

TABLE 6.3 Summary of Significant Frequencies from Fourier Analyses of Time-Series Data Sets

DATA SET	WINDOW	GRAIN	FREQUENCIES (YEARS)		
			PRIMARY	SECONDARY	TERTIARY
RAINFALL	39 yr	day	1	0.25	0.3
	39 yr	month	1	0.25	0.3
	44 yr	year	6	8.00	11.0
WATER STAGE	22 yr	day	1	7.00	3.0
		month	11	1.00	3.0
WATER FLOW	44 yr	month	1	8.00	22.0
PAN EVAPORATION	22 yr	month	1	11.00	5.0

regions of self-similarity, although the reasons for this result are unclear. Temporal patterns in the stage and flow reflect dominant frequencies in the interplay among the faster dynamics of the atmosphere, the intermediate speeds of the surface water, and the longer-term variations in vegetation, climate, and sea level.

These analyses support the theory that ecosystems are structured around a few keystone variables of mixed spatial and temporal dimensions. Dramatic patterns of discontinuities appear as a result of the interactions within and between hierarchical levels in space and time. This emerging viewpoint of ecosystem structure and dynamics may provide a better basis for understanding the dynamics of the Everglades and hence help to meet multiple management objectives in this unique ecosystem.

7

DISCONTINUITIES IN THE GEOGRAPHICAL RANGE SIZE OF NORTH AMERICAN BIRDS AND BUTTERFLIES

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ELUCIDATING LARGE-SCALE patterns in plant and animal assemblages is a key step toward understanding ecosystem dynamics and their likely responses to current and future regional and global threats. An attribute that has been widely used in this context is body size because of its well-known relationship with physiological, morphological, and population-level traits (Peters 1983; Schmidt-Nielsen 1984; Niklas 1994; Calder 1996). For example, body size in plant and animal assemblages has been used to characterize energy and nutrient pool sizes as well as fluxes in ecosystems (Kimmel 1983; Wen, Vezina, and Peters 1994; Cyr and Peters 1996; Cyr, Downing, and Peters 1997). In addition, it has been used to understand variation in species diversity (Harris, Piccinin, and van Ryn 1983) and to evaluate the response of ecosystems to disturbance, including climate change (Sprules and Munwar 1986; Jacobs 1999). Less used in this context have been home range and geographical range size, two attributes that have a strong spatial component and that therefore may be informative of processes underlying the distribution of individuals and populations in space (Brown, Stevens, and Kaufman 1996; Maurer and Taper 2002).

The *geographical range* is the basic biogeographical unit and represents the total area over which a species is found (Brown, Stevens, and Kaufman 1996; Gaston and Blackburn 2000). It has been described in terms of its structure and size. Whereas *structure* indicates "how" population demographic attributes are distributed in space (Brown 1984; Villard and Maurer 1996; Brewer and Gaston 2003), *size* indicates the range of abiotic and biotic conditions that a species can tolerate (Gaston and He 2002, and references therein). *Shape*, a third attribute of geographical range, has been postulated to reflect the limitation of ecological factors, including the physical structure of continents (Rapoport 1982; Ruggiero

We are grateful to William Beltrán, Andres Cuervo, Sylvia Heredia, and Rodney Rodríguez for helping put together the bird and butterfly data sets and to Craig Stow and Jennifer Skillen for their valuable comments on early versions of this manuscript. This work was funded by National Science Foundation grant NSF-CREST (HRD no. 0206200).

2001). Thus, the geographical range reflects past and present conditions influencing the large-scale spatial dynamics of plant and animal populations.

Of these three attributes, geographical range size may be particularly informative of processes underlying the origin and maintenance of species diversity. First, the frequency of small and large geographical ranges may suggest conditions favoring speciation and extinction, including such conditions as the expansion and contraction of geographical ranges within given taxa and regions (Gaston and Blackburn 1997; Vilenkin and Chikatunov 1998; Webb and Gaston 2000; Crisp et al. 2001; Jablonski and Roy 2003). Second, the distribution of geographical range size may be used to compare assemblages and to establish whether a similar suite of processes can explain large-scale patterns of species diversity (Gaston 1998; Gaston et al. 1998; Paulay and Meyer 2002). Third, geographical range size is an important criterion in identifying species' vulnerability to large-scale disturbances, such as those resulting from human activities (Terborgh and Winter 1983; Kunin and Gaston 1993; Mace 1994; Angermeier 1995; Arita et al. 1997; Jones, Purvis, and Gittleman 2003). Finally, understanding patterns in the distribution of geographical range size may help design plans for the long-term preservation of the evolutionary and biogeographical processes that underlie the origin of species diversity (de Klerk et al. 2002; Hughes, Bellwood, and Connolly 2002; Jansson 2003).

Geographical range size has been expressed in several ways, depending on whether range maps, information on species' latitudinal/elevational limits, presence/absence, and abundance for a given region are available (Gaston 1994; Brown, Stevens, and Kaufman 1996; Gaston et al. 1996; Quinn, Gaston, and Arnold 1996). In general, species differ widely in the size of their geographical range such that a large number of species are narrowly distributed, whereas a small number are widely distributed (Gaston 1990, 1998; Brown, Stevens, and Kaufman 1996; but see Hughes, Bellwood, and Connolly 2002). In more quantitative terms, these right-skewed distributions of range size have been shown to resemble unimodal, continuous, log-normal distributions (Gaston 1996; Gaston and Blackburn 1997), and several explanations for such patterns have been proposed (for a summary, see Gaston and Blackburn 2000; McGeoch and Gaston 2002). Surprisingly, most of the explanations are based on processes operating over ecological or short-term scales that do not necessarily match the long-term scales associated with evolutionary and biogeographical processes involved in the origin, expansion, and extinction of species.

Alternatively, one may ask whether the distribution of geographical range sizes exhibits patterns of discontinuity or multimodality, as has been shown for body size (Holling 1992). A multimodal distribution in range size suggests the presence of discontinuities, and it follows from Holling's Textural Discontinuity

Hypothesis (TDH) that modes in range size should be associated with attributes that are discontinuous in space and time and that are known to have influenced evolutionary and biogeographical processes. The distinctive nature of landforms and the characteristic rates of processes that give rise to them (Brundsen 1996) offer a natural way to evaluate the TDH (Holling 1992) in a biogeographical context. For example, unusual geological substrates and landforms, including mountains, are well known for harboring species with restricted geographical ranges (Van der Werff 1992; Tuomisto and Poulsen 1996; Printaud and Jaffré 2001; de Klerk et al. 2002). Likewise, landscapes covering extensive areas, whether as a result of natural or anthropogenic processes, harbor species that have large geographical ranges (Terborgh and Winter 1983; Duncan, Blackburn, and Veltman 1999). And species' distributions are known to cluster in space, allowing the identification of geographical regions with unique characteristics (Hagmeier and Sults 1964).

Here we focus on North American birds and butterflies to address three questions. Does the distribution of geographical range sizes for these two taxa exhibit multiple modes? Do the distributions of geographical range sizes of these two unrelated volant taxa exhibit similarities? And are the modes and discontinuities in the size distribution of geographical ranges related in a meaningful way with landscape attributes?

METHODS

We restricted our analysis to North America defined as the continental mass that includes the United States, Canada, and Greenland; in some few instances, we included species whose geographical range extends into northern Mexico (fig. 7.1). The area occupied by the first three countries totals approximately 21.5 by 10⁶ km², representing 14% of the Earth's land surface. Within this area, we included only those species whose geographical range falls completely within the boundaries described. This means that year-round residents and intracontinental migrants, but not intercontinental migrants, were included in our study. Although such restriction substantially decreased our sample size, it generated a more homogeneous group of species whose geographical ranges were more likely to be influenced by processes shaping North America as described earlier. It is well known that the majority of intercontinental migrants reported in North America belong to taxa that originated in the Neotropics (Levey and Stiles 1992). In addition, their geographical ranges are depicted as highly disjunct; breeding and wintering grounds do not overlap, raising the issue of how to measure their range size. In total, 136 species of birds and 288 species of butterflies met the criteria described here (see appendixes 7.1 and 7.2).

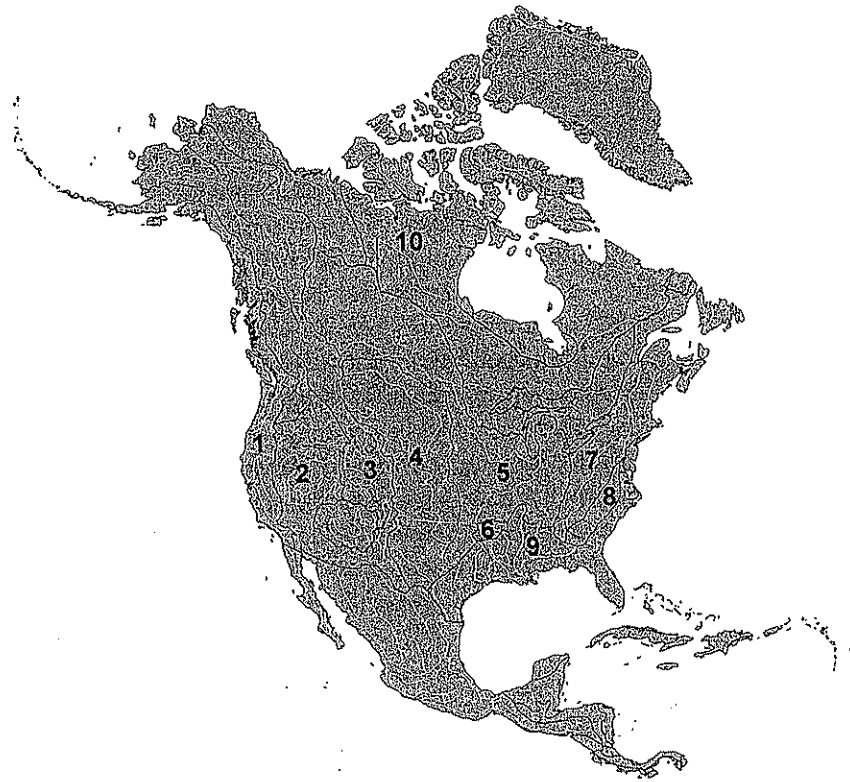


FIGURE 7.1 Map of North America showing main physiographic units (black lines) and Bailey's ecoregions (white lines). Numbers correspond to physiographic units: Pacific Mountain System (1), Intermontane Plateaus (2), Rocky Mountain System (3), Interior Plains (4), Interior Lowlands (5), Interior Highlands (6), Appalachian Highlands (7), Piedmont (8), Atlantic Plain (9), and Canadian Shield (10).

