ORNITOLOGIA NEOTROPICAL 2: 40—43, 1991

TROPICAL BIRD SPECIES NUMBERS IN SECOND-GROWTH *VS.* PRIMARY FOREST HABITATS AT LARGE SCALES

David A. Wiedenfeld *

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-2043, U.S.A.

Key words: Deforestation, Amazonia, diversity, range size, forest, edge.

Destruction of tropical forests is becoming a major concern, as an area of tropical forest larger than Costa Rica is being cut down each year (Wilson 1988). To maintain biological diversity, it will be necessary not only to preserve primary habitats that still exist, but also to renew some habitats that have already been exploited. For example, in the tropics, some attention is being given to re-establishing or regenerating forests on areas where the primary forest has already been cut (Cairns 1988). This, of course, requires a period when a site has on it a young, second-growth forest, with a complement of animal and plant species different from the primary association.

Establishing large second-growth forest areas is not irrelevant to maintaining biodiversity and to conservation efforts, because second-growth forests sometimes support a greater diversity of species than do primary forests (e.g., Lugo 1988) per unit of area. Forest-restricted bird species, however, may have smaller geographic ranges compared to edge and second-growth species. If this is true, then conversion of a large area of primary forest to second-growth might reduce the area's diversity by wiping out some forest species, even though diversity at any one point within the region of former primary forest might be increased when occupied by second-growth species. Therefore I decided to test the idea that forest species in the tropics do not have smaller geographic ranges than do edge species.

METHODS

To avoid any potential bias, I chose bird lists for which the author had already assigned a habitat-use category for each species, such as "edge" or "forest". Following this criterion, I chose lists of all bird species at two localities, one in Amazonia on the Río Tambopata, southeastern Peru (Parker, unpublished), and one in Central America at Barro Colorado Island, Panama (Willis & Eisenmann 1979). These lists are not necessarily the most up-to-date for these localities. This is unimportant, because the reason for using lists prepared by others was to obtain independent species pools, and so that I not choose the species to be included myself and potentially bias the results. I excluded all temperate-zone migratory species, and I included all species in the taxonomic list from the Trochilidae (hummingbirds) through the Fringillidae (siskins), except for the kingfishers and swallows. This includes all Trogoniformes, Coraciiformes except Alcedinidae, all Piciformes, and all Passeriformes except the Hirundinidae. This restricts the lists to the smaller woodland- or edge-dwelling species and excludes some groups such as water birds, hawks, and vultures, because it is difficult to decide if those birds are using forest or edge habitat. Through the rest of this paper, I will refer to the group of species that can live in second-growth forests and edge habitats as "edge" species. Some of these birds also occur in primary forests; however, if they occur at all in edge or successional habitats I will call them edge species. Only species restricted to primary forests will be referred to as "forest" species.

To obtain an index to the relative sizes of geo-

* *Current address:* Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A.

graphic ranges (range-size index), I divided the New World into 14 regions of roughly equal size, and used information on ranges from Meyer de Schauensee (1982). If a species occurred in a region at all, I counted it for the whole region. Information in Meyer de Schauensee (1982) on ranges may be inaccurate with respect to details. Because I used only the presence or absence of species within large regions to count for the entire region, the inaccuracies in range details should not be important as long as the inaccuracies are smaller than one of the 14 regions. Next, I determined the area of the regions in which each species occurred. Clearly, this technique will over-estimate the area of a species' range, possibly by a large factor. Species which have narrow, linear ranges would be counted in many regions, although the actual area of their ranges might not be large. This source of bias should be consistent for both forest and edge species, however, and the area of the regions in which a species occurs should be a valid index to geographic range size. Another source of bias could be that edge species have more linear ranges than forest species. Use of the range-size index then would over-estimate the size of edge species' ranges relative to forest species' ranges. This analysis was not designed to answer the question of whether one group has more linear ranges than the other.

To compare the geographic ranges of the forest and edge species I used the non-parametric Kolmogorov-Smirnov two-sample test (K-S test), a conservative test.

To test the validity of my range-size index, I compared the ranges of *Tangara* measured by the range-size index with the areas measured directly from accurate maps in Isler & Isler (1987) using a digital planimeter. This comparison shows that the two methods give about the same statistical results ($D = 0.191$, n.s.). One difference is that the cumulative frequency distribution calculated from the Isler & Isler (1987) maps is much smoother than the more step-like distribution produced by the range-size index. More importantly, ranges measured directly from the Isler & Isler (1987) maps using the planimeter show a median range to be about 300,000 km², but the ranges measured by the range-size index are about twice that large.

