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Heritability of Geographic Range Sizes Revisited:
A Reply to Hunt et al.

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Hunt et al. (2005) revisit the issue of range size heritability following our recent article on this topic (Webb and Gaston 2003). In that article, we showed that the range sizes of closely related species tend to be highly dissimilar and argued that this provided evidence to counter Jablonski's (1987) claim that range size was a heritable species-level trait. Hunt et al. do not dispute the fact that the species pairs that we examined have highly asymmetric range sizes; however, they claim that the statistical technique that we used to assess the significance of this asymmetry is flawed. They then return to correlation analyses to support their assertion that range size is indeed heritable. While some points of technical interest are raised, we disagree with their conclusions and feel that the analyses that they present provide little insight into the ultimate questions driving studies such as that of Webb and Gaston (2003) and Jablonski's (1987) original paper on the topic—namely, to identify important factors in the determination of a species' range size and in the generation of species–range size distributions. In responding to the concerns raised by Hunt et al., we first defend our simple null model of range size similarity. We then make explicit our initial objection to the correlation analyses favored by Jablonski (1987) and by Hunt et al. by showing how a simple but apparently feasible mechanism, rooted in individual-level biology or

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in sampling artifact, can reproduce observed patterns without requiring the species-level heritability of range size as a species-level trait.

Null Models of the Similarity of Range Sizes of Closely Related Pairs of Species

In the critique of our methodology, Hunt et al. correctly point out that if two range sizes are drawn at random from a distribution of ranges, the null expectation of the asymmetry (where asymmetry $= 1 - S/B$, with S the smaller range size in a pair and B the larger) of the two ranges will approach 0.5 only when the overall distribution of ranges is uniform. Given the right-skewed nature of most species–range size distributions (including the two that we initially analyzed), they suggest that the null expectation of asymmetry will generally be rather higher than 0.5 and support this with simulations of random pairings of ranges from various distributions.

While accepting this result, we disagree that expected asymmetry should be constrained by the shape of the observed species–range size distribution, a topic that we expand on below. However, it is possible to modify our measure of expected asymmetry to account for this apparent bias. First, we fit a suitable distribution to our avian range size data. We prefer the negative binomial distribution to an exponential distribution because it captures the discrete nature of most range size measures. The fit of the negative binomial distribution to our data is shown in figure 1A. We then calculated for each observed value of B (the larger range in a pair) the mean value of those observations in a sample of 10,000 random draws from a negative binomial distribution (with the same parameters as shown in figure 1A) that were >0 and $\leq B$. This is the null expectation of S, the smaller range in the pair, constrained by the shape of the observed species–range size distribution. Expected values of S for each B were converted into asymmetry values as shown above, and observed asymmetry was then compared to this expectation. In doing so, we find no evidence that the ranges of bird sister species are less symmetrical than expected (fig. 1B). Asymmetry was less than expected in 47 of 103 cases, a
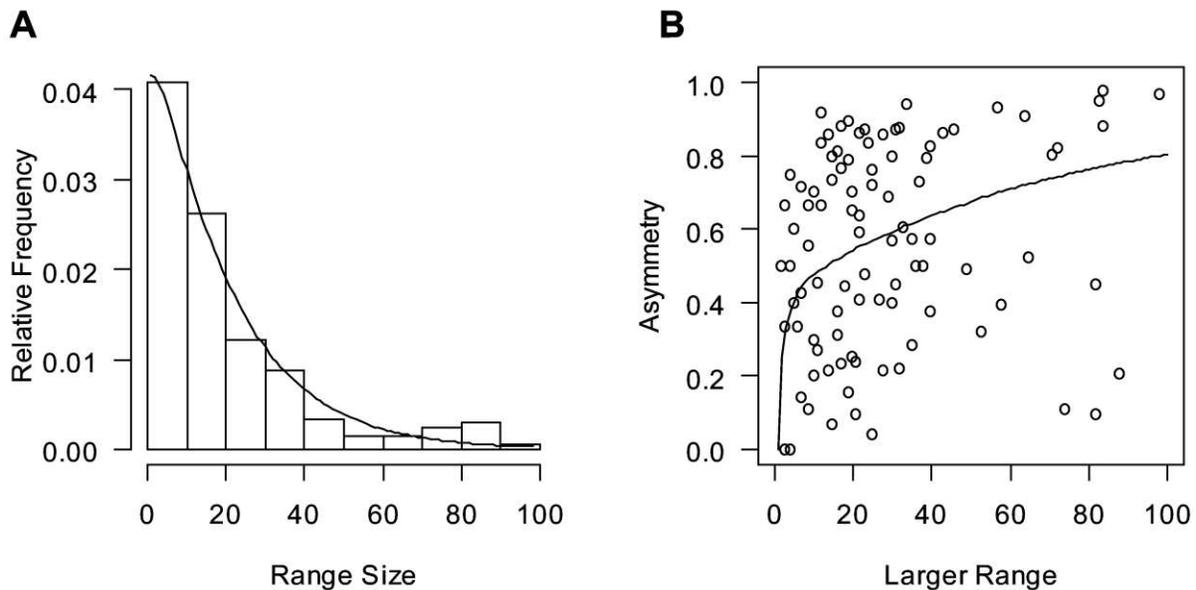
A

