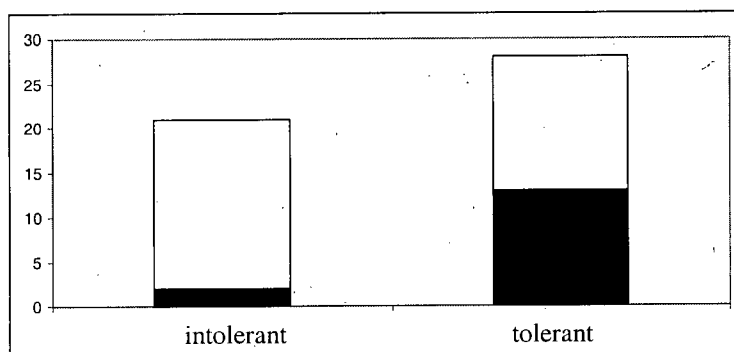


Figure 4.2: Relative proportions of specialist species among risk-intolerant and risk-tolerant candidate species. White = non-specialist, black = specialist. Y axis = frequency count.

Trait	Association with risk tolerance	Statistic (df = 2,47 for regression tests)	Phylogenetic signal in trait
Ln Geographic range size	-	T = -2.47, p=0.02 (slope = -1.27)	Yes. TFSI, p = 0.003
√ Number of habitat types used + 0.5	-	T = -2.03, p = 0.048 (slope = -0.2)	Yes. TFSI, p = 0.032
Specialism (binary variable)	+	LR = 13.3, p = 0.01	Yes. Runs Test, p = 0.012
√ Number of food types exploited +0.5	ns	T = -0.61, p = 0.54	Yes. TFSI, p = 0.007
Ln Population density	ns	T = 1.5, p = 0.14	Yes. TFSI, p = 0.001
Ln female body mass	ns	T = 0.18, p = 0.86	Yes. TFSI, p = 0.001
Ln Biomass per km ²	ns	T = 1.36, p = 0.18	Yes. TFSI, p = 0.001
Ln Birthrate (births per year)	ns	T = -0.70, p = 0.49	Yes. TFSI, p = 0.001

Table 4.1: Results of analysis of possible predictors of risk-tolerance. The T statistics refer to a T-test of whether the slope of phylogenetic regressions of the trait against tolerance/ intolerance was significantly different from zero. LR = the likelihood ratio from Pagel's (1994) method, a phylogenetically-corrected contingency test. TFSI = test for serial independence (Abouheif 1999).

DISCUSSION

Extinction risk tolerance and diversification rates

Clade diversity differences are strongly influenced by differences in extinction risk tolerance, even in the most recent two million years. The ability to survive short-term range-restriction causes lineages to diversify more quickly than if they were unable to tolerate range restriction.

Obviously, lack of extinction will increase clade species numbers in general. But a species' ability to survive periods when its entire population is confined to a very small area may also be important in several speciation processes. Several studies have argued that range fragmentation during periods of climate change probably triggered speciation in many species e.g. in Pleistocene refugia over the two million years studied here (Haffer 1997, Bonaccorso et al. 2006). In speciation by peripheral isolate formation or by founder migration, the new proto-species similarly occupies a very small area at first (Mayr 1963, Templeton 1980, Carson and Templeton 1984). In both cases, reproductively isolated populations will only be able to take advantage of the opportunity for speciation presented by allopatry if they initially survive at a very low population size.

Biological correlates of extinction risk tolerance in species

Unexpectedly, risk tolerance is correlated with a smaller geographic range and with specialist niches, at least in primates. In plants, rare species are also more able to tolerate the genetic consequences of habitat fragmentation than are common ones (Honnay and Jacquemyn 2006). These findings appear to contradict both theoretical expectations and paleontological findings that species persistence is associated with a large geographic range size and a wide ecological niche (Hansen 1980, McKinney 1997, Maurer and Nott 1998, Jablonski and Hunt 2006). However, the mechanisms involved in risk-tolerance will be very different from those associated with risk-avoidance. Persistence on islands implies an ability to tolerate several thousand years of high extinction risk (risk

tolerance). Intuitively, this ability may be enjoyed more by species whose biology already permits them to exist in few habitats or at a small geographic range size on mainlands. Persistence in the paleontological record, on the other hand, will often reflect traits that permit a species to avoid the risk of extinction (risk avoidance).

The results have implications for the study of rarity itself. Many authors have regarded rare species as extinction-prone. However, rarity is often poorly explained by the known correlates of extinction-proneness (Kunin and Gaston 1993, Kunin and Gaston 1997, Harcourt 2006). This study suggests that rare species may actually be extinction-resistant (and that is what allows them to survive as rare without falling over the brink). If rare species have any traits in common, these may well be traits that explain risk-tolerance, rather than risk-proneness (Kunin and Gaston 1993).

Rare and specialist species are more at risk than common species in IUCN threat listings (IUCN 2000). This study suggests that it is important for conservation biologists not to class rare species as threatened simply because they are rare, since rarity may often indicate species which tolerate risk well. On the other hand, if anthropogenic threats disrupt the normal ability of rare species to tolerate the risk of small population size, then rare species will be highly endangered by human impacts (Mace and Kershaw 1997, Webb et al. 2001). Indeed, many of the primate subspecies which have survived 10,000 years on the islands are listed as highly endangered today (IUCN 2000). It will be important to determine in future whether or not natural risk-tolerance in rare species translates into tolerance of anthropogenic impacts.

Many previous studies of landbridge islands (or pseudo-islands on mountaintops) found that species absent from the islands tended to have small geographic range, large body size, narrow niche breadth and low population density. This was interpreted as evidence that these traits cause extinction-proneness, since they all imply low population size on an island (Brown 1971, Diamond 1974, Faaborg 1979, Graves and Gotelli 1983, Patterson 1984, Foulfopoulos and Ives 1999, Harcourt and Schwartz 2001).

The discrepancy between these findings and those of the present study is probably related to two differences in method. Firstly, many previous studies used birds, which can easily colonise near-shore islands (Diamond 1974, Faaborg 1979, Graves and Gotelli 1983). Colonisation ability is associated with abundant, widespread and generalist species (Maurer and Nott 1998) and so may well explain the overrepresentation of high-density species on the islands, since it swamps the influence of extinction (Graves and Gotelli 1983).

Some studies that controlled for colonisation have still concluded that low density, small geographic range and specialisation promote extinction (Brown 1971, Patterson 1984, Foufopoulos and Ives 1999, Harcourt and Schwartz 2001, Harcourt et al 2002). However, all these studies quantified extinction risk by measuring the minimum island size on which a species or genus can be found in a landbridge (or mountaintop) archipelago, rather than using mainland controls. The assumption in these studies is that every species or genus was omnipresent across the entire pre-flooding landmass, and its absence from smaller islands today reflects extinction (Foufopoulos and Ives 1999, Harcourt and Schwartz 2001, Harcourt et al 2002).