DISCONTINUITY IN GEOGRAPHICAL RANGE SIZE

We used published range maps of North American birds (National Geographic Society 2002) and butterflies (Scott 1986) to obtain geographical range-size data. Therefore, we express geographical range size in terms of extent, or the total area over which a species has been recorded, irrespective of range structure and shape (Brown, Stevens, and Kaufman 1996; Gaston and Blackburn 2000). For intracontinental migrants, we summed the breeding and wintering ranges to obtain a single figure for the size of their geographical range. We followed a three-step procedure to estimate the size of the geographical ranges. First, we scanned (600 dpi) the published range maps and processed the digital maps to eliminate pixels

representing political boundaries and labels. Second, we used a clustering algorithm based on an eight-neighborhood rule to identify and measure the number of pixels in each cluster of the black-and-white range map images (Imagine, ERDAS). Last, we converted the number of pixels into metric units based on a model that predicts area (km^2) from pixel number. For this purpose, we selected from the range maps those features with known areas, such as states and provinces of the United States and Canada, and processed them as described here. This selection was necessary because the scale of the range maps differed between butterflies and birds, as well as within birds.

Geographical range-size data obtained in this fashion may have some limitations that need to be addressed. First, range maps can be generated using different methods that reflect predicted distribution based on habitat preferences, or the actual distribution based on field or museum observations or both (Brown, Stevens, and Kaufman 1996). Whereas we know that this latter method was used to generate the butterfly map ranges (Scott 1986), we do not know how the bird maps were prepared. Second, these maps, in contrast to those derived from coordinated large-scale censuses, are likely to provide a relatively crude estimate of the real size of geographical ranges and do not reflect the structure of the geographical range (Maurer 1994). However, maps derived from coordinated efforts are available only for limited taxa or geographical regions or both. Third, range maps generated by different authors are likely to be based on maps differing in terms of their projection or scale or both, as was the case with the bird and butterfly maps we used. Such difference may introduce an important source of error when data sets based on different maps are compared. Last, the size of small geographical ranges may be underestimated because of the small scale of the base maps. In spite of these limitations, range maps represent the best source of information available to estimate sizes of geographical ranges and make comparisons across taxa.

We used the Gap Rarity Index (GRI) to identify aggregations (or modes) and discontinuities (or gaps) in the size distribution of geographical ranges (Restrepo, Renjifo, and Marples 1997). The GRI method tests whether discontinuities in an observed distribution of rank-ordered data are unlikely in data sampled from a continuous unimodal log-normal distribution fit to the observed data. First, a continuous unimodal distribution is obtained by constructing a normal kernel density estimate that uses the smallest window width (h) that smoothes the observed frequency distribution (Silverman 1986). Second, absolute gaps in a variable of interest are measured, $d_i = s_{i+1} - s_i$, where s_i is the \log_{10} of i th geographical range size in rank-size-ordered data, and their significance was tested based on the index, D_i . This index is a statistic measuring the proportion of simulated absolute gaps smaller than the observed, and it is obtained by sampling the continuous unimodal distribution ten thousand times (Restrepo, Renjifo, and Marples 1997).

CLUSTERS OF SPECIES IN GEOGRAPHICAL SPACE

The geographical range of a species reflects the gamut of abiotic and biotic conditions influencing a species' life span in space and time and therefore is indicative of a species' history. Broad-scale subdivisions of land based on terrain structure and geology—that is, physiographic units—are ideal to classify species in geographical space. Such a map exists for the United States (Fenneman and Johnson 1946; Vigil, Pike, and Howell 2002), but not for the entire region considered in this study (but see Barton, Howell, and Vigil 2003). Instead, we used Bailey's (1998) map of North American ecosystems, or ecoregions, which reflects physiographic units to some extent. In addition, the resolution of the ecoregions was fine enough to allow a detailed characterization of birds and butterflies' geographical ranges, especially those restricted to small areas. We refer to major physiographic provinces (Fenneman and Johnson 1946) to report our results (fig. 7.1).

After differentiating ecoregions represented on both coasts into east and west to account for the different origins of the land (King and Beikman 1974), we identified for each species the ecoregions falling within the limits of the range maps. We recorded ecoregions as present or absent irrespective of whether the ecoregion was widely or narrowly represented. We ran a cluster analysis using Sorensen's index as a distance measure to avoid the double zero problem and using flexible beta ($\beta = -0.25$) as the group linkage method to build dendrograms (Legendre and Legendre 2003). We used branches in the dendrogram at 50% of similarity to distinguish clusters of species occupying similar geographical regions, hereafter referred to as *zooregions* (Hagmeier and Sults 1964). The misplacement of some species in the clusters was unavoidable, in part because of the scale of the range maps and our inability to identify ecoregions within the range maps. This misplacement may have resulted in the inclusion of some ecoregions that were not really represented within the boundaries of the published maps. We classified each species according to aggregation in geographical range size and zooregion, and we used chi-square tests to evaluate whether affiliation to a given aggregation was independent from affiliation to a given zooregion.

RESULTS

The geographical ranges of birds and butterflies exhibited a right-skewed distribution and overlapped over a wide range of values (4.9 by 10^4 to 1.3 by 10^7 km²), yet butterflies exhibited the smallest and birds the largest geographical ranges (3.8 by 10^4 km² and 1.51 by 10^7 km², respectively) (fig. 7.2). The observed distribution of bird and butterfly geographical range sizes did not differ

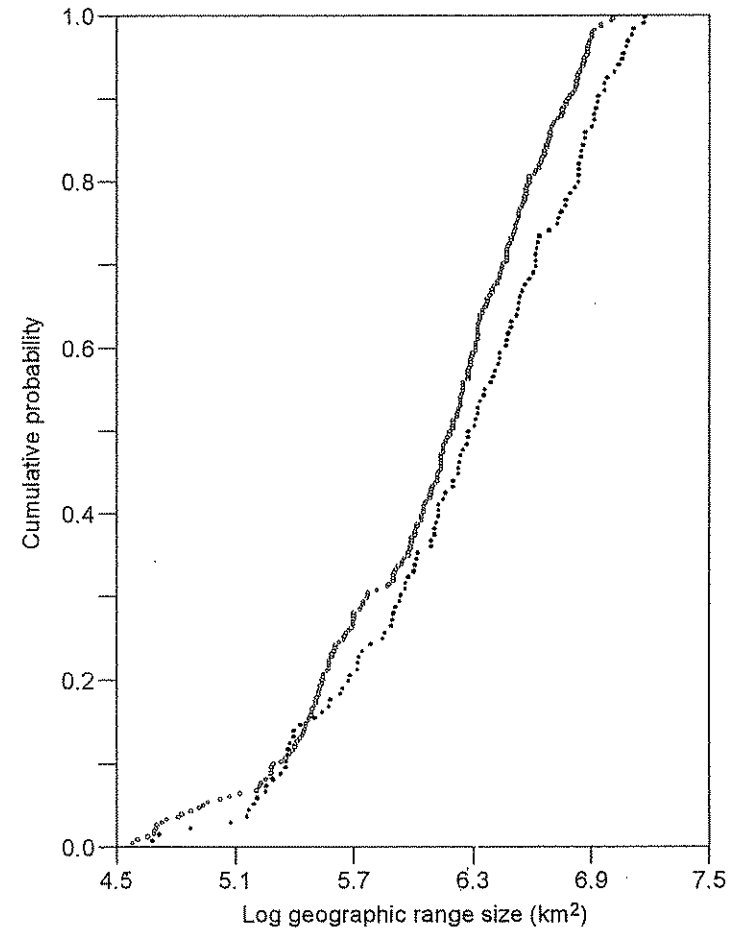


FIGURE 7.2 Observed cumulative distribution function of geographical range size of North American birds (●) and butterflies (○).

($K-S=0.1327$, $P=0.07$) (fig. 7.2). When compared against an expected log-normal distribution, however, the observed distribution of butterfly geographical ranges ($K-S=0.08$, $P=0.03$), but not of bird geographical ranges ($K-S=0.06$, $P=0.69$), was significantly different (fig. 7.3). This difference suggests that properties other than the mean and standard deviation, the two parameters that describe the shape of log-normal distributions, may be responsible for the similarities between the two observed distributions. One possibility is that the observed distributions exhibit patterns of discontinuity and aggregation.

DISCONTINUITY IN GEOGRAPHICAL RANGE SIZE

An examination of the cumulative density curves shows a large discontinuity at approximately 5.8 km^2 (log-transformed value or $6.0 \text{-by-} 10^5 \text{-km}^2$ untransformed value) in both data sets, hereafter referred to as the 6GAP (figs. 7.3 and 7.4). Furthermore, changes in the slope of the cumulative density curves of the observed data in several regions suggested additional discontinuity when compared to the expected log-normal cumulative density curves. We identified seven aggregations in the distribution of geographical range sizes of butterflies ($P=0.006$) and birds ($P=0.002$) using the GRI method (fig. 7.4). This analysis confirmed the presence of the discontinuity found at approximately 5.8 km^2 (log-transformed value) as well as of other discontinuities already observed in the cumulative density curves of the two taxa. Below the 6GAP, we identified three and two aggregations in the bird and butterfly data sets, respectively. In this region, there seems to be a match in aggregation 1 in each of the data sets and between aggregation 2 for butterflies and aggregations 2 and 3 for birds. Above the 6GAP, we found four and five aggregations in the bird and butterfly data sets, respectively. Aggregations 4 and 5 for birds seem to match aggregation 3 for butterflies, but any resemblance thereafter is less obvious.