B

Figure 1: *A*, Species–range size distribution for the 206 bird species analyzed by Webb and Gaston (2003). The solid curve shows the fitted negative binomial distribution, with maximum likelihood parameter estimates *R* (the measure of aggregation) = 1.115 and *p* (the probability of success) = 0.055. *B*, Actual range size asymmetry plotted against the size of the larger range of each pair of avian sister species. The line shows expected asymmetry if the shape of the species–range size distribution is assumed to be fixed, as proposed by Hunt et al. Here, for each value of *B* (the size of the bigger range), the mean of all possible values of *S* (the size of the smaller range) was taken to be the mean of all instances of a range ≤*B* and >0 occurring in 10,000 random draws from a negative binomial distribution with parameters *R* and *p* as in *A*.

split that is not unusually extreme (binomial probability of ≤47 values out of 103 being less than expected = 0.2153). A similar result was obtained for the mollusks, with asymmetry less than expectation in 37 species pairs, greater than expected in 40 pairs, and equal to expectation in 18 pairs (binomial probability of ≤37 values out of 77 being less than expected = 0.4099). Thus, even accepting Hunt et al.'s criticism, there is no evidence that species pairs in either data set have ranges more similar than expected, suggesting little "heritability" of range size.

Despite this broad support for our original conclusions, we disagree with the rationale behind requiring the null distribution of range size asymmetry to be contingent on the observed species–range size distribution. This argument has some parallels with the broader debate over the use of null models in ecology (e.g., Gotelli 2001). How much biological information should be included when generating a null distribution of asymmetry? Hunt et al. argue that the appropriate null distribution of asymmetry is that obtained from random pairing of the observed range sizes. However, this calls into question just what exactly would be the significance of such a restricted notion of range size heritability. Under this scenario, heritability is only allowed to work within the bounds of the observed species–range size distribution: a new daughter species (for

example) will tend toward a range size determined by the parameters of the existing species–range size distribution rather than toward the range size of its ancestor. Species-level selection will not shape the species–range size distribution, counter to Jablonski's (1987, p. 362) statement that "the spectrum of geographic ranges within clades can be shaped by selection at the species level; other factors being equal, mean geographic range should increase through a clade's history." Rather, there is a tacit admission that, given the observed species–range size distribution, the ranges of closely related species are likely to be rather dissimilar on average. This makes the interesting prediction that the degree of range size asymmetry will co-vary with the shape of the overall species–range size distribution. However, it is difficult to see how such results would be interpreted: for instance, would the shape of the species–range size distribution be considered as evidence of the strength of range size heritability? Or would similar levels of heritability be allowed to produce contrasting patterns of asymmetry, depending on the shape of the species–range size distribution under consideration?