These studies also assume, however, that a population spanning an entire area would be found on all of the small patches of land left behind when that area fragmented. This is unlikely to be true in all cases. Individuals in low-density populations occur in localized clumps, and so there are many areas within their geographic range where they do not occur (Gregory et al. 1998; see also Gaston 2003 and for a summary of how most species are at low densities in most parts of their geographic range). Habitat specialisation will also cause a species to be absent from many areas within its range, and species with small range sizes similarly tend to occur as fragmented populations (Maurer and Nott 1998). The random expectation is therefore that low-density, narrowly-distributed species with specialised habitat requirements will not be found on small areas of land after insularization. Their absence from landbridge islands could reflect a sampling effect, rather than evidence that they have non-randomly gone extinct.

Studies which used a mainland control group instead of archipelagoes have not found strong connections between extinction and population density, generalism or other correlates of population size (Karr 1982, Gotelli and Graves 1990). Indeed, there appears to be no general association between minimum population size and risk of extinction (Brook et al. 2006) and common species are often lost from landbridge islands (Karr 1982, Gotelli and Graves 1990). Since the sampling expectation is that narrowly-distributed specialists should be underrepresented on islands, their overrepresentation in the current study represents particularly compelling evidence of their risk-tolerance.

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CHAPTER 5: CONCLUSION

The overall question behind the studies presented here was: Why are some families more species-rich than others? Since families can be of very different ages to each other and may even be paraphyletic, it makes more sense evolutionarily to ask why clades of the same age have different numbers of species from each other.

When clades are the same age, differences in the number of species that they contain must be due to differences in their speciation and extinction rates. This thesis then examined whether a species-level trait, geographic range size, influenced speciation and extinction rates in such a way as to explain differences in clade diversity. The second chapter examined the degree to which range size shows heritability, following a suggestion by Webb and Gaston (2003) that only heritable species traits can affect clade diversification rates. It found that range size is weakly heritable. The third chapter found that geographic range size has a positive but non-linear effect on rates of diversification in primates, and that this strongly suggested a hump-shaped relationship between speciation rate and geographic range size. Chapter four separated out the effect of extinction on clade diversity. It showed that primate clades which are able to tolerate the risk of extinction have significantly higher diversification rates. It also showed that habitat specialisation and small geographic range size were associated with extinction risk-tolerance.

Range size heritability and evolution

According to Lewontin's (1970) original prescriptions for the study of natural selection at any level, a trait must be heritable before its influence on fitness can be meaningfully studied. When selection at the level of species or clades is being studied (Eldredge and Gould, Okasha 2003, Jablonski 2007), "fitness" takes on the special meaning of "diversification rate", the net differences between species births and species deaths.

Several very different tests have been proposed for heritability at the species level (Jablonski 1987, Gittleman and Kot 1990, Ricklefs and Latham 1992, Taylor and Gotelli 1994, Pagel 1999, Webb et al. 2001, Freckleton et al. 2002, Webb and Gaston 2003, Qian and Ricklefs 2004, Hunt et al. 2005, Webb and Gaston 2005) and these have made it difficult to approach the question of range size heritability, since they give different results. Chapter 2 argues that there are two distinct concepts of heritability being tested for in the studies cited. The first is “phylogenetic signal”, meaning that on average, closely-related species are more similar to each other in trait value than non-relatives. The second is a “general null expectation of heritability”, under which a trait is regarded as heritable if close relatives are more similar to each other than would be expected under a null model. For example, Webb and Gaston (2003) defined a trait as heritable if the ratio of sister species trait values was less than one-third/ two thirds. Chapter 2 goes on to show that if the general null expectation is informed by a model of evolution, geographic range size shows heritability under both tests.

How can a weakly-heritable trait impact clade diversity?

In studies of clade diversity differences, the more relevant concept of heritability is phylogenetic signal. The strength of phylogenetic signal indicates how much trait values will be preserved within a lineage as evolution progresses (Felsenstein 1985, Blomberg et al. 2003). If trait values are only weakly preserved, then any impact the trait has on the probability of a species diversifying will not be transmitted to that species’ descendants. Weak phylogenetic signal therefore implies a weak effect on clade diversity.

Chapter 2 found that although phylogenetic signal does exist in range size in North American birds, it is weak. This may be particularly true for birds, since their high dispersal capacity is likely to cause rapid changes in range size. But phylogenetic signal is often weak in non-avian taxa (e.g. Jones et al. 2005, Waldron 2007). It is indeed widely observed that close relatives may have very different range sizes in many groups of species (Arita 1993, Gaston 1998, Webb et al. 2001). The mode of inheritance for geographic range size may often be for the ancestor to split into two unequal parts. Indeed, chapter 2 showed that the two areas resulting from such a split are expected to be

highly asymmetric in size. Chapter 2 therefore provides further evidence that range size differences between close relatives will often be large.

Since range sizes are so varied across the modern members of a clade, it seems unlikely that will have consistent effects of diversification rate throughout the evolutionary history of a clade. This would appear to make range size a poor candidate to be a trait influencing clade-level diversity. However, there are a number of ways in which strong heritability may not be a necessary prerequisite to studying selection on a species-level trait. These will be discussed in the summary of chapter 3.

The relationship between range size and clade diversity

Chapter 3 demonstrates that if a clade is simply defined as a species and one or two of its descendants, then range size has a significant effect on the probability of a clade diversifying. And if we only focus on clades consisting of one species and its daughter, the question of heritability becomes moot, since we only ask how a species' range size affects its probability of giving birth to a new species.

The "triplets test", which compares two sister clades with one and two extant species respectively, removes the prerequisite of trait heritability. It also minimizes two major problems associated with the evolutionary study of range size: the extreme lability of range size over time (Overpeck and Webb 1992, Brown 1995, FAUNMAP working group 1996, Davis and Shaw 2001, Losos and Glor 2003, Lyons 2003, 2005); and the fact that speciation itself influences average clade range size so much that it is difficult to study the reverse effect (Gaston and Blackburn 1997). The triplets test does not require any reconstruction of ancestral range size, only that the relative range sizes of two species should be preserved over a short period of geological time.

Using the triplets test, there is extremely strong evidence that range size is positively correlated with the rate of diversification, at least in primates. However, because the test is dependent upon at least one extant speciation event, it may miss lineages in which there has been no speciation for a long time, or in which extinction has erased all species

births. One such case seems to be species with extremely large range sizes. Chapter 3 shows that these have a lower rate of diversification than species with medium-sized ranges, reversing the general positive relationship. Although this downturn might be expected from the right-skewed distribution of range sizes, a randomization test found that the downturn is stronger than would be expected at random.

Could a weakly-heritable trait still impact long-term diversity differences?

