DISPERAL, VICARIANCE, AND CLOCKS: HISTORICAL BIOGEOGRAPHY AND SPECIATION IN A COSMOPOLITAN PASSERINE GENUS (ANTHUS: MOTACILLIDAE)

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Abstract.—Dispersal and vicariant hypotheses have for decades been at odds with each other, notwithstanding the fact that both are well-established natural processes with important histories in biogeographic analyses. Despite their importance, neither dispersal nor vicariant methodologies are problem-free. The now widely used molecular techniques for generating phylogenies have provided a mechanism by which both dispersal- and vicariance-driven speciation can be better tested via the application of molecular clocks; unfortunately, substantial problems can also exist in the employment of those clocks. To begin to assess the relative roles of dispersal and vicariance in the establishment of avifaunas, especially intercontinental avifaunas, I applied a test for clocklike behavior in molecular data, as well as a program that infers ancestral areas and dispersal events, to a phylogeny of a speciose, cosmopolitan avian genus (Anthus; Motacillidae). Daughter-lineages above just 25 of 40 nodes in the Anthus phylogeny are evolving in a clocklike manner and are thus dateable by a molecular clock. Dating the applicable nodes suggests that Anthus arose nearly 7 million yr ago, probably in eastern Asia, and that between 6 and 5 million yr ago, Anthus species were present in Africa, the Palearctic, and North and South America. Speciation rates have been high throughout the Pliocene and quite low during the Pleistocene; further evidence that the Pleistocene may have had little effect in generating modern species. Intercontinental movements since 5 million yr ago have been few and largely restricted to interchange between Eurasia and Africa. Species swarms on North America, Africa, and Eurasia (but not South America or Australia) are the product of multiple invasions, rather than being solely the result of within-continent speciation. Dispersal has clearly played an important role in the distribution of this group.

Key words.—Anthus, dispersal, historical biogeography, molecular clock, vicariance.

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“The null hypothesis of vicariance biogeography is not a law.”
Bremer 1992

Dispersal theories have dominated the history of biogeography (Humphries and Parenti 1986), but dispersal could accommodate any distribution, making it resilient to rejection. Therefore, dispersal theories have been regarded by some as unscientific (Rosen 1978; Nelson and Platnick 1981). Vicariance theories currently dominate biogeographic analyses, and vicariance has proven a powerful tool in identifying areas of endemism and the underlying historical events that created such areas, both at regional and continental scales.

However, testing vicariant theories may be as difficult as testing dispersal theories because two substantial problems exist with vicariant methods. First, the “test” of vicariant hypotheses has been the search for concordance in distribution patterns, as predicted by a geological event in Earth history. Topological congruence of distributions between area-cladograms of two or more lineages (e.g., sister-taxon from each lineage are physically isolated by the same geographic barrier) has often been interpreted as evidence for congruent temporal isolation (Cunningham and Collins 1994). However, given the cyclical nature of many geological and climatological processes, this interpretation can be tenuous. Although taxa have single histories, areas can have multiple histories with respect to the taxa being considered (Cracraft 1988). Thus, although several lineages may be topologically and geographically congruent, suggesting a shared history, the congruent patterns may in fact have originated at very different times; this phenomenon is known as pseudocongruence (Cunningham and Collins 1994).

Additionally, if vicariance explains a pattern, the concordance of modern-day species distributions and areas must be indicative of past vicariant events and not merely a reflection of distributions modified by dispersal. A barrier to more rigorous tests of vicariant methodology has been the inability to roughly correlate the timing of species divergences between codistributed groups and the inability to roughly correlate these divergences with the timing of vicariant events.

Second, vicariance theorists have tended to reject dispersal as a primary causal factor in the development of concordant patterns (e.g., Ball 1975; Cracraft 1986, 1991; Mayden 1988; but see Bowen and Grant 1997). However, because both dispersal and vicariance are well-established natural processes, neither explanation can be discounted a priori (Morrone and Crisci 1995). Indeed, concordant dispersal patterns can explain area congruence as easily as vicariance, especially for adjacent areas (Hedges et al. 1994).

In the rush to establish vicariant explanations as more rigorous than explanations relying on dispersal, proponents of the vicariant method have ignored several important realities. One is that similarities in intercontinental avifaunal assemblages can reasonably, and perhaps more plausibly, be explained by dispersal theories simply because many avian groups are too young to have been affected by continental drift. Equally convincing examples of assemblages (avian or not) that must have resulted from dispersal events can be found on any island of volcanic origin. Another reality is, in essence, hidden in the central tenet of vicariance theory. This central tenet requires that ancestral taxa were stable and wide-
spread (but see Zink and Hackett 1988) and that modern species distributions have resulted from speciation/fragmentation of the ancestral distribution, which was achieved via biotic “dispersion” (Cracraft 1991; Avise 1992). It should be immediately apparent that not only does this requirement allow the possibility of a reduced ancestral area (sensu Bremer 1992), but more importantly some dispersal across barriers is almost certainly required to explain the occurrence of the widespread ancestor (Ronquist 1997). Thus, if dispersal can play a role in developing intercontinental or island avifaunas and in establishing widespread taxa, then it is difficult to exclude the possibility of dispersal from any biogeographic scenario.

The advent of molecular techniques to elucidate species relationships has provided a means by which both dispersal and vicariant biogeographic hypotheses can be tested rigorously. Molecular phylogenies generate branch lengths and degrees of divergence between taxa, which should be correlated with divergence times (e.g., Bermingham et al. 1992; Brumfield and Capparella 1996; Bowen and Grant 1997; Klicka and Zink 1997); these times can be related to potential vicariant events. Depending on the relative ages of species divergence and vicariant events, assessments can be made of whether a dispersal hypothesis (barrier older than species divergence) or vicariant hypothesis (barrier age and species divergence similar) better explains the observed distributions. Indeed, molecular data have been used to test explicit vicariant and dispersal models (e.g., Bermingham et al. 1992; Klein and Brown 1994; Patton et al. 1994; Brumfield and Capparella 1996; Bowen and Grant 1997), and dispersal is often implicated as having been a key factor in biogeographic history. Molecular data have also been used to challenge the archetypal vicariant model, speciation in Pleistocene refugia (Haffer 1969, 1974; Mayr and O’Hara 1986) and in explaining modern distributions for a number of sister-taxon erroneously thought to have diverged during the Pleistocene Epoch (e.g., Zink and Slowinski 1995; Klicka and Zink 1997).

