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On the Heritability of Geographic Range Sizes

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ABSTRACT: Within taxonomic groups, most species are restricted in their geographic range sizes, with only a few being widespread. The possibility that species-level selection on range sizes contributes to the characteristic form of such species–range size distributions has previously been raised. This would require that closely related species have similar range sizes, an indication of "heritability" of range sizes at the species level. Support for this view came from a positive correlation between the range sizes of closely related pairs of fossil mollusc species. We extend this analysis by considering the relationship between the geographic range sizes of 103 pairs of contemporary avian sister species. Range sizes in these sister species show no evidence of being more similar to each other than expected by chance. A reassessment of the mollusc data also suggests that the high correlation was probably overestimated because of the skewed nature of range size data. The fact that sister species tend to have similar life histories and ecologies suggests that any relationship between range sizes and biology is likely to be complicated and will be influenced by historical factors, such as mode of speciation and post-speciation range size transformations.

Keywords: geographic range size, heritability, speciation, birds, molluscs.

Geographic range sizes can vary enormously even between closely related species (Brown et al. 1996; Gaston and Chown 1999). As yet, we do not know precisely what governs the possession of a particular range size by any one species (Gaston 1998). One possibility, raised by Jablonski (1987), is that the frequency distribution of geographic range sizes of species within clades (the species–range size distribution) is shaped by selection at the species level (we discuss higher-level selection below). This conclusion rested largely on the documentation of statistically significant positive correlations between the geographic range sizes of closely related pairs of fossil mollusc species and on the argument that this constitutes evidence for the species-level heritability of range sizes. Although analyses of the range sizes of a small number of sister species pairs from various contemporary taxa have failed to find a similar pattern (Gaston 1998; Webb et al. 2001), Jablonski's (1987) study continues to be cited regularly, either as the single bona fide example of species-level heritability of range sizes (e.g., Burns 1992; Ricklefs and Latham 1992; Lawton 1993, 1995; Lloyd and Gould 1993; Taylor and Gotelli 1994; Grantham 1995; McKinney 1995, 1997*a*; Brown et al. 1996; Chown 1997; Price et al. 1997; Holman 1999; Barraclough and Vogler 2000) or as a caveat added to statements suggesting that range sizes may not pass between "generations" (i.e., from ancestral to descendant species) in the same manner as, say, facets of the biologies of individual organisms (e.g., Blackburn et al. 1997; Kunin 1997; Quinn et al. 1997; Chown et al. 1999; Gaston and Chown 1999).

In addition to range size heritability being a necessary prerequisite for species selection to be invoked as a general mechanism for creating observed patterns of range sizes, a more thorough demonstration of range size heritability would have further important consequences. For example, one explanation for apparent heritability of range sizes would be that geographic range sizes are determined by life-history, ecological, or physiological characters (Lawton 1993; Emlet 1995; Brown et al. 1996). Such traits may evolve independently within species, but changes will be relatively minor, and close relatives will tend to resemble each other because of common descent (or "history of lineage"; Brown et al. 1996). From this, it might be possible to identify robust biological correlates of range size and related variables such as extinction proneness, which would be of theoretical interest as well as of potential benefit for conservation (e.g., Angermeier 1995). Conversely, if evidence from other taxa fails to corroborate the findings of Jablonski (1987), then this would suggest that "history of place" factors (Brown et al. 1996; see also Emlet 1995)—such as mode of speciation, abiotic environmental history, or chance—may interact with (or even dominate)

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biology in the determination of a species' geographic range and in the creation of clade-level species–range size distributions.

Here, we investigate the phenomenon of range size heritability by examining the similarity in the global geographic range sizes of a wide selection of contemporary avian sister species pairs. We then reexamine Jablonski's (1987) results with reference to our findings. Finally, in light of our conclusions, we discuss some of the processes that seem likely to influence the form of species–range size distributions.

Heritability and Levels of Selection

The debate about the levels in the biological hierarchy on which selection acts has persisted for decades (see Lloyd 2000 for a recent review). Some ideas, such as Wynne-Edwards's (1962) conjecture that individuals will often act for the "good of the species," have not stood up to rigorous examination (e.g., Dawkins 1989). However, this need not mean that group-level selection processes are impossible (Lloyd and Gould 1993). Lewontin (1970) argues that any entity that meets certain criteria may evolve by natural selection. These criteria require that individuals within a population differ with regard to the trait in question, that different phenotypes have different rates of survival and reproduction, and that both the trait and its correlation with fitness are heritable to some degree. These conditions specify no particular mechanism of inheritance, only a correlation in fitness between parent and offspring; this means that selection may act on any entity in nature that has both heritable variation and reproduction (Lewontin 1970). On this foundation, Eldredge and Gould (1972) developed the idea of species selection to explain how macroevolutionary trends might originate if species differ in characters that make them prone to extinction or unusually likely to speciate (Sterelny 2001). As defined by Grantham (1995, p. 305), "species selection occurs when the differential reproduction or extinction of species is caused by heritable differences in the fitness of species-level traits."

Despite initial disagreements and misunderstandings, the possibility of species selection is now generally accepted (Sterelny 2001). However, there is less agreement as to its importance. Dawkins (1986), for instance, acknowledges that species selection might explain the pattern of species existing in the world at any one time as well as changes in these patterns through geological time, but he remains more interested in explaining "complex, well-designed mechanisms like hearts, hands, eyes and echolocation" (p. 265). Lloyd and Gould (1993) agree that species selection will not explain Dawkins's complex adaptations but argue that "a theory of evolution has many more, and equally important, things to do" (p. 595). Gould (1994, 1998), in particular, stresses the potential macroevolutionary importance of a general theory of natural selection that can operate at any level.