Interest in diversification rates originally arose from the observation that families or genera contain very different numbers of species from each other (Marzluff and Dial 1991, Guyer and Slowinski 1993). Studies of the impact of range size on clade diversity have implicitly followed this early lead by defining clades at approximately the genus or family level (e.g. Barraclough et al. 1998, Owens et al. 1999, Cardillo et al. 2003, Isaac et al. 2005, Phillimore et al. 2006). Does the strong positive influence of range size at the level of individual species imply that range size can have an effect on the diversity of family-level clades?

Older clades usually consist of several species, all with very different range sizes from each other (Arita 1993, Gaston 1998, Webb et al. 2001). Even if an ancestor had a large range size, it is thought unlikely that geographic range size could continue to drive diversification in that ancestor's lineage when range size is so weakly and so variably inherited (Gaston and Blackburn 1997, Webb and Gaston 2003, Waldron 2007). Indeed, the process of diversification may have subdivided any formerly large ancestral range into small pieces.

However, it is possible that even a poorly-heritable trait may have an impact on long-term clade diversity. Under random probabilities of speciation, a lineage which has speciated once will lead to a much larger clade over time than a sister lineage which has not speciated at all (Yule 1924). The one-species head start may therefore be all that a clade needs to achieve significantly greater species diversity than its sister. This implies that the impact range size has on the relative diversification rates of a single pair of species in chapter 3 may explain differences in the diversity of those sister lineages much

later, after multiple speciation events. Heritability may not be a necessary prerequisite, since it can be replaced by this kind of grandfathering effect.

In addition, the highly asymmetric inheritance of range size (chapter 2) may mean that a species with a large range size often gives rise to one daughter that has a range size almost as large, even if the other daughter has a much smaller range size. This would also lead to the prolonging of range size's impact through several speciation events, even though sister species would appear to have very different range sizes from each other (i.e. low heritability). Such a process would potentially lead to extensive "ladderization" in phylogenies (i.e. where a single species successively gives birth to all other members of a clade). The model in chapter 2 could be extended to explore the likelihood of these kinds of effects, of their impact on clade diversity, and indeed of their potential influence on the distribution of range sizes within a clade (Webb and Gaston 2003, 2005).

How the impact of range size on extinction risk affects clade diversity

Chapter 3 finds that range size has a strong effect on diversification rates in young clades of primates. Clade diversity and clade diversification rate are the products of the dual processes of speciation and extinction. As with other studies of diversification rate (e.g. Gaston and Blackburn 1997, Cardillo et al. 2003, Phillimore et al. 2006), chapter 3 was unable to directly address the question of whether the main impact of range size was on speciation rate or on extinction rate.

Chapter 4 therefore explored the relationship between species distributions and extinction. Small distributions (and by implication small population sizes) are widely associated with high extinction risk (Jablonski 1986, 1987, 1995, 2005, 2007, Gaston 1994, 1998, 2003, Mace and Kershaw 1997, McKinney 1997, Gaston and Blackburn 2000, Purvis et al. 2000). However, chapter 4 differs from the majority of studies on range size and extinction rate in exploring how well species survive being confined to a limited area, rather than the degree to which they avoid extinction risk by sustaining large and/or widespread populations.

The ability to survive range restriction was defined as “risk tolerance”. If greater risk tolerance contributes to higher clade diversity, then diversity differences between clades can partly be attributed to lack of extinction. Chapter 4 shows very strong empirical evidence of a positive relationship between extinction risk tolerance and diversification rate in primates. It suggested that risk tolerance enhances diversity in two ways: firstly by preventing the pruning of species from clades; and secondly because opportunities for speciation in peripatry or allopatry may often be tied up with temporary periods of range restriction. For example, habitat fragmentation due to climate change (Haffer 1997, Bonaccorso et al. 2006) will only cause speciation if the separate populations are both able to survive fragmentation and range reduction.

Chapter 4 also investigated the species-level traits which are correlated with risk tolerance, and came to the surprising conclusion that these are habitat specialisation and small geographic range. Species with small range sizes or small populations are usually thought to be at risk of extinction (Jablonski 1986, 1987, 1995, 2005, 2007, Lande 1993, Lawton 1994, Gaston 1994, 1998, 2003, Mace and Kershaw 1997, McKinney 1997, Gaston and Blackburn 2000, Purvis et al. 2000). Chapter 4 suggests it may be profitable to investigate the biological or environmental factors that allow such rare species to persist in spite of that risk.

Since small range size is associated with risk-tolerance and risk tolerance is associated with faster diversification, it is tempting to conclude that small range size promotes faster diversification. This would directly contradict the finding of Chapter 3, that larger range sizes cause faster diversification rates. However, chapter 4 did not directly investigate whether small range size or habitat specialisation of entire clades promotes faster diversification. In fact, the tests used are not appropriate to address such a question. Chapter 3 models various possible modes of speciation and their impact on geographic range size. It then asks whether present-day range sizes of entire clades show a signal of a positive relationship between range size and diversification rate in the past. Chapter 4 suggests that individual species with small ranges survive certain extinction scenarios

better. But it does not address range sizes in the clades to which those species belong, nor seek to relate them to past diversification rates.

In other words, species with risk-tolerance belong to more diverse clades, but do not necessarily give birth to new species themselves. Chapters 3 and 4 need not be contradictory. In fact, they may reflect complementary processes. Large range sizes probably cause faster speciation. If speciation leads to the asymmetrical division of a large ancestral range, as predicted by chapter 2, its daughter species will often have a large and small range respectively. If the high-risk, narrowly-distributed species does not persist, the speciation potency of its widespread ancestor will leave no trace in present-day clade diversity.

Future lines of research

Several avenues of further enquiry are opened up by these three studies. Firstly, each took a single taxon to demonstrate a novel approach to the questions being asked. Other taxa could also be tested, especially where the conclusions are so counterintuitive e.g. in chapter 4.

The model of range size evolution developed for chapter 2 has so far only been used to model the symmetry between sister species' range sizes. The model is also valid for the evolution of individual ranges, and could address such interesting questions as whether the skewed distribution frequently seen with taxon range sizes is the result of random processes, or whether it suggests non-random speciation and extinction. Chapter 3 could use such a model to test whether range-size-driven, short-term differences in diversification rate can indeed lead to long-term differences in clade range sizes.

Chapter 4, if its results prove robust, suggests a need for ecological theory to explain why rare species are risk-tolerant. It also has many implications for conservation planning, such as whether it would be possible to predict the kinds of species biology that will be most and least threatened by habitat loss. Conservation is in urgent need of informed models that allow it to plan ahead in place of its often reactive mode of operation.

Further studies of risk-tolerance and the ecology of species with small populations could help it achieve this goal.

The Evolution of Geographic Range Size

Gaston and Webb's (2003) null expectation test (my term) does not define species-level heritability in the commonly-used sense of phylogenetic signal (Blomberg et al. 2003). Under some models of evolution it leads to the same conclusions about heritability as phylogenetic signal (Hunt et al. 2005, Waldron 2007). Under others, the conclusions are different (Webb and Gaston 2003, 2005).