Despite the power they bring to biogeographic analyses, molecular methods are not without limitations because rates of molecular evolution can vary within and between lineages, and this variation invalidates the clock used to date events. Although taxa with a good fossil record can be used to calibrate a specific clock (e.g., Brown et al. 1982; Martin et al. 1992; Krajewski and King 1996; Friesen and Anderson 1997), the great majority of taxa lack a fossil record suitable for calibrating clocks and thus investigators must use a rate calibrated for other groups, a problematic (Martin et al. 1992) but unavoidable approach. Many studies have implicitly assumed rate homogeneity across lineages and calculated divergence times based on some measure of difference between those lineages. This uncritical approach is inescapable under certain conditions (i.e., parsimony analysis), but relative rate tests that use branch length information (e.g., from neighbor-joining and maximum-likelihood algorithms) have been available for at least two decades (e.g., Sarich and Wilson 1973).

The avian passerine genus Anthus (pipits; Motacillidae) is a good group with which to investigate the relative roles of dispersal and vicariance in the development of avifaunas and, in particular, intercontinental avifaunas. Anthus has a cosmopolitan distribution and currently includes about 40 species (Clancey 1990; Sibley and Monroe 1990), although recent work has suggested that there are at least several more (Zink et al. 1995; Voelker 1999). Distributions range from single continent endemics (about 30) to species that breed on multiple continents (six). Three species are confined to islands, and a few breed primarily on one continent and winter on another. Collectively, Anthus species breed in a wide variety of habitats, including tundra, grassland, and bushveld; no Anthus species breeds in tropical forest.

In assessing the relative roles of dispersal and vicariance in Anthus, I use the phylogenetic relationships determined from molecular sequence data (Voelker 1999) in conjunction with area cladograms, as well as several new methods for inferring ancestral areas and dispersal events (Bremer 1992; Ronquist 1996). I also employ a recently devised test for clocklike behavior in molecular sequence data (Takezaki et al. 1995) to determine at which nodes daughter-lineages within Anthus are evolving in a manner consistent with a molecular clock. By roughly dating these nodes, I am able to assess whether dispersal or vicariant events may better explain the observed distribution pattern.

METHODS

Phylogeny, Distributions, and Area Cladograms

To assess the historical biogeography of Anthus, I converted a maximum-likelihood (ML) phylogeny of the group (Voelker 1999) to area cladograms. Biogeographic analyses of individual groups are undeniably important; but to extract their full potential, these studies should facilitate broad comparisons among many such analyses, and this is best accomplished using similar areas for reconstructing area cladograms. Thus, where possible, I used areas defined by previous avian biogeographic analyses (e.g., Crowe and Crowe 1982; Cracraft 1985). For geographic regions for which I did not find previously defined areas of endemism, I defined areas based solely on Anthus breeding distributions (Ali and Ripley 1973; Flint et al. 1984; Cramp 1988; Ridgely and Tudor 1989; Clancey 1990; Sibley and Monroe 1990; Keith et al. 1992). Individual species were then scored as present or absent in each defined area.

To determine intercontinental and continent-to-island movements, the areas I used were North America, South America, Eurasia, Africa, Australia, South Georgia Island, and the Canary and Madeira Island groups (Canary Islands hereafter). To determine area relationships within continents, I refined the intercontinental-distributions cladogram to more accurately reflect within-continent distributions.

There are very few barriers to movement that can be used to convincingly divide most of the Palearctic into smaller areas. An exception is the Yenisey River, or the area between the Yenisey and the Ural Mountains, which forms an eastern or western boundary for many avian species, including some Anthus species (see Flint et al. 1984). Because of the lack of widespread (i.e., across taxa) barriers, I recognize just six areas to account for the distributions of the largely Palearctic clade (Fig. 1A) and base these mostly on distributions of Anthus (see Ali and Ripley 1973; Flint et al. 1984; Cramp
Fig. 1. Areas used to delimit Anthus distributions for (A) the Palearctic clade; dashed lines are used to indicate that these regions are not previously defined as avian centers of endemism. (B) The South American clade; in general, these areas are centers of endemism defined by Cracraft (1985). For reference, the shared Bolivian, Argentine, Chilean border is approximately at the junction of the Northern Andean, Chaco, and Chilean Andean centers. (C) The African/Eurasian clade; these regions, except the Canary Islands, were defined as major passerine avifaunal zones by Crowe and Crowe (1982).

1988): (1) western Palearctic (west of Urals/Yenisey); (2) eastern Palearctic (east of Urals/Yenisey and north of Lake Baikal); (3) eastern Asia (Lake Baikal south through Indonesia and east of the Himalayas); (4) the Himalayas; (5) Africa north of the Sahara; and (6) North America, which this clade has invaded.

For the clade composed primarily of South American species, distributions generally correspond to previously recognized areas of endemism (i.e., Peruvian arid coast center, Chaco center, Chilean Andean center, and Patagonian center; Cracraft 1985), and I use them here (Fig. 1B). I also use the Andes, from the northwestern tip of Argentina (i.e., Provincias Jujuy and Salta) northward and the eastern “lowlands,” from northeastern Argentina through Uruguay and Brazil (Fig. 1B); each of these areas as I define them is a composite of several areas of endemism (see Cracraft 1985). Finally, I include both South Georgia Island and North America to account for the remaining species in this clade.

To account for distributions of the Asian component of
the large African/Asian clade, I recognized those areas used for the Palearctic clade, plus an area from the Saudi Peninsula to the Burmese mountain barrier (Ripley and Bebber 1990) on the Indian-Burmese border. Within Africa, species distributions were based on the six sub-Saharan regions delimited by Crowe and Crowe (1982) for avian passerine taxa (Fig. 1C) plus a seventh region consisting primarily of South Africa (which combines Crowe and Crowe [1982] districts nine and ten of zone five; Fig. 1C), due to two endemic species and several disjunct populations of other species that occur there (see Clancey 1990). These African zones were also used to account for distributions of the sokokensis/brachyurus/caffer clade. Finally, I use the Canary Islands as an area.

### Biogeography, Area Relationships, and Ancestral Areas

I used dispersal-vicariance analysis (DIVA: Ronquist 1996) to reconstruct ancestral distributions on the phylogeny and the direction of dispersal events between areas. Briefly, DIVA searches for the optimal reconstruction of ancestral areas by assuming current distribution are the result of vicariant events (i.e., allopatric speciation), while recognizing that dispersal and extinction are possible (Fig. 2). By dealing explicitly with dispersal and extinction events (see Fig. 2A, B), but involving them only when vicariance fails as an explanation (i.e., minimizing occurrence, thus a parsimony criteria) in ancestral reconstructions, DIVA provides optimal solutions (as scores) that require fewer such events than do cladistic methods. An advantage of DIVA is that it does not require a posteriori explanations and/or a priori data manipulation, which can be common in other methods (Ronquist 1997). Other important benefits are that the method does not restrict widespread distributions to terminals or force ancestral distributions to consist only of single areas (Ronquist 1997). However, it should be noted that dispersals are often underestimated by DIVA because similar distributions between species will be interpreted as shared vicariant history (F. Ronquist, pers. comm.); as stated above, this does not necessarily have to be the case (Hedges et al. 1994).

