Hummingbird Conservation: Discovering Diversity Patterns in Southwest U.S.A.

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Abstract—*Using data obtained in 2002 and 2003 from sites in the Hummingbird Monitoring Network, we investigated the effect of geographic factors—latitude, longitude, and elevation—and year on hummingbird diversity patterns in Southwestern U.S.A. In California, none of these factors affected hummingbird richness but elevation significantly affected abundance. In southeastern Arizona, longitude and elevation significantly affected richness; year affected abundance. For all sites, elevation and longitude affected richness, year and elevation affected abundance. We compared these results with global hummingbird diversity patterns and suggest that the distribution of forest and rainfall patterns are likely important factors for conserving hummingbird diversity and abundance.*

Introduction

The north end of the Madrean Archipelago region of southeastern Arizona has the greatest number of hummingbird species in the United States and Canada (Johnsgaard 1983). Hummingbirds occur only in the New World and are the second most diverse family of birds there (Schuchmann 1999). Their distribution shows a strong latitudinal gradient (Greenewalt 1960) where the highest numbers of species live in the tropics. As one travels either north or south of the equator, hummingbird richness, defined as the number of hummingbird species in an area, declines (figure 1). Ecuador lies along the equator, is about the size of Colorado, and has 130 species (Ortiz Crespo 2003). Southeastern Arizona at latitudes between 31°N and 33°N has 15 regularly occurring species (Tucson Audubon Society 1995). Based upon this latitudinal distribution pattern, other regions farther south in the United States should be more likely candidates for this northern diversity center. Yet, south Texas has only nine and Big Bend National Park has ten regularly occurring hummingbird species.

In addition to richness, diversity is measured by the abundances of species in a region. This second component to diversity is poorly understood for hummingbirds (Schuchmann 1999). One reason for this missing knowledge is that techniques used to monitor other land birds fail to adequately monitor hummingbird populations (Rich et al. 2003). Two studies in southeastern Arizona (Wethington and Russell 2003; Wethington et al., in press) show that sites there support large numbers of hummingbirds, particularly during southbound migration. Thus, southeastern Arizona supports high richness and high abundance for North America. Identifying factors that make this region an important diversity center for hummingbirds is important for their conservation in the Madrean Archipelago region.

The Hummingbird Monitoring Network (HMN) is a group of scientists, citizens, land managers, and property owners who are committed to maintaining the diversity and abundance of hummingbirds. We began monitoring hummingbird populations in Arizona and California in 2002 (figure 2) with the following research goals. (1) To determine the best long-term monitoring sites for hummingbirds in Western United States and Northwestern Mexico; (2) to effectively sample their

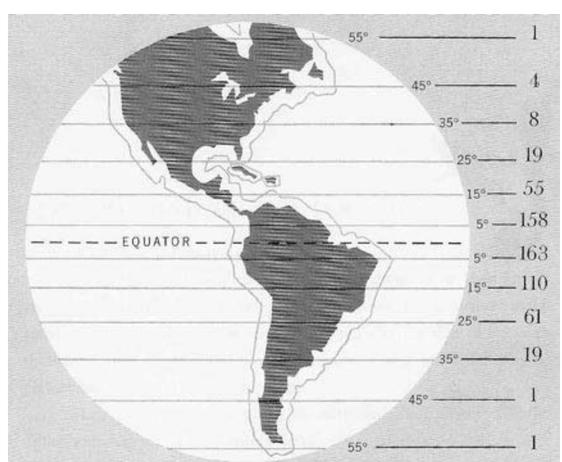

Figure 1—Map of the number of hummingbird species occurring at different latitudes (Greenewalt 1960).

Figure 2—General location of HMN's monitoring sites in California and Arizona.

populations sizes to detect trends; and (3) to use the resulting information for hummingbird conservation. Our research is a systematic banding study that generates knowledge about hummingbird diversity, abundance, productivity, and survivorship at a number of sites. We choose monitoring sites based upon geographic factors, such as elevation, longitude, and latitude, and vegetation types. Thus, HMN provides information about areas that support a high diversity and abundance of hummingbirds and that are important for breeding and migration success. HMN also tracks the timing of hummingbird occurrence and their seasonal movement patterns. This paper describes diversity patterns discovered during our first two field seasons and then discusses possible implications of these patterns.

