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Geographic range size and evolutionary age in birds

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Together with patterns of speciation and extinction, post-speciation transformations in the range sizes of individual species determine the form of contemporary species–range-size distributions. However, the methodological problems associated with tracking the dynamics of a species' range size over evolutionary time have precluded direct study of such range-size transformations, although indirect evidence has led to several models being proposed describing the form that they might take. Here, we use independently derived molecular data to estimate ages of species in six monophyletic groups of birds, and examine the relationship between species age and global geographic range size. We present strong evidence that avian range sizes are not static over evolutionary time. In addition, it seems that, with the regular exception of certain taxa (for example island endemics and some threatened species), range-size transformations are non-random in birds. In general, range sizes appear to expand relatively rapidly post speciation; subsequently, and perhaps more gradually, they then decline as species age. We discuss these results with reference to the various models of range-size dynamics that have been proposed.

Keywords: geographic range size; evolutionary age; range-size transformations; birds

1. INTRODUCTION

The majority of species are rare. This observation is clearly illustrated by the fact that the frequency distribution of geographic range sizes (the species–range-size distribution) for a taxonomic group tends to have a very strong right skew (e.g. Gaston 1994, 1996, 1998; Gaston & Chown 1999). On a global scale, such distributions must be a product of three processes: speciation, extinction and evolution of the range sizes of individual species between speciation and extinction (Price *et al.* 1997; Barraclough *et al.* 1998; Gaston 1998). Speciation adds range sizes to the species–range-size distribution and its effects upon the distribution will depend upon the probability that species with different range sizes will speciate and the way in which the ancestral geographic range is partitioned between the two daughter species. Extinction removes range sizes from the distribution and its effects will depend upon the probability of species with different range sizes going extinct. Post-speciation transformations in the geographic range sizes of individual species will also influence the form of contemporary species–range-size distributions. Here, the effects will depend on the form that the transformations take, which in turn will be determined by the relative inputs of a number of environmental, ecological and evolutionary factors (Miller 1997).

Despite their undoubted importance, the study of range-size transformations is plagued by methodological problems and there is no generally accepted model for the long-term temporal dynamics of species' geographic range sizes (Gaston 1996). In order to plot the course of a species' range size over time, we would ideally need information on its range size from its origination at speciation until its eventual demise at extinction (Gaston & Kunin 1997). However, because species with restricted range sizes are less likely to be preserved or discovered as fossils than more abundant species (McKinney 1997), it follows

that any period in a species' life span during which it occurred in a restricted area is also unlikely to be recorded. Thus, although the fossil record may reliably record the maximum distributional extent of a species over its entire duration, it is unlikely to provide sufficiently detailed information on the dynamics of its range size at a finer temporal scale. Despite such problems, consideration of the limited evidence available has resulted in several models being proposed to describe the form that range-size transformations may take (see Gaston 1998; Gaston & Blackburn 1997; Gaston & Kunin 1997; Gaston & Chown 1999). For example, observing that the range sizes of molluscs arising in the two million years (Myr) before the end-Cretaceous mass extinction (and whose geological durations were truncated by this event) were indistinguishable from the range sizes of molluscs arising in the previous 14 Myr, Jablonski (1987) inferred that a species' geographic range size is determined early in its history and remains more or less constant throughout its existence. This 'stasis' model allows for major fluctuations in a species' range size during origination and extinction, provided that these periods of flux are short relative to the geological durations of species; once range sizes have reached their stasis level, range-size transformations will have a minimal effect on the species–range-size distribution. Alternatively, geographic range sizes may increase over time (an 'age and area' model; Willis 1922); this period of increase would presumably culminate in a rapid decline to extinction or disappearance through cladogenesis (Gaston & Chown 1999). Some evidence of a positive correlation between the 'age' of individual species (defined as the number of nodes separating a species from the root of the cladogram) and their geographic range size is presented by Taylor & Gotelli (1994); Miller (1997) documents an increase in the overall range sizes of fossil marine genera in the Ordovician, although it is uncertain whether this represents an increase in the range of individual species or increased species richness within genera. Alternatively,

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range sizes may initially expand post-speciation, before reaching a maximum extent and then declining towards extinction. This is similar to the concept of a 'taxon cycle' (Wilson 1961; Ricklefs & Cox 1972); supporting evidence includes the fact that among West Indian passerine birds, putatively older taxa tend to have smaller ranges than their younger relatives (Ricklefs & Cox 1978; Ricklefs & Bermingham 1999). The relative amount of time spent in phases of increase and decline, and the duration of the period of maximal range size, will influence the extent to which this model will be distinguishable from the previous models. Finally, range sizes may change in an idiosyncratic manner post-speciation.