When the ancestral distribution was determined by DIVA to be composed of all, or nearly all, possible areas used to define the distribution of Anthus, I used the "maxareas" option to limit the range of ancestral distributions to no more than two areas. This approach determines what the most likely ancestral distribution would be if that distribution was restricted to smaller areas (Ronquist 1996).

In addition to DIVA, I used the ancestral areas method of Bremer (1992), which provides an alternative to narrative dispersal-from-centers-of-origin scenarios. The method is cladistic, assumes no particular speciation mechanism, and relies solely on the topological information of the area cladogram. Species are replaced on a phylogeny by the presence of each area in its overall distribution. Two parsimony analyses that assume irreversibility of character states are then conducted to determine the number of gains and losses of each area. For each area, the number of gains is divided by the number of losses, and the area with the highest gain/loss value is set to a value of one (or, 100% probability of being part of the ancestral area). Values for the other areas are rescaled to provide relative probabilities for each area being part of the ancestral area for the group; areas that are basal are more likely parts of the ancestral area than are areas occurring only near terminal branches. Note that these searches look for the most basal branch above which an area is completely present or completely absent; thus, this method is not inferring an ancestral area simply by assessing the relative density of species (whereas this is the determining factor for "centers-of-origin" hypotheses).

### Molecular Clock

To test whether lineages within Anthus are evolving in a clocklike fashion, I applied the two-cluster test (Takezaki et al. 1995) to an ML topology of the genus (Voelker 1999); I previously established that, overall, Anthus species cytochrome b is not evolving in a clocklike manner (Voelker 1999). The two-cluster test generates a neighbor-joining tree (based on Tamura-Nei distance) and uses this tree to examine the hypothesis that a molecular clock is in effect along two lineages (\( b_A, b_B \)) diverging from an interior node of the tree. Briefly, the test assesses whether the difference (\( b \)) in length between left (L) and right (R) daughter-lineages at a node is significantly different from zero. CP is the confidence probability (\( 1 - P \)-value of the test), with larger values indicating increasing certainty of rejecting a molecular clock, but only CP values of 95% or greater reject a clock outright. Thus, lineages at a given node must be very different from one another to be rejected as clocklike under this test.

If a molecular clock can be inferred at a node linking two daughter-lineages, I use 2% sequence divergence per million years in applying dates. Clock values at or near 2% have been inferred from several studies of disparate avian lineages (Shields and Wilson 1987; Tarr and Fleischer 1993; Wood and Krajewski 1996; Fleischer et al. 1998). Because branch height (\( h \) in Table 1) is the mean branch length between two daughter-lineages, that value is the expected value after correcting for the assumption of 2% per million-year divergence (i.e., 1% along each lineage). I also provide node dates based on ML branch lengths, to compare whether date estimates based on these branch lengths are similar or dissimilar to those dates generated by neighbor-joining (i.e., the two-cluster test). Because the two-cluster method is computationally intensive (see Takezaki et al. 1995), I use the mean of ML branch lengths along each daughter-lineage to date clocklike nodes (at 2% per million years), and do this only for nodes at which both daughter-lineages can be traced through other clocklike nodes to terminal clocklike nodes. This is a slight improvement on the now-traditional method of using percent sequence divergence between two lineages (e.g., Klicka and Zink 1997) because it allows a qualitative assessment of whether branch lengths actually appear similar. Finally, I used percent sequence divergence (uncorrected) to provide a third time estimate at clocklike sister-species nodes.
Fig. 2. Examples of the calculations made by the dispersal-vicariance (DIVA; Ronquist 1996; A–C) and Bremer's (1992) ancestral area (D, E) methods. DIVA searches for optimal (simplest) ancestral areas by assuming that current distributions are the result of vicariance events and by assigning a cost to inferred dispersal (A) or extinction events (B). In (C), DIVA would invoke vicariance to explain the distributions of the taxa occurring only in locations A or B, with zero cost (score) for this event. Other methods would be forced to explain the distributions by inferring two extinctions (Ronquist 1997). A final score of zero means that no dispersal or extinction events were required to explain the distribution of a group. In Bremer's method, species trees are converted to area cladograms, and two parsimony analyses assuming irreversibility of characters are conducted (D, E). The first analysis assumes the ancestral area is empty and the number of gains for each area is assessed, whereas the second assumes the ancestral area is full and the number of losses of each area is assessed. Then, for each area, the number of gains is divided by the number of losses, the area with the highest gain/loss value is set to a value of one (or 100% probability of being part of the ancestral area), and the other areas are rescaled to provide relative probabilities for each area being part of the ancestral area for the group. In (D), all areas have an equal probability of having been part of an ancestral area, whereas, in (E), area A has a much higher probability (100%) of having been part of an ancestral area than do areas B (50%), C (33%), or D (33%).

RESULTS AND DISCUSSION

Molecular Clock and Dating Nodes

Despite the evidence that, overall, Anthus cytochrome b is not evolving in a clocklike manner (Voelker 1999), there are 25 of 40 nodes at which daughter-lineages are evolving in a manner consistent with a molecular clock according to the two-cluster test (Fig. 3, Table 1). Approximate dates can be inferred at each these 25 nodes. A second date (based on mean ML branch lengths) can be inferred for 13 nodes (Table 1; see Methods).

In general, dates based on ML branch length averaging are
greater than dates associated with the two-cluster test, although in most cases the differences fall within the standard error estimates of the two-cluster test (Table 1). However, note that the standard error estimates (which can themselves be dated) can cover a substantial portion of a given divergence time estimate (Table 1). Large standard error estimates suggest that attempts to unambiguously identify a specific cause of vicariant speciation may be difficult, especially when events are recent and periodic, such as Pleistocene glacial cycles. Nevertheless, these dates overwhelmingly support the conclusion that diversification in Anthus was high in the Pliocene (ca. 7–2 million yr ago) and low in the Pleistocene (2–0 million yr ago; Fig. 4); other avian groups show a similar pattern (e.g., Zink and Slowinski 1995; Klicka and Zink 1997).