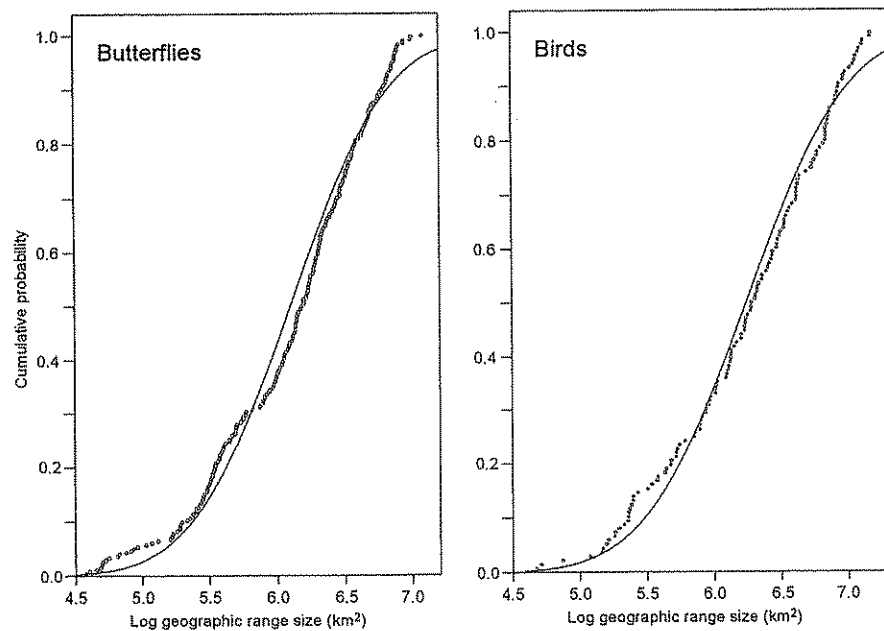


FIGURE 7.3 Observed (O) and expected (black line) cumulative distribution functions of geographical range size of North American butterflies and birds. The expected cumulative distribution functions correspond to a log-normal distributions with parameters estimated from the data. There is a large discontinuity in the observed distributions at approximately 5.8 km^2 (log-transformed data). We refer to this discontinuity as the 6GAP.

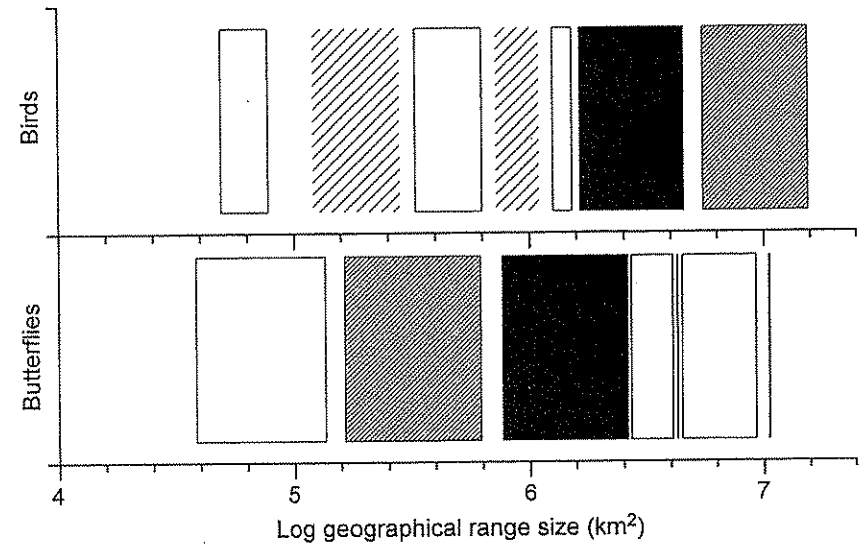


FIGURE 7.4 Identified discontinuities and aggregations in the distribution of geographical range size of North American birds and butterflies resulting from the GRI analysis. Changes in color and hatching from white to black indicate a greater percentage of species falling within each aggregation, with black indicating the largest percentage.

CLUSTERS OF SPECIES IN GEOGRAPHICAL SPACE

For birds, we identified six major clusters, or zooregions (fig. 7.5). Zooregion 1 included species restricted to small areas in the Pacific Mountain System (California and Baja California) and small areas of the Intermontane Plateaus (southwestern United States). Zooregion 2 was represented by species found in the Interior Plains (southwestern United States), in some instances reaching into the southern Rocky Mountain System and the Intermontane Plateaus. Species found in the Atlantic Plain and increasingly extending into the Piedmont, Appalachian Highlands, and Interior Highlands were grouped in zooregion 3. A small group of species found in the Pacific Mountain System of the northwestern United States (including Alaska) and western Canada defined zooregion 4. Species found mostly in the Rocky Mountain System and the Intermontane Plateaus defined zooregion 5. Finally, species found in the Pacific Mountain System, Intermontane Plateaus, and Rocky Mountain System from Alaska to northern California, Arizona, and New Mexico and then extending into the Canadian Shield (Laurentian Upland and Lowland), Interior Highlands, Appalachian Highlands, and Atlantic Plain were grouped in zooregion 6.

Butterflies clustered in geographical space in a similar, but not identical, manner as birds clustered (fig. 7.6). We identified seven major zooregions, the first

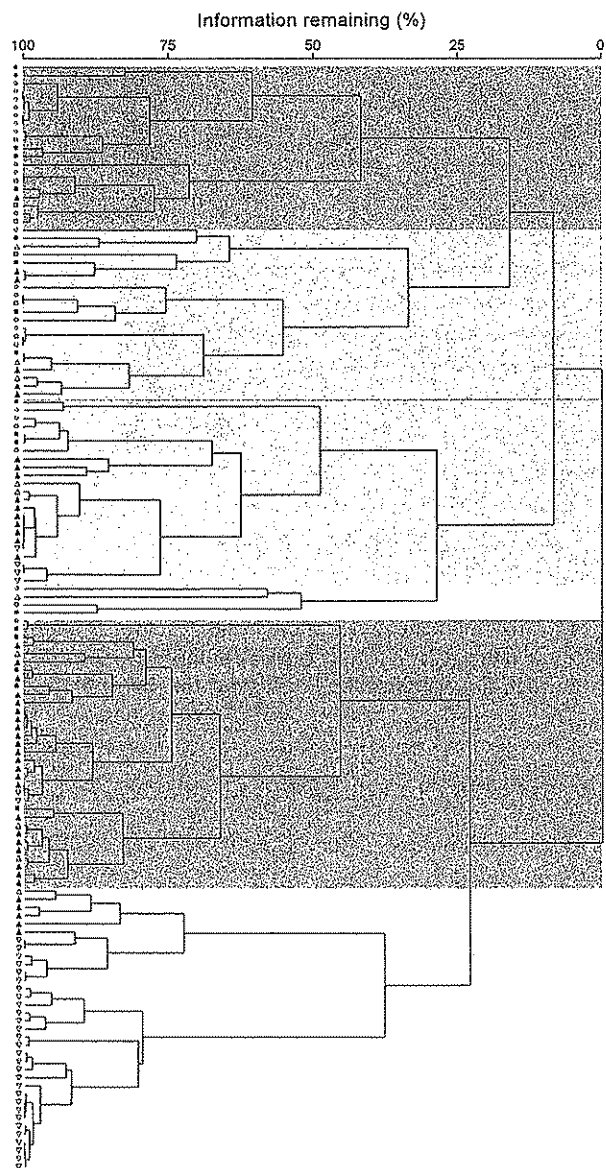


FIGURE 7.5 Dendrogram showing clusters of North American birds based on the occurrence of ecoregions within their geographical ranges. Each species is also identified with a symbol indicating aggregation number affiliation: aggregation 1 (●), aggregation 2 (○), aggregation 3 (□), aggregation 4 (■), aggregation 5 (△), aggregation 6 (▲), and aggregation 7 (▽). Species' clusters are identified with the large gray and white boxes.

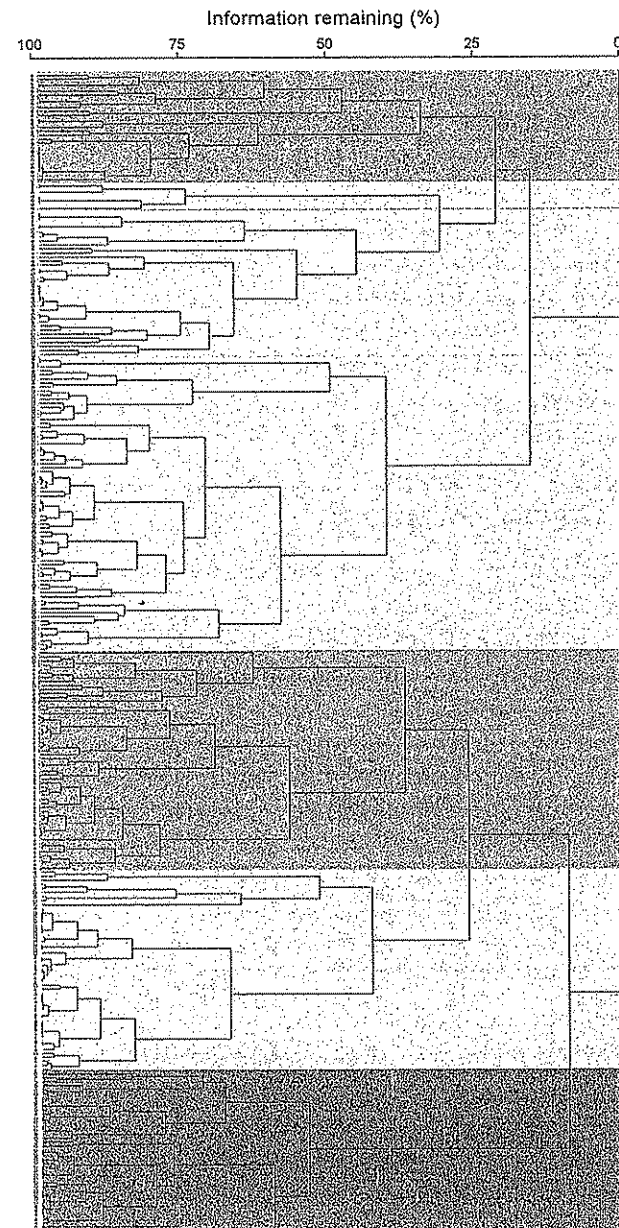


FIGURE 7.6 Dendrogram showing clusters of North American butterflies based on the occurrence of ecoregions within their geographical ranges. Each species is also identified with a symbol indicating aggregation number affiliation: aggregation 1 (●), aggregation 2 (○), aggregation 3 (□), aggregation 4 (■), aggregation 5 (△), aggregation 6 (▲), and aggregation 7 (▽). Species' clusters are identified with the large gray and white boxes.