The question that we addressed was rather different, its interpretation straightforward. We asked, Are the range sizes of sister species more similar to one another than expected from a uniform distribution? We maintain that

this is a sensible question, and it avoids some of the circularity inherent in Hunt et al.'s proposal by avoiding the requirement that the form of the underlying species–range size distribution is known a priori. Even in the simplest case this would require decisions to be made as to which species to include in this distribution—presumably all those that existed in the phylogenetic tree, whether extant or extinct. Frequently, more complex issues may also affect this decision. For instance, although species–range size distributions are generally strongly right skewed (Gaston 1998, 2003), there are circumstances under which this is not the case. The Late Cretaceous gastropod data provide a good example, as these species have been shown (Jablonski 1986) to consist of two subgroups, differentiated on the basis of larval developmental mode, each with very different species–range size distributions (fig. 2A). Because larval mode is phylogenetically a relatively stable trait (12 of 16 families listed in Jablonski's [1986] article contain species of only one of the larval modes), it would be perfectly justifiable to analyze planktotrophs and nonplanktotrophs separately, requiring separate null distributions of range size asymmetry.

Such effects may be rather common: for instance, the overall species–range size distribution of shorefish in the tropical eastern Pacific is composed of distinct distributions of insular and continental species (Mora and Robertson 2005). For the bird species in our data set, there does not appear to be a single trait with equivalent influence on range size. However, sampling effects might easily influence range size distributions, for instance, if commoner species were more likely to be included in phylogenetic and distributional data sets. Similar effects may occur if range sizes are estimated over only a portion of the global distributional extent of the clade in question (see below). Our simple null model means that broad patterns in the similarity of range sizes can be identified for any group of species. Of course, further analysis may then be interesting to investigate mechanisms behind the observed patterns. For instance, one might ask whether asymmetry differs between major taxonomic groups within a data set or whether it correlates with ecology, life history, and so on. Results can also be applied to more general questions regarding the species–range size distribution; for instance, What form would the species–range size distribution take if range sizes were heritable? or, equivalently, Is the form and phylogenetic structure of the species–range size distribution compatible with a scenario of range size heritability? The answer to this second question would generally appear to be no. Such questions could not be addressed if the underlying form of the species–range size distribution needs to be estimated before analysis of range size similarity, as proposed by Hunt et al. We now argue that the correlation analyses that they favor also

have little potential to provide insight into the fundamental ecological and evolutionary questions that drive studies into patterns of range sizes.

Using Rank Correlations to Assess Range Size Heritability

In the second part of their comment, Hunt et al. use rank correlations between the range sizes of pairs of species to reaffirm their view that range sizes are heritable. Rank correlations essentially perform parametric statistics on the ranked data, and as such they are applied to situations in which the raw data do not meet the assumptions of parametric analysis. This is clearly the case for paired species range size data, as can be seen from figure 1*C* and 1*D* in Jablonski (1987) and figure 2*B* in Webb and Gaston (2003). Implicit in the use of rank correlation is that ranking the data removes any features that will bias the analysis. The characteristics of the paired species range size data sets that concern us do not appear to be removed by ranking, however; a frequency distribution of the ranks in Hunt et al.'s figure 4, for example, would retain considerable right skew because of the influence of multiple tied ranks. Of course, this does not explain the disappearance of any correlation when range sizes are randomly shuffled, and the positive correlation that Hunt et al. report among species pairs that both have large ranges is intriguing (although, of course, excluding pairs in which only one species had a large range means that the most dissimilar pairs are excluded; the correlation between species pairs in Hunt et al.'s data set in which at least one species has a range >500 km is somewhat lower [$r_s = 0.33$, $n = 58$, cf. 0.38, $n = 34$ when both species have a range >500 km], and we note that there is no such correlation in the small range–small range pairs [$r_s = 0.065$, $n = 37$]).