Determining which, if any, of these models is operating is fundamental to understanding species–range–size distributions. In addition, if range sizes do change considerably post-speciation, then in many circumstances this may have serious repercussions for any reconstructions of past biogeographic events that are based on the modern distributions of species (Chesser & Zink 1994; Barraclough *et al.* 1998; Gaston 1998; Voelker 1999). One potentially fruitful method of pursuing the study of range-size transformations may be to consider interspecific variation in range sizes of contemporary species as representative of an intraspecific relationship (Gaston 1998), which assumes that changes will be consistent enough between lineages for them to have a general biological meaning and to become apparent as a statistical effect (Ricklefs & Bermingham 1999). We adopt this approach and examine the relationship between global geographic range size and species age in several groups of birds. The key to this approach is to be able to estimate species age (Ricklefs & Bermingham 1999); we estimate the ages of extant species from molecular phylogenies. The quantity and quality of phylogenetic information available for birds is one of the reasons why they are an ideal group for the study of range-size transformations. In addition, it is easy to envisage the range sizes of highly mobile taxa such as birds changing extensively over time as ecological and environmental conditions vary (Chesser & Zink 1994; Price *et al.* 1997). Finally, estimates of global distribution (at least in broad terms) are available for most avian species.

It is unlikely that this method will allow any firm conclusions to be drawn as to precisely which of the above models is operating in any one case. For example, a pure stasis model, even if post-speciation increase and pre-extinction decline in range size were instantaneous, could only be distinguished from a random model if each species within a group attained an identical or very similar range size, which is certainly not the case. However, assuming that range-size transformations within groups are broadly both qualitatively and quantitatively similar, then general patterns of post-speciation range-size expansion or contraction may become apparent (Webb *et al.* 2000), and thus increase understanding of the distribution of range sizes among contemporary taxa.

2. METHODS

(a) *Data and analysis*

For reasons outlined below, we consider separately groups of closely related species (e.g. families or genera). We use only

phylogenies that include all or nearly all of the extant species in a monophyletic group: Old World *Acrocephalus* and *Hippolais* reed warblers (27 out of 33 species; Helbig & Seibold 1999); New World *Dendroica* wood warblers (24 out of 27 species; Lovette & Bermingham 1999); albatrosses (all 14 species; Nunn *et al.* 1996); gannets and boobies (all nine species; Friesen & Anderson 1997); New World *Icterus* orioles (all 25 species; Omland *et al.* 1999); and storks (16 out of 19 species; Slikas 1997). Published distribution maps were obtained for all species included in these phylogenies except four Far Eastern species of *Acrocephalus* warbler (Harrison 1985; Cramp 1992; Del Hoyo *et al.* 1992; Curson *et al.* 1994; Urban *et al.* 1997; Jaramillo & Burke 1999); these were converted to estimates of global geographic range size by transferring them onto an equal-area WORLDMAP grid (Williams 1996). The grid employed here has squares of 10° longitude, each with an area of ca. 611 000 km². For most groups, the overall range size (breeding and non-breeding ranges) was used. However, for the albatrosses it was felt that breeding range (islands on which breeding occurs) might provide a more realistic measure of the area occupied by each species as a whole. The coarse scale of our range-size estimates means that such measures of breeding range size will encompass short-range foraging trips but not the extensive oceanic wanderings of individual birds, which would inflate estimates of overall range size. For this group then, we consider separately breeding and overall ranges. Plots of global geographic range size (log₁₀ transformed) against species age were produced for each group, and any emergent patterns were analysed using linear or quadratic regressions as appropriate.