composed of species restricted to sites in the Pacific Mountain System (California). Zooregion 2 grouped butterfly species found mostly in the Intermontane Plateaus (southwestern United States and extending into northern Mexico). Species found in the Intermontane Plateaus and Interior Plains of the southwestern United States were grouped in zooregion 3. Species found in the Rocky Mountain System, northern Intermontane Plateaus, and Pacific Mountain System of the United States were grouped in zooregion 4. Species restricted to small areas in the Pacific Mountain System of northwestern Canada and extending into the northern Pacific Mountain System of the United States, Intermontane Plateaus, Rocky Mountain System, Interior Plains, and Canadian Shield were grouped in zooregion 5. Species found in the Interior Lowlands and Appalachian Highlands were in zooregion 6. Finally, those species distributed in the Atlantic Plain were grouped in zooregion 7.

DISCONTINUITY IN GEOGRAPHICAL RANGE SIZE AND CLUSTERS OF SPECIES IN GEOGRAPHICAL SPACE

We classified bird species according to the size of their geographical range (aggregation number) and zooregion, and we found a significant association between these two variables ($\chi^2 = 131.9$, $df = 20$, $P = 0.0001$) (table 7.1; fig. 7.5). An examination of the post hoc individual cell values revealed that species with

TABLE 7.1 Number of North American Bird Species Classified in Terms of Their Geographical Range Size (Aggregation Number) and Zooregion (Cluster of Species in Geographical Space)

	CLUSTERS OF SPECIES IN GEOGRAPHICAL SPACE					
	ZOO_1	ZOO_2	ZOO_4	ZOO_5	ZOO_6	ZOO_3
AGGREGATION 1	2	0	0	0	0	1
AGGREGATION 2	9	4	1	1	0	2
AGGREGATION 3	5	5	1	0	0	2
AGGREGATION 4	3	4	1	5	0	2
AGGREGATION 5	0	3	1	3	1	2
AGGREGATION 6	1	5	0	22	5	10
AGGREGATION 7	0	0	0	2	29	4

Note: Zooregions 1 and 2 and aggregations 1 and 2 were pooled to carry out the statistical analysis described in the text.

TABLE 7.2 Number of North American Butterflies Classified in Terms of Their Geographical Range Size (Aggregation Number) and Zooregion (Cluster of Species in Geographical Space)

	CLUSTERS OF SPECIES IN GEOGRAPHICAL SPACE						
	ZOO_1	ZOO_2	ZOO_3	ZOO_4	ZOO_5	ZOO_6	ZOO_7
AGGREGATION 1	9	2	7	0	0	0	0
AGGREGATION 2	18	5	19	7	1	6	14
AGGREGATION 3	0	0	10	55	4	16	20
AGGREGATION 4	0	0	0	2	0	4	2
AGGREGATION 5	0	0	0	1	1	1	2
AGGREGATION 6	0	0	0	8	45	23	1
AGGREGATION 7	0	0	0	0	4	0	0

Note: Zooregions 1 and 2 and aggregations 6 and 7 were pooled to carry out the statistical analysis described in the text.

small geographical ranges (aggregations 1 and 2) were represented more often than expected in zooregions 1 and 2. Likewise, species in aggregations 6 and 7 were found more often than expected in zooregions 5 and 6, respectively.

The butterfly zooregions were significantly associated with geographical range size ($\chi^2 = 305.6$, $df = 25$, $P = 0.0001$) (table 7.2; fig. 7.6). We found that species with small geographical ranges (aggregations 1 and 2) were found more often than expected in zooregions 1 through 3. These ranges were followed by medium-size geographical ranges (aggregation 3) found more often than expected in zooregion 4. The largest geographical ranges (aggregations 6 and 7) were found more often than expected in zooregions 5 and 6.

DISCUSSION

The distribution of geographical range sizes for North American birds and butterflies was discontinuous, characterized by aggregations and discontinuity (gaps). Moreover, the location of aggregations and gaps in the two data sets exhibited important similarities. Further, there is a strong association between aggregations in the size distribution of geographical ranges and clusters of species in geographical space. Taken altogether, these three findings support the idea that discontinuities

and aggregations in the distribution of geographical range size may reflect large-scale spatial attributes as predicted by the TDH (Holling 1992).

Although this is the first time to our knowledge that Holling's TDH has been tested in a biogeographical context, some earlier work has shown that when geographical range size is expressed in terms of site occupancy, bimodal distributions arise (Hanski 1982). Specifically, there is a high frequency of species that are locally sparse and regionally uncommon and of species that are locally abundant and regionally common; in between these two extremes fall species with intermediate site occupancies. It has been proposed that such patterns may result from biological processes (low environmental heterogeneity) or artefactual effects (small sampling extents) (for a recent review, see McGeoch and Gaston 2002). Yet the distribution of geographical range size of mammals in North America (Simpson 1964) and of birds in the Neotropics (Gaston and Blackburn 1997), two large and heterogeneous regions, seems to be bimodal.

The 6GAP at approximately 600,000 km² (untransformed value) was a distinctive feature in both the bird and the butterfly data sets. In the bird data, we clearly identified three aggregations ($n=33$ species, or 24% of the total) below this value, and most of the member species were found in the Pacific Mountain System (California) and the southern Intermontane Plateaus (Texas, New Mexico, Arizona, and northern Mexico). A very small fraction of the species falling within these three aggregations were restricted to the Atlantic Plains, either to the central sand dunes of Florida or to a narrow strip along the coastline, extending increasingly inwards. In the butterfly data, we identified two aggregations below the 6GAP ($n=88$ species, or 31% of the total), and, as for birds, these aggregations included mostly species found in the southern Pacific Mountain System (California), the Intermontane Plateaus, and the Interior Plains. Unlike for birds, however, we found many more butterfly species with small ranges centered in the Interior Plains (Texas) and the Atlantic Plains. In fact, this finding may have contributed to our recognition of an additional zooregion for butterflies, zooregion 7. For the most part, however, the 6GAP separated butterfly species and bird species with small geographical ranges (less than 1% of the size of the North American continent) that seem to be associated with complex or relatively recent landforms, or both (Fenneman and Johnson 1946; King and Beikman 1974). These landforms are ecotonal in character in two ways. First, they developed along the margins of the stable core of North America and are relatively new from a geological perspective. Second, they are currently influenced by a subtropical climate.

In the bird data set, we identified four aggregations above the 6GAP. Aggregations 4 and 5 had few species distributed more or less evenly among the six zooregions, whereas aggregations 6 and 7 included the largest number of species (not only above the gap, but overall) and were characteristically associated with zooregions 5 and 6, respectively. The attributes of the geographical ranges of species

belonging to aggregations 4 and 5 are thus apparently "transitional" in character in that these species, unlike species with smaller or larger ranges, are not strongly associated with any zooregion. This conclusion is illustrated by the following two examples. First, although most birds considered in our analyses have their geographical ranges within the North American continent as defined in this work, we included a few that extended south to central Mexico. These species were found in aggregations 4 and 5, and the inclusion of this additional piece of land apparently introduced a source of heterogeneity not found within the area that we defined as the North American continent. In other words, this landform left an imprint on the size distribution of geographical ranges. Second, within a given zooregion some species had "unusual" geographical ranges. For example, three species in aggregation 4 found in the Pacific Mountain System had narrow but very long geographical ranges extending along most of the coast of Canada and the United States (*Sphyrapicus ruber* and *Calypte anna*) or along the coast of the United States and Mexico (*Calypte costae*). Other species were all-year residents (*Strix occidentalis* and *Lagopus leucurus*) that have disjunct populations such that their geographical ranges include dissimilar ecoregions. In contrast to aggregations 4 and 5, aggregation 6 had the largest number of species (32%), the vast majority of which had geographical ranges within the Rocky Mountain System and the Intermontane Plateaus of the United States. Aggregation 7 had the second-largest number of species (26%), but these species, unlike most of the species in aggregation 6, were found distributed across the continent in an east-west direction either centered in the Canadian Shield physiographic unit or entering the Rocky Mountain System and the Appalachian Highlands. Only two species had ranges spanning most of the study area (*Junco hyemalis* and *Colaptes auratus*), but these ranges were nevertheless smaller than the total area.

For butterflies, we found a large aggregation above the 6GAP (106 species, or 37% of the total) that included species with geographical ranges centered in the Rocky Mountain System and Intermontane Plateaus. This aggregation mirrors aggregation 6 for birds. Aggregations 4 and 5 had very few butterfly species and, as found for birds, had "unusual" geographical ranges for the zooregion in which they fell. They marked a transition between aggregations 3 and 6, the latter including species with geographical ranges running predominantly in an east-west direction, as was the case for birds.