RESULTS

For the Río Tambopata list (119 edge species, 188 forest species) the K-S test is significant ($D = 0.316$, $p < 0.001$), showing the forest species to have smaller ranges than the edge species. About 70 percent of forest species have ranges equal to or smaller than the 44th rank (14,106,000 square km), while less than 40 percent of edge species have ranges smaller than this.

A histogram of the ranges (Fig. 1) shows that a few edge species have very large ranges. The largest of these belongs to the house wren, *Troglodytes aedon*. The six largest ranges are all of edge species. Two edge and two forest species are tied for the smallest range size, but seven of the nine smallest ranges are of forest species.

The Barro Colorado Island list included 125 edge and 51 forest species. For this list, the K-S test indicates that the forest species have smaller ranges than the edge species with a probability of 0.06 ($D = 0.197$). About 75 percent of the forest species have ranges smaller than the 35th rank (14,834,000 square km), but only about 55 percent of the edge species do.

A histogram of the ranges of the Barro Colorado Island birds (Fig. 2) shows that the four largest ranges belong to edge species, but six of the eight smallest also belong to edge species. The histogram also shows an interesting bimodal distribution in range sizes. I interpret these two peaks to be the group of species with a primarily Central American distribution and the group of species that also occur on the Barro Colorado Island, but have a primarily South American distribution. I have not analyzed the ranges,

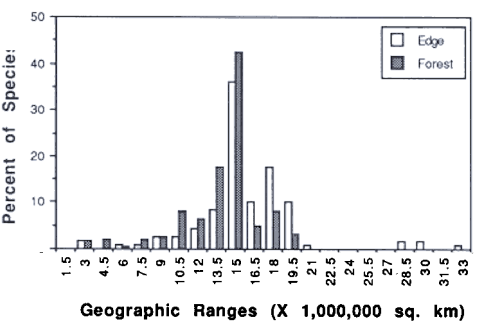

FIG. 1. Distribution of geographic range sizes of birds from Río Tambopata, Peru, list.

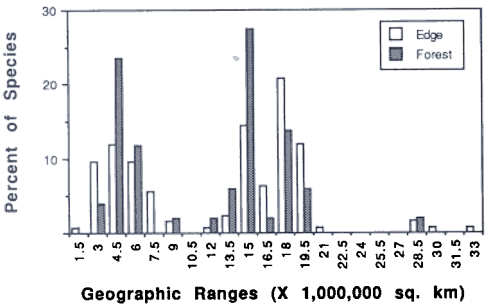

FIG. 2. Distribution of geographic range sizes of birds occurring on Barro Colorado Island, Panama.

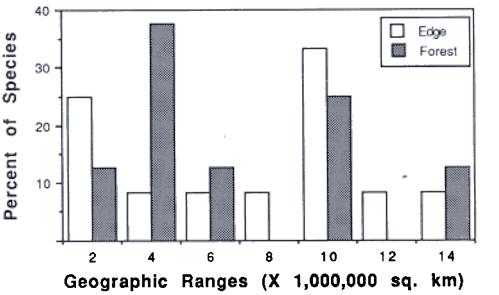

FIG. 3. Distribution of geographic range sizes for birds in the genus *Synallaxis*.

however, to determine if this is correct. Once again, there is a small group of species with very large ranges.

To compare species with a common phylogenetic background, I examined the three genera with the most species in South America, *Synallaxis* (spinetails), *Myrmotherula* (antwrens), and *Tangara* (tanagers). In the genus *Synallaxis* (12 edge and 8 forest species), the K-S test was non-significant (D = 0.292), but the forest species again tended to have smaller ranges (Fig. 3). Three of the four largest ranges in this genus are of edge species, although three of the four smallest were also edge species.

Myrmotherula contains four edge and 17 forest species. In this genus, the K-S test indicates significantly smaller ranges in the forest species ($D = 0.750$, $p < 0.05$), although the sample size of edge species is small. All forest species have ranges of less than the 17th rank (14,106,000 square km), whereas only one of the four edge species does (Fig. 4). It is clear that in this genus, edge species are much more widespread than forest species.