Study Sites and Methodology

Study Sites

Table 1 describes HMN's monitoring sites. In 2002, there were nine in Arizona, two in California. In 2003, we expanded to 13 in Arizona and five in California. Six sites in Arizona and two in California were monitored during both years. Sites were classified into elevation, latitude, and longitude classes.

Monitoring Protocol

At least five commercial hummingbird feeders with a sugar solution of one part sugar to four parts water were maintained at each site while hummingbirds were present. At sites where feeder number could not be controlled, the number of feeders in the area was recorded. Hummingbirds were trapped and banded once every two weeks from early March to late October. Trapping and banding began within one half-hour of sunrise and continued for five hours, but was delayed if the temperature was below 38 °F. We used two Hall traps (Russell and Russell 2001) that each covered one feeder. The other feeders were taken down and were not accessible to hummingbirds during the banding period. At the banding table, birds were identified, aged, and sexed in chronological order and were held no longer than 30 minutes. The bander determined how many birds that he/she could safely band within this time limit. When the number of birds waiting to be processed was reached, the bander requested the trappers to stop trapping. While they were not actively catching birds, they recorded the number of birds that entered the trap. They also recorded all birds that escaped while actively trapping.

Statistical Analyses

We used the numbers of hummingbird species captured and observed at a site during a monitoring session and the daily estimated abundance of individuals to identify hummingbird diversity patterns. The abundance estimate includes both the number of individuals captured and one-tenth the number of birds counted at the trap but not captured. We assumed that hummingbirds fed once every 30 minutes and that the feeders were their sole source of nectar. Thus, one hummingbird would visit a feeder 10 times during a monitoring session (2 visits/hour * 5 hours). We used ANOVA to determine which geographic factor—elevation, latitude, and longitude—and if year affected the estimated abundance and species richness values among our sites. We used a standard $P < 0.05$ to indicate statistical significance. Values presented are means ± SD. All analyses were done with AXUM 6.0.

Results

We ran two sets of ANOVA analyses on the monitoring data. In the first set, the data for dependent variables—species richness and estimated abundance—were taken from each monitoring day at each site. This provided large sample sizes, included all the variability in the data, and had high statistical power. For the second set of analyses, we averaged the dependent variables from each site and year. This eliminated much of the variability encountered at a site within a year but likely provided statistical significance values that are more realistic. The mean values for species richness and estimated abundance were essentially equal in both analyses.

In California, where sample sizes are small, geographic factors and year had no significant effect on richness, but elevation significantly affected the estimated abundance (table 2, figures 3 and 4). Richness averaged 3.1 ± 1.3 species for all geographic and year classes. The average estimated abundance varied by elevation and averaged 27.1 ± 19.8 individuals (n = 58) at low elevations and 81.3 ± 53.5 (n = 30) at mid elevations.

In Arizona, elevation and longitude significantly affected richness (table 2, figures 3 and 4). With increased statistical power, year also had an effect. Mid elevation sites in the western Arizona longitudinal class (table 1) had the highest species richness. In 2002, species richness was 6.1 ± 2.1 (n = 28) and in 2003, 5.3 ± 2.1 (n = 62). Low elevation sites had 3.5 ± 1 (n = 12) and 2.8 ± 1 (n = 32) species in 2002 and 2003, respectively. High elevation sites had 3.5 ± 1.7 (n = 10) and 2.8 ± 1.4 (n = 12). At the eastern HMN Arizona sites, richness at mid-elevation sites was 4.2 ± 1.5 (n = 36)

Table 1—Description of HMN monitoring site. The geographic factors—elevation, latitude, and longitude—and vegetation type are given for each site. The years of monitoring, the number of monitoring days, and the number of days defined as migration days are also provided. A migration day is defined if there were more than 100 trap visits within a monitoring session. The number of migration days directly affects the estimated abundance for a site. Each site is also classified into different geographic classes. We defined three elevation, three longitude, and three latitude classes. Low elevation sites occur at less than 1,200 m; mid elevation sites between 1,200 m and 1,800 m; and high elevation site over 1,800 m. Ranges of latitude defined these classes. The most southern sites occur between 31° and 32°, the next between 32° and 33°, and the most northern class between 33°00″ and 34°30″. Longitudinal classes fall within the following ranges: Eastern Arizona sites between 109° and 110°30″, Western Arizona sites between 110°30″ and 111°40″, and California sites between 116° and 117°30″.