One caveat to this conclusion is that I lack an Anthus-specific estimate to account for the time involved in ancestral species divergences; such a correction would shift the dates provided in Table 1 closer to the present. Moore (1995) and Edwards (1997) suggested a value of 350,000 yr to account for prespeciation divergence time. Correcting for this value would potentially shift only one date into the (very early) Pleistocene. Avise and Walker (1998) and Arbogast and Slowinski (1998) have also discussed methods to account for

<table>
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<tr>
<th>Node</th>
<th>Daughter-lineages (L, R)</th>
<th>δ</th>
<th>CP (%)</th>
<th>h (SE)</th>
<th>Time (MYA) ± SE</th>
<th>Time (MYA) (ML estimate)</th>
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<td>brachyurus &gt; cafer</td>
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<td>15.86</td>
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<td>78</td>
<td>77 &lt; 76</td>
<td>0.00200</td>
<td>3.20</td>
<td>0.0479 (0.0036)</td>
<td>4.79 ± 360,000</td>
<td>—</td>
</tr>
<tr>
<td>80</td>
<td>godlewski &gt; 78</td>
<td>0.00047</td>
<td>5.58</td>
<td>0.0471 (0.0040)</td>
<td>4.71 ± 400,000</td>
<td>—</td>
</tr>
<tr>
<td>79</td>
<td>nyssae &lt; novaeseelandiae</td>
<td>0.01076</td>
<td>71.98</td>
<td>0.0679 (0.0064)</td>
<td>6.79 ± 640,000</td>
<td>8.201</td>
</tr>
<tr>
<td>81</td>
<td>79 &gt; 80</td>
<td>0.02034</td>
<td>99.96</td>
<td>0.0587 (0.0039)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>50</td>
<td>richardi &lt; Rufulus</td>
<td>0.01366</td>
<td>98.58</td>
<td>0.0227 (0.0034)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>82</td>
<td>50 &lt; 81</td>
<td>0.00654</td>
<td>78.50</td>
<td>0.0489 (0.0036)</td>
<td>4.89 ± 360,000</td>
<td>—</td>
</tr>
<tr>
<td>48</td>
<td>lineivis &lt; crenatus</td>
<td>0.02357</td>
<td>99.74</td>
<td>0.0430 (0.0048)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>72</td>
<td>48 &gt; hoeshi</td>
<td>0.01592</td>
<td>97.74</td>
<td>0.0479 (0.0045)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>73</td>
<td>62 &gt; sylvanus</td>
<td>0.00320</td>
<td>31.82</td>
<td>0.0622 (0.0052)</td>
<td>6.22 ± 520,000</td>
<td>—</td>
</tr>
<tr>
<td>74</td>
<td>73 &gt; 82</td>
<td>0.00314</td>
<td>44.48</td>
<td>0.0638 (0.0040)</td>
<td>6.38 ± 400,000</td>
<td>—</td>
</tr>
<tr>
<td>70</td>
<td>74 &gt; 72</td>
<td>0.00198</td>
<td>25.86</td>
<td>0.0662 (0.0037)</td>
<td>6.62 ± 370,000</td>
<td>—</td>
</tr>
</tbody>
</table>

1 These values are greater than those at more basal nodes (see text).
ancestral diversity and species divergence estimates, but their methods have been questioned by Klicka and Zink (1998, 1999). Because Klicka and Zink (1997, 1998, 1999) dealt exclusively with passerine birds in their analyses, it seems appropriate here to apply a divergence value of 2% per million years between species, and to assume that their correction of 200,000 yr may on average account for ancestral divergences in most passerine species. Employing the latter value does not change the conclusion that diversification in *Anthus* has been highest in the Pliocene.

Not surprisingly, the percent sequence divergence method does a good job of approximating time estimates at clocklike sister-species nodes. The method does particularly well when the sister-species split is recent; there is little difference between percent sequence divergence (not shown) and two-cluster test dates. The most serious problem with using percent sequence divergence in biogeographic analyses is that it is not possible to determine which lineages are diverging in a clocklike fashion with this method.

One difficulty with the inference of clocklike behavior for daughter-lineages is potential rate heterogeneity across the tree. For example, above node 56, only node 43 (*correndera (1)/antarcticus*) and node 45 (*hellmayri (1)/bogotensis*) can be inferred to be diverging according to a clock (Fig. 3). However, because the daughter-lineages above node 56, each of which contains one of these sister-pairs, are not diverging in a clocklike manner, it would seem difficult to apply the same divergence rate to nodes 43 and 45 or between these nodes and other terminal nodes elsewhere on the tree that may themselves not be connected through clocklike nodes.

Despite the probability that some divergence rates are different, using one rate across all clocklike nodes (with two exceptions, see below) to obtain a rough time estimate seems reasonable for three reasons. First, rate heterogeneity is usually moderate when closely related sequences (i.e., taxa) are used (Takezaki et al. 1995); the clocklike behavior at basal nodes within *Anthus* supports this idea. Second, sampling error may be a contributing factor to heterogeneous lineages (Takezaki et al. 1995). Several *Anthus* species were not available for molecular analysis and, conceivably, adding these taxa could result in more clocklike nodes depending on their placement in the phylogeny. Obviously, additional taxa could also change relationships and inferences of dates at certain nodes. Third, there do not appear to be alternative methods to address this dilemma.

Applying dates to nodes 65 and 79 was not possible, because assigning rough dates according to a uniform *Anthus* rate would result in each being older than more basal nodes. One possible explanation for this is the two-cluster tests’ reliance on neighbor joining to generate branch lengths. Neighbor-joining accuracy in recovering trees decreases both when the number of taxa included increases and when branch lengths are short (Strimmer and von Haeseler 1996); both apply to this study (Fig. 3; Voelker 1999). An alternative
**Ancestral Areas**

The results of the ancestral area reconstructions suggest several alternative possibilities for *Anthus* (Fig. 5, Table 2). Bremer’s (1992) method of determining ancestral areas suggests that Africa, Eurasia, and South America are near-equivalent probable alternatives (Table 2A). However, if island-endemic distributions are excluded as distinct areas and instead considered part of the nearest continent, only Africa and Eurasia remain as probable candidates for the *Anthus* ancestral area (Table 2B). Clearly, this method is sensitive to tree topology and distribution.

DIVA reconstruction suggests that either Africa or Eurasia is the most likely ancestral area for *Anthus* (Fig. 5, Table 2). When only continental distributions are recognized, 16 dispersal events are required to explain those distribution patterns (Table 3). Virtually all of these dispersals occur at terminal tips (i.e., are not inferred as ancestral areas at terminal nodes; see Fig. 5) and for four of the species (not *similis*) with multiple-continent distributions, the distribution on one continent makes up a tiny fraction of total distribution (see below). Certainly, intercontinental movements have been important to the development of this group; in Africa, Eurasia, and North America, *Anthus* species are polyphyletic and clearly not part of a single within-continent radiation (Fig. 5).