For the moment, we will accept that these rank correlations are valid and that Hunt et al.'s suggestion that the range sizes of pairs of mollusk and bird species are significantly correlated needs to be explained. We maintain that the high rank correlation coefficients appear to be at odds with what, to most eyes surely, remain unconvincing plots (e.g., fig. 3*A*; Hunt et al. 2005, fig. 4), particularly if the regression lines are removed (Hunt et al. acknowledge [p. 134] that their ranked data do not meet the assumptions of linear least squares regression yet curiously still include the line on their figure). This becomes vividly apparent when the results for range sizes are compared to traits, such as body size, that are undoubtedly conserved across phylogenies (fig. 3*B*). In our initial article, we suggested that plots of pairs of range sizes appear to generate a significant rank correlation due principally to an excess of small range–small range pairs, plus a very few outlying large range–large range pairs. Hunt et al. counter that this
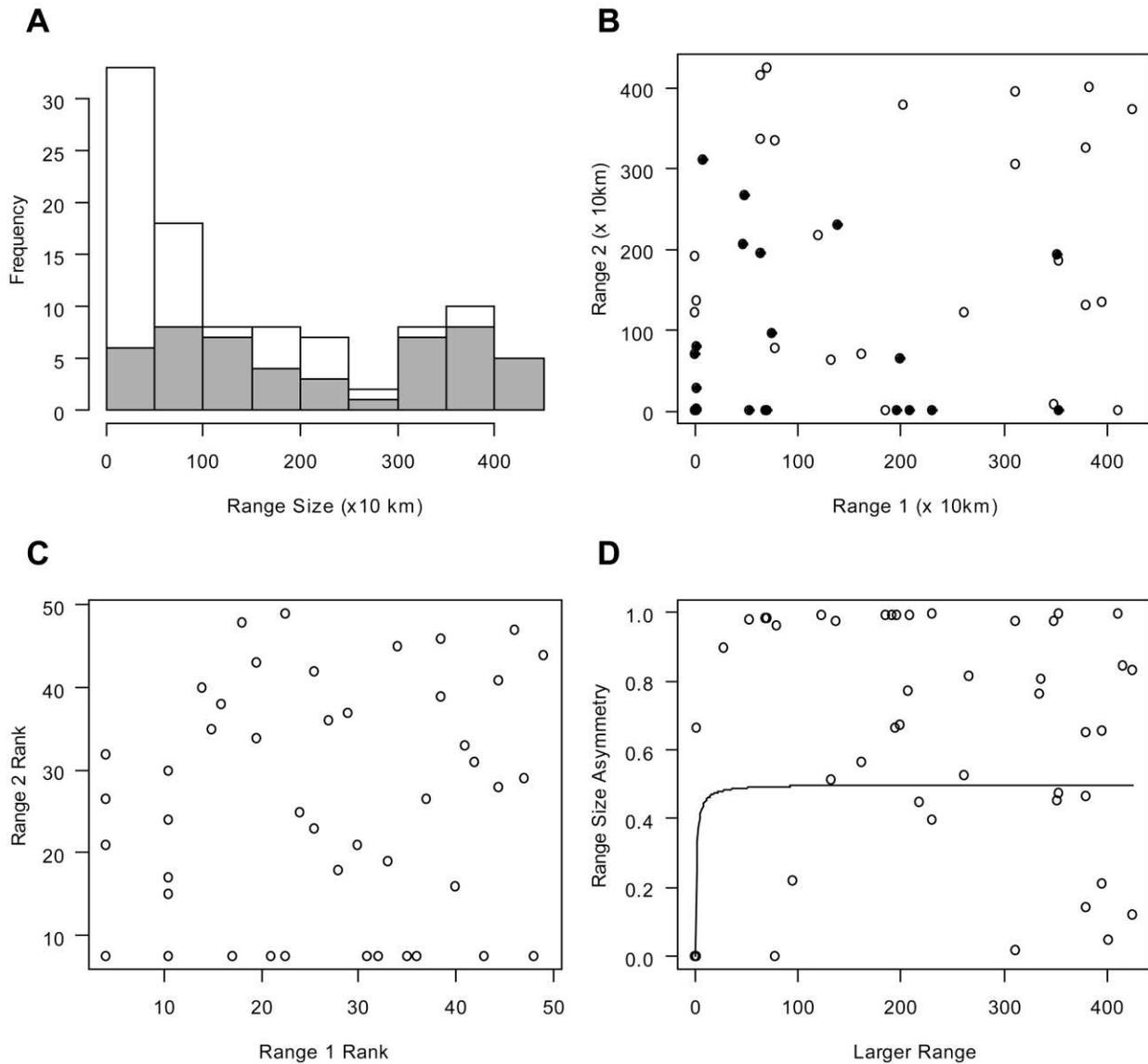
Figure 2: *A*, Species–range size distribution for Late Cretaceous gastropod mollusks with different larval dispersal modes: nonplanktotrophic (*open bars*; $n = 50$), which are small range biased, and planktotrophic (*filled bars*; $n = 49$), which are larger range biased (data from Jablonski 1986). The typically right-skewed overall species–range size distribution (total height of bars) can be seen as the sum of the two rather different distributions. *B*, *C*, Typical manifestations of raw (*B*) and ranked (*C*) range size pairs created by pairing the range size data shown in *A* at random, within larval modes (i.e., random pairs of planktotroph ranges and random pairs of nonplanktotroph ranges). Considering all 49 pairs of range sizes, the relationship was positive ($r = 0.22$, $r_s = 0.22$). However, there was no relationship within the nonplanktotroph (solid circles in *B*; $r = 0.01$, $r_s = 0.02$) or the planktotroph (open circles in *B*; $r = -0.02$, $r_s = -0.09$) pairs. *D*, Asymmetry in the randomly paired range sizes shown in *B* and *C*. Asymmetry exceeds the measure of expected asymmetry (*solid line*) of Webb and Gaston (2003) for 33 of 49 pairs and equals expectation on four occasions, suggesting significant asymmetry (binomial probability of exceeding expectation on 33/45 occasions = 0.0004). Mean absolute asymmetry = 0.63.