Rather than prolonging the debate about heritability, it is more valuable to recognise that Webb and Gaston are asking a different but potentially more interesting question about range size. How is geographic range size inherited at speciation, and how does it evolve over the lifetime of a species? Several studies have attempted to infer the evolution of range size from looking at the pattern of range sizes in closely-related species of different ages (Taylor & Gotelli 1994, Gaston & Blackburn 1997, Webb & Gaston 2000, Jones et al. 2005). They have generally found conflicting patterns: range size seems sometimes to decrease, sometimes to increase and sometimes to show a humped trajectory with species age (Webb & Gaston 2000, Jones et al. 2005). But by taking into account how range size is inherited at speciation, clearer patterns may emerge. For example, chapter 2 and 3 suggests that the difference between the range sizes of close relatives may decline over time. This could imply patterns such as the more widespread sister declining whilst the narrowly-distributed one grows in size. Indeed, if widespread species have high rates of vicariant speciation (Rosenzweig 1995), they may constantly be losing parts of their distributional area (often without trace). This would lead to a steady decline in range size over time, but only for widespread species. Current studies implicitly combine all species irrespective of their histories of speciation and so would be unable to detect such patterns.

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APPENDIX 2.1: Sister species pairs of North American birds and their range size symmetry

Sister species 1	Sister species 2	Range symmetry
<i>Aechmophorus occidentalis</i>	<i>Aechmophorus clarkii</i>	0.44
<i>Agelaius phoeniceus</i>	<i>Agelaius tricolor</i>	0.01
<i>Ammodramus henslowii</i>	<i>Ammodramus bairdii</i>	0.68
<i>Ammodramus nelsoni</i>	<i>Ammodramus caudacutus</i>	0.04
<i>Amphispiza belli</i>	<i>Poocetes gramineus</i>	0.19
<i>Anas rubripes</i>	<i>Anas platyrhynchos</i>	0.27
<i>Archilocus colubris</i>	<i>Archilocus alexandri</i>	0.51
<i>Baeolophus bicolor</i>	<i>Baeolophus atricristatus</i>	0.16
<i>Baeolophus inornatus</i>	<i>Baeolophus ridgwayi</i> (or <i>griseus</i>)	0.21
<i>Calamospiza melanocorys</i>	<i>Chondestes grammacus</i>	0.30
<i>Calcarius pictus</i>	<i>Calcarius ornatus</i>	0.80
<i>Callipepla californica</i>	<i>Callipepla gambelii</i>	0.77
<i>Calypte anna</i>	<i>Calypte costae</i>	0.94
<i>Catharus bicknelli</i>	<i>Catharus minimus</i>	0.03
<i>Contopus sordidulus</i>	<i>Contopus virens</i>	0.86
<i>Cyanocitta stelleri</i>	<i>Cyanocitta cristata</i>	0.46
<i>Dendroica castanea</i>	<i>Dendroica fusca</i>	0.85
<i>Dendroica graciae</i>	<i>Dendroica nigrescens</i>	0.71
<i>Dendroica pensylvanica</i>	<i>Dendroica striata</i>	0.31
<i>Dendroica pinus</i>	<i>Dendroica dominica</i>	0.95
<i>Dendroica townsendi</i>	<i>Dendroica occidentalis</i>	0.48
<i>Dolichonyx oryzivorus</i>	<i>Xanthocephalus xanthocephalus</i>	0.86
<i>Empidonax affinis</i>	<i>Empidonax oberholseri</i>	0.18
<i>Empidonax alhorum</i>	<i>Empidonax traillii</i>	0.62
<i>Empidonax difficilis</i>	<i>Empidonax occidentalis</i>	0.35
<i>Euphagus cyanocephalus</i>	<i>Euphagus carolinus</i>	0.64
<i>Icterus abeillei</i>	<i>Icterus galbula</i>	0.07
<i>Icterus spurius</i>	<i>Icterus fuertesi</i>	0.13
<i>Junco hyemalis</i>	<i>Junco phaeonotus</i>	0.06
<i>Limnothlypis swainsonii</i>	<i>Protonotaria citrea</i>	0.51

Sister species 1	Sister species 2	Range symmetry
<i>Loxia curvirostra</i>	<i>Loxia leucoptera</i>	0.80
<i>Megascops asio</i>	<i>Megascops kennicottii</i>	0.69
<i>Melospiza georgiana</i>	<i>Melospiza lincolni</i>	0.81
<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	0.96
<i>Passerella iliaca</i>	<i>Spizella arborea</i>	0.70
<i>Passerina caerulea</i>	<i>Passerina amoena</i>	0.52
<i>Passerina versicolor</i>	<i>Passerina ciris</i>	0.91
<i>Pheucticus melanocephalus</i>	<i>Pheucticus leudovicianus</i>	0.90
<i>Pica pica</i> (or <i>hudsonia</i>)	<i>Pica nuttalli</i>	0.02
<i>Picoides nuttalli</i>	<i>Picoides scalaris</i>	0.07
<i>Picoides tridactylus</i>	<i>Picoides arcticus</i>	0.69
<i>Pipilo aberti</i>	<i>Pipilo crissalis</i>	0.54
<i>Pipilo maculatus</i>	<i>Pipilo erythrophthalmus</i>	0.90
<i>Poecile gambeli</i>	<i>Poecile atricapillus</i>	0.28
<i>Poecile hudsonica</i>	<i>Poecile rufescens</i>	0.12
<i>Polioptila melanura</i>	<i>Polioptila californica</i>	0.11
<i>Quiscalus major</i>	<i>Quiscalus mexicanus</i>	0.04
<i>Sayornis phoebe</i>	<i>Sayornis nigricans</i>	0.56
<i>Seiurus noveboracensis</i>	<i>Seiurus motacilla</i>	0.30
<i>Selasphorus sasin</i>	<i>Selasphorus rufus</i>	0.03
<i>Sialia sialis</i>	<i>Sialia mexicana</i>	0.35
<i>Sitta pygmaea</i>	<i>Sitta pusilla</i>	0.78
<i>Sphyrapicus ruber</i>	<i>Sphyrapicus nuchalis</i>	0.42
<i>Spizella pusilla</i>	<i>Spizella breweri</i>	0.51
<i>Sturnella neglecta</i>	<i>Sturnella magna</i>	0.96
<i>Toxostoma bendirei</i>	<i>Toxostoma cinereum</i>	0.07
<i>Toxostoma crissale</i>	<i>Toxostoma lecontei</i>	0.91
<i>Toxostoma curvirostre</i>	<i>Toxostoma ocellatum</i>	0.06
<i>Toxostoma longirostre</i>	<i>Toxostoma rufum</i>	0.05
<i>Tympanuchus cupido</i>	<i>Tympanuchus pallidicinctus</i>	0.90
<i>Vermivora cryoptera</i>	<i>Vermivora pinus</i>	0.74
<i>Vermivora luciae</i>	<i>Vermivora ruficapilla</i>	0.59
<i>Vireo solitarius</i>	<i>Vireo cassinii</i>	0.30
<i>Wilsonia canadensis</i>	<i>Cardellina rubrifrons</i>	0.13
<i>Wilsonia citrina</i>	<i>Setophaga ruticilla</i>	0.36

APPENDIX 2.2

ERRATUM: The broken tile model with uniform distribution of barriers across the range shape

In chapter 2, I produced a null model of the geographic division of one species into two species by a vicariance barrier. Specifically, the model defined a random expectation of the expected symmetry between the range sizes of the two daughter species that would arise immediately following a vicariance event.