Eldredge and Gould (1972) saw their work as contributing toward such a unified theory of natural selection, which is why the term "species selection" was not coined until later (by Stanley 1975; see Gould and Eldredge 1977). Under this view, species selection can lead to genuine species-level adaptations by acting on traits that are only emergent at the species level. Such traits can only be assigned to species, not to individual members (for instance, individuals are male or female, but only groups have a sex ratio). In such cases, species take on the properties of individuals (Hull 1980; Gould 1998), with a clade of species becoming analogous to a population of individuals; this effectively negates the "defection" objection to group selection (Sterelny 2001).

Despite the growing consensus that species selection may be responsible for temporal patterns in the fossil record and indeed for the pattern of species existing in the world at any one time (Gould and Eldredge 1977; Dawkins 1986; Lloyd 2000), it has been hard to find empirical evidence for its occurrence (Sterelny 2001). Those searching for such evidence have looked at geographic range size because it is a species-level trait that clearly varies between species and that seems likely to be related to fitness (i.e., the probability of speciation and extinction; see Rosenzweig 1995; Chown 1997; McKinney 1997*b*; Gaston 1998). The final requirement for species selection is that variation is heritable, which has been harder to demonstrate (Sterelny 2001); this is why Jablonski's (1987) study has been influential. For instance, in a review of the thinking behind higher-level selection, Lloyd (2000) presents a convincing argument that such selection is possible, but the only empirical study that she cites in support of species selection is that of Jablonski (1987). It therefore seems valuable to subject the issue of range size heritability to further empirical examination.

First, however, it is worth stating explicitly what heritability means and how it might be applied to the species level. In quantitative genetics, the heritability of a trait is the proportion of phenotypic variability in the trait that is accounted for by additive genetic variation (Ayala 1982; Cook 1991; Stearns 1992). Values of heritabilities can range between 0 (phenotypic variance is entirely due to differences in the environment) and 1 (phenotypic differences are entirely genetic in origin; Ayala 1982; Cook 1991). Although this quantitative genetic concept of heritability has been applied more or less intact to levels above the individual (e.g., Wade and McCauley 1980; Wade and Griesemer 1998; Griesemer and Wade 2000), Jablonski (1987) cautioned against pushing the analogy too far, given the complex nature of "inheritance" at speciation. In his analyses, Jablonski (1987) applied the methods of quantitative genetics (i.e., parent-offspring regressions, correlations of sibling values; Cook 1991; Stearns 1992; Falconer and Mackay 1996) in an attempt simply to quantify the degree to which similarities in a species-level trait (geographic range size) are due to common descent. We agree that the notion of species-level heritability may be a useful descriptive tool. For instance, it seems reasonable (conceptually at least) to divide species traits into phylogenetic (inherited) and specific values (Cheverud et al. 1985); this is essentially what happens in analyses of phylogenetic constraints and evolutionary transitions (e.g., McKitrick 1993; Johnson et al. 1999). When we refer to heritability, then, we use it only as a useful means to refer to the degree of similarity between relatives.

Bird Data

Methods

We identified 103 avian sister species pairs from the phylogenetic literature (table 1). Global geographic range size was estimated for each species by transferring published distribution maps (Harrison 1985; Cramp 1988, 1992; del Hoyo et al. 1992, 1994, 1996; Curson et al. 1994; Ridgely and Tudor 1994; Urban et al. 1997; Jaramillo and Burke 1999) onto an equal-area WorldMap grid (Williams 1996) except in the wildfowl, for which the number of WorldMap squares occupied was already known (D. A. Callaghan, unpublished data). The grid employed here has squares of 10° longitude, each with an area of approximately 611,000 km^2. We acknowledge that this measure is rather crude, but it is practical, and interspecific differences in geographic range size are such that it is sufficient for the examination of broad macroecological patterns (e.g., Gaston and Blackburn 2000).

Jablonski (1987) documented the relationship between the range sizes of ancestral and descendant species (a parent-offspring situation) and estimated the heritability of range sizes using the regression coefficient b (Falconer and Mackay 1996). Recognizing that his data clearly departed from normality (and thus violated the assumptions of parametric regression), he also calculated Spearman's rank correlation coefficients (r_s). Using pairs of sister species (whose range sizes also clearly depart from normality), we could mimic this approach by estimating heritability as the correlation (r) of range sizes within the pairs (Falconer and Mackay 1996), backing this up with rank correlation. However, we take an alternative approach for the following reasons. First, a large concentration of small range–small range pairs (the points near the origin on Jablonski's [1987] fig. 1*C*, 1*D*; see our fig. 2) will exert a strong influence not only on parametric analyses (e.g., Thomson et al. 1996) but also possibly on rank correlations (T. J. Webb, unpublished data). This will lead to an overestimation of the strength of any relationship and certainly to an inflated estimate of heritability. Estimates may be increased further by outliers (points with both high leverage and large residuals), which will exert a strong influence on any correlation analysis (Samuels 1989; Sokal