should be taken as evidence of a genuine relationship. Here we make explicit our concerns with this approach by showing how a simple constraint on the pairing of range sizes can apparently reproduce observed patterns without implying species-level range size heritability.

We start from the observation that species–range size distributions may be considered as nested sets of two or more subdistributions, as outlined above. This suggests to us an analogy with comparative analyses, wherein species are not considered as independent data points because of
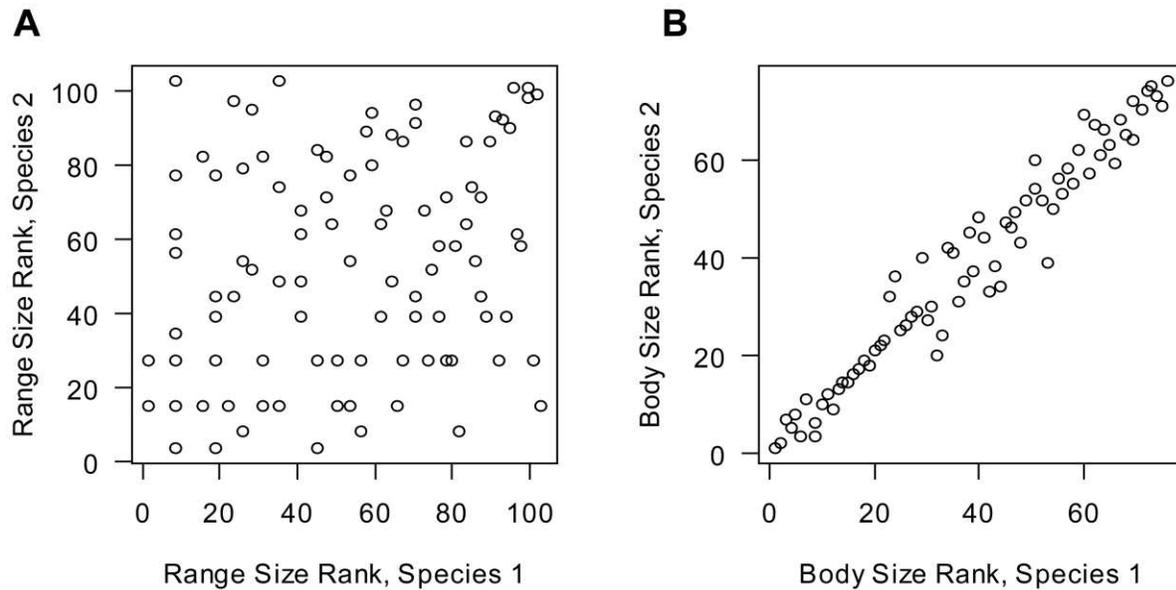
Figure 3: *A,* Ranked global breeding range sizes (see Webb and Gaston 2003 for more details) for our 103 avian sister species pairs. The significant correlation ($r_s = 0.29$, $n = 103$, $P = .0032$) is seen by Hunt et al. as adequate evidence that range sizes are heritable at the species level in this group. Our method (Webb and Gaston 2003) suggested that the ranges of sister species actually tend to be rather dissimilar, which seems reasonable given that sister species ranks differ by nearly 30 on average, with a maximum difference of 94. *B,* We contrast this with a trait that clearly is phylogenetically conserved in this assemblage, body size ($r_s = 0.98$, $n = 76$, $P < .00001$). Here, the mean difference in ranks is 3.5, with a maximum difference of 14.