(b) *Estimating taxon age from molecular phylogenies*

Data on pairwise genetic divergences between species obtained from published molecular phylogenies were converted to approximate times since divergence (figure 1a). This analysis assumes that genetic divergence is proportional to time, a contentious issue (Klicka & Zink 1997) with rates of molecular evolution being influenced by such factors as body size, generation time and metabolic rate (Martin & Palumbi 1993). Such effects should be minimal if only groups of closely related species are considered (Klicka & Zink 1997; Fleischer *et al.* 1998; Voelker 1999), although this will not correct for other potential sources of rate heterogeneity, such as population history (e.g. frequency of bottlenecks: Klicka & Zink 1997; Gaggiotti & Excoffier 2000). Despite the problems associated with the idea of a molecular clock, it has been widely employed (albeit with considerable caution) in the reconstruction of past biogeographic events in avian speciation (e.g. Zink *et al.* 1991, 1999; Bermingham *et al.* 1992; Randi 1996; Seibold & Helbig 1996; Wink *et al.* 1996; Klicka & Zink 1997; Bloomer & Crowe 1998; Cicero & Johnson 1998; Johnson & Sorenson 1998; Pasquet 1998; Garcia-Moreno *et al.* 1999; Lovette & Bermingham 1999; Lovette *et al.* 1999; Ricklefs & Bermingham 1999; Sorenson *et al.* 1999). All of these studies have used the consensus rate of 2% divergence of mitochondrial DNA per Myr, estimated for non-passerine (geese; Shields & Wilson 1987) and passerine (Hawaiian honeycreepers; Tarr & Fleischer 1993; Fleischer *et al.* 1998) birds; estimates for albatrosses (1.6–2.9%; Nunn *et al.* 1996) and cranes (0.7–1.7%; Krajewski & King 1996) are also close to this 2% consensus rate. We therefore employ this rate of 2% Myr⁻¹ (although we use the appropriate rates calculated by Nunn *et al.* (1996) for our analysis of the albatrosses). If another rate is operating in any one of the groups, then providing it is

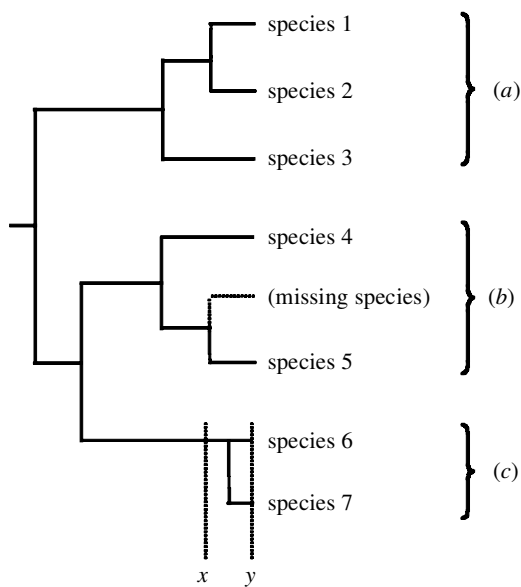


Figure 1. The method and potential problems associated with estimating species age from molecular phylogenies. (a) The ages of species 1 and 2 are estimated by converting the pairwise percentage sequence divergence between them to an estimate of time since divergence, using the consensus figure of 2% sequence divergence per million years. The age of species 3 is estimated in the same way, except that the mean of the pairwise sequence divergences between species 3 and species 1 and between species 3 and species 2 is used. (b) Species missing from the phylogeny, whether extant or extinct, may cause the ages of species included in the phylogeny to be overestimated. Here, the ages of both species 4 and species 5 are estimated by the pairwise sequence divergence between them, whereas species 5 actually originated more recently from its common ancestor with the missing species. (c) If an ancestral species persists after giving rise to a daughter species, its age will be underestimated by this method. Here, sampling species at point *y*, the ages of both species 6 and species 7 are estimated by the pairwise sequence divergence between them, whereas in fact the age of species 6 should be estimated by the average pairwise sequence divergence between it and species 4 and 5. This is illustrated by the fact that we would obtain an older age estimate for species 6 if we had sampled it earlier in its evolutionary history (point *x*).

constant across the group, it would cause only a rescaling of the age axis in our species age–range–size plots. Even if molecular evolution does not proceed in a strictly clock-like manner, degrees of divergence should at least be correlated with divergence times (Klein & Brown 1994; Voelker 1999), and so for the purposes of our analyses any qualitative patterns observed under the assumption of a molecular clock should be robust to moderate violations of this assumption.

Any species, whether extant or extinct, missing from the phylogeny may cause the ages of certain species to be overestimated (Gaston & Blackburn 1996; figure 1*b*). This effect will be exacerbated if the missing species is sister to a species included in the phylogeny that has no other close relatives; conversely, a species missing from a speciose clade resulting from a rapid burst of speciation should have only a minimal effect on age estimates. As well as seeking phylogenies including all extant members, then, we tried to avoid groups for which there is strong evidence of high rates of extinction in the recent past.

A further potential problem with our method of estimating taxon age involves uncertainty over the prevalence of ancestral

species that persist after giving rise to daughter species: modern cladists tend to downplay the importance of such speciation events, whereas palaeontologists are more comfortable with it (Gaston & Chown 1999). If they do occur, these events may lead to an underestimation of the age of the persisting ancestor (figure 1*c*). The effect of such speciation events on our analyses will depend on which of the models of range–size transformations is operating and at what stage in its life span a species is most likely to give rise to a daughter species. For example, if the ranges of widespread species fragment over time, any isolated population that persists and diverges sufficiently from its ancestor will remove evidence of range sizes declining as a species ages.