Monitoring sites	Monitoring years		Monitoring days 2002	Monitoring days 2003	Migration days 2002	Migration days 2003	Elevation (m)	Elevation	Longitude	Dominant vegetation type
ARIZONA – Eastern Sites										
TNC Aravaipa Canyon	2002	2003	13	13	1	1	1,001	32°52	110°24	Desert Riparian
Private Residence, Klondyke	2002	2003	11	13	3	0	1,065	32°51	110°20	Mesquite/Grasslands
Private Residence, Fort Grant	2002	2003	13	14	6	1	1,496	32°37	109°56	Mesquite/Grasslands Oak/Riparian nearby
Private Residence, Rock Creek	2002		10		1		1,526	31°53	109°28	Oak/Mesquite/ Riparian
NPS Chiricahua Nat'l Mon.		2003		14		1	1,616	32°00	109°21	Oak/Pine
Private Residence, Paradise	2002	2003	12	13	4	2	1,688	31°56	109°13	Riparian/Oak/Pine
USFS Visitor Center, Mt Graham		2003		8		0	2,870	32°42	109°54	Pine/Fir
ARIZONA – Western Sites										
Tohono Chul Park		2003		14		0	765	32°20	110°58	Desert/Garden
Tanque Verde Guest Ranch, Tucson	2002		12		0		840	32°14	110°41	Desert/Mesquite Riparian nearby
NPS Tumacacori Hist. Park		2003		17		7	975	31°34	111°02	Mesquite/Riparian
NPS Coronado Nat'l Mem.		2003		16		0	1,615	31°20	110°15	Oak/Pine
Chuparossa Inn, Madera Canyon	2002	2003	14	16	1	0	1,621	31°42	110°52	Riparian/Oak/Pine
TNC Ramsey Canyon Preserve		2003		16		0	1,686	31°26	110°18	Riparian/Oak/Pine
Private Residence, Miller Canyon	2002	2003	14	15	3	3	1,745	31°25	110°17	Orchard/Oak/Pine/ Riparian
NOAO Kitt Peak Observatory		2003		12		4	2,065	31°57	111°35	Juniper/Oak
Private Residence, Summerhaven	2002		9		5		2,420	32°26	110°45	Pine/Fir
CALIFORNIA										
UC Motte Rimrock Reserve,		2003		16		1	350	33°48	117°15	Desert Scrub
BLM Big Morongo		2003		16		0	805	34°03	116°34	Mesquite
Private Residence, Yucca Valley	2002	2003	11	15	0	0	1,030	34°07	116°28	Desert Scrub
NAS Bear Paw Sanctuary		2003		9		3	1,358	34°06	116°58	Oak/Pine
Private Residence, San Jacintor Mtns.	2002	2003	9	12	3	5	1,405	33°35	116°36	Pine

and 4 ± 1.5 (n = 41) species in 2002 and 2003, at low elevation sites, 3.2 ± 1.3 (n = 23) and 2.7 ± 1.2 (n = 26) and at high elevations 2.4 ± 0.9 (n = 9) in 2003. There were no high elevation sites in 2002.

Year significantly affected abundance estimates at sites in Arizona (table 2, figures 3 and 4). Low elevation sites averaged 31.5 ± 19.6 individuals (n = 35 days) in 2002 and 29.4 ± 32.8 (n = 58) in 2003. Mid elevation sites averaged 75.6 ± 54.4 (n = 64) in 2002 and 34.4 ± 34.9 (n = 103) in 2003. High elevation sites averaged 75.7 ± 54.4 (n = 10) in 2002 and 44.1 ± 60.8 (n = 21) in 2003. At the eastern Arizona high elevation site in 2003, the abundance values likely underestimated the population since feeders ran dry often.

When all sites are combined, the results for species richness is dominated by the Arizona patterns. The results for estimated abundance shows both elevation, which was significant in California, and year, which was significant in Arizona, as significant factors (table 2).

Table 2—Results of the ANOVA analyses. Two sets of analyses were done. In the first set, hummingbird richness and estimated abundances were averaged for each site in each year. In the second set, the richness and estimated abundances were evaluated from data taken from each monitoring day at each site. The factors that showed significant effects are in bold.