Within-continent analyses may also shed light on alternative ancestral areas for *Anthus* because, at this level, areas can be refined to reflect finer distribution patterns. The ancestral reconstruction for the African/Asian clade suggests either that Eurasia (Himalayas + Mongolia–Southeast Asia) or Mongolia–Southeast Asia + South Africa comprise the ancestral area (Fig. 6A). Furthermore, moving up the tree from the base, node reconstructions suggest that several waves from Asia have occurred into Africa; although the reverse is also true, such events are seen in single-species distributions and are not inferred at nodes (see below). Also note that an eastern Palearctic (or the entire Palearctic) origin is inferred for the largely Palearctic clade (Fig. 6B).

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**Table 2.** Ancestral area reconstructions based on Bremer’s (1992) method. Ancestral area scores are probabilities that a given area is part of the ancestral area for the group. (A) Using all five continents and recognizing the two island endemic areas occupied by *Anthus*. Eurasia, South America, and perhaps Africa are most likely to have been part of an *Anthus* ancestral area. (B) By restricting distributions to continents by including island endemics with nearest continent, Eurasia and Africa are most likely to have been part of an *Anthus* ancestral area.

<table>
<thead>
<tr>
<th>Area</th>
<th>Gains</th>
<th>Losses</th>
<th>Gains/Losses</th>
<th>Ancestral area</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Africa</td>
<td>5</td>
<td>6</td>
<td>0.83</td>
<td>0.83</td>
</tr>
<tr>
<td>Eurasia</td>
<td>9</td>
<td>9</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Australia</td>
<td>1</td>
<td>5</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>North America</td>
<td>2</td>
<td>10</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>South America</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Canary Islands</td>
<td>1</td>
<td>8</td>
<td>0.125</td>
<td>0.125</td>
</tr>
<tr>
<td>South Georgia Island</td>
<td>1</td>
<td>7</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>(B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Africa</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>0.91</td>
</tr>
<tr>
<td>Eurasia</td>
<td>9</td>
<td>8</td>
<td>1.1</td>
<td>1</td>
</tr>
<tr>
<td>Australia</td>
<td>1</td>
<td>5</td>
<td>0.2</td>
<td>0.18</td>
</tr>
<tr>
<td>North America</td>
<td>2</td>
<td>10</td>
<td>0.2</td>
<td>0.18</td>
</tr>
<tr>
<td>South America</td>
<td>3</td>
<td>5</td>
<td>0.6</td>
<td>0.54</td>
</tr>
</tbody>
</table>
TABLE 3. Number of dispersals inferred by dispersal-vicariance analysis to explain the present distributions of each clade of pipits. A purely vicariant explanation would result in a score of zero.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Number of areas allowed for reconstruction</th>
<th>Maximum of two areas</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Anthus</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>African/Eurasian</td>
<td>21</td>
<td>28</td>
</tr>
<tr>
<td>South American</td>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>Paleartic</td>
<td>9</td>
<td>13</td>
</tr>
</tbody>
</table>

Taken together, these points suggest the likelihood of an eastern Asian origin for Anthus, over any alternative area.

**Initial Intercontinental Movements**

Both the structure of the ML tree (Fig. 3) and the divergence time estimates (Fig. 4, Table 1) suggest that Anthus achieved much of its current cosmopolitan distribution (i.e., present on most continents) early in its history, about 6 million yr ago (Fig. 7); subsequent intercontinental movements (i.e., successful colonizations) were, until recently, few and largely restricted to movement between Africa and Eurasia (Fig. 7). Several species having multiple-continent distri-

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**Fig. 6.** Within-continent ancestral area reconstructions for Anthus clades, using dispersal-vicariance analysis. The maximum number of possible ancestral areas for each clade was set at two. (A) The African/Eurasian clade; (B) the Paleartic clade; (C) the South American clade.
butions do not share this distribution with sister or more basal taxa (i.e., a more restricted distribution is given at the next most basal node), which implies that there has been a recent burst of dispersal and/or speciation events of very late Pliocene-early Pleistocene age (3–1 million yr ago; Figs. 3, 4, Table 1). These recent events have been speciation/dispersal events either between Africa and Eurasia, or into North America (Fig. 3). The number of intercontinental movements at both the base and at the tips of the *Anthus* phylogeny suggest that movement between continents may have been constant throughout the development of the group; however, during much of *Anthus* history, this movement either did not generate species or successful intercontinental colonists have since gone extinct (see below).

The initial movement of *Anthus* from Eurasia into Africa (about 6.5 million yr ago; Fig. 7) was likely facilitated by climate and habitat changes that resulted in an increase in grasses (i.e., more open habitats) both in Pakistan and east Africa from 9 to 5 million yr ago (see Vrba 1985, 1993); most African *Anthus* are found in open habitats. This change to more open habitat was evident on several continents and was apparently the result of a net global cooling (Vrba 1993).

According to molecular clock dates (Table 1), *Anthus* entered South America nearly 6 million yr ago, most likely from North America (Fig. 7). Although no surviving North American species supports this hypothesis, the invasion of South America by an extinct North American ancestor(s) is more plausible than dispersal to South America from Asia. Molecular clock dates for the North-South American movements as well as the open habitat associations of all members of the South American pipit clade suggest that suitable open habitats were present in Central America prior to the final closure of the Panamanian Land Bridge in the mid-Pliocene, about 3–2.5 million yr ago (Pitman et al. 1993). Indeed, present-day Central America has been near northwestern South America for 45 million yr (Pitman et al. 1993), with an Alaskan-type archipelago connection between North and South America in place since the mid-Miocene (ca. 12–10 million yr ago; Pitman et al. 1993); the high mountains of Central America could well have been occupied by grasslands prior to land-bridge closure. Also, tropical forest were likely less extensive about 5–3 million yr ago, as the result of climatic/habitat shifts due to the primary uplift of the northern Andes and the emergence of the coastal lowlands from Colombia to Peru (DeVries 1987; Megard 1992) and general global cooling.

**Intracontinental Area Relationships and “Recent” Intercontinental Movements**

**African/Eurasian and sokokensis Clades**

The ancestral area of the African/Eurasian clade is inferred to consist of either the Himalayas + Mongolia–Southeast Asia or the Himalayas + South Africa (Fig. 6A). Twenty-eight dispersals (maxareas = 2) are required to explain this reconstruction; an unconstrained analysis also requires a large number of dispersals (21), with virtually all areas inferred as ancestral (Table 3).

Clearly, there have been several interchanges between
Africa and Eurasia; these interchanges occur both deep within the African/Eurasian clade as well as at terminal tips. In general, avian distributions suggest that the main route between Africa and Eurasia has been across the Saudi-Indian region, which connects the northeast arid region and Mongolia–Southeast Asia (Figs. 1, 7), rather than a Saharan-Mediterranean route (Moreau 1952; Short and Horne 1990). This route is supported by Anthus distributions: cinnamonosus, which is widespread in Africa, has a limited distribution on the Saudi Peninsula; similis, which is also widespread in Africa, has a continuous distribution through the Saudi-Indian region; whereas the distribution of rufulus, which is widespread in Southeast Asia, is found westward to Pakistan (Ali and Ripley 1973; Clancey 1990; Keith et al. 1992).