Table 1: Taxonomic makeup of the sister-species pairs used in the bird analysis

Family	Number of sister-species pairs	Source of phylogeny
Partridges and ptarmigans (Phasianidae)	2	Ellsworth et al. 1995; Randi 1996
Screamers (Anhimidae)	1	Livezey 1997*a*
Ducks, geese, and swans (Anatidae)	45	Livezey 1986, 1991, 1995*a*, 1995*b*, 1995*c*, 1996*a*, 1996*b*, 1997*a*, 1997*b*
Cranes (Gruidae)	4	Krajewski and Fetzner 1994
Kittiwakes (Laridae)	1	Crochet et al. 2000
Auks (Alcidae)	6	Friesen et al. 1996
Gannets and boobies (Sulidae)	2	Friesen and Anderson 1997
Storks (Ciconiidae)	4	Slikas 1997
Penguins (Spheniscidae)	1	O'Hara 1989
Albatrosses (Diomedeidae)	6	Nunn et al. 1996
Tit-tyrants (Tyrannidae)	3	Roy et al. 1999
Thrashers (Mimidae)	2	Zink et al. 1999
Nuthatches (Sittidae)	2	Pasquet 1998
Gnatcatchers (Certhiidae)	1	Zink and Blackwell 1998
Old World warblers (Sylviidae)	10	Price et al. 1997; Helbig and Seibold 1999
Pipits (Motacillidae)	1	Voelker 1999
New World warblers (Parulidae)	5	Lovette and Bermingham 1999
New World blackbirds (Icteridae)	7	Lanyon 1994; Omland et al. 1999

and Rohlf 1995). The method employed below reduces the influence of outliers. Finally, Jablonski (1987) was able to assign his ancestral species (defined as that within each species pair with the geologically older first occurrence) to the horizontal axis (note that if both species first appeared in the same stratigraphic layer, the species whose name came first alphabetically was assigned to this axis). In sister species pairs, however, there is no a priori reason to assign members of each pair to a particular axis; this would therefore necessitate randomizing the order of species within each pair, calculating r_s and r, and then repeating this process many times to generate frequency distributions of the coefficients. The method outlined below removes this requirement. An alternative method, assigning all the range sizes in the data set to species at random and then assessing any correlations, was also rejected because it is not clear to what extent it is desirable to randomize ranges from taxa as disparate as, for example, albatrosses and warblers.

The method employed here examines the similarity in the range sizes of sister species by comparing the smaller range size within the pair to the larger range size. This allows a measure of range size symmetry to be calculated and compared with the situation that would arise if the smaller range size within a pair was a random fraction of the larger range size. Note that symmetry in contemporary range sizes is simply a convenient way to assess the similarity in the present-day ranges of relatives and implies nothing about the way that range sizes are apportioned between sister species at speciation; neither does it imply an ancestral range size that was the sum of the two contemporary range sizes. Clearly, this method does not enable us to put a numerical value on our estimate of range size heritability, certainly not one that is comparable with the estimates used in population genetics studies of organismal traits. However, as outlined above, we consider the term "heritability" here to be shorthand for quantifying the degree of similarity in a trait between closely related species rather than a strict analogue of the term used in quantitative genetics. If range size were heritable in this looser sense, then the range sizes of sister species should be more similar to each other (i.e., more symmetrical) than would be expected by chance. Applying this method to pairs of integers generated to fit the assumptions of parametric correlation analysis has shown that even marginally significant positive correlations obtained in such cases will be reflected in significant degrees of symmetry being reported (T. J. Webb, unpublished data).

In fact, we consider range size asymmetry rather than symmetry. We define the actual range size asymmetry, $\mathrm{Asy}_{\mathrm{act}}$, of sister species pairs as

$$\mathrm{Asy}_{\mathrm{act}} = 1 - \frac{S}{B}, \tag{1}$$

where S is the smaller range size in the pair and B is the bigger range size. Therefore, species with identical ranges ($S/B = 1$) have an asymmetry of 0, and species with very differently sized ranges ($S/B \to 0$) have an asymmetry approaching 1. Because of the way we have measured range sizes (they must always take a positive integer value), the degree of asymmetry possible in a given case will be constrained by the size of the largest range size. Thus, if $B = 2$, S can only equal 1 or 2, and so asymmetry can equal either 0 or 0.5; if $B = 100$, asymmetry therefore equals $1 - (S/100)$, with S taking any integer value between 1 and 100. In general, if the smaller range size within a pair were a random fraction (up to and including 1) of the larger range, then averaging over many pairs for each value of B would give an average degree of asymmetry, $\mathrm{Asy}_{\mathrm{exp}}$, for a given value of B equal to

$$\mathrm{Asy}_{\mathrm{exp}} = \frac{1}{B}\left[\frac{1 + 2 + 3 + \cdots + (B - 1)}{B}\right]. \tag{2}$$

This simplifies to

$$\mathrm{Asy}_{\mathrm{exp}} = \frac{B - 1}{2B}. \tag{3}$$

With large values of B, $\mathrm{Asy}_{\mathrm{exp}}$ approaches the 0.5 that would be expected if range sizes were not constrained to take whole number values. Note that if B is an even number, $\mathrm{Asy}_{\mathrm{act}}$ can never precisely equal $\mathrm{Asy}_{\mathrm{exp}}$. However, there will always be an equal number of possible values of $\mathrm{Asy}_{\mathrm{act}}$ above and below $\mathrm{Asy}_{\mathrm{exp}}$. Values of B, the biggest range in each of the 103 sister species pairs in our data set, range from 2 to 98. We therefore generated expected degrees of asymmetry for every integer in this range and compared the actual degree of asymmetry for the 103 sister species pairs with the appropriate value of $\mathrm{Asy}_{\mathrm{exp}}$.