			Species richness						Estimated abundance					
			Averaged values per site per year			Values per monitoring day			Averaged values per site per year			Values per monitoring day		
Sites	**Factors**	**DF**	**n**	**f stat**	**p**	**n**	**f stat**	**p**	**n**	**f stat**	**p**	**n**	**f stat**	**p**
All sites			29			379			29			379		
	Elevation	2		7.74	**<0.01**		44.2	**<0.001**		4.63	**<0.03**		16.9	**<0.001**
	Longitude	2		5.28	**<0.02**		18.7	**<0.001**		0.97	>0.39		2.52	>0.08
	Latitude	2		0.30	>0.58		1.76	>0.18		1.09	>0.30		2.57	>0.11
	Year	1		2.17	>0.15		8.83	**<0.01**		4.86	**<0.04**		22.5	**<0.001**
California			7			88			7			88		
	Elevation	1		0.01	>0.91		0.00	>0.96		41.2	**<0.01**		47.2	**<0.001**
	Year	1		0.07	>0.80		0.04	>0.83		0.45	>0.54		0.34	>0.55
Arizona			22			291			22			291		
	Elevation	2		8.22	**<0.01**		44.4	**<0.001**		1.90	>0.18		7.33	**<0.001**
	Longitude	1		6.31	**<0.03**		24.1	**<0.001**		0.33	>0.57		0.94	>0.33
	Latitude	1		0.09	>0.77		0.15	>0.70		0.17	>0.68		0.17	>0.68
	Year	1		2.09	>0.16		8.72	**<0.01**		7.01	**<0.02**		30.0	**<0.001**

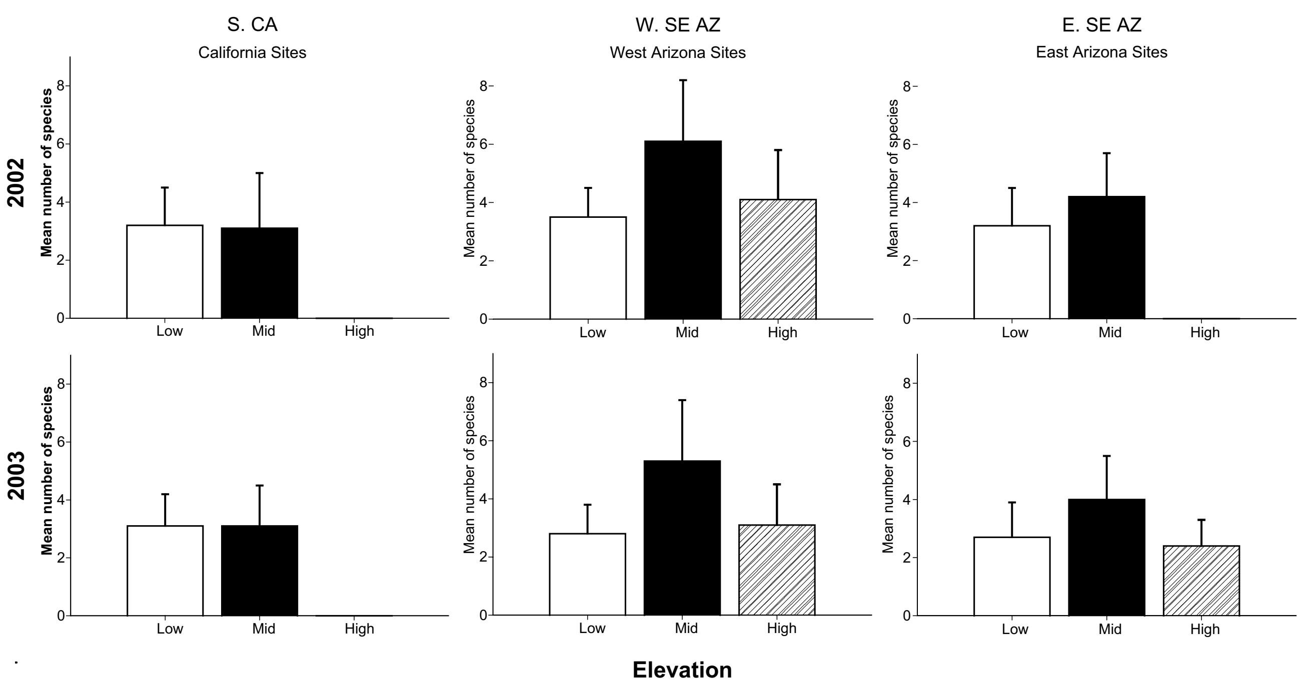

Figure 3—Species richness distributions for hummingbirds at HMN monitoring sites. Each graph shows results of each longitude, elevation, and year class. Mean richness values (± SD) are shown. Geographic factors and year had no significant effect on richness in California. In Arizona elevation and longitude significantly affected richness.