In addition, movement across the Saudi-Indian region is implied from the sister-relationship of novaseelandiae (Australia) and nyassae (Africa; Fig. 7); a less plausible alternative is dispersal across the Indian Ocean. Unfortunately, a molecular clock date for the nyassae/novaseelandiae divergence (node 79, Fig. 3; see above) is not available, but the structure of the ML tree (Fig. 3) indicates that this is a fairly old split and thus may be contemporary with early Pliocene (ca. 4 million yr ago) faunal turnover in Australia, which is accompanied by an increase in open habitat (i.e., grassland) mammals (Tedford 1985).

Only the breeding distribution of campestris, which is widespread across Eurasia but also found in limited areas of Africa north of the Sahara, suggests an invasion route via dispersal across the Mediterranean (Fig. 7), despite a pre-Pleistocene land-bridge connection between Sicily and Tunisia (Moreau 1952), which could have facilitated intercontinental exchange.

Most of the inferred dispersal events between Africa and Eurasia (Figs. 6A, 7) appear to predate the flooding of the Red Sea, 4–3.5 million yr ago (Hsiu et al. 1977; Table 1). This implies that the Red Sea may have played a role in fragmenting ancestral species ranges, even though it has never been much wider than present (Moreau 1952).

The distributions of species in the sokokensis clade (not shown) also supports southward movement from the northeast arid region; sokokensis is restricted to a narrow coastal forest belt of this region and is sister to brachyrurus and caffer (Fig. 5), which share distributions in the southern savannah and South Africa. Speciation patterns in eight Afrotropical land bird orders strongly support isolation of the northeast arid region from the rest of Africa due to (presumably repeated) eastward expansion of tropical forests (Fry 1986).

Micromammal fossils (Wesselman 1985), pollen changes (Bonnefille 1983), and disjunct sister-species distributions of open habitat francolins (Phasianidae; Crowe et al. 1992) suggest another major shift to more grassy/open habitats (see above) began about 3 million yr ago both across the northeast arid region and southward (i.e., the “arid-corridor” of Wintenburg 1996). This second major shift to grassy/open habitats implies a reexpansion of tropical forest and more humid climates between 5–3 million yr ago. Molecular divergence date estimates between the aforementioned francolin species (Crowe et al. 1992) and at node 58 (Fig. 3, Table 1; see above) are concordant with this reexpansion. Divergence during this period can also be inferred for the melindae/similis (1) and longicaudatus/vaalenis sister-pairs (Table 1). Plausible biogeographic interpretations are not possible for these sister-pairs, unfortunately, because the ranges of similis (1) and longicaudatus are presently unknown. It is worth noting, however, that melindae, like sokokensis, is also restricted to coastal areas of Kenya and Somalia (Britton and Britton 1978; Keith et al. 1992) and that vaalenis, like caffer and brachyrurus, is distributed primarily in southern Africa (Clancey 1990; Keith et al. 1992).

A subsequent cooling/drying period is supported by several lines of evidence dating from the late Pleistocene to early Holocene. During that period, east African montane glaciers were several thousand meters lower than present (Osmaston 1965, as cited in Livingstone 1975) and fossil pollen records suggest that intermediate-altitude montane grasses were able to connect currently isolated montane grasslands (Livingstone 1975, 1993). It is almost certainly the case that these dry-wet cycles repeat in conjunction with Earth’s orbital changes (Livingstone 1993; Vrba 1993; Kutzbach and Liu 1997) and that the African climates have fluctuated for at least several million years (Livingstone 1975; Coetzee 1986, 1993, and references therein; Van Zinderen Bakker 1986). Similar evidence from southwest Asia to Nepal suggests that an analogous pattern of climatic cycling has occurred in the region over at least the past 4 million yr (papers in Jain 1989). These climatic shifts would likely have increased the potential for Anthus movements through, and speciation in, Africa and the Palearctic.

The development of African or southwest Asian mountain systems have not likely had an important role in speciation within the African/Eurasian clade. Much of the southern and eastern African mountain systems have been in place for 20 million yr, and although some volcanic mountains are between 5–2 millions yr old, none form continuous barriers (Visser 1984; Burgess et al. 1996; Young 1996). Generally continuous tectonic activity has been recorded from across southwest Asia, but this activity would not result in complete barriers to movement or a vicariant speciation event (papers in Jain 1989; Alavi 1994).

A dispersal event must be inferred to explain the presence of the endemic Anthus species on the Canary Islands (berthelotti). Although there has been speculation that the eastern Canaries were once connected to the African mainland (where berthelotti’s sister, campestris, does have a limited breeding distribution; Fig. 6A), no compelling proof exists for such a land bridge (Schmincke 1976).

South American Clade

Results of a within-continent DIVA reconstruction (maxareas=2) suggest that the northern Andes and either the Patagonian center or the eastern lowlands forms the Anthus ancestral area within South America (Figs. 1B, 6C). Thirteen dispersals are required by this reconstruction (Table 3). Unconstrained maxareas requires only nine dispersals (Table 3), but gives an ancestral area reconstruction consisting of all possible areas.

When the number of potential ancestral areas is limited,
northern Andean–lowland connections are inferred at several
nodes and the northern Andes is the sole ancestral area in-
ferred at two near-basal nodes (Fig. 6C). This might imply
that the northern Andes have served as the route by which
Anthus entered South America from the north; distributions
of high altitude species of the rodent genus Akodon indicate
a similar route (Hoffstetter 1986). Either the Patagonian cen-
ter or eastern lowlands are suggested as the ancestral area
for the furcatus group and possibly for the antarcticus/cor-
rendera correndera sister-pair (South Georgia cannot be in-
ferred as ancestral; Fig. 6C).

Several lines of evidence suggest that a connection between
the northern Andes and the eastern lowlands (see also da
Silva 1995) is more likely than an Andean-Patagonian con-
nection. First, about 1.2 million yr ago, glaciers entirely cov-
ered both Chile, between at least 40°S latitude and Tierra del
Fuego (inclusive), and southern Patagonia; in both regions
glaciers reached the continental shelves (Rabassa and Clap-
perton 1990). In northern Patagonia, glaciers extended up to
200 km east of the Andean front ranges (Rabassa and Clapp-
perton 1990), which may have left little suitable pipit habitat
in this region. Thus, species distributions that include these
areas must be the result of “recent” range expansion. This
is supported by the molecular clock dates available for this
clade (Fig. 3, Table 1), which suggest that the most recent
speciation events predate this period of extensive glacial ac-
tivity. Second, there is evidence of past gallery and subtrop-
ical forest connections across the Chaco center linking the
forest foothills of the northern Andes and eastern lowlands
(Vuilleumier 1971; Short 1975; Nores 1992; Iriondo and Gar-
cia 1993).