Two non-mutually exclusive explanations may account for these results. First, aggregations and discontinuities in the distribution of geographical range size are the result of changes in the shape of the geographical ranges, which in turn are influenced, if not constrained, by the structure of the landforms where the species originated. Second, range expansion or contraction over a species' life span may have translated into changes of geographical range shape and size, and therefore into changes in the overall distribution of range sizes at a continental scale. We speculate that underlying these two explanations is a problem of

geographical range allometry and, more specifically, of the occurrence of scale breaks most likely resulting from the ways in which landscapes are structured at large scales. These hypotheses can be easily tested by examining the distribution of geographical range size of plant and animal assemblages from other continents of equivalent area and range of climate, but of different structure.

The qualitative similarities between birds and butterflies above the 6GAP, however, were not matched in terms of the correspondence of aggregations and discontinuities. One reason for this result may be that differences between the bird and butterfly maps were ultimately reflected in the size and shape of the ranges. Also, the level of detail in the two sets of maps may have affected our ability to discern which ecoregions were found within the ranges. Alternatively, the lack of correspondence of aggregations and discontinuities above the 6GAP in both data sets may reflect real differences in the way birds and butterflies, two taxa that differ greatly in size, perceive and exploit resources. The occurrence of a larger number of butterflies in each aggregation-zooregion combination may provide support to this idea.

The simultaneous examination of geographical range size and ecoregions provides tremendous insight into the processes underlying the distribution of attributes used to characterize species assemblages. In particular, the distribution of geographical range size has previously been characterized in most instances as a continuous, unimodal, right-skewed distribution that may become normal or slightly left skewed when log transformed. Instead, we found several aggregations of varying size clearly associated with landscape attributes. These findings may have implications in terms of how we define endemic species, how we predict which geographical range sizes are likely to expand or contract, and perhaps which areas deserve special conservation status because many species seem to originate in them.

APPENDIX 7.1 North American Bird Species Included in the Study of Discontinuities in Geographical Range Size

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
CATHARTIDAE	<i>Gymnogyps californianus</i>	48,893.40	1
CORVIDAE	<i>Aphelocoma coerulescens</i>	52,664.61	1
CORVIDAE	<i>Pica nuttalli</i>	76,695.89	1
PHASIANIDAE	<i>Tympanuchus pallidicinctus</i>	121,726.58	2
EMBERIZIDAE	<i>Ammodramus caudacutus</i>	146,754.99	2
EMBERIZIDAE	<i>Plectrophenax hyperboreus</i>	150,598.00	2
EMBERIZIDAE	<i>Aimophila carpalis</i>	160,181.28	2
FRINGILLIDAE	<i>Carduelis laurencei</i>	165,634.29	2
FRINGILLIDAE	<i>Leucosticte australis</i>	183,919.68	2
EMBERIZIDAE	<i>Pipilo aberti</i>	185,375.69	2
PARIDAE	<i>Poecile sclateri</i>	199,200.96	2
EMBERIZIDAE	<i>Ammodramus maritimus</i>	216,923.62	2
MIMIDAE	<i>Toxostoma redivivum</i>	231,778.70	2
PARIDAE	<i>Baeolophus inornatus</i>	234,654.83	2
MIMIDAE	<i>Toxostoma lecontei</i>	236,188.01	2
EMBERIZIDAE	<i>Agelaius tricolor</i>	238,812.84	2
PICIDAE	<i>Picoides nuttallii</i>	245,561.42	2
POLIOPTILIDAE	<i>Polioptila californica</i>	254,167.75	2
TIMALIIDAE	<i>Chamaea fasciata</i>	254,762.01	2
PICIDAE	<i>Picoides albolarvatus</i>	276,036.31	2
EMBERIZIDAE	<i>Pipilo crissalis</i>	323,744.90	3
EMBERIZIDAE	<i>Quiscalus major</i>	349,633.87	3
PICIDAE	<i>Colaptes chrysoides</i>	383,256.72	3

APPENDIX 7.1 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
PHASIANIDAE	<i>Tympanuchus cupido</i>	387,283.86	3
PARIDAE	<i>Baeolophus wollweberi</i>	437,230.08	3
ODONTOPHORIDAE	<i>Oreortyx pictus</i>	447,287.38	3
CORVIDAE	<i>Corvus caurinus</i>	480,633.52	3
MIMIDAE	<i>Toxostoma benüirei</i>	486,047.02	3
CORVIDAE	<i>Aphelocoma ultramarina</i>	530,984.16	3
PICIDAE	<i>Melanerpes uropygialis</i>	531,370.05	3
EMBERIZIDAE	<i>Aimophila aestivalis</i>	537,033.51	3
ODONTOPHORIDAE	<i>Callipepla gambelii</i>	563,372.01	3
STRIGIDAE	<i>Micrathene whitneyi</i>	617,440.32	3
VIREONIDAE	<i>Vireo vicinitor</i>	721,610.06	4
FRINGILLIDAE	<i>Leucosticte atrata</i>	734,140.31	4
SITTIDAE	<i>Sitta pusilla</i>	791,941.02	4
STRIGIDAE	<i>Strix occidentalis</i>	796,937.33	4
TROCHILIDAE	<i>Calypte costae</i>	810,120.02	4
PICIDAE	<i>Picoides borealis</i>	828,931.32	4
PARIDAE	<i>Baeolophus rufescens</i>	879,115.83	4
TROCHILIDAE	<i>Calypte anna</i>	887,002.66	4
PHASIANIDAE	<i>Centrocercus urophasianus</i>	932,101.98	4
PARIDAE	<i>Baeolophus griseus</i>	936,687.33	4
ODONTOPHORIDAE	<i>Callipepla californica</i>	959,438.99	4
EMBERIZIDAE	<i>Ammodramus bairdii</i>	1,037,495.49	4
POLIOPTILIDAE	<i>Poliioptila melanura</i>	1,040,316.48	4
PICIDAE	<i>Sphyrapicus ruber</i>	1,060,857.59	4

APPENDIX 7.1 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
MIMIDAE	<i>Toxostoma crissale</i>	1,079,588.16	4
EMBERIZIDAE	<i>Calcarius mccownii</i>	1,252,168.22	5
CORVIDAE	<i>Gymnorhinus cyanocephalus</i>	1,266,450.19	5
EMBERIZIDAE	<i>Ammodramus henslowii</i>	1,303,476.69	5
CORVIDAE	<i>Corvus ossifragus</i>	1,309,994.28	5
PHASIANIDAE	<i>Lagopus leucurus</i>	1,335,954.86	5
EMBERIZIDAE	<i>Ammodramus nelsoni</i>	1,358,267.16	5
EMBERIZIDAE	<i>Pipilo fuscus</i>	1,369,034.07	5
SITTIDAE	<i>Sitta pygmaea</i>	1,370,127.16	5
EMBERIZIDAE	<i>Aimophila ruficeps</i>	1,440,839.10	5
CORVIDAE	<i>Corvus cryptoleucus</i>	1,502,145.14	5
MIMIDAE	<i>Toxostoma curvirostre</i>	1,624,583.52	6
REMIZIDAE	<i>Auriparus flaviceps</i>	1,628,039.49	6
PICIDAE	<i>Sphyrapicus thyroideus</i>	1,720,874.50	6
MOTACILLIDAE	<i>Anthus spragueii</i>	1,729,808.87	6
TROGLODYTIDAE	<i>Campylorhynchus brunneicapillus</i>	1,748,492.01	6
EMBERIZIDAE	<i>Aimophila cassinii</i>	1,767,703.44	6
CORVIDAE	<i>Aphelocoma californica</i>	1,811,037.86	6
EMBERIZIDAE	<i>Calcarius pictus</i>	1,900,925.60	6
EMBERIZIDAE	<i>Amphispiza belli</i>	1,932,016.92	6
CORVIDAE	<i>Nucifraga columbiana</i>	1,933,806.13	6
FRINGILLIDAE	<i>Carpodacus cassinii</i>	2,067,875.81	6
PICIDAE	<i>Melanerpes lewis</i>	2,086,872.01	6

APPENDIX 7.1 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
EMBERIZIDAE	<i>Zonotrichia querula</i>	2,149,974.72	6
EMBERIZIDAE	<i>Calcarius ornatus</i>	2,163,255.55	6
PARIDAE	<i>Poecile carolinensis</i>	2,199,436.03	6
PHASIANIDAE	<i>Derdragapus obscurus</i>	2,330,278.15	6
PARIDAE	<i>Poecile gambeli</i>	2,343,351.63	6
TURDIDAE	<i>Sialia mexicana</i>	2,512,742.54	6
TROCHILIDAE	<i>Archilochus alexandri</i>	2,570,849.52	6
EMBERIZIDAE	<i>Zonotrichia atricapilla</i>	2,637,925.13	6
EMBERIZIDAE	<i>Dendroica pinus</i>	2,735,331.67	6
MIMIDAE	<i>Oreoscoptes montanus</i>	2,775,922.45	6
EMBERIZIDAE	<i>Calamospiza melanocorys</i>	2,807,039.10	6
EMBERIZIDAE	<i>Pipilo chlorurus</i>	2,985,712.21	6
PICIDAE	<i>Picoides scalaris</i>	3,008,385.58	6
TROGLODYTIDAE	<i>Catherpes mexicanus</i>	3,059,461.11	6
TURDIDAE	<i>Ixoreus naevius</i>	3,182,726.29	6
STRIGIDAE	<i>Otus kennicotis</i>	3,196,894.34	6
EMBERIZIDAE	<i>Spizella breweri</i>	3,399,900.45	6
EMBERIZIDAE	<i>Ammodramus leconteii</i>	3,439,489.14	6
PICIDAE	<i>Melanerpes carolinus</i>	3,451,570.76	6
PICIDAE	<i>Sphyrapicus nuchalis</i>	3,523,635.80	6
PARIDAE	<i>Baeolophus bicolor</i>	3,621,328.15	6
FRINGILLIDAE	<i>Leucosticte tephrocotis</i>	3,748,610.12	6
ACCIPITRIDAE	<i>Buteo regalis</i>	3,944,000.16	6
TROGLODYTIDAE	<i>Thryothorus bewickii</i>	4,173,406.16	6