(c) Excluded taxa

There are two groups of taxa that are expected regularly to deviate from any emergent relationship between species age and geographic range size. First, island species derived from a widespread continental relative are unlikely subsequently to recolonize the mainland, especially as island species tend to move towards more central island habitats and become more specialized in their habitat requirements as they age (Wilson 1961; Ricklefs & Cox 1978; Ricklefs & Bermingham 1999). This will therefore limit the opportunity for range expansion among island endemics, at least at the scale of our estimates of geographic range size. The situation in the albatrosses may be somewhat different because these birds evidently have the dispersal capabilities to increase their range sizes even if they have evolved on isolated oceanic islands (the wandering albatross *Diomedea exulans*, for example, breeds on several such islands; Harrison 1985). In this group only, then, there was no *a priori* exclusion from formal statistical analysis of species endemic to a single island or island group.

The second group of species expected to deviate from any general relationship between species age and geographic range size includes those species that have suffered recent declines in range size due to anthropogenic factors. We assume that all species whose historical range has been reduced to such a degree that the number of 10° longitude squares occupied has also declined will be listed as globally threatened. We therefore identified all species in the studied groups listed as globally threatened by Collar *et al.* (1994), and by examining the justification given by Collar *et al.* for inclusion on the list we determined which of these species historically occupied more grid squares than they do today. All such species were excluded from formal statistical analysis.

3. RESULTS

(a) Old World *Acrocephalus* and *Hippolais reed warblers*

In this group there is evidence of a decline in range sizes as species age (figure 2*a*). The one conspicuous outlying point is the Seychelles warbler *Acrocephalus sechellensis*, which, being endemic to the Seychelles, is excluded from analysis. The other *Acrocephalus* species included in this data set that may warrant exclusion under the criteria outlined in §2(c) is the aquatic warbler *Acrocephalus paludicola*. The range of this species ‘... has contracted sharply eastwards since the turn of the [20th] century’ (Collar *et al.* 1994, p. 167); although it is not a conspicuous outlier, its range size is smaller than those of other species of a similar age. Excluding these two