The broken tile model should be expected to produce a uniform distribution of breaks in two dimensions across the simulated range shape (a rectangle). It has since been pointed out to me (D. Irwin, personal communication) that this is not properly achieved by the program as it was written. The program created barriers by picking a random entry point for the barrier on the circumference of the range and then picking a random angle of departure. However, this procedure causes barriers to occur near the edges of the simulated range shape more often than would be expected for a uniform distribution, and thus artificially reduces the expected symmetry.

A uniform distribution of breaks can be achieved computationally by creating a larger polygon surrounding the range shape, much as the shape of a continent would surround the geographic range of an endemic species. Random points are then chosen from a uniform distribution of x and y coordinates within the larger polygon, and a barrier (a line) is extended outwards at a random angle from each such point. If the barrier bisects the range shape, then the symmetry of the two parts is calculated as in the original model.

I carried out such a simulation, using the same parameter sets as the original program. The larger polygon was a 10,000 by 10,000 square, in which was centrally nested a rectangle of height 100. The rectangle's length was a multiple (between 1 and 10) of the height. It is possible that the size of the larger polygon might affect the results, and so I performed a similar set of simulations using squares of differing sizes, from 20,000 square units to 100,000 square units.

Using this corrected simulation method, the expected symmetry values are somewhat different from those reported in chapter 2, being higher or lower depending on the shape of the range (appendix table 2.2.1). The effects of limiting barrier length are also different under the new simulation: in general, shapes which are not perfectly square have their expected symmetry more extensively reduced by limitations on barrier length than in the erroneous simulation.

Since the broken tile only gives an expectation for the moment of speciation, the original paper also modelled the evolution of range size symmetry. This model of range symmetry evolution uses the output of the broken tile to define its starting parameters. Since these parameters change under the corrected simulation, I repeated the simulations of range symmetry evolution. I used two sets of input: firstly, pairs of ranges from the output of the square tile (1:1), and secondly, pairs from a broken tile simulation that used

the average height:width ratio found in the bird data, namely 1:1.6. The original paper used the output from the square tile only, a point that was not made explicit then.

The average symmetry for timestep 1 in the range evolution model is therefore 0.29 (in either case, see appendix table 2.2.1) rather than the original figure of 0.21. Appendix figure 2.2.2 shows an example plot of a typical trajectory for range symmetry evolution and should replace figure 2.2 from the original paper. In spite of the different starting point, the maximum range symmetry achieved at any timestep in 5 repetitions of the simulation was still 0.32, the same as that reported in the original paper.

Whilst the change in starting value would clearly cause a higher average symmetry in the second simulation than that reported in the original paper (see appendix figure 2.2.2), average symmetry was not used as an expectation in the second simulation. This is because expected symmetry of a given sets of sister pairs depends on what point of the trajectory each of them has reached at a given moment. This cannot be easily modeled, both because different sets of sister pairs will have different relative ages, and because the average value for any given timestep varies with each run of the model. I therefore chose the maximum symmetry achieved as the expectation, rather than average symmetry (see the original paper). This expectation that should be conservative; in any set of species pairs, not all pairs (and probably none of them) will be at this maximum value in the present. Whereas the change in the first simulation affects the average, it does not appear to affect the maximum and the conclusion of the second simulation remains unaffected.

Indeed, these changes affect none of the conclusions of the original paper. The observed symmetry between the range sizes of sister species of North American birds (0.48) is still considerably higher than the symmetry expected under null models of range size evolution.

Notwithstanding, I was unable to find a programming solution for ellipses using the new approach, and so the conclusions based on ellipses in the Discussion (namely that ellipses have a lower expected symmetry than rectangles) should be disregarded until it can be proven.

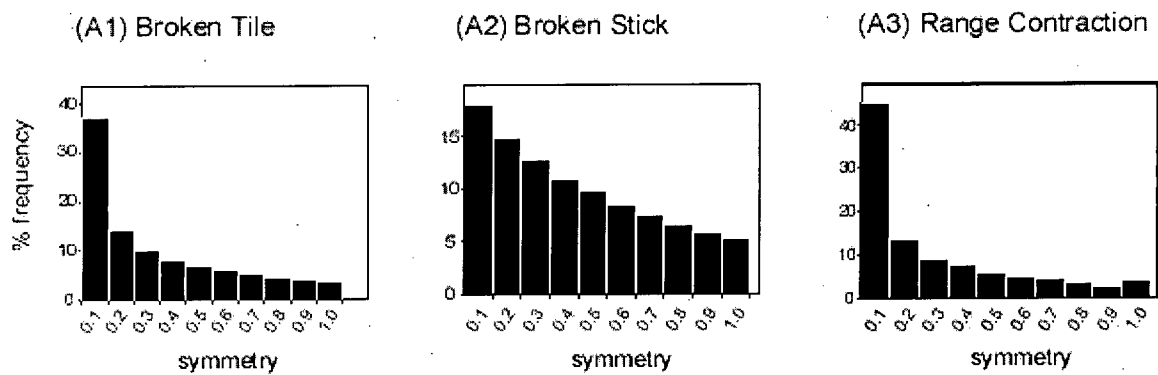
I

Model	Long side:short side ratio of the rectangle		
	1	1.6	10
(A1) Broken tile	0.29 (0.20, 0.08)	0.29 (0.07, 0.05)	0.35 (0.01, 0.007)
(A2) Broken stick	0.39	NA	NA
(A3) Range-contraction	0.25	0.25	0.25 (0.28 if using a uniform distribution)

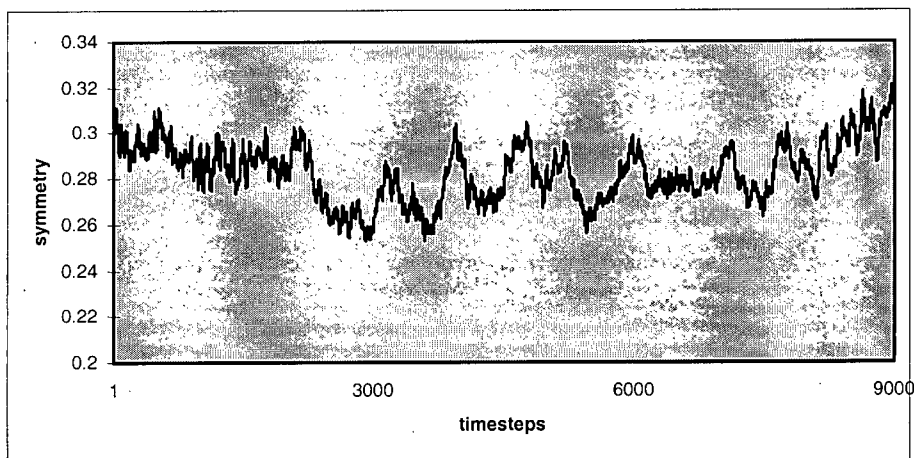
II

Model	Long side:short side ratio of the rectangle		
	1	1.6	10
(A1) Broken tile	0.21 (0.19, 0.07)	0.26 (0.20, 0.04)	0.36 (0.32, 0.01)

Appendix Table 2.2.1: Expectations for the mean symmetry (small/large ratio) between sister species' range sizes at the moment of speciation, and assuming vicariant speciation. Numbers in parentheses for model A1 show the effects of limiting maximum barrier length inside the range to 1.2 times and 1 times the rectangle's shorter side respectively. In the case of model A2, the long side:short side ratio is not relevant since the model breaks a one-dimensional line. Results for model A3 are the same for lognormal and uniform distribution of range size radii, except where shown (see chapter 2 text). I: The results from the corrected simulation. Broken stick and range-contraction results are not affected, but are reproduced for completeness. II: The vicariance scenario results from the original and erroneous simulation, for comparison.



Appendix figure 2.2.1: Expected frequency distributions of symmetry between sister species range sizes at the moment of speciation. Models A1 and A3 show results for a longside:shortside ratio of 1. The model A3 figure used a uniform distribution of radii to model range size; a lognormal distribution yielded very similar results (see text).



Appendix figure 2.2.2: A typical trajectory of range symmetry evolution using a model of random drift. The line shows the average of smaller range/larger range for 250 sister species pairs.

APPENDIX 3.1: Primate phylogeny and triplet range sizes

I updated the Vos and Mooers (2006) tree as follows: the genus *Ateles* is comprised of the four species *A. belzebuth*, *A. marginatus*, *A. geoffroyi* and *A. paniscus* (Collins and Dubach 2000, 2001, Nieves et al. 2005); *Saimiri sciureus*, *S. oesterdii* and *S. ustus* were conservatively treated as a polytomy, not least because *S. oesterdii* may have been artificially introduced into Central America and so could be the product of a non-natural speciation event (Cropp and Boinski 2000); the *Papio/Theropithecus* clade diverged from *Lophocebus* approximately 4 million years ago (Tosi et al. 2005) i.e. earlier than in Vos and Mooers (2006); *Alouatta sara* was elevated to species status as sister to *Alouatta seniculus* (with divergence time greater than 2 million years ago), with *A. macconelli* as the sister to this pair (Cortes-Ortiz et al. 2003); and *Semnopithecus entellus* gave rise to both *Semnopithecus (Trachypithecus) johnii* and *Semnopithecus (Trachypithecus) vetulus* (Karanth 2000). Since the order of divergence of these last two is uncertain, I took the more conservative arrangement of the triplet and made *T. johnii* sister to *Semnopithecus* (this affects none of the conclusions).

Primate distribution maps were taken from Wolfheim (1987), Fooden (1982), Rylands et al. (1993) Ford (1994), Oates et al. (1994), Garbutt (1999), Cortes-Ortiz et al. (2003), Gursky (2003), Oates (2006), The African Mammal database (online), and InfoNatura (2005).

singleton	pair	range single (km ² /10,000)	range pair (km ² /10,000)
<i>Ateles hybridus</i>	<i>A. belzebuth</i>	24.3	466.4
	<i>A. geoffroyi</i>		102.1
<i>Brachyteles</i>	<i>Lagothrix flavicauda</i>	47.2	3.1
	<i>L. lagotricha</i>		351.9
<i>Pithecia aequatorialis</i>	<i>P. monachus</i>	11.3	233.2
	<i>P. albicans</i>		9.3
<i>Callicebus dubius</i>	<i>C. cupreus</i>	21.1	107
	<i>C. calligatus</i>		7.2
<i>Alouatta macconelli</i>	<i>A. sara</i>	69.3	183.7
	<i>A. seniculus</i>		497.5

singleton	pair	range single (km ² /10,000)	range pair (km ² /10,000)
Aotus nigriceps	A trivirgatus	166.3	77.9
	A azarai		108.5
Callithrix pygmaea	C argentata	148.3	121.8
	C humeralifera		32.3
Leontopithecus chrysomela	L. rosalia	2.8	7
	L chrysopygus		6
Saguinus nigricollis	S fuscicollis	65.9	198.3
	S tripartitus		6.1
Saguinus imperator	S labiatus	23.1	25.7
	S mystax		95.2
Hylobates moloch	H agilis	6.9	28.4
	H lar		79.3
Hylobates leucogenys	H concolor	28.8	15.1
	H gabriellae		22.5
T vetulus	Semnopithecus entellus	4.6	343.5
	Trachypithecus johnii		2.3
Pygathrix roxellana	P bieti	2.5	2.8
	P brelichi		0.2
Procolobus verus	P badius	47.4	54.3
	P pennantii		177.1
Colobus angolensis	C guereza	225.2	257.4
	C polykomos		93.8
Lophocebus	Papio	261.3	1345.8
	Theropithecus		22.1
Macaca fuscata	M cyclopis	26.2	3.2
	M mulatta		590.6
Cercopithecus solatus	C lhoesti	1.4	34.6
	C preussi		8.1
Cercopithecus erythrotis	C cephus	10.4	84.5
	C ascanius		292.8
Microcebus coquereli	M murinus	4.4	11.5
	M rufus		10.5
Propithecus diadema	P tattersalli	5.1	0.1
	P verreauxi		9.3
Eulemur coronatus	E fulvus	1.1	13
	E macaco		0.8
Hapalemur simus	H aureus	0.4	0.9
	H griseus		10.8
Loris tardigradus	Nycticebus coucang	74.3	358.1
	N pygmaeus		51
Lepilemur leucopus	L dorsalis	2.3	0.9
	L edwardsi		2.2

Appendix 3.1 table 1: Primate triplets and their range sizes.

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APPENDIX 4.1: Candidate primate clades, their presence or absence on the islands for which they are candidates, and their biological attributes.

CLADE	SU RV IV E	SP P	DIV RAT E	co nti ne nt	GRS	density	fmass	bioD	pri mf or	se cfo r	rivf or	sw am p	mo nta ne	wo od sa v	dry for	op en	hu ma n	ha bit ats	>2 ha b	fruit see d	veg etat ion	ins ect	gu m	flo we rs	me at	die ts	byr
Euoteles elegantulus	1	1	0.00	1	72.5	18.5	0.28	5.18	1	1	1	0	0	0	0	0	1	4	1	1	0	1	1	0	0	3	1
Galago zanzibaricus	1	1	0.00	1	148.2	147.5	0.14	20.65	1	1	0	0	0	0	0	0	0	2	0	1	0	1	1	0	0	3	2
Galago demidoff	1	1	0.00	1	506.8	65	0.06	3.9	1	1	0	0	0	0	0	0	0	2	0	1	0	1	1	0	0	3	1.5
Otolemur garnetti	1	1	0.00	1	83.5	118.5	0.73	86.51	1	0	1	0	0	1	0	0	1	4	1	1	0	1	1	0	0	3	1.8
Otolemur crassicaudatus	1	1	0.00	1	497.1	88	1.24	109.1	1	0	1	0	1	1	0	0	1	5	1	1	0	1	1	0	0	3	2
Galago alleni	1	1	0.00	1	52.9	17.5	0.25	4.375	1	1	0	1	1	1	1	0	1	7	1	1	0	1	1	0	0	3	1
Galago senegalensis	1	1	0.00	1	790.7	31	0.23	7.13	1	0	0	0	0	1	0	0	0	2	0	1	0	1	1	0	0	3	2.6
Galago moholi	0	1	0.00	1	517.3	103	0.19	19.57	1	0	0	0	0	1	0	0	0	2	0	1	0	1	1	0	0	3	2.6
Periodicticus potto	0	1	0.00	1	344.9	8.5	1.15	9.775	1	1	1	1	1	1	0	0	1	7	1	1	0	1	1	0	0	3	1.1
Arctocebus calabarensis	0	1	0.00	1	103.9	4.5	0.25	1.125	1	1	0	0	0	1	0	0	1	4	1	1	0	1	0	0	0	2	1
Nycticebus coucang	1	1	0.00	2	358.1	20	1	20	1	1	0	0	0	0	0	0	1	3	1	1	0	1	0	0	1	3	1.4
Lepilemur dorsalis	1	2	0.35	4	0.9	57	0.64	36.48	1	1	0	0	0	0	0	0	1	3	1	1	1	0	0	1	0	3	1
Hapalemur griseus	0	1	0.00	4	10.8	54.5	0.8	43.6	1	1	0	0	0	0	1	0	0	3	1	0	1	0	0	0	0	1	1

CLADE	SU RV IV E	SP P	DIV RAT E	co nti ne nt	GRS	density	fmass	bioD	pri mf or	se cfo r	riv or	sw am p	mo nta ne	wo od sa v	dry for	op en	hu ma n	ha bit ats	>2 ha b	fruit see d	veg etat ion	ins ect	gu m	flo we rs	me at	die ts	byr
Eulemur macaco	1	1	0.00	4	0.8	129	1.8	232.2	1	1	0	0	0	0	0	0	1	3	1	1	1	1	0	1	0	4	1
Microcebus coquereli	0	1	0.00	4	4.4	50	0.38	19	1	0	1	0	0	0	1	0	1	4	1	1	1	1	1	1	0	5	1.5
Microcebus murinus	0	1	0.00	4	11.5	214	0.07	14.98	1	0	1	0	0	1	1	0	0	4	1	1	0	1	1	0	1	4	2.2
Cheirogaleus major	0	1	0.00	4	9.9	80.3	0.36	28.91	1	1	0	0	0	0	0	0	1	3	1	1	1	1	0	1	1	5	2.5
Tarsius spectrum	1	1	0.00	2	4.6	340	0.11	37.4	1	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0.9
Tarsius syricta	1	1	0.00	2	9.2	340	0.11	37.4	1	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	2	1
Tarsius bancanus	1	1	0.00	2	56.0	98	0.12	11.76	1	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	2	1
Alouatta pallata	1	1	0.00	3	73.8	15	5.84	87.6	1	0	1	1	0	0	0	0	0	3	1	1	1	0	0	0	0	2	0.6
Alouatta seniculus	1	2	0.35	3	566.7	23.5	5.54	130.2	1	1	1	1	1	0	0	0	0	5	1	1	1	0	0	0	0	2	0.7
Ateles geoffroyi	0	1	0.00	3	102.1	20.8	7.89	164.1	1	1	0	0	1	0	0	0	0	3	1	1	1	1	0	1	0	4	0.3
Cebus capucinus	1	2	0.35	3	45.7	28	2.68	75.04	1	1	0	1	0	0	1	0	0	4	1	1	1	1	1	1	1	6	0.6
Pongo pygmaeus	0	1	0.00	2	33.7	2.75	37.8	104	1	0	0	1	1	0	0	0	0	3	1	1	1	1	0	0	1	4	0.3
Pan troglodytes	0	2	0.35	1	255.0	1.1	37.65	41.42	1	1	1	0	1	1	1	0	0	6	1	1	1	1	1	1	1	6	0.3
Hylobates muelleri	0	1	0.00	2	19.0	10.2	5.6	57.12	1	1	0	0	0	0	1	0	0	3	1	1	1	1	1	1	0	5	0.4
Hylobates lar	0	1	0.00	2	79.3	6.4	5.4	34.56	1	0	0	1	0	0	1	0	0	3	1	1	1	1	1	1	0	5	0.4

CLADE	SU RV IV E	SP P	DIV RAT E	co nti ne nt	GRS	density	fmass	bioD	pri mf or	se cfo r	rivf or	sw am p	mo nta ne	wo od sa v	dry for	op en	hu ma n	ha bit ats	>2 ha b	fruit see d	veg etat ion	ins ect	gu m	flo we rs	me at	die ts	byr
Hylobates agilis	0	1	0.00	2	28.4	16.9	5.6	94.64	1	0	0	1	0	0	1	0	0	3	1	1	1	1	0	1	0	4	0.4
Trachypithecus obscurus + T. cristatus	1	4	0.69	2	64.5	116	6.38	740.1	1	0	1	1	0	0	0	0	0	3	1	1	1	0	0	1	0	3	0.5
Presbytis rubicunda + P. melalophos	1	4	0.69	2	68.9	36.6	6.215	227.5	1	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0	3	0.5
Nasalis larvatus	0	1	0.00	2	75.4	5.9	9.88	58.29	1	0	1	1	0	0	0	0	0	3	1	1	1	0	0	1	0	3	1
Procolobus pennantii	1	1	0.00	1	5.0	178.2	8.2	1461	1	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0	3	0.5
Procolobus badius	1	1	0.00	1	1.0	178.2	8.2	1461	1	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0	3	0.5
Colobus satanas	1	1	0.00	1	32.4	12.3	7.4	91.02	1	0	0	0	1	0	0	0	0	2	0	1	1	0	0	1	0	3	0.5
Colobus angolensis	0	1	0.00	1	203.9	6.9	6.67	46.02	1	0	1	0	1	0	1	0	0	4	1	1	1	0	0	0	0	2	0.5
Mandrillus leucophaeus	1	2	0.35	1	11.5	6.7	15	100.5	1	1	1	0	0	0	0	0	0	3	1	1	1	1	0	0	1	4	1
Cercocebus torquatus	0	1	0.00	1	140.5	23.4	5.9	138.1	1	1	1	1	0	0	0	0	0	4	1	1	0	1	0	0	0	2	0.9
Lophocebus albigena	0	1	0.00	1	261.3	39.85	5.645	225	1	0	1	1	0	0	0	0	0	3	1	1	1	0	0	0	0	2	0.5
Papio	0	1	0.00	1	1345.8	6.8	11.68	79.42	1	1	1	0	0	1	0	1	0	5	1	1	1	1	1	1	1	6	0.8
Macaca nigra	1	7	0.97	2	2.6	11.8	5.5	64.9	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	5	0.9
Macaca nemestrina	0	1	0.00	2	306.0	11.7	6.37	74.53	1	1	1	0	0	0	0	0	0	3	1	1	1	1	0	1	1	5	0.9
Macaca arctoides	0	1	0.00	2	207.0	5.3	12	63.6	1	0	0	0	0	0	1	0	0	2	0	1	1	1	0	1	1	5	0.7

CLADE	SU RV IV E	SP P	DIV RAT E	co nti ne nt	GRS	density	fmass	bioD	pri mf or	se cfo r	riv or	sw am p	mo nta ne	wo od sa v	dry for	op en	hu ma n	ha bit ats	>2 ha b	fruit see d	veg etat ion	ins ect	gu m	flo we rs	me at	die ts	byr
Macaca mulatta + M. fuscata	1	3	0.55	2	308.4	9.3	5.62	52.27	1	0	0	1	1	1	1	0	0	5	1	1	1	1	0	1	1	5	1
Chlorocebus aethiops	0	1	0.00	1	1378.9	95.8	3.3	316.1	1	1	1	1	1	1	1	1	1	9	1	1	0	1	0	0	1	3	1
Cercopithecus preussi	1	3	0.55	1	8.1	8.5	10	85	1	1	0	0	1	0	0	0	0	3	1	1	1	1	0	0	1	4	0.7
Cercopithecus pogonias	1	4	0.69	1	122.6	13.4	3	40.2	1	1	0	0	0	0	0	0	0	2	0	1	1	1	0	0	1	4	0.7
Cercopithecus erythrotis	1	5	0.80	1	10.4	24.7	30	741	1	1	0	0	0	0	0	0	0	2	0	1	1	1	0	0	1	4	0.7
Cercopithecus nictitans + Cercopithecus mitis	1	2	0.35	1	264.6	33.35	3.855	128.6	1	1	1	0	1	0	1	0	0	5	1	1	1	1	0	0	1	4	0.7

KEY:

SURVIVE, tolerant = 1, intolerant = 0.

Divrate = diversification rate of the clade that the species belong to.

continent, 1 = Africa, 2 = Asia, 3 = Neotropics, 4 = Madagascar.

GRS = geographic range size in km2 (divided by 10,000)

Density = population density in individuals per km2

Fmass = bodyweight of female in kg

BioD = biomass per km2

For habitat and diet categories, 1 = exploited, 0 = not exploited.

Habitat categories: "Rivfor" is riverine or gallery forest, "swamp" includes mangrove, "woodsav" includes savannah and open woodland and bush, "dryfor" is dry seasonal forest.

For diet, "vegetation" includes leaves and other vegetative parts of plants.

Habitats = count of possible habitats exploited

>2hab indicates specialism, 1 = two or fewer habitats exploited, 0 = greater than two habitats exploited.

Diets = count of diets exploited

Byr = births per year

Geographic range size data was taken from Waldron (chapter 3). Population density data was taken from Harcourt et al. (2005), supplemented by Happel et al. (1987), Thomas (1991), Nowak (1999). The value for *C. lhoesti* in Harcourt et al. (2005) was also assigned to *C. preussi*. Body mass data was taken from Harcourt et al. (2005) supplemented by Fa et al. (1995) and Nowak (1999). Habitat and diet data were taken from Happel et al. (1987), Wolfheim (1987) and Nowak (1999). Habitats and diets were classed as exploited if they appeared in any source. Births per year data was taken from , with missing species supplemented from Fa et al. (1995) and Nowak (1999). Where Nowak did not give exact values, approximate values were calculated as $365 / \text{interbirth interval} \times \text{litter size}$ where IBI was available, else as $\text{average litter size} \times \text{breeding seasons per year}$ if births were seasonal, or as $\text{average litter size} \times 365 / (\text{gestation length (days)} + \text{weaning period (days)})$ for non-seasonal breeders. Reproductive data for the closest relative was used in the case of the data-deficient candidates *G. moholi*, *G. senegalensis*, *H. muelleri*, *H. agilis*, *P. rubicunda*, *C. angolensis*

APPENDIX 4.2: Landbridge islands and areas of islands

ISLAND	AREA km2
Basilan	501
Batam	399
Billiton/Belitung	4830
Bintan	1173
Bioko	1935
Bohol	3821
Bunguran Selatan	231
Coiba	50
Dinagat	769
Galang	80
Karimata	179
Kundur	315
Langkawi inc Dayang Bunting	479
N Borneo	20
Natuna	1605
N Sulawesi1	20
N Sulawesi2	30
N Sulawesi3	20
Nosy Be	290
Peleng	2346
Pemba	890
Penang	280
Phangan	170
Phuket	800
Pulau Sugi	54
Natuna Besar	1605
Serasan	104
Siargao	416
Singapore	700
Tarutao	250
Tioman	140
Togian	180
Trinidad	4828
Wanshan	20
Yaku	524
Zanzibar	1575

Unnamed islands were islands drawn on primate distribution maps whose names could not be unequivocally identified. Sources for island size were the UNEP database <http://islands.unep.ch>, supplemented by Heaney (1984), Harcourt and Schwartz (2001) and Lammertink et al. (2002). The size of unnamed islands was measured directly by

digitising them from distribution maps into ArcGIS 9.2 and then calculating their areas with ArcGIS 9.2 utilities (ESRI 2005). Sources do not specify on which islands of the Wanshan group *Macaca mulatta* is found; I therefore treated the group as a single island and assigned it an area of 20km² based on an average of the larger islands.

Sources for primate distributions and primate presence on islands were Wolfheim (1987), Fooden (1982), Butynski et al. (1994), Oates et al. (1994), Rabarivola et al. (1996), Shukor (1996), Rylands et al. (1993), Garbutt (1999), Harcourt (1999), Harcourt and Schwartz (2001), Gursky (2003), Brandon-Jones et al. (2004), Oates (2006), The African Mammal database (online), and InfoNatura (2005).

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