APPENDIX 7.1 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
CAPRIMULGIDAE	<i>Phalaenoptilus nuttallii</i>	4,224,045.37	6
PHASIANIDAE	<i>Tympanuchus phasianellus</i>	4,228,093.52	6
FALCONIDAE	<i>Falco mexicanus</i>	4,231,703.52	6
EMBERIZIDAE	<i>Spizella pusilla</i>	4,306,910.57	6
TURDIDAE	<i>Sialia cucoroides</i>	4,335,942.32	6
PICIDAE	<i>Melanerpes erythrocephalus</i>	4,454,873.42	6
STRIGIDAE	<i>Otus asio</i>	4,980,413.52	6
MIMIDAE	<i>Toxostoma rufum</i>	5,475,720.86	7
PICIDAE	<i>Picoides arcticus</i>	5,535,010.53	7
PHASIANIDAE	<i>Meleagris gallipavo</i>	5,745,221.01	7
TURDIDAE	<i>Myadestes townsendi</i>	5,981,241.13	7
EMBERIZIDAE	<i>Pipilo maculatus</i>	6,054,404.84	7
STRIGIDAE	<i>Strix varia</i>	6,345,958.06	7
PARIDAE	<i>Poecile hudsonicus</i>	6,680,823.14	7
PICIDAE	<i>Dryocopus pileatus</i>	6,966,758.31	7
FRINGILLIDAE	<i>Coccothraustes vespertinus</i>	6,999,336.80	7
CORVIDAE	<i>Cyanocitta cristata</i>	7,008,286.42	7
LANIIDAE	<i>Lanius ludovicianus</i>	7,023,979.92	7
PHASIANIDAE	<i>Bonasa umbellus</i>	7,180,719.96	7
SITTIDAE	<i>Sitta carolinensis</i>	7,250,946.56	7
PHASIANIDAE	<i>Dendragapus canadensis</i>	7,378,870.52	7
STRIGIDAE	<i>Aegolius acadicus</i>	7,496,170.88	7
FRINGILLIDAE	<i>Carpodacus purpureus</i>	7,563,130.25	7
CORVIDAE	<i>Perisoreus canadensis</i>	8,139,837.84	7

APPENDIX 7.1 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
PARIDAE	<i>Poecile atricapillus</i>	8,321,408.04	7
EMBERIZIDAE	<i>Quiscalus quiscula</i>	8,362,835.65	7
TROGLODYTIDAE	<i>Cistothorus palustris</i>	8,577,547.55	7
EMBERIZIDAE	<i>Euphagus carolinus</i>	8,711,199.08	7
EMBERIZIDAE	<i>Zonotrichia albicollis</i>	8,780,431.01	7
EMBERIZIDAE	<i>Passerella iliaca</i>	9,419,367.36	7
EMBERIZIDAE	<i>Spizella arborea</i>	9,498,511.88	7
FRINGILLIDAE	<i>Carduelis tristis</i>	9,808,459.52	7
REGULIDAE	<i>Regulus satrapa</i>	10,668,588.22	7
CORVIDAE	<i>Corvus brachyrhynchus</i>	11,210,082.59	7
PICIDAE	<i>Picoides pubescens</i>	11,531,589.52	7
SITTIDAE	<i>Sitta canadensis</i>	11,722,684.16	7
EMBERIZIDAE	<i>Melospiza melodia</i>	12,248,430.24	7
EMBERIZIDAE	<i>Zonotrichia leucophrys</i>	12,390,931.26	7
FRINGILLIDAE	<i>Carduelis pinus</i>	13,028,008.42	7
ACCIPITRIDAE	<i>Haliaeetus leucocephalus</i>	13,298,938.88	7
PICIDAE	<i>Colaptes auratus</i>	14,994,305.15	7
EMBERIZIDAE	<i>Juncq hyemalis</i>	15,068,746.85	7

APPENDIX 7.2 North American Butterfly Species Included in the Study of Discontinuities in Geographical Range Size

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
PIERIDAE	<i>Colias behrii</i>	38,451.08	1
HESPERIIDAE	<i>Agathymus evansi</i>	41,385.10	1
HESPERIIDAE	<i>Polites mardon</i>	46,403.81	1
LYCAENIDAE	<i>Lycaena hermes</i>	49,569.46	1
LYCAENIDAE	<i>Plebejus emigdionis</i>	50,495.99	1
HESPERIIDAE	<i>Hesperia miriamae</i>	51,036.47	1
LYCAENIDAE	<i>Callophrys dumetorum</i>	51,499.74	1
NYMPHALIDAE	<i>Chlosyne chinatiensis</i>	54,588.18	1
LYCAENIDAE	<i>Plebejus neurona</i>	57,290.56	1
HESPERIIDAE	<i>Amblyscirtes unnamed</i>	66,478.67	1
NYMPHALIDAE	<i>Speyeria adiaeste</i>	68,872.21	1
HESPERIIDAE	<i>Atrytonopsis cestus</i>	77,133.79	1
HESPERIIDAE	<i>Thorybes diversus</i>	84,005.57	1
LYCAENIDAE	<i>Fixsenia polingi</i>	87,943.33	1
HESPERIIDAE	<i>Celotes limpia</i>	93,579.73	1
HESPERIIDAE	<i>Agathymus stephensi</i>	107,940.98	1
HESPERIIDAE	<i>Agathymus remingtoni</i>	120,140.32	1
HESPERIIDAE	<i>Agathymus alliae</i>	134,501.56	1
NYMPHALIDAE	<i>Phyciodes orseis</i>	165,154.33	2
HESPERIIDAE	<i>Agathymus polingi</i>	168,011.14	2
LYCAENIDAE	<i>Calephelis wrighti</i>	171,871.69	2
NYMPHALIDAE	<i>Coenonympha haydenii</i>	172,798.22	2
LYCAENIDAE	<i>Philotis sonorensis</i>	183,530.55	2

APPENDIX 7.2 Continued

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
NYMPHALIDAE	<i>Boloria natazhati</i>	193,336.34	2
HESPERIIDAE	<i>Agathymus neumoegeni</i>	195,266.62	2
HESPERIIDAE	<i>Atrytonopsis lunus</i>	195,652.67	2
HESPERIIDAE	<i>Atrytonopsis deva</i>	195,961.52	2
HESPERIIDAE	<i>Piruna polingii</i>	197,351.32	2
HESPERIIDAE	<i>Problema bulenta</i>	201,057.44	2
HESPERIIDAE	<i>Amblyscirtes fimbriata</i>	220,514.62	2
NYMPHALIDAE	<i>Speyeria diana</i>	231,710.21	2
HESPERIIDAE	<i>Amblyscirtes nereus</i>	240,203.42	2
HESPERIIDAE	<i>Euphyes arpa</i>	244,295.60	2
NYMPHALIDAE	<i>Chlosyne hoffmanni</i>	251,939.49	2
NYMPHALIDAE	<i>Boloria kriemhild</i>	259,351.75	2
NYMPHALIDAE	<i>Erebia vidleri</i>	259,660.59	2
HESPERIIDAE	<i>Euphyes berryi</i>	266,609.58	2
HESPERIIDAE	<i>Agathymus aryxna</i>	273,249.73	2
PIERIDAE	<i>Colias eurydice</i>	279,117.77	2
HESPERIIDAE	<i>Pyrgus xanthus</i>	285,912.33	2
LYCAENIDAE	<i>Satyrium auretorum</i>	286,761.65	2
LYCAENIDAE	<i>Philotiella speciosa</i>	292,398.06	2
LYCAENIDAE	<i>Callophrys lanoraieensis</i>	292,475.27	2
HESPERIIDAE	<i>Hesperia lindseyi</i>	296,953.51	2
HESPERIIDAE	<i>Atrytonopsis pittacus</i>	306,990.94	2
HESPERIIDAE	<i>Stinga morrisoni</i>	309,538.90	2
HESPERIIDAE	<i>Megathymus ursus</i>	312,472.92	2

APPENDIX 7.2 Continued

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
LYCAENIDAE	<i>Euphilotes spaldingi</i>	314,557.61	2
HESPERIIDAE	<i>Hesperia columbia</i>	320,657.28	2
HESPERIIDAE	<i>Amblyscirtes phylace</i>	327,065.80	2
NYMPHALIDAE	<i>Chlosyne californica</i>	328,687.23	2
HESPERIIDAE	<i>Megathymus cofaqui</i>	333,242.68	2
HESPERIIDAE	<i>Nastra neamathia</i>	338,570.24	2
NYMPHALIDAE	<i>Euphydryas gillettii</i>	338,879.08	2
HESPERIIDAE	<i>Ochlodes agricola</i>	340,500.51	2
PAPILIONIDAE	<i>Papilio brevicauda</i>	346,831.81	2
NYMPHALIDAE	<i>Oeneis nevadensis</i>	352,854.27	2
HESPERIIDAE	<i>Hesperia dacotae</i>	356,405.98	2
PIERIDAE	<i>Anthocharis lanceolata</i>	357,255.30	2
HESPERIIDAE	<i>Agathymus mariae</i>	358,876.73	2
HESPERIIDAE	<i>Amblyscirtes cassus</i>	370,844.43	2
LYCAENIDAE	<i>Satyrium tetra</i>	381,267.92	2
HESPERIIDAE	<i>Cogia outis</i>	381,267.92	2
HESPERIIDAE	<i>Amblyscirtes texanae</i>	383,815.88	2
LYCAENIDAE	<i>Lycaena gorgon</i>	384,515.78	2
LYCAENIDAE	<i>Callophrys johnsoni</i>	395,860.80	2
HESPERIIDAE	<i>Poanes aaroni</i>	397,636.65	2
HESPERIIDAE	<i>Atrytonopsis python</i>	405,203.33	2
PIERIDAE	<i>Colias occidentalis</i>	412,692.80	2
LYCAENIDAE	<i>Callophrys hesseli</i>	413,850.96	2