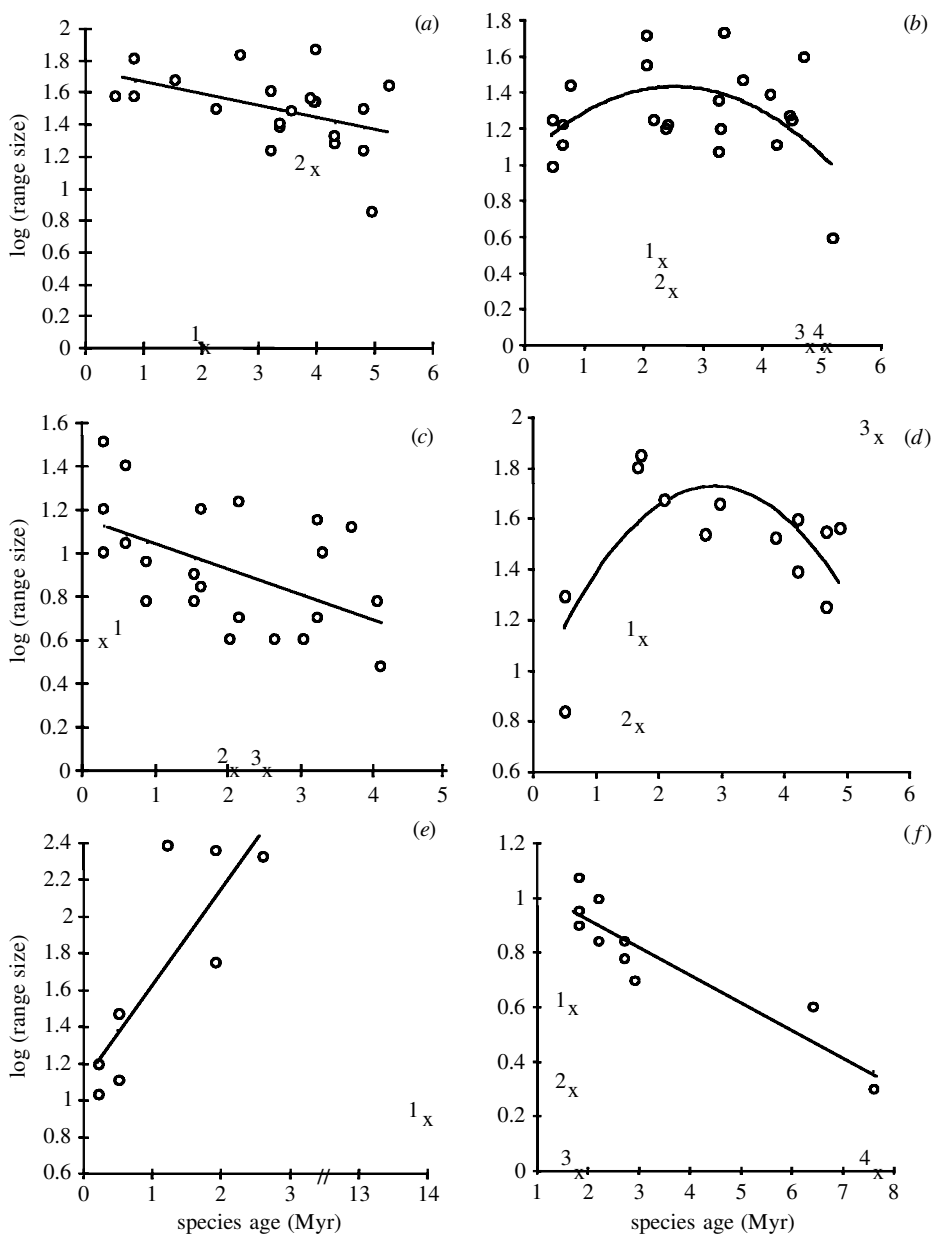


Figure 2. Plots of global geographic range size against species age (Myr). Crosses represent species excluded from regression analysis (see §3 for details). (a) Old World *Acrocephalus* and *Hippolais* reed warblers; 1, Seychelles warbler *Acrocephalus sechellensis*, 2, aquatic warbler *Acrocephalus paludicola*. (b) New World *Dendroica* wood warblers; 1, olive-capped warbler *Dendroica pityophila*, 2, Adelaide's warbler *Dendroica adelaidae*, 3, whistling warbler *Catharopeza bishopi* and arrow-headed warbler *Dendroica pharetra*, 4, plumbeous warbler *Dendroica plumbea*. (c) New World *Icterus* orioles; 1, black-backed oriole *Icterus abeillei*, 2, St Lucia, Martinique and Montserrat orioles *Icterus laudabilis*, *Icterus bonana* and *Icterus oberi*, 3, Jamaican oriole *Icterus leucopteryx*. (d) Storks; 1, oriental white stork *Ciconia boyciana*, 2, Storm's stork *Ciconia stormi*, 3, black stork *Ciconia nigra*. (e) Gannets and boobies; 1, Abbott's booby *Papasula abbotti*. (f) Albatrosses; 1, Buller's albatross *Diomedea bulleri*, 2, shy albatross *Diomedea cauta*, 3, Amsterdam albatross *Diomedea amsterdamensis*, 4, short-tailed albatross *Diomedea albatrus*.

taxa, the decline in range size with age in this group is significant ($b = -0.075 \pm 0.034$ (s.e.m.), $r^2 = 0.202$, d.f. = 20, $p = 0.041$).

(b) New World *Dendroica* wood warblers

In the *Dendroica* warblers (figure 2b) there is a general curvilinear relationship (increase followed by decrease) between species age and geographic range size, with two conspicuous outliers, the West Indian endemic olive-capped warbler and Adelaide's warbler (*Dendroica pityophila* and *Dendroica adelaidae*). Excluding these species, along with the other West Indian endemics *Dendroica*

pharetra, *Dendroica plumbea* and *Catharopeza bishopi*, quadratic regression provides a significantly better fit to the data than does linear regression (F -test, $F_{1,18} = 5.48$, $p < 0.05$; Zar 1996, p. 448), explaining 23.5% of the variation in range sizes observed in this group ($b_1 = 0.313 \pm 0.142$, $b_2 = -0.062 \pm 0.027$, $r^2 = 0.235$, d.f. = 18, $p = 0.089$; linear regression, $b = -0.009 \pm 0.039$, $r^2 = 0.003$, d.f. = 19, $p = 0.824$).