Results

Figure 1 shows the actual degree of range size asymmetry in the 103 sister species pairs ($\mathrm{Asy}_{\mathrm{act}}$; *circles*) compared with the degree of asymmetry expected if the smaller range size within each pair was simply a random fraction of the larger one ($\mathrm{Asy}_{\mathrm{exp}}$; *solid line*). If range sizes were heritable, most points would be below the solid line on figure 1. A random distribution of points above and below the line on figure 1 would suggest that range sizes are randomly distributed within sister taxa, whereas a preponderance of points above the line would suggest that sister species tend

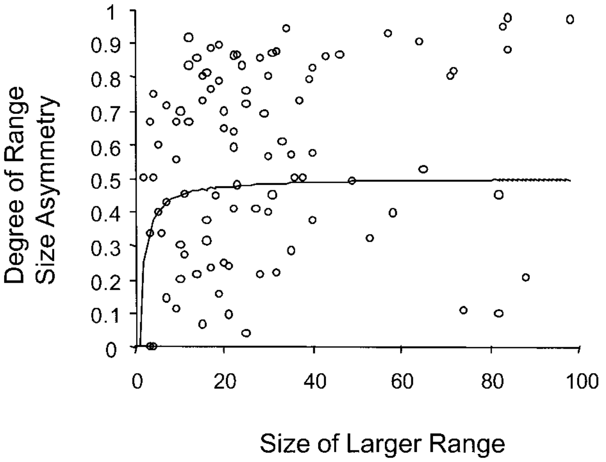

Figure 1: Actual degree of range size asymmetry for 103 pairs of contemporary avian sister species (*open circles*). The solid line represents the average expected degree of asymmetry if the smaller range in a pair were simply a random fraction of the larger range.

to have unusually asymmetric range sizes. In fact, 61 points fall above the line and 36 below it, with six falling on the line. Such a distribution is highly unlikely to result from chance variation around the expected values (one-sample sign test, $P = .0148$). Observed values of asymmetry are significantly greater than those expected under a null hypothesis of random symmetry; the mean difference ($\pm$SEM) from the expected value for a given B (i.e., the mean distance of points from the solid line in fig. 1) is 0.095 ± 0.026, which is significantly >0 ($df = 102$, $t = 3.65$, $P = .0002$). In other words, there is a tendency for avian sister species to have ranges significantly less symmetrical than would be expected at random. There is certainly no evidence of range size heritability.

Bearing on Jablonski's Results

There are various reasons why the bird data presented above may seem to contradict Jablonski's (1987) assertion: birds and molluscs are clearly very different, and fossil and contemporary data may not be comparable. Here, however, we treat the mollusc data as comparable with our bird data and examine the consequences of subjecting it to the kind of analysis used above. Such a comparison is of interest because if the range sizes of avian sister species are plotted against each other, the resulting plot is not overly dissimilar to those obtained by Jablonski (1987; our fig. 2). As in the molluscs, there is a high concentration of points near the origin (i.e., there are many small range–small range species pairs), with a large scatter across the rest of the span of range sizes on both axes. Indeed, had we performed an analysis identical to that of Jablonski (1987), we too may have concluded that range size was a heritable species-level trait, because there is a significant positive correlation between the range sizes of avian sister species (after randomizing the order of species within each of the 103 sister species pairs 1,000 times, mean ± SEM $r_s = 0.260 \pm 0.0003$; $r = 0.269 \pm 0.0003$; $P < .05$ for every randomization and for both statistics). However, we showed above that the range sizes of avian sister species are actually less similar than would be expected by chance. This suggests that heritabilities estimated from data like those plotted in figure 2 may be artifactually exaggerated because of the highly skewed nature of range size data.

Methods

Jablonski's (1987) figure 1*D* shows the relationship between range sizes of 95 pairs of closely related gastropod species (see our fig. 2*A*). (Note that we report results from the gastropod data because Jablonski [1987] reported a higher estimate of range size heritability for gastropods [0.63 ± 0.08] than for bivalves [0.55 ± 0.08]. All our conclusions also hold for bivalves.) We measured the position on both axes of each of the pairs in which at least one species has a range of >500 km ($n = 56$). By our measurements, range sizes in these species span approximately 20 to 4,340 km on each axis. Range sizes in these taxa are measured as the linear extent of occurrence along an outcrop belt, with a precision of ± 20 km. All of the ranges can therefore be represented by integers between 1 (20/20) and 217 (4,340/20). Degree of asymmetry in range sizes (Asy_{act}) was calculated for each pair using equation (1), and expected degree of asymmetry (Asy_{exp}) was determined by solving equation (3) for $B = 1$ to 217.

The remaining 39 points on Jablonski's (1987) figure 1*D* (our fig. 2*A*), in which both species have a range of <500 km (i.e., an integer value between 1 and 25), are represented as a solid box signifying more than 20 points by Jablonski (1987). We explore several scenarios as to how these points may be distributed, which are designed to represent the extremes of what is likely, as well as a more realistic situation. First, under a random scenario, 39 random integers were generated between 1 and 25; these were set to be B ranges. Corresponding S ranges were obtained by rounding a random fraction of each B range to the nearest integer. Next (maximum symmetry scenario), B ranges were generated as in the random scenario, and each B range was paired with an identical S range (i.e., $\text{Asy}_{\text{act}} = 0$ in every case). In a complementary simulation termed "maximum asymmetry," B ranges were constrained to be random integers between 13 and 25, and S ranges were all set to equal 1 (i.e., $0.92 < \text{Asy}_{\text{act}} < 0.96$). Finally, asymmetry calculated for the 56 measurable spe-