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
LYCAENIDAE	<i>Habrodais grunus</i>	426,976.83	2
HESPERIIDAE	<i>Hesperia woodgatei</i>	456,317.01	2
HESPERIIDAE	<i>Oligoria maculata</i>	457,089.12	2
LYCAENIDAE	<i>Callophrys fotis</i>	467,126.55	2
LYCAENIDAE	<i>Apodemia nais</i>	475,774.18	2
HESPERIIDAE	<i>Amblyscirtes reversa</i>	497,624.90	2
HESPERIIDAE	<i>Zestusa dorus</i>	503,184.09	2
HESPERIIDAE	<i>Oarisma powesheik</i>	504,959.94	2
LYCAENIDAE	<i>Celastrina nigra</i>	508,588.86	2
HESPERIIDAE	<i>Euphyes pilatka</i>	510,827.98	2
LYCAENIDAE	<i>Calephelis borealis</i>	512,603.83	2
LYCAENIDAE	<i>Plebejus lupini</i>	547,966.47	2
HESPERIIDAE	<i>Ochlodes yuma</i>	555,455.93	2
HESPERIIDAE	<i>Atrytonopsis vierecki</i>	574,141.00	2
HESPERIIDAE	<i>Panoquina panoquin</i>	575,685.22	2
NYMPHALIDAE	<i>Speyeria nokomis</i>	595,528.44	2
HESPERIIDAE	<i>Piruna pirus</i>	598,230.83	2
HESPERIIDAE	<i>Amblyscirtes carolina</i>	607,032.88	2
PIERIDAE	<i>Anthocharis cethura</i>	665,636.03	3
HESPERIIDAE	<i>Euphyes dukesi</i>	762,458.63	3
NYMPHALIDAE	<i>Oeneis alberta</i>	764,852.17	3
LYCAENIDAE	<i>Calephelis muticum</i>	806,237.26	3
LYCAENIDAE	<i>Euphilotes rita</i>	808,476.38	3
HESPERIIDAE	<i>Amblyscirtes simius</i>	810,406.66	3

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
NYMPHALIDAE	<i>Cercyonis meadii</i>	828,010.76	3
LYCAENIDAE	<i>Calephelis virginiensis</i>	829,014.51	3
LYCAENIDAE	<i>Ministrymon leda</i>	855,883.94	3
LYCAENIDAE	<i>Callophrys mossii</i>	887,849.29	3
PAPILIONIDAE	<i>Papilio palamedes</i>	896,651.34	3
LYCAENIDAE	<i>Satyrium kingi</i>	918,965.32	3
HESPERIIDAE	<i>Systasea zampa</i>	957,339.19	3
LYCAENIDAE	<i>Satyrium fuliginosum</i>	961,122.53	3
HESPERIIDAE	<i>Amblyscirtes alternata</i>	990,694.34	3
HESPERIIDAE	<i>Polites sonora</i>	992,624.62	3
LYCAENIDAE	<i>Lycaena arota</i>	1,001,658.30	3
HESPERIIDAE	<i>Megathymus streckeri</i>	1,003,820.21	3
HESPERIIDAE	<i>Hesperia attalus</i>	1,004,283.48	3
LYCAENIDAE	<i>Phaeostrymon alcestis</i>	1,040,109.38	3
HESPERIIDAE	<i>Hesperia meskei</i>	1,040,418.23	3
LYCAENIDAE	<i>Lycaena cupresus</i>	1,048,525.38	3
PIERIDAE	<i>Artogeia virginiensis</i>	1,068,368.61	3
HESPERIIDAE	<i>Ywretta rhesus</i>	1,075,085.96	3
HESPERIIDAE	<i>Poanes massasoit</i>	1,112,919.35	3
HESPERIIDAE	<i>Amblyscirtes eos</i>	1,121,721.41	3
HESPERIIDAE	<i>Poanes yehi</i>	1,134,152.38	3
NYMPHALIDAE	<i>Phyciodes pallida</i>	1,150,135.06	3
HESPERIIDAE	<i>Pholisora libya</i>	1,150,984.38	3

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
NYMPHALIDAE	<i>Speyeria edwardsii</i>	1,152,528.60	3
HESPERIIDAE	<i>Amblyscirtes aenus</i>	1,169,206.17	3
NYMPHALIDAE	<i>Speyeria egleis</i>	1,190,902.46	3
HESPERIIDAE	<i>Polites draco</i>	1,238,232.81	3
HESPERIIDAE	<i>Euphyes conspicua</i>	1,240,626.35	3
NYMPHALIDAE	<i>Neonympha areolata</i>	1,258,076.03	3
LYCAENIDAE	<i>Lycaena nivalis</i>	1,264,561.76	3
NYMPHALIDAE	<i>Boloria epithore</i>	1,273,827.08	3
NYMPHALIDAE	<i>Erebia magdalena</i>	1,312,200.95	3
HESPERIIDAE	<i>Erynnis telemachus</i>	1,341,772.76	3
PAPILIONIDAE	<i>Parnassius clodius</i>	1,353,045.56	3
HESPERIIDAE	<i>Erynnis lucilius</i>	1,353,894.89	3
NYMPHALIDAE	<i>Lethe portlandia</i>	1,377,984.72	3
HESPERIIDAE	<i>Amblyscirtes oslari</i>	1,399,449.38	3
LYCAENIDAE	<i>Satyrium californica</i>	1,411,725.92	3
LYCAENIDAE	<i>Satyrium behrii</i>	1,415,895.32	3
HESPERIIDAE	<i>Hesperopsis alpheus</i>	1,416,744.64	3
HESPERIIDAE	<i>Pyrgus ruralis</i>	1,417,130.69	3
HESPERIIDAE	<i>Amblyscirtes aesculapius</i>	1,423,925.26	3
NYMPHALIDAE	<i>Limenitis lorquini</i>	1,439,599.10	3
HESPERIIDAE	<i>Hesperia viridis</i>	1,443,305.22	3
NYMPHALIDAE	<i>Chlosyne palla</i>	1,451,952.86	3
HESPERIIDAE	<i>Problema byssus</i>	1,475,347.79	3

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
NYMPHALIDAE	<i>Lethe creola</i>	1,477,200.85	3
LYCAENIDAE	<i>Callophrys irus</i>	1,506,541.03	3
LYCAENIDAE	<i>Plebejus shasta</i>	1,555,570.02	3
NYMPHALIDAE	<i>Speyeria hydaspe</i>	1,557,809.14	3
NYMPHALIDAE	<i>Chlosyne leanira</i>	1,614,713.64	3
LYCAENIDAE	<i>Satyrium caryaevorus</i>	1,617,338.82	3
LYCAENIDAE	<i>Satyrium saepium</i>	1,618,574.19	3
HESPERIIDAE	<i>Hesperia ottoe</i>	1,626,218.08	3
NYMPHALIDAE	<i>Cercyonis sthenele</i>	1,693,237.23	3
HESPERIIDAE	<i>Hesperia pahaska</i>	1,697,252.20	3
LYCAENIDAE	<i>Euphilote enoptes</i>	1,727,055.65	3
NYMPHALIDAE	<i>Speyeria coronis</i>	1,734,004.64	3
HESPERIIDAE	<i>Thorybes confusus</i>	1,755,546.51	3
HESPERIIDAE	<i>Polites sabuleti</i>	1,755,932.56	3
HESPERIIDAE	<i>Hesperia sassacus</i>	1,756,241.41	3
LYCAENIDAE	<i>Lycaena heteronea</i>	1,782,801.99	3
PAPILIONIDAE	<i>Papilio indra</i>	1,794,229.22	3
LYCAENIDAE	<i>Callophrys sheridanii</i>	1,806,042.50	3
LYCAENIDAE	<i>Euphilotes battoides</i>	1,816,697.62	3
HESPERIIDAE	<i>Pyrgus scriptura</i>	1,817,469.73	3
HESPERIIDAE	<i>Hesperia nevada</i>	1,834,610.57	3
NYMPHALIDAE	<i>Limenitis weidemeyerii</i>	1,912,593.68	3
LYCAENIDAE	<i>Lycaena mariposa</i>	1,923,943.70	3

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
LYCAENIDAE	<i>Calycopis cecrops</i>	1,926,954.93	3
NYMPHALIDAE	<i>Chlosyne harrisii</i>	1,931,896.43	3
HESPERIIDAE	<i>Atrytone arogos</i>	1,945,639.99	3
NYMPHALIDAE	<i>Neominois ridingsii</i>	1,971,814.52	3
LYCAENIDAE	<i>Lycaena rubidus</i>	1,978,145.82	3
NYMPHALIDAE	<i>Euphydryas editha</i>	1,981,774.74	3
HESPERIIDAE	<i>Euphyes bimacula</i>	2,006,791.10	3
LYCAENIDAE	<i>Glaucopsyche piasus</i>	2,029,259.50	3
LYCAENIDAE	<i>Satyrium sylvinus</i>	2,081,531.35	3
PAPILIONIDAE	<i>Papilio eurymedon</i>	2,081,608.56	3
PIERIDAE	<i>Pieris chlorodice</i>	2,093,421.84	3
HESPERIIDAE	<i>Hesperia juba</i>	2,110,331.05	3
NYMPHALIDAE	<i>Oeneis uhleri</i>	2,137,200.48	3
LYCAENIDAE	<i>Callophrys affinis</i>	2,139,439.60	3
PIERIDAE	<i>Anthocharis midea</i>	2,146,465.80	3
NYMPHALIDAE	<i>Speyeria idalia</i>	2,166,772.29	3
HESPERIIDAE	<i>Poanes viator</i>	2,168,934.20	3
PIERIDAE	<i>Euchloe hyantis</i>	2,176,269.25	3
PAPILIONIDAE	<i>Eurytides marcellus</i>	2,185,225.72	3
NYMPHALIDAE	<i>Nymphalis californica</i>	2,209,933.24	3
NYMPHALIDAE	<i>Oeneis macounii</i>	2,228,155.04	3
HESPERIIDAE	<i>Ochlodes sylvanoides</i>	2,274,404.43	3
HESPERIIDAE	<i>Hesperia metea</i>	2,297,799.36	3
PIERIDAE	<i>Neophasia menapia</i>	2,364,123.61	3