(c) *Icterus* orioles

As observed in the Old World reed warblers, in the New World *Icterus* orioles (figure 2c) there seems to be a

general trend of decreasing range sizes as species age. The principal outliers here are West Indian endemics. Excluding these island outliers, the linear negative relationship between species age and geographic range size is significant ($b = -0.092 \pm 0.042$, $r^2 = 0.177$, d.f. = 23, $p = 0.041$). The other conspicuous outlying point in this data set is the black-backed oriole *Icterus abeillei*. This species is a Mexican endemic, which until recently was considered conspecific with the North American Bullock's and Baltimore orioles (*Icterus bullockii* and *Icterus galbula*; Jaramillo & Burke 1999). It may therefore represent the position of recently differentiated oriole species, which then tend to rapidly increase their range sizes before the gradual decline. Excluding this species improves the fit of the regression line ($b = -0.115 \pm 0.041$, $r^2 = 0.269$, d.f. = 22, $p = 0.011$; this line is shown in figure 2c), although it does not significantly change its slope ($t = 0.389$, d.f. = 43, $p > 0.5$).

(d) Storks (*Ciconiidae*)

Among the storks (figure 2d) there appears to be a general trend of increasing range sizes post-speciation with a subsequent decline as species age. Three species fall conspicuously outside this general relationship. The oriental white stork *Ciconia boyciana* is excluded from analysis because its current range covers fewer grid squares than was historically the case (Collar *et al.* 1994). Storm's stork *Ciconia stormi* is another relatively young species with a restricted range, but here there is no evidence of a substantial recent decline in range size (Collar *et al.* 1994). This species, for whatever reason, seems to be analogous to an island species: unable to expand its range post-speciation, it seems likely to go extinct at a relatively young age. Finally, the black stork *Ciconia nigra* appears to have a very large range despite its old age. The phylogenetic position of this species with respect to its congeners is rather uncertain (Slikas 1997), although in each phylogenetic hypothesis illustrated by Slikas (1997) *C. nigra* is the most basal member of the *Ciconia* clade, so increased phylogenetic resolution is unlikely to alter significantly the estimate of its age. However, although it meets neither of the criteria for exclusion, it seems to occur at low densities throughout its range, with a world population of perhaps a few thousand pairs, compared to the 150 000 or so pairs of European white storks *C. ciconia* occupying a similar global range size (Del Hoyo *et al.* 1992). As it prefers undisturbed open woodland habitat (Del Hoyo *et al.* 1992), it seems likely that although the overall extent of *C. nigra*'s occurrence may not have declined sufficiently to be detectable by our crude measure of range size, the range size so measured will in fact include extensive areas of habitat no longer occupied by this species. Excluding the three outlying species, over 50% of the observed variation in range sizes amongst storks is explained by quadratic regression analysis of range size on age ($b_1 = 0.557 \pm 0.175$, $b_2 = -0.097 \pm 0.031$, $r^2 = 0.503$, d.f. = 12, $p = 0.030$), a significant improvement on the linear model ($F_{1,10} = 9.41$, $p < 0.05$).

(e) Gannets and boobies (*Sulidae*)

In the gannets and boobies (figure 2e) there is a pattern among non-threatened species of range expansion

with increasing species age. This increase is significant ($b = 0.532 \pm 0.146$, $r^2 = 0.689$, d.f. = 7, $p = 0.011$) and relatively rapid, with maximum range sizes reached by an age of about 2 Myr. Unfortunately, there are no species of intermediate age in this group, and the only old species (Abbott's booby *Papasula abbotti*) qualifies for exclusion from analysis because it has been extirpated from at least two widely separated breeding localities during the last three centuries (Collar *et al.* 1994). It is therefore impossible to infer what happens to Sulids as they pass into middle and old age.

(f) Albatrosses (*Diomedeidae*)

In the albatrosses (figure 2f), the pattern seems to be one of rapid increase in breeding range size followed by a gradual decrease as species age: the two youngest species have relatively restricted range sizes, but maximum range sizes are observed in species only marginally older, with a significant decline in range sizes thereafter ($b = -0.100 \pm 0.016$, $r^2 = 0.836$, d.f. = 9, $p = 0.0002$). For this analysis, two species in addition to the two youngest species were omitted. The oldest species in the group, the threatened short-tailed albatross *Diomedea albatrus*, is excluded because it no longer breeds on islands in several grid squares where it was previously found; these extinctions have been primarily due to exploitation for feathers (Collar *et al.* 1994). The Amsterdam albatross *Diomedea amsterdamensis*, is endemic to a single island, but as stated in §2(c) this may not be an appropriate criterion for the exclusion of albatross species due to their high dispersal capabilities. However, particularly when humans enter the equation, it may often be the fate of newly differentiated species to remain endemic to a single island and risk early extinction, which unfortunately seems likely in *D. amsterdamensis* (Collar *et al.* 1994). It is also worth noting that the specific status of this albatross is not universally accepted and it may be better considered a race of the wandering albatross *Diomedea exulans* (Del Hoyo *et al.* 1992). Overall range size also declines significantly with age in this group ($b = -0.138 \pm 0.049$, $r^2 = 0.445$, d.f. = 11, $p = 0.018$); only *D. albatrus* and *D. amsterdamensis* were excluded from this analysis, the two youngest species having already achieved large overall range sizes.