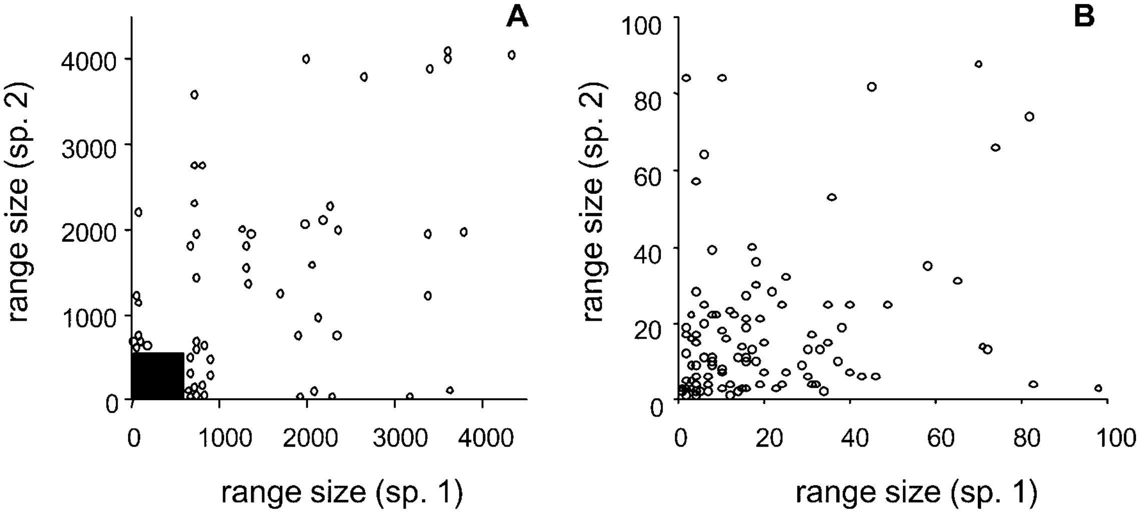

Figure 2: *A*, Relationship between the geographic range sizes (linear extent of range; km) of 95 pairs of ancestor-descendant (species 1–species 2) pairs of late Cretaceous gastropod mollusc species (redrawn from Jablonski 1987). The solid box represents 39 pairs of species, both having a range size <500 km. There is a highly significant positive correlation ($r_s = 0.65$, $P < .001$), and the regression slope (heritability) is 0.63. *B*, Analogous plot for the range sizes of 103 pairs of contemporary avian sister species. Here too there is a highly significant positive correlation ($r_s = 0.27$, $P < .01$), and heritability (estimated for sister species as the product moment correlation coefficient, *r*) is also 0.27; this is despite the fact that range sizes within these species pairs are actually less similar than would be expected if the smaller range in a pair were simply a random fraction of the larger range.

cies pairs had an interquartile range of 0.24 to 0.88, which corresponds to a ratio of S/B of between 0.12 and 0.76. We therefore created a realistic scenario by generating *B* ranges as in the random scenario, and we obtained corresponding *S* ranges by rounding to the nearest integer a random fraction between 0.12 and 0.76 of each *B* range. We ran 100 replicates of each of these scenarios. In each iteration of each scenario, the 39 values of $\mathrm{Asy}_{\mathrm{act}}$ calculated according to the appropriate scenario were combined with the 56 values of $\mathrm{Asy}_{\mathrm{act}}$ that were directly measurable. We recorded the number of points falling above, on, and below the line representing expected asymmetry, and we tested departures from equality using one-sample sign tests. We also recorded the mean distance of points from this line and performed a *t*-test to determine the significance of this departure.

Results

Considering only the 56 measurable points, there was no trend for either unusually high or unusually low levels of asymmetry between species pairs (fig. 3, *open circles*: 32 points above the line, 23 below, one on the line; one-sample sign test, $P = .28$). Mean distance of points from the line was 0.060 ± 0.0442, which is not significantly different from 0 ($t = 1.36$, $P = .18$), although the trend is toward greater degrees of asymmetry than expected, the opposite of what would be the case were range sizes heritable.

The results obtained after combining these 56 points with the remaining 39 points generated according to the four scenarios tested are shown in table 2; typical plots obtained in each case are shown in figure 3. It is clear (table 2) that the distribution of the 39 small range–small range species pairs has a big effect on the overall levels of asymmetry in range sizes seen in this group (which is not surprising, since they represent more than 40% of all species pairs). When range sizes within all of these species pairs were identical (maximum symmetry scenario), overall levels of range size symmetry in this group were greater than expected (i.e., $\mathrm{Asy}_{\mathrm{act}} < \mathrm{Asy}_{\mathrm{exp}}$). When the smaller range size in a pair was unrelated to the size of the larger range (random scenario), overall levels of range size symmetry were no different to those expected at random ($\mathrm{Asy}_{\mathrm{act}} = \mathrm{Asy}_{\mathrm{exp}}$). When range sizes in this group were very dissimilar (maximum asymmetry), overall levels of range size symmetry were less than expected (i.e., $\mathrm{Asy}_{\mathrm{act}} > \mathrm{Asy}_{\mathrm{exp}}$). Interestingly, the realistic scenario also suggests that overall levels of range size symmetry are less than expected. Under this scenario, in all 100 simulations, the mean $\mathrm{Asy}_{\mathrm{act}}$ is greater than $\mathrm{Asy}_{\mathrm{exp}}$; in more than half of these simulations, a *t*-test would have concluded that this difference was significant (table 2).