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
HESPERIIDAE	<i>Nastra lherminier</i>	2,390,915.83	3
NYMPHALIDAE	<i>Lethe appalachia</i>	2,395,394.06	3
NYMPHALIDAE	<i>Cercyonis oetus</i>	2,410,913.48	3
HESPERIIDAE	<i>Staphylus hayhurstii</i>	2,428,826.43	3
LYCAENIDAE	<i>Lycaena epixanthes</i>	2,469,671.05	3
NYMPHALIDAE	<i>Speyeria callippe</i>	2,534,991.55	3
NYMPHALIDAE	<i>Boloria napaea</i>	2,545,569.46	3
LYCAENIDAE	<i>Plebejus icarioides</i>	2,691,498.25	4
HESPERIIDAE	<i>Achalarus lyciades</i>	2,697,983.97	4
NYMPHALIDAE	<i>Chlosyne gabbii</i>	2,758,440.19	4
NYMPHALIDAE	<i>Euphydryas phaeton</i>	2,772,106.53	4
HESPERIIDAE	<i>Pompeius verna</i>	2,812,565.10	4
LYCAENIDAE	<i>Satyrium edwardsii</i>	2,840,669.90	4
PAPILIONIDAE	<i>Papilio troius</i>	2,849,780.80	4
HESPERIIDAE	<i>Euphyes dion</i>	2,911,240.76	4
HESPERIIDAE	<i>Erynnis baptisiae</i>	3,022,579.02	5
LYCAENIDAE	<i>Fixsenia favonius</i>	3,029,528.01	5
LYCAENIDAE	<i>Apodemia mormo</i>	3,034,392.30	5
PIERIDAE	<i>Euchloe creusa</i>	3,037,866.80	5
HESPERIIDAE	<i>Erynnis martialis</i>	3,039,333.80	5
HESPERIIDAE	<i>Amblyscirtes hegon</i>	3,083,189.65	6
PIERIDAE	<i>Colias pelidne</i>	3,116,930.86	6
HESPERIIDAE	<i>Poanes zabulon</i>	3,189,045.93	6

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
PIERIDAE	<i>Euchloe olympia</i>	3,197,230.30	6
HESPERIIDAE	<i>Thorybes bathyllus</i>	3,251,278.00	6
HESPERIIDAE	<i>Hesperia leonardus</i>	3,314,668.23	6
HESPERIIDAE	<i>Erynnis horatius</i>	3,347,328.48	6
LYCAENIDAE	<i>Satyrrium acadica</i>	3,351,034.61	6
PAPILIONIDAE	<i>Papilio zeicaon</i>	3,365,859.12	6
NYMPHALIDAE	<i>Speyeria mormonia</i>	3,441,989.17	6
PIERIDAE	<i>Anthocharis sara</i>	3,475,035.48	6
PAPILIONIDAE	<i>Parnassius phoebus</i>	3,490,091.62	6
HESPERIIDAE	<i>Polites origenes</i>	3,512,328.39	6
NYMPHALIDAE	<i>Phyciodes batesii</i>	3,557,419.61	6
LYCAENIDAE	<i>Callophrys henrici</i>	3,620,809.85	6
HESPERIIDAE	<i>Atrytonopsis hianna</i>	3,699,951.12	6
LYCAENIDAE	<i>Plebejus optilete</i>	3,738,633.83	6
NYMPHALIDAE	<i>Lethe anthedon</i>	3,760,175.70	6
LYCAENIDAE	<i>Lycaena xanthoides</i>	3,779,246.82	6
NYMPHALIDAE	<i>Euphydryas chalcedona</i>	3,814,532.24	6
NYMPHALIDAE	<i>Erebia epipsodea</i>	3,858,156.46	6
NYMPHALIDAE	<i>Lethe eurydice</i>	3,943,320.19	6
LYCAENIDAE	<i>Feniseca tarquinius</i>	3,966,637.91	6
PIERIDAE	<i>Pieris sisymbrii</i>	3,979,300.52	6
LYCAENIDAE	<i>Lycaena dorcas</i>	4,197,344.38	6
NYMPHALIDAE	<i>Chlosyne gorgone</i>	4,217,959.72	6
NYMPHALIDAE	<i>Polygona comma</i>	4,430,212.76	6

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
LYCAENIDAE	<i>Satyrrium calanus</i>	4,434,613.79	6
HESPERIIDAE	<i>Polites mystic</i>	4,515,608.12	6
LYCAENIDAE	<i>Lycaena hyllus</i>	4,553,441.51	6
HESPERIIDAE	<i>Poanes hobomok</i>	4,652,039.96	6
LYCAENIDAE	<i>Callophrys niphon</i>	4,689,718.93	6
NYMPHALIDAE	<i>Megisto cymela</i>	4,714,580.87	6
PIERIDAE	<i>Colias alexandra</i>	4,829,393.63	6
LYCAENIDAE	<i>Plebejus melissa</i>	4,838,041.26	6
HESPERIIDAE	<i>Ancyloxypha numitor</i>	4,944,438.02	6
PIERIDAE	<i>Colias interior</i>	4,988,448.29	6
PIERIDAE	<i>Colias scudderii</i>	5,016,398.67	6
NYMPHALIDAE	<i>Speyeria aphrodite</i>	5,018,406.16	6
NYMPHALIDAE	<i>Oeneis polyxenes</i>	5,038,017.75	6
PIERIDAE	<i>Colias nastes</i>	5,101,562.40	6
NYMPHALIDAE	<i>Chlosyne nycteis</i>	5,216,375.16	6
LYCAENIDAE	<i>Callophrys eryphron</i>	5,262,624.55	6
LYCAENIDAE	<i>Callophrys polios</i>	5,484,451.75	6
PIERIDAE	<i>Euchloe ausonides</i>	5,741,873.23	6
NYMPHALIDAE	<i>Oeneis chryxus</i>	5,836,919.97	6
LYCAENIDAE	<i>Satyrrium lyparops</i>	5,841,707.05	6
NYMPHALIDAE	<i>Speyeria cybele</i>	5,855,450.61	6
NYMPHALIDAE	<i>Polygona satyrus</i>	6,040,062.11	6
HESPERIIDAE	<i>Erynnis persius</i>	6,070,946.51	6

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
LYCAENIDAE	<i>Callophrys gryneus</i>	6,241,505.61	6
NYMPHALIDAE	<i>Boloria bellona</i>	6,382,878.95	6
HESPERIIDAE	<i>Polites peckius</i>	6,509,041.72	6
NYMPHALIDAE	<i>Phyciodes morpheus</i>	6,637,829.67	6
NYMPHALIDAE	<i>Polygonia progne</i>	6,784,453.36	6
HESPERIIDAE	<i>Epargyreus clarus</i>	6,798,969.03	6
LYCAENIDAE	<i>Harknclenus titus</i>	6,809,392.51	6
HESPERIIDAE	<i>Polites themistocles</i>	6,919,649.82	6
HESPERIIDAE	<i>Euphyes ruricola</i>	6,924,900.17	6
PAPILIONIDAE	<i>Papilio machaon</i>	7,039,172.45	6
HESPERIIDAE	<i>Erynnis icelus</i>	7,145,337.57	6
PIERIDAE	<i>Pieris callidice</i>	7,351,645.37	6
HESPERIIDAE	<i>Amblyscirtes vialis</i>	7,359,134.83	6
HESPERIIDAE	<i>Carterocephalus palaemon</i>	7,433,643.45	6
NYMPHALIDAE	<i>Speyeria atlantis</i>	7,475,723.44	6
LYCAENIDAE	<i>Plebejus idas</i>	7,659,948.89	6
NYMPHALIDAE	<i>Boloria eunomia</i>	7,802,094.34	6
LYCAENIDAE	<i>Everes amyntula</i>	7,814,756.94	6
NYMPHALIDAE	<i>Polygonia faunus</i>	7,827,805.60	6
LYCAENIDAE	<i>Callophrys augustus</i>	7,894,361.48	6
LYCAENIDAE	<i>Lycaena helloides</i>	7,961,843.90	6
LYCAENIDAE	<i>Plebejus saepiolus</i>	8,076,116.18	6
NYMPHALIDAE	<i>Polygonia gracilis</i>	8,097,271.99	6

APPENDIX 7.2 *Continued*

FAMILY	SPECIES	GEOGRAPHICAL RANGE SIZE (KM ²)	AGGREGATION NUMBER
NYMPHALIDAE	<i>Cercyonis pegala</i>	8,176,953.74	6
NYMPHALIDAE	<i>Aglais milberti</i>	8,342,571.34	6
NYMPHALIDAE	<i>Boloria selene</i>	9,092,676.20	6
NYMPHALIDAE	<i>Limenitis arthemis</i>	9,094,606.48	6
LYCAENIDAE	<i>Glaucopsyche lygdamus</i>	10,210,305.43	7
NYMPHALIDAE	<i>Coenonympha tullia</i>	10,403,332.93	7
PAPILIONIDAE	<i>Papilio glaucus</i>	12,537,676.60	7