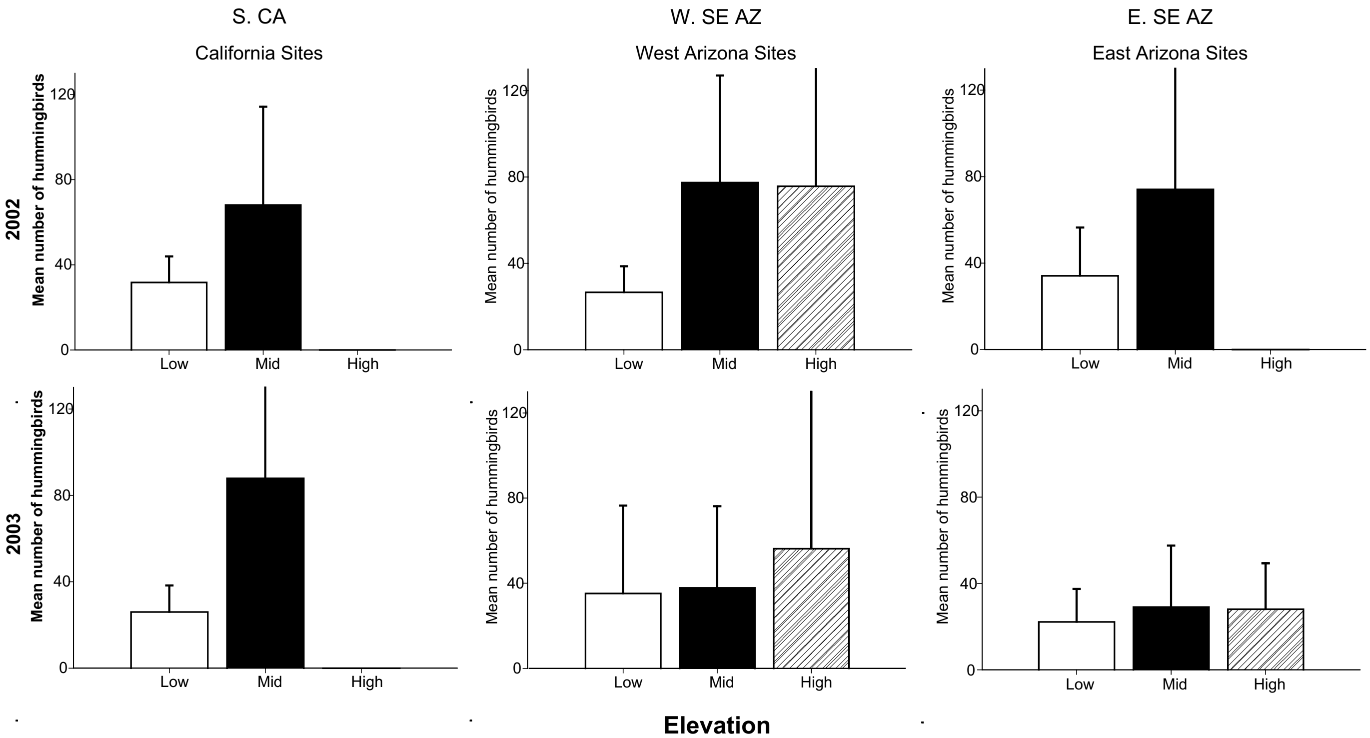

Figure 4—Estimated abundances for hummingbirds at HMN monitoring sites. Each graph shows results of each longitude, elevation, and year class. Mean abundance values (± SD) are shown. Elevation affected abundance in California and year in Arizona.

Discussion

A central goal of conservation is to preserve areas that represent and maintain the diversity of a region (Cabeza and Moilanen 2001; Margules and Pressey 2000). Thus, effective conservation of hummingbirds requires an understanding of factors that promote their diversity and of areas that currently are important for breeding and migration success. The diversity patterns that we identify at the northern end of hummingbird diversity are likely affected by their global patterns emanating from the neotropics. For example, the number of hummingbird species in the neotropics is greatest in the humid forests at elevations between 1,800 and 2,500 m (Schuchmann 1999). Areas lower in elevation but still in moist forest habitats also support high hummingbird richness (Becker and Lopez 1997).

Our results indicate that elevation significantly affects hummingbird richness at their northern center of diversity. The elevations with the highest species richness at HMN sites ranged from 1,500 m to 1,800 m. Both the tropical and temperate elevations where hummingbird richness is greatest occur at middle elevations.