In *Tangara*, there was no significant difference between the forest and edge species' ranges (D = 0.214, with 14 edge and 21 forest species), although the three largest ranges are of edge species, and the edge species did tend to have the larger ranges (Fig. 5). As at Barro Colorado Island, however, several of the smallest ranges also belong to edge species.

DISCUSSION

In general it seems to be true that forest species have smaller ranges than do edge species. The large species pools from both localities and for one of the three genera examined indicated significant differences, using the conservative K-S test,

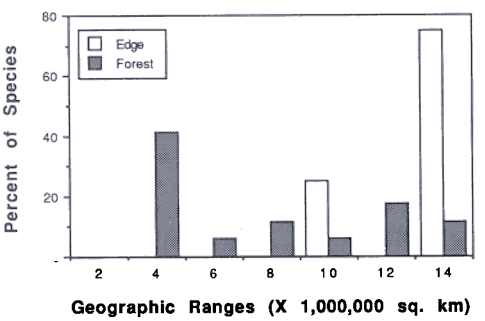

FIG. 4. Distribution of geographic range sizes for birds in the genus *Myrmotherula*.

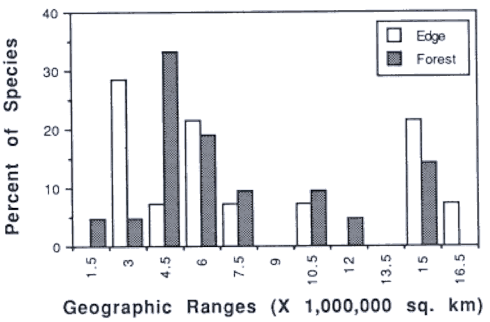

FIG. 5. Distribution of geographic range sizes for birds in the genus *Tangara*, using range sizes computed from the range-size index.

and in the two non-significant tests the trend was for forest species to have smaller ranges. This analysis also was conservative in another way: some species of birds occur only in naturally-made second-growth or edge habitats, and shun man-made second-growth. These species probably best should be considered with the forest species. If they have small ranges as the natural forest species do, then the difference between range sizes of forest and natural edge species would be even greater.

Because forest species have relatively small ranges, clearing a large fraction of the Amazonian forest in one block and replacing it with second growth could extinguish an important fraction of forest species. Their identity would depend of course on exactly what part of Amazonia was cut down and what species' ranges still overlapped with the remaining forest. Even so, because of the possibly higher diversity of second-growth species, the number of species in the second-growth at any point within the region might be higher than it was at that same point before the destruction.

The differences in distribution patterns of edge and forest species at large scales are relevant to the problem of whether to create one large reserve for the preservation of species diversity, or several smaller, scattered reserves. Because forest species tend to have smaller ranges, it appears it would be necessary to have several forest reserves at different places (so that each species would occur in at least one reserve), rather than a single, large reserve. Of course, each reserve would still have to be large enough to maintain a healthy population of the species within it. Ironically, if one were designing reserves for second-growth or edge species within a large area of forest, fewer reserves would be necessary.

ACKNOWLEDGEMENTS

This manuscript benefitted from discussions with C. A. Chase III and S. K. Robinson. I thank G. R. Graves, J. V. Remsen, K. V. Rosenberg, and D. S. Simberloff for useful comments on the manuscript.

REFERENCES

Cairns, J., Jr. (ed.) 1988. Rehabilitating damaged ecosystems. Boca Raton, Florida.

Isler, M. L., & P. R. Isler. 1987. The tanagers, natural history, distribution, and identification. Washington, D. C.

Lugo, A. E. 1988. Estimating reductions in the diversity of tropical forest species. Pp. 58—70 *in* Wilson, E. O. (ed.): Biodiversity. Washington, D. C.

Meyer de Schauensee, R. 1982. A guide to the birds of South America. 2nd edition. Philadelphia.

Parker, T. A., III. Birds of the Tambopata Nature Reserve, Puerto Maldonado, Madre de Dios, Peru. Unpublished.

Willis, E. O., & E. Eisenmann. 1979. A revised list of birds of Barro Colorado Island, Panama. Smithsonian Contributions to Zoology No. 291.

Wilson, E. O. 1988. The current state of biological diversity. Pp. 3—18 *in* Wilson, E. O. (ed.): Biodiversity. Washington, D. C.

Accepted 4 April 1991.