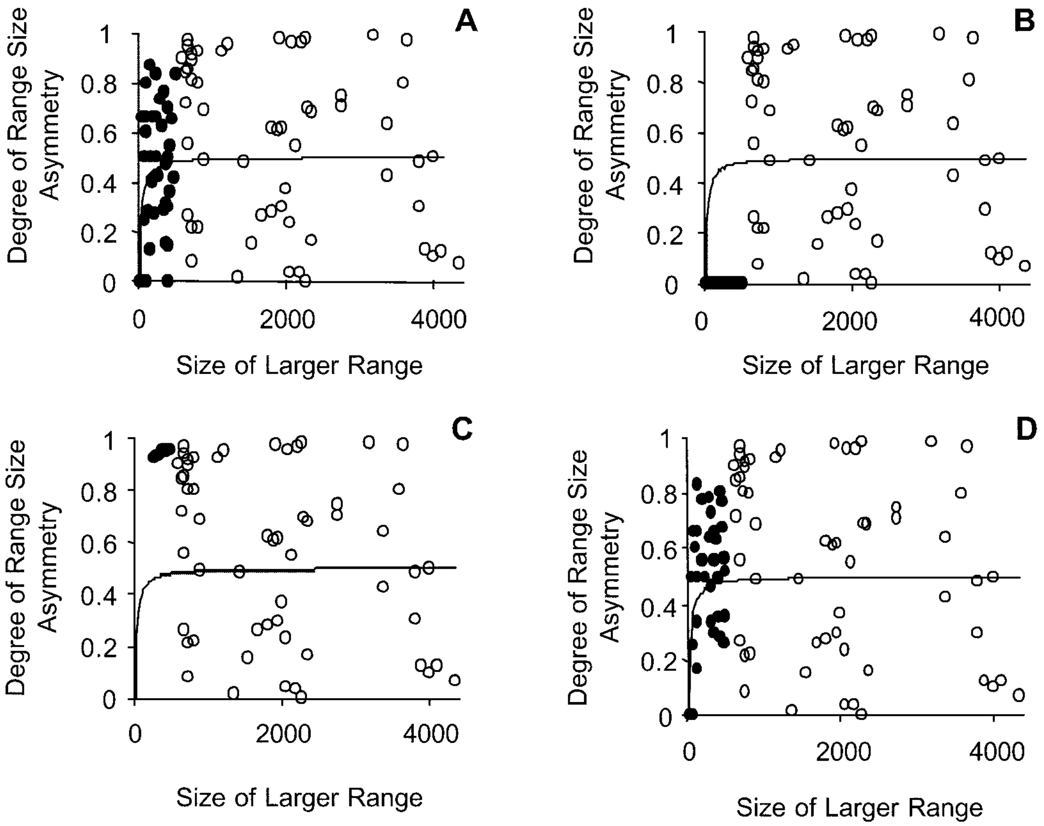

Figure 3: Actual degree of range size asymmetry for 56 pairs of closely related late Cretaceous gastropod species, in which at least one species in each pair has a range size >500 km (*open circles*). The solid line represents the average expected degree of asymmetry if the smaller range in a pair were simply a random fraction of the larger range. Solid circles represent degrees of asymmetry obtained from a typical example of generating range sizes for the remaining 39 small range–small range pairs under the following scenarios: *A*, random; *B*, maximum symmetry; *C*, maximum asymmetry; *D*, realistic.

Discussion

We have argued that the concept of heritability at the species level can be useful for assessing the potential influences of common descent and subsequent independent evolution on shaping patterns of similarity in species-level traits between closely related species. One such species-level trait is geographic range size. On the basis of an analysis of fossil molluscs, Jablonski (1987) argued that geographic range size was heritable at the species level. If this were the case, then we would expect to observe a high degree of symmetry between the range sizes of sister species. In fact, we observe the opposite: we document significant levels of asymmetry between the range sizes of 103 pairs of contemporary avian sister species.

This result led us to reassess the high values of range size heritability reported by Jablonski (1987) for late Cretaceous molluscs. His heritability estimates were obtained, as he recognized, by applying parametric statistics to data that clearly departed from normality. Had we taken the same approach, we might equally have concluded that range sizes were heritable (although our estimate for birds, $h^2 = 0.27$, would be somewhat lower than the heritabilities of 0.55–0.63 presented by Jablonski [1987]). Applying our methods to Jablonski's gastropod data (in which he estimated heritability of range sizes to be 0.63 ± 0.08), we failed to detect significant levels of range size symmetry in the 56 pairs of species from this data set whose ranges we could measure directly from Jablonski's (1987) figure 1*D*. In the remaining 39 pairs, both species had restricted ranges. Generating such pairs under several scenarios produced contrasting patterns of overall range size symmetry. There does not seem to be a compelling reason to expect unusually high or low degrees of range size symmetry in these species pairs, however, and we feel that constraining range size symmetry in these pairs to levels similar to that observed in the other 56 pairs is a reasonable assumption.

Table 2: Summary of results from simulations to assess the degree of asymmetry in the ranges of closely related gastropod molluscs

	Median frequency			No. of significant	Mean difference		No. of significant
Scenario	$Asy_{act} > Asy_{exp}$	$Asy_{act} = Asy_{exp}$	$Asy_{act} < Asy_{exp}$	sign tests	of Asy_{act} from Asy_{exp}^{a}	Mean value of t^a	t-tests
Random	50	4	41	2	.03 ± .019 (−.014 to .086)	1.06 ± .608 (−.429 to 2.720)	6
Maximum symmetry	32	3	60	100	−.14 ± .007 (−.154 to −.120)	−3.80 ± .164 (−4.143 to −3.374)	100
Maximum asymmetry	71	1	23	100	.23 ± .0003 (.228 to .230)	6.88 ± .005 (6.867 to 6.892)	100
Realistic	53	5	37	25	.06 ± .012 (.026 to .089)	2.00 ± .421 (.902 to 3.181)	54

Note: Data from Jablonski (1987). Within any one scenario, sign tests and t-tests were only ever significant ($P < .05$) in one direction. Under the maximum symmetry scenario, all significant results were in the direction of greater levels of symmetry than expected ($Asy_{act} < Asy_{exp}$). Under all other scenarios, all significant results were in the direction of greater levels of asymmetry than expected ($Asy_{act} > Asy_{exp}$). All t-tests were based on levels of asymmetry in all 95 pairs; n for sign tests depended on the number of occasions that $Asy_{act} = Asy_{exp}$.

[a] Values reported are means of 100 simulations ± SD (minimum to maximum).