4. DISCUSSION

As expected, given the theoretical and methodological problems outlined in §1, the relationship between species age and geographic range size does not appear to be a simple one. Within taxa, range sizes are clearly not adhering precisely to any one of the models outlined in §1, and different models may be operating in different taxonomic groups. However, despite the inevitable noise introduced into the relationships by the rather crude estimates of both species age and geographic range size, a random model can be rejected in all of the data sets employed, which strongly suggests that post-speciation range-size transformations themselves do not occur entirely at random. In the *Acrocephalus* and *Hippolais* warblers, the *Icterus* orioles and the albatrosses there is a general trend of decreasing range sizes with increasing species age, over the majority of ages considered. In the

New World *Dendroica* warblers and the storks the pattern is more curvilinear, with the decline in range sizes following a more gradual increase. The gannets and boobies provide the only evidence that a simple 'age and area' model (Willis 1922) may be operating, with a trend for increasing range sizes as species age, but the lack of middle- to old-aged species and the position of Abbott's booby suggest that in this group too range sizes may decline as species pass into middle and old age.

Although the 'age and area' model (Willis 1922) implies that species range sizes increase gradually over time, both Jablonski's (1987) stasis model and the taxon cycle concept (Wilson 1961; Ricklefs & Cox 1972, 1978) predict that post-speciation, species' ranges expand rapidly to their maximum extents (over less than 0.5 Myr in the Lesser Antillean avifauna; Ricklefs & Bermingham 1999). Our data tend to support this second prediction (figure 2): in all groups, maximum range sizes are reached by an age of about 2 Myr. Further evidence for this pattern might be provided if there were more very young species in our data sets; if these tended to have small ranges, this would suggest that the rapid expansion in range sizes does follow immediately post-speciation. There are two possible reasons why such species might be lacking. First, it might be the usual fate of newly formed species with very small range sizes (for instance peripheral isolates) to go extinct more or less straight away, with only an exceptional few persisting long enough to embark upon the phase of expansion (Chesser & Zink 1994). Alternatively, it might be that such species are 'hidden' from our analyses, as they are currently considered as subspecific taxa of older and more widespread species. As a preliminary attempt to investigate this second possibility, we plotted global geographic range size against taxon age for every *Acrocephalus* and *Hippolais* taxon (subspecies as well as monotypic full species) included in the phylogeny of Helbig & Seibold (1999) for which distribution maps were available ($n = 27$; figure 3). It can be seen that whereas the relationship for full species only was significantly negative (figure 2a), here (excluding species as before) a positive relationship results ($b = 0.079 \pm 0.040$, $r^2 = 0.138$, d.f. = 26, $p = 0.056$). Because including subspecies means that species with subspecies will undergo a reduction in both taxon age and range size (the range sizes of subspecies rarely overlapping to any degree), this result suggests that differentiation occurs in fairly young, widespread taxa: it is young to middle-aged taxa whose ages and ranges have decreased to cause the positive relationship, whereas the position of older taxa in figure 3 is similar to that in figure 2a. Indeed, the increase in range size with age in figure 3 seems to slow down and even reverse at ages over about 4 Myr (although this trend is not strong enough to favour quadratic over linear regression, $F_{1,24} = 1.367$, $p > 0.25$). It is possible that a curvilinear relationship between age and range size, such as that observed in the *Dendroica* warblers, may result from confusion over the specific status of taxa included in the study.

Following the initial expansion, the stasis model then predicts that species' range sizes remain at this maximum extent until an equally rapid decline prior to extinction, whereas under a taxon-cycle model the decline begins earlier but is much more gradual, as populations across