Noting avian distributional patterns, Fjeldså (1990; see
also Roy et al. 1997) suggested that rainshadows and asso-
ciated temperature changes have created opportunities for
arid woodland and humid shrub (i.e., “lowland”) species to
enter high-altitude Bolivian valleys; indeed, some of these
“lowland” species occur above 4000 m. Bates and Zink
(1994), using a molecular phylogeny of Leptopo gon flycatch-
ers, were able to support evolution into the Andes for that
genus. Despite this example of using well-supported phy-
logenies, which could allow directionality of movements to
be inferred, the “lowland-to-highland” theory appears to be
driving recent biogeographic interpretations (Fjeldså 1992;
citations in Maijer and Fjeldså 1997).

The pattern inferred from the South American cladogram
(Fig. 6C) suggests Andean-to-lowland movement. Sick
(1985) had suggested Andean-to-lowland movement to ex-
plain the presence of several avian species in the Itatiaia
highlands of southeastern Brazil; the nearest relatives to the
unique flora of this region are found in the Bolivian Andes.
Patton and Smith (1992), using molecular data, suggested
Akodon from low altitudes were derived from high-alti-
tude ancestors living in the Andean puna zone. Clearly, di-
rectionality is not generalizable across taxa.

Repeated Chaco dispersal corridors coupled with extensive
vicariant events in the Andes (Gansser 1973; Van der Ham-
men and Cleef 1986; Saeebrier et al. 1988; Seltzer 1990) may
be driving pipit speciation in South America. Roy (1997) has
suggested a similar pattern of repeated montane vicariant
events as the driving speciation mechanism in an African
passerine genus. Additional samples of Anthus taxa occuring
in the Andes (subspecies of furcatus, hellmayri, and corren-
dera), as well as samples from the two other lowland species
(chacoensis and nattereri) not included in this study, may
elucidate this proposed pattern, as should planned studies of
other South American genera with distributions similar to
Anthus.

Dispersal by an ancestral population to South Georgia Is-
land (Fig. 7) and subsequent isolation from continental pop-
ulations must be inferred to explain speciation between c.
correndera and antarcticus (Fig. 6C); South Georgia has been
separated from South America for 45 million yr (Brown and
Gibson 1983). A molecular clock date (Table 1; but see
above) suggests that the isolation took place roughly 1.5
million yr ago, a period when much of southern Argentina
was covered by glaciers (Rabassa and Clapperton 1990), thus
increasing the distance from the Falklands and South Georgia
to the nearest source of mainland Anthus.

North America was invaded from South America by a lu-
tescens (South American/spragueii (North American) an-
cestor roughly 4 million yr ago (Figs. 6C, 7). Based on this
divergence date, dispersal prior to final uplift of the Panam-
ian Land Bridge is inferred, and ancestral movements northward
would have been facilitated by generally continuous open
habitat across the Americas at about this time (Vrba 1993;
see above).

Vicariance via tropical forestation of Central America
may have contributed to final separation of the spragueii/
lutescens ancestral range. Currently, lutescens has a con-
tinuous breeding distribution from Panama to Argentina (ex-
cluding western and central Amazonia), as well as an iso-
lated distribution in the Peruvian arid coast center (Fig. 6C).
Although I do not have samples from the disjunct popula-
tion, I would predict that the divergence between these
breeding groups will be consistent with the final uplift of
the northern Andean Cordilleras, about 2.5 million yr ago,
and subsequent forestation of coastal areas (see Brumfield
The intervening region (i.e., coastal lowlands of Colombia
and Ecuador) between the lutescens distributional areas is
covered with evergreen forest (Brumfield and Capparella
1996), expansion of which would have been aided by in-
creased rain associated with the uplifting Andes and south-
ward expansion of warm-water currents; fossil molluscan
fauna suggest the latter occurred near the Pliocene/Pleis-
tocene boundary (Devries 1987).

Paleartic Clade

Either the entire Paleartic or the eastern Paleartic are
inferred as the ancestral area for this group (maxareas = 2),
and 14 dispersals are required to explain the distributions
(Fig. 6B). Again, assuming unconstrained ancestral areas in-
vokes fewer dispersals (12; Table 3) and gives an ancestral
area consisting of all possible areas.

North America can be inferred as part of an ancestral area
at nodes throughout most of this clade, and Enghoff (1996;
but see Ronquist 1997) supported a western Nearctic ances-
tral area for many taxa. However, inferring a North American
ancestral area is likely an artifact of relatively recent colo-
nizations by Anthus species. Except for rubescens (North America), North American distribution of other species in this clade constitute a very small fraction of their total range (see below). A second analysis (not shown) that removed North America from all but the rubescens (North America) distribution confirmed this assumption; all other possibilities remain the same at these nodes.

As suggested for other Anthus clades, mountain-building events or dispersal over existing mountains do not seem to be driving speciation in the Palearctic clade. However, a fair number of species ranges are bounded on either the east or west by the Ural–Yenisey River area (see Flint et al. 1984), and I suggest the following scenario to explain these distributions.

Frenzel (1968) has shown that extensive glaciers covered much of northern Eurasia, except northeasternmost Siberia, and broad areas to the south of these glaciers were covered by tundra. I hypothesize that the combination of glaciers and environmental changes, which are recorded from the past 2.5 MY in the Chinese Loess Plateau (Kukla and An 1989; An et al. 1991), have acted in concert and their combined actions of reducing habitat variety (i.e., little forest) and generally rendering the remaining habitat (tundra) inhospitable (due perhaps to high winds that deposited sediment in the Loess Plateau from deserts to the northwest [i.e., near the Ural–Yenisey region]) may serve to explain the present range boundaries of several avian species in the central Palearctic.

This hypothesis can be tested. There are 44 glacial-to-interglacial shifts recorded in the plateau, with three major shifts dated at 2.4, 1.2, and 0.5 million yr ago (Kukla and An 1989). This suggests that by dating divergences between sister-taxa whose distributions are interrupted by the Ural–Yenisey region (or even between sister-taxa that overlap to some extent in this region), we may be able to determine whether changing environments that generated the Loess Plateau are correlated with divergence events within and between Palearctic species. These environmental effects could also explain patterns of distributions bordered to the north or south by the plateau region; during the last glacial period, the Chinese coastline was 800–1000 km farther east (An et al. 1991), which would certainly have had an impact on habitats east of the plateau. Unfortunately, the two possible tests of these ideas within Anthus (hodgsoni-trivialis sister-pair across the Palearctic; richardi-rufulus sister-pair across China) are not dated (Table 1). The general structure of this Palearctic clade, however, suggests that the isolation of roseatus in the Himalayas about 4.5 million yr ago (Table 1) could be the result of glacial effects (assuming a longer cycle than is recorded in the plateau); most other species in the cervinus subclade are distributed farther north (Fig. 6B).