This realistic scenario led to the conclusion that range sizes were certainly no more symmetrical than expected at random and probably less. Thus, it seems that here too there is no great trend for closely related species to be constrained to similar magnitudes of geographic range size.

Similar results are therefore obtained using birds and molluscs, despite the great differences between these taxa that may translate into differences in factors influencing any perceived heritability of range sizes—such as mode of speciation, dispersal ability, or habitat (e.g., terrestrial or marine)—or in taxonomic opinion as to what constitutes a species (Purvis and Hector [2000] show that such differences of opinion can be considerable). Ricklefs and Latham (1992) have demonstrated that different patterns can arise in taxa far less distinct than birds and molluscs (herbaceous vs. woody plant genera). In addition, Jablonski's (1987) analysis used fossil species, whereas we considered the contemporary range sizes of extant species. Good fossil data record the total extent of a species' range over its entire life span or a substantial part thereof (Gaston 1998); they may therefore be compromised if species' ranges move around while remaining more or less constant in size. Contemporary data, however, record a snapshot of where a species has recently been distributed and so do not account for transformations in the size of species' ranges over time (Gaston 1998). The broad convergence of conclusions based on contemporary bird and fossil mollusc data therefore suggests that an absence of similarity in the range sizes of close relatives may be rather general.

Why should range size be apparently unrelated to phylogeny in this way? To answer this question, we need to consider the processes that act to determine a species' range size. Sister species come into existence when speciation occurs through cladogenesis. Speciation in birds is probably predominantly allopatric (e.g., Anderson and Evensen 1978; Mayr 1982; Chesser and Zink 1994; Peterson et al. 1999; Turelli et al. 2001), although other models are certainly possible (e.g., Schliewen et al. 1994; Rosenzweig 1995; Dieckmann and Doebeli 1999; Via 2001). Allopatric models of speciation dictate that cladogenesis involves the divergence of geographically isolated populations. In other words, an ancestral geographic range size encompasses a

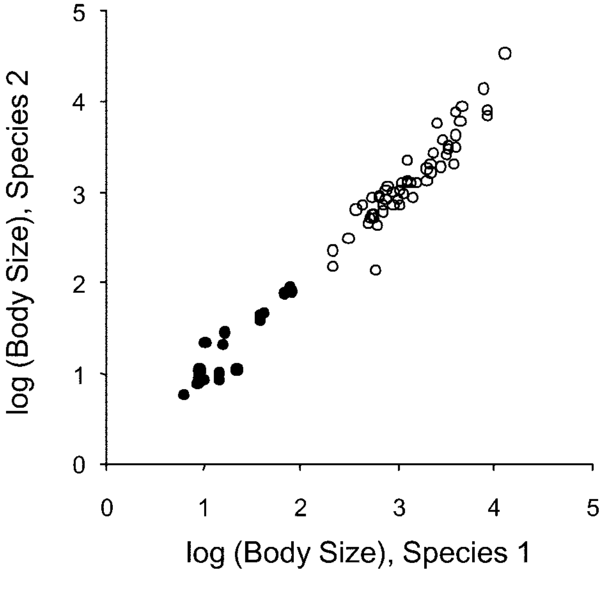

Figure 4: Relationship between body sizes (maximum body mass [g] reported for either sex in Dunning [1993]) within 76 pairs of contemporary avian sister species (*solid circles*, passerines; *open circles*, nonpasserines). The positive correlation is highly significant (all 76 pairs: $r = 0.98$, $P < .001$; 19 passerine pairs: $r = 0.93$, $P < .001$; 57 nonpasserine pairs: $r = 0.94$, $P < .001$), indicating that sister species tend to have similar body sizes. Note that this figure is analogous to figure 2*B*.

Table 3: Habitat categories used to classify the species in the avian data set

Broad habitat classification	Subcategories/nesting sites
Marine pelagic	Open ground
	Cliffs
	Heavy vegetation
	Burrows
Aquatic	Bogs, swamps, marshes, etc.
	Open freshwater, standing (lakes, ponds, etc.)
	Open freshwater, running (rivers, streams, etc.)
	Coastal (estuaries, brackish lagoons, etc.)
Forest	Deciduous woodland
	Coniferous woodland
	Open woodland, orchards, etc.
	Scrub, shrubs, brush, etc.
Open areas	Desert, barrens, rocky ground, etc.
	Tundra, moors, uplands, etc.
	Grassland, savanna, etc.
	Farmlands, gardens, etc.
Urban	Towns

Note: Adapted from habitat descriptions given in Sibley and Monroe (1990, 1993).

number of populations, and each resultant sister species will constitute a subset of these. Are they likely to receive a roughly equal portion of the ancestral range? Certain models of speciation suggest not. For instance, daughter species with rather asymmetric range sizes will result from speciation through peripheral isolation (Glazier 1987; Price et al. 1997; Gaston and Chown 1999; Barraclough and Vogler 2000). Vicariance too will often result in daughter species with different range sizes, especially if the ancestral range size were large; vicariance in an ancestral species with a small range size can only result in two daughter species also with small ranges (Gaston and Chown 1999; Webb et al. 2001).

Immediately following a speciation event, then, we might often expect nascent sister species to have rather different range sizes. However, range sizes are not static and are likely to change over time as ecological and environmental conditions vary (Ricklefs and Latham 1992; Chesser and Zink 1994; Price et al. 1997). Indeed, from a separate analysis in the same 1987 article that we have been concerned with here, Jablonski concludes that in the mollusc taxa under consideration, range sizes expand very rapidly postspeciation. It is therefore unlikely that the contemporary distributions (in the case of extant species) or total distributional extent over their life span (in the case of fossil species) of sister species will reflect their relative range sizes at speciation (see also Chesser and Zink 1994; Friesen and Anderson 1997; Webb and Gaston 2000). This dynamic nature of geographic ranges means that the high degrees of asymmetry in the contemporary range sizes of avian sister species cannot be taken as evidence of, for example, a high frequency of speciation by peripheral isolation.