their shared evolutionary history (see, e.g., Harvey and Pagel 1991). For instance, Nee et al. (1991) showed that a general negative relationship between abundance and body size in British birds arose largely because of a division between passerines (small bodied, abundant) and nonpasserines (large bodied, scarce); the sample size for this comparison is two, and there is no relationship within either group. Likewise, species pairs may not be independent of each other, particularly in analyses with very broad taxonomic scope (our analyses covered nine avian orders). As in the example of the British birds, the Late Cretaceous gastropods can also be split into phylogenetically distinct groups (on the basis of larval development mode); and furthermore, these groups differ in range size (fig. 2*A*). Thus, species pairs may be drawn from the small range-biased nonplanktotrophs or from the larger range-biased planktotrophs, but it will be rare to observe a pair consisting of one member from each group. Under such a situation, the null distribution of correlation coefficients presented by Hunt et al. in their figure 3 will not be appropriate. Rather, one should retain the major subdivision of the data set when randomizing range size pairs. To illustrate this effect, we created random pairs of ranges from each of the subdistributions shown in figure 2*A* and calculated the overall correlation (across 49 species pairs)

as well as the correlations within 24 planktotroph pairs and 25 nonplanktotroph pairs. This procedure was repeated 10,000 times; typical iterations are shown in figure 2*B* and 2*C*. Over all pairs, the mean ($\pm$SD) correlation was 0.22 ± 0.117, with a mean rank correlation of 0.23 ± 0.112. These positive correlations occurred despite the lack of any relationship within the planktotroph (mean $r = 0.00 \pm 0.208$, mean $r_s = 0.00 \pm 0.209$) or the nonplanktotroph pairs (mean $r = 0.00 \pm 0.206$, mean $r_s = 0.00 \pm 0.206$). The correct interpretation of this result is that larval mode (in this example) and range size are associated, but given the lack of a relationship within either larval mode, we would not consider this to be evidence of heritability. This conclusion is supported by an analysis of the asymmetry in range sizes of these pairs (fig. 2*D*; actual asymmetry exceeded expected asymmetry in a mean of 35.2 ± 2.80 out of 49 pairs). Note that the results quoted here do not bear direct comparison to those reported by Hunt et al. because the composition of the data sets is rather different, with little overlap in the species for which larval mode data were available from Jablonski (1986) and the species pairs analyzed by Jablonski (1987), Webb and Gaston (2003), and Hunt et al. However, we believe that the positive correlation that we document

from what might be termed constrained random pairing of ranges is noteworthy.

Discussion

In our original article (Webb and Gaston 2003), after analyzing both a large group of extant birds and an assemblage of Late Cretaceous gastropod mollusks, we found no evidence to suggest that range size could in any meaningful sense be said to be heritable at the species level. We based this conclusion on the premise that heritability of range sizes would be reflected in the range sizes of close relatives being unusually similar and the observation that in fact they tend to be highly dissimilar. We note that our requirement for significant similarity to be recognized was extremely lenient: the smaller range in a pair could average 51% the larger range yet still be considered highly similar; the fact that we still fail to find significant similarity is telling. Hunt et al. point out that the behavior of the particular metric that we used, Asy, is sensitive to the frequency distribution of the trait of interest. More specifically, when the distribution of the trait (e.g., range size) is right skewed, then closely related species will tend to be dissimilar on average (although this need not be the case: species–body size distributions also have strong right skew, yet the body sizes of species pairs are highly symmetric). We have argued that this objection implies a very restricted notion of heritability, although even when we impose it, the ranges of close relatives in neither data set that we analyzed would be classed as significantly similar.