Latitude affects hummingbird diversity throughout the New World, but did not influence species richness or abundance at HMN sites. The latitudes at our sites differ by only three degrees. It is likely that this latitudinal pattern of diversity occurs at larger spatial scales than our study.

Longitude significantly affected hummingbird richness at HMN sites. Yet, this geographic factor has not been identified as a factor in a global diversity pattern for hummingbirds. This unexpected longitudinal effect occurred within Arizona as well as across all our sites. More species occurred in the western Madrean Archipelago region of southeastern Arizona than in the eastern area or in California. HMN western sites in Arizona occurred from the Baboquiviri Mountains in the west to the Huachuca Mountains in the east. The eastern sites occurred east of the Huachuca and Santa Catalina Mountains and included sites in or near the Pinaleno and Chiricahua Mountains. Since hummingbirds occur in humid forests of the tropics, rainfall patterns may be a factor in this geographic affect. Using thirty-year average rainfall amounts reported for areas in southeastern Arizona on the NOAA website (www.wrh.noaa.gov/tucson/climate/seaz_new_rainfall_normals.html), annual rainfall at the weather stations near HMN western sites averaged 23.4 inches whereas rainfall near HMN eastern sites averaged 21.3 inches. Although the difference in rainfall might not be significant, the valley between our eastern and western Arizona also indicates a potential difference in moisture availability. In this valley called Sulfur Springs Valley, vegetation from the Chihuahuan Desert meets the vegetation of the Sonoran Desert (MacMahon 1985). On average, the Chihuahuan Desert is drier than the Sonoran Desert, which has two rainy seasons instead of one. Also, the Mojave Desert, a drier desert than the Sonoran Desert, separates HMN's California sites from the forests of the Sierra Madre (MacMahon 1985).

Although hummingbirds live in virtually all habitats, their diversity appears most dependent on forest habitats throughout the Americas. In 1999, twenty-five hummingbird species were listed as threatened or endangered, but none in the United States and Canada. Of these 25, all but two rely on forests for at least one stage of their life history (Schuchmann 1999). In the Madrean Archipelago region, the mid-elevation range, which supports the greatest number of species, also supports the most diverse forest types. It is likely that maintaining these forest are critical to hummingbird diversity there. A review of the eleven Birds of North America (BNA) accounts for hummingbirds that occur in southeastern Arizona indicate that nine of these species rely on forests for breeding (Baltosser and Russell 2000; Baltosser and Scott 1996; Calder 1993; Calder and Calder 1992, 1994; Powers 1996; Powers and Wethington 1999; Russell 1996; Scott 1994; Wethington 2002; Williamson 2000).

So, why is southeastern Arizona the northern center of hummingbird diversity and not south Texas or Big Bend National Park? South Texas is near sea level and is not forested. The lack of nearby forests likely eliminates a number of species from south Texas. Additionally, forest and elevation maps of Mexico (URL: http://www.unep-wcmc.org/habitats/mountains/cam.htm) show that the area in Mexico bordering south Texas is low elevation and not forested.

These maps suggest that the region south of Big Bend has similar elevations as the region south of HMN's southeastern Arizona sites, but that these mountain ranges are not forested like the area south of southeastern Arizona. An additional difference between the regions south of Big Bend and southeastern Arizona is rainfall patterns. When hummingbird species distribution and rainfall maps of the New World are compared (figures 5 and 6), correlation between hummingbird species richness and average rainfall emerges for Central and South America. It appears that average rainfall and forests are good predictors for hummingbird richness in forested areas.

The factors affecting hummingbird abundance are much less studied than the distribution of hummingbird species (Schuchmann 1999). Often, the abundance of available food, nectar and insects, is suggested as a major factor affecting the abundance of hummingbirds (see BNA references). In HMN's results, the year of monitoring in Arizona significantly affected the abundance of hummingbirds. This temporal variation of their abundance between years suggests that abundance is likely affected by environmental conditions such as food availability. 2002 and 2003 were years of virtually no winter rains and below normal summer rains in southeastern Arizona. It is likely that nectar resources continued to decline during our monitoring seasons and that lowered nectar resources could have affected abundance values.

This exploration of hummingbird diversity suggests that factors affecting hummingbird diversity throughout the New World help explain patterns discovered at their northern center of diversity and are likely important for maintaining hummingbird diversity in the Madrean Archipelago region. These factors are rainfall patterns and the distribution of forests. By studying diversity patterns for the