Anthus rubescens is probably two species (based on migratory route and molecular differences; see Zink et al. 1995; Voelker 1999), and corresponding North American and Eurasian mtDNA lineages diverged from each other at about the Pliocene/Pleistocene boundary (Table 1), presumably after the invasion of North America (Fig. 7). Even with a divergence time estimate, determining whether this speciation event occurred due to vicariance as the Beringian Land Bridge submerged or after dispersal into North America during a period when the bridge was submerged seems difficult (but see below), given the complex history of Beringia with respect to avian lineages with trans-Beringian distributions (Zink et al. 1995).

Anthus cervinus is present in both western Alaska (Seward Peninsula) and Eurasia (where it is widely distributed). The distribution of cervinus is certainly a recent dispersal event into North America (Fig. 7), rather than a population that has survived in western Alaskan glacial refugia. Because much of western Alaska was ice-free during the Wisconsin glacial (Porter et al. 1983), a wider present distribution should be expected for cervinus because ample habitat would have been available (tundra).

Anthus pratensis, which is widely distributed across Eurasia, has a limited distribution on eastern Greenland. This is clearly the result of a recent dispersal (Fig. 7) because Greenland was covered by glaciers almost continually during the Quaternary (Brown and Gibson 1983). Several other avian species have also colonized Greenland from Eurasia (e.g., fieldfare, Turdus pilaris; northern wheatear Oenanthe oenanthe).

Relative Roles of Dispersal and Vicariance

Dispersal has clearly played an important role in shaping the cosmopolitan distribution of Anthus (Fig. 7). The repeated occurrence, during migration, in North America of several species that breed in the Palearctic suggests that dispersal will continue to play an important role. Molecular clock dates (Table 1) suggest that the two interchanges between South and North American predated the final uplift of the Panamanian Land Bridge. Island distributions clearly resulted from dispersal. Furthermore, very limited distributions of several primarily Eurasian species in North America strongly suggest recent colonizations (Fig. 7), almost certainly since the last glaciation. Dispersal across barriers seems a credible explanation for the limited distribution of several species on the Saudi Peninsula and for the sole species found in North Africa.

Beringia is clearly not a barrier to intercontinental dispersal by pipits as evidenced by the colonization of western Alaska by cervinus and the recurrence of still other pipit species on the Aleutians (American Ornithologists’ Union 1983); nor is the North Atlantic an insurmountable barrier, as evidenced by the colonization of Greenland by pratensis. Numerous records of a variety of birds crossing these water barriers can be found annually in ornithological journals.

Admittedly, the Bering Sea is not a huge barrier in terms of distance; however, it is certainly wider than presumed barriers to dispersal invoked from other regions (e.g., riverine barriers; Capparella 1992). One problem with invoking (or accepting) dispersal has been that we generally lack knowledge of how often and how far a given species disperses (other than the occasional site record, see above). In a recent study of an avian hybrid zone, Rohwer and Wood (1998) were able to show, using museum specimens, that hermit and Townsend warblers (Dendroica occidentalis and D. townsendi, respectively) can be found breeding well away from ”usual” breeding areas; the nearly 20 records included
fledglings, and showed dispersal distances ranging between 40 km and 265 km. These observations indicate that, ultimately, the ability to disperse across barriers may not constrain the distributional spread of many avian lineages, at least in cases where areas are fairly close. The constraint on successful colonization is likely whether or not an area is suitable for invasion; successful invasion could be hindered by, for instance, competition from residents or lack of suitable habitat. However, the combination of distant suitable habitats and unsuitable intervening habitats (tropical forests) would almost certainly explain why we do not see interchange between North and South America or between the Palearctic and Australia, at the tips of the *Anthus* phylogeny/ cladogram.

Climatic shifts are the most likely vicariant events driving speciation between African and Eurasian forms. Vicariance may also be driving intracontinental speciation in *Anthus*. However, it should be noted that in some cases vicariance is simply inferred as more likely in a program designed to make that assumption. For instance, molecular clock dates are generally unavailable for ancestral nodes in the South American clade (Fig. 3, Table 1), as are approximate dates for the inferred vicariant events that may be driving speciation there (i.e., climate/vegetational shifts across the Chaco/Pampas). Assuming good dates were available for these events, those dates would perhaps not be time compatible and dispersal across barriers would indeed be implicated. Indeed, molecular studies of a number of marine taxa have unequivocally implicated dispersal, rather than plate tectonics, as the primary explanation of biogeographic distributions (Bowen and Grant 1997 and references therein).

Avifaunal community buildup via separate invasions of more distantly related congeners, rather than within-region speciation, has been recently documented in *Phylloscopus* warblers in the Palearctic (Richman 1996). The key to implicating dispersal in that study was the use of a molecular phylogeny and comparisons of island (Japan) versus mainland communities. A similar pattern is evident from a phylogeny of titmice (Paridae) subgenera (Slikas et al. 1996). By replacing each species on the titmouse phylogeny (Slikas et al. 1996, fig. 3A) with its respective continental distribution (Asia or North America), it is apparent that several invasions of North America have occurred during the evolutionary history of this family. The same general pattern of buildup of species communities through multiple invasions, rather than solely within-region speciation events, is also apparent within *Anthus* (e.g., Fig. 5). Given the lack of long-term barriers to movement between regions across several continents, I suggest that most attempts to assess the role of dispersal in biogeographic scenarios will underestimate its relative importance.

Biogeographic studies have made important strides in the past few decades. However, there is still room for improvement, and the first step may be accepting the possibility that dispersal plays a primary role in biogeographic histories; the need for taking this step has been sounded by others (e.g., Hedges et al. 1994; Bowen and Grant 1997). The present study and others have directly or indirectly implicated dispersal as an integral factor in the development of regional and continental species-swarms in several distinct avian lineages. Furthermore, our ability to roughly date lineage splits allows, for the first time, fairly accurate assessment of the roles of dispersal and vicariance regardless of the scale at which biogeographic analyses are performed. By failing to explore both dispersal and vicariance as primary explanations and by failing to rigorously test for a molecular clock, biogeographic hypotheses of both the dispersalist and the vicariant acolyte are prone to narrative storytelling.

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