Clearly, measuring asymmetry is not without problems. For instance, although asymmetry does co-vary with the relationship between simulated pairs of ranges (stronger correlations are reflected in lower Asy values; T. J. Webb, unpublished analysis), artificially correlated data do not always have asymmetry significantly lower than expected. We therefore suggest that our measure of asymmetry be used with some caution, although we maintain that it provides useful information, whether in an absolute sense (e.g., bird ranges have a mean asymmetry of 0.55) or as a relative measure to be entered into further analysis of correlates of asymmetry. Hunt et al. advocate the use of rank correlations to assess the similarity of pairs of range sizes, but we feel that this method too has significant problems. For instance, we have shown that significant rank correlations can easily be generated with a single realistic constraint to the pairing of range sizes, leading to artificially inflated estimates of heritability. Even if we ignore all statistical issues, however, we maintain that the reality of the observed patterns is better reflected in the observations that one species of a pair of avian sisters will have a range size that is on average only 45% that of its sister, or that in nearly a quarter (23%) of fossil gastropod

ancestor-descendant pairs, the smaller of the two range sizes is <10% the size of the larger, than in heritability values estimated from rank correlations. Indeed, our initial use of the Asy statistic was motivated by the high heritability values attributed to what is clearly a highly phylogenetically variable trait.

It should also be noted that the calculated asymmetries in range sizes are likely to be underestimates. For instance, the very crude scale of our range size estimates (the resolution of the grid is 10° longitude) undoubtedly hides much greater dissimilarity in the birds, and geographical scale may also play a role in the mollusk data. Our data for birds covered global distributions, whereas the mollusk data are from a single province. This means that, for instance, species pairs consisting of two widely distributed species at the provincial scale may in fact consist of species with much more dissimilar ranges at the global scale. Hunt et al. counter in their appendix B (in the online edition of the *American Naturalist*) that there is a positive correlation between the total and within-province ranges of present-day mollusks, and so within-province range size should be a reasonable surrogate of total range size. This is based on results reported by Jablonski and Valentine (1990) showing a positive correlation between within-province and outside-province range size in a group of mollusks. However, the correlations, while clearly significant, are rather low ($r_s = 0.29$, $n = 212$); this certainly does not preclude a situation where, for example, two species that are widespread within the province (and hence have very similar ranges at this scale) may have much less similar ranges at the global scale. In fact, this is exactly what is seen in the data set that Jablonski and Valentine analyze: 70 of the species in this data set have the (identical) maximum within-province range, but the extra-provincial ranges of these species vary by a factor of over 300 (data from Jablonski and Valentine 1990). A similar argument would apply to the unpublished results reported by Hunt et al. in appendix B—most of the U.S. Coastal Plain species occurring in Mexico may well be widespread in the U.S. fauna, but this does not mean that all widespread U.S. species also occur in Mexico.

Evidence for range size heritability would have important implications for ecology, evolution, and biogeography. For instance, because closely related species tend to be biologically very similar, if their range sizes were also similar, this would suggest a role for biology in the determination of range size. We agree with Hunt et al. that more studies are needed in this area and that modern phylogenetic methods may provide a more robust method to estimate the phylogenetic signal in traits such as range size. A good example is the method described by Freckleton et al. (2002; see also Pagel 1999). We suspect that range size is unlikely to commonly show a strong phy-

logenetic signal using such a method. This is certainly true for birds at a regional scale (Great Britain; T. J. Webb, unpublished data), and even in cases where complete phylogenetic independence of range sizes is rejected, the signal appears to be weak (Jones et al., forthcoming; see also examples in table 1 of Freckleton et al. 2002). Results obtained using other methods (e.g., partitioning of variance between taxonomic levels) in groups of mollusks (Pfenninger 2004), birds (Gaston and Blackburn 1997; Blackburn et al. 1998; Gaston 1998; Webb et al. 2001), mammals (Arita 1993; Brown 1995; Diniz-Filho and Tôrres 2002), plants (Qian and Ricklefs 2004), and other taxa (Gaston 1998) agree that the majority of variation in range size remains unexplained by phylogeny. Of course, none of these phylogenetic effects is entirely analogous to heritability as used here. Nevertheless, it is difficult to see why the range sizes of species pairs should be consistently more similar to each other than expected by chance if this were not due to some inherited characteristic, which should therefore be traceable through the phylogeny and observable as a significant phylogenetic effect. In other words, we take these findings of a lack of phylogenetic signal in range size to imply a general lack of range size heritability. Consideration of evolutionary processes suggests reasons for why this should be so: models of allopatric speciation will almost always lead to asymmetrical range sizes of daughter species (Gaston and Chown 1999), and there is little reason to expect the subsequent evolution of allopatric species pairs in different biotic and abiotic environments to mirror each other (Ricklefs and Latham 1992).

The significant (and rather high) positive rank correlations reported by Hunt et al. appear to run counter to this general finding that variation in range size is not explained by phylogeny (i.e., is not heritable). However, we have developed here our initial, rather vague objection to the use of rank correlations—namely, that positive relationships result from a combination of skew and outliers in the data—to propose a mechanism that may explain much of the relationship by analogy to other comparative studies. By recognizing that cross-species analyses of broad taxonomic scope may often include phylogenetically distinct groups of species with differing species–range size distributions, we have shown that simply constraining species pairs to be drawn from the same subdistribution of ranges can result in high positive correlations across all species but not between species in the same subgroup. Of course, this will remain a hypothesis until confronted with real data; however, we believe that, despite our rather incomplete data, the plots of ranked and raw data shown in figure 2*B* and 2*C* bear a tantalizing resemblance to plots obtained from real pairs of range sizes (e.g., fig. 3*A*; Jablonski 1987, fig. 1*C*, 1*D*; Webb and Gaston 2003, fig. 2*B*;

Hunt et al. 2005, fig. 4). We therefore propose that although range sizes show very little phylogenetic pattern and are not heritable at the species level in any kind of strict sense, certain phylogenetically conserved individual-level traits bias clades toward smaller or larger range sizes, such that the overall species–range size distribution is actually composed of different individual distributions with different means and degrees of skew. (Alternatively, sampling issues involving which species from different groups are included in the "overall" species–range size distribution may lead to similar biases.) At some level this is clearly true—major taxa differ in their average range sizes (Brooks et al. 2001), so that a species–range size distribution could be plotted for birds and mollusks combined, for example, that would consist of separate bird and mollusk distributions with different parameters. We suggest that one reason why the apparent heritability of range sizes in gastropods is higher than that in birds is the existence of an individual-level trait (developmental mode) in gastropods that apparently influences range size (Jablonski 1986). Note that we are not claiming a definitive role for developmental mode in the observed patterns in the gastropods, just using it as an apparently plausible example to illustrate our point, based on our reading of the relationship between larval dispersal and range size in these species. Any such traits in birds (which may include, e.g., patterns of habitat use) are likely to be less evident, hence leading to weaker patterns. Vermeij (1996) further develops this objection to species-level heritability of range sizes (namely, that patterns emerge "as a species-level manifestation of traits that are inherited by individual organisms" [p. 370]).

In conclusion, we stand by our assertion that very closely related species can have very different geographic range sizes, in clear contrast to phylogenetically constrained traits such as body size (fig. 3). Our measure of range size asymmetry clearly captures this fact, whereas Hunt et al.'s study reveals little of interest with respect to large-scale ecological or evolutionary patterns. We suspect that their results may be due to treating two or more distinct groups of species as homogeneous; however, even if their statistical techniques are accepted, most of the variability in range sizes remains unexplained by phylogeny, and range size therefore cannot be considered to be a strongly heritable trait. We would certainly be uncomfortable making any prediction about the range size of a species based on knowledge of the range sizes of its relatives, other than the vague statement that, if a species is widely distributed, its closest relative probably is not. We feel that a situation in which range size is reasonably independent of phylogeny (due to historical and geographical contingencies; see, e.g., Taylor and Gotelli 1994) but the maximum range size that a species can attain is potentially constrained by interacting features of its biology

(heritable at the individual level) is a more plausible explanation of the observed patterns than one requiring heritability of range size as a species-level trait.

Acknowledgments

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