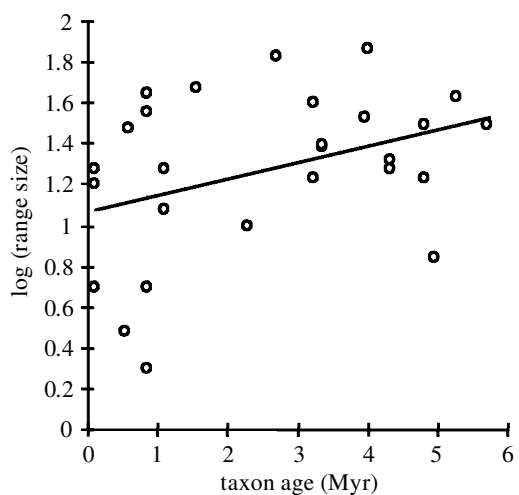


Figure 3. Global geographic range size plotted against taxon age for 27 out of 34 subspecies and monotypic full species of *Acrocephalus* and *Hippolais* Old World reed warblers recognized by Helbig & Seibold (1999). Species were excluded as in figure 2a and are not shown. See §4 for details of regression.

the range differentiate and some go extinct until the species persists only as an endemic with a very restricted range (Wilson 1961; Ricklefs & Cox 1972, 1978). Our data appear to favour this second scenario (see the comparatively long periods of range-size decline in all groups except the gannets and boobies in figure 2), although it is possible that a stasis model could generate such a pattern if species within a group had differing life spans.

As outlined in §2(c), two groups of taxa regularly deviated from the general patterns documented in figure 2. First, island endemics evidently have tiny range sizes regardless of their age. However, such species do tend to be of middle to old age, which suggests that taxa recently colonizing islands are likely still to be considered subspecific to their continental ancestor. Older species that have differentiated to full species status on islands may be unable to recolonize the mainland, thus limiting their potential for range expansion. Of course, post-speciation changes in range sizes are likely even among island endemics, as new islands are colonized and other populations go extinct (see, for example, Ricklefs & Bermingham 1999). However, the crude scale of resolution in our range-size estimates (where, for example, the entire Lesser Antilles are contained within two grid squares) is unlikely to show such patterns.

The other conspicuous outlying points in the plots in figure 2 represent those threatened species that have suffered recent and large-scale declines in their range sizes, probably due to human activities. We discuss elsewhere the potentially dire consequences for future avian diversity of disrupting 'natural' patterns of rarity (Webb *et al.* 2000), but it is worth emphasizing the three ways in which the human factor might impact upon a general pattern of rapid expansion to maximum range sizes followed by a decline prior to extinction: first, young species may be unable to expand their ranges (e.g. the youngest storks *Mycteria cinerea* and *Mycteria leucocephala* (figure 2d) are listed in Collar *et al.* (1994) as 'vulnerable' and 'near threatened', respectively; it therefore seems

unlikely that a period of range expansion is imminent in either species); second, species of middle age may suffer marked declines (e.g. the endangered stork *C. boyciana* (figure 2d) and the vulnerable *Acrocephalus paludicola* (figure 2a)); and third, old species may be hastened towards extinction (e.g. the endangered albatross *D. albatrus* (figure 2f) and the vulnerable booby *P. abbotti* (figure 2e)). One further point is that species declines may result from fragmentation across a species' entire range, as well as from contraction into a small area of the original range (Lawton 1993); the crude measures of range size used here are more likely to identify the latter pattern of decline than the former (see the anomalous position of the black stork *C. nigra* in figure 2d).

5. CONCLUSIONS

Previous interpretations of biogeographic history have often suffered from the fact that it has been impossible to estimate the relative ages of the populations involved independently of the geographical patterns that they show (Ricklefs & Cox 1972). By employing independent, molecular-derived estimates of age, we have been able to document broad relationships between the age of individual species and their global geographic range sizes in several groups of biologically rather dissimilar birds. These relationships provide strong support for the notion that avian range sizes are dynamic and that dispersal has played a vitally important role in shaping the current species–range–size distribution (e.g. Chesser & Zink 1994; Voelker 1999; Zink *et al.* 2000), implying that caution should be used in applying the current distributions of species to processes that have taken place in the distant past (Chesser & Zink 1994; Gaston & Chown 1999). However, our data also indicate that these post-speciation range–size transformations do not occur entirely at random; rather, there is some suggestion of a general pattern of an increase in range sizes immediately post-speciation followed by a subsequent decline towards extinction. This consistency suggests that organismal phylogenies can preserve important information about the historical distributions of species (see also Zink *et al.* 2000). As more accurate information on the phylogenetic relationships between bird species becomes available, and as estimates of geographic range sizes are refined, these patterns may become clearer, but if generally true, the expectation of rarity at both ends of a species' lifetime may explain to a certain extent the highly asymmetrical form of the species–range–size distribution. This distribution is likely to become more highly skewed, as the position of threatened species in the species–age–range–size relationships provides further evidence of the disruptive effect that humans are having upon global avian biodiversity.

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