The question of whether the lack of a strong relationship between the range sizes of sister species is consistent through time could be addressed through consideration of the age of sister species used in our analyses. For instance, sister species might tend to have similar range sizes

Table 4: Congruence between the habitat categories of 97 pairs of sister species for which habitat descriptions were given in Sibley and Monroe (1990, 1993)

	No. of species pairs	
	Broad habitat types	Habitat subcategories
Habitat classification of sister species identical	84	45
Habitat of more generalist species encompasses all habitat types occupied by more specialist species	10	24
Overlap in habitat types occupied by sister species is not complete	2	17
Sister species occupy different habitats	1	11

Note: Broad habitat types and habitat subcategories refer to the two levels of classification shown in table 3.

soon after speciation and then evolve independently until any correlation disappears (Ricklefs and Latham 1992), although models of allopatric speciation suggest that this is unlikely. Alternatively, sister species might tend toward similar range sizes even if their range sizes immediately after speciation are rather different; the lack of symmetry between the range sizes of contemporary species pairs suggests that this too is unlikely. The current rate of production of high-quality, relatively complete species-level molecular phylogenies means that such issues are now becoming tractable. For instance, in an investigation into the likely mode of speciation in a number of groups of organisms (birds, fish, and insects), Barraclough and Vogler (2000) examined the total area occupied by all species occurring below nodes of different ages within a phylogeny. They compared this clade-level range size with that of a sister clade and examined range size symmetry as a function of node age. The youngest comparisons were between recently split sister species, which tended to have highly dissimilar range sizes. Most of the older comparisons were between two clades, each containing several species, but it would be possible to adapt this approach to consider only sister species pairs of varying ages.

Is there any reason to expect that the ranges of close relatives will become more (or less) similar over time? History of lineage explanations of range size (Brown et al. 1996), which suggest that a species' geographic range size is determined by features of its life history, ecology, or physiology, would predict that species with similar biologies will tend to have similar range sizes. Under this scenario, the high degree of asymmetry in the range sizes of avian sister species would be due to differences in biology or ecology between close relatives. As a preliminary investigation into whether differences in the range sizes of avian sister species could be attributed principally to differences in biology, we consider a life-history variable (body size) and an ecological variable (habitat), estimates of which are available for most species in our data set (Sibley and Monroe 1990, 1993; Dunning 1993). Body size is highly conserved within avian sister species pairs (fig. 4), presumably because of common descent. Many life-history traits of birds and other animals are correlated with body size (e.g., Gaston and Blackburn 2000), and so this similarity in the body sizes of sister species will tend to be indicative of broadly similar life histories. Could differences in habitat requirements explain differences in the range sizes of sister species? We used the habitat descriptions given in Sibley and Monroe (1990, 1993) to classify 97 of the 103 species pairs in our data set into broad habitat categories and further into subcategories (table 3). Almost all species occupy the same broad habitat type as their sister (table 4); in addition, there is usually considerable (and quite often complete) overlap between the habitat subcategories used by sister species (table 4). If ecology or life history were playing the major role in determining distributional extent in these species, then we would expect to see a high degree of symmetry between the range sizes of sister species pairs; this is not the case. Of course, rigorous comparative tests may reveal certain traits that often covary with range size (number of habitat types used seems an obvious candidate). The purpose of these general examples, however, is to highlight the fact that considerable variation in range size exists even within groups of closely related species that have broadly similar life histories and ecologies.

One possible explanation for this result is that very small differences in biology may have a disproportionate effect on range size. Alternatively, biology might have little influence on range size. Rather, history of place factors (Brown et al. 1996) may predominate. These may include stochastic events in the abiotic environmental history experienced by different species in different areas as well as historical legacies resulting from the mode and geographic location of the speciation event that gave rise to a species. Marine molluscs may shed some light here. In marine bivalves, body size has played a role in both Pleistocene and contemporary range expansions (Roy et al. 2001). In addition, those species of late Cretaceous molluscs with planktotrophic larvae tend to have larger ranges than those with nonplanktotrophic larvae (Jablonski 1986), and closely related species will tend to resemble each other because evolutionary changes in developmental mode are infrequent in this lineage (Jablonski 1986). We might therefore expect to observe somewhat similar ranges in closely related species in these taxa. However, the role of body size in range expansion is complex (Roy et al. 2001), and Jablonski (1987, p. 362) states that "variance of geographic range within each larval mode—or any other single trait—is high." It seems most likely that the size of a geographic range is not entirely independent of biology, but neither is there a simple causative relationship between certain life-history or ecological traits and distributional extent. Rather, range sizes will result from the combined influences of individual biological characteristics, interactions with competing species, and abiotic environmental effects (Davis et al. 1998; Case and Taper 2000). The relative roles of these factors and the fact that all will vary in time and space may explain why closely related species can have very different range sizes.

Conclusions

Our results provide little support for the notion that species selection on geographic range sizes has played a significant role in shaping contemporary species–range size distributions, a result supported by the fact that most variation in range sizes within lineages tends to be explained at low taxonomic levels (Gaston 1998; Webb et al. 2001). Indeed, in the absence of a heritable basis to geographic range size, species selection cannot be invoked as an important force in the evolution of species–range size distributions. While (potentially heritable) features of its life history, ecology, or physiology will doubtless influence the extent to which a species can spread, its geographic range may in fact be less constrained by phylogeny than by accidents of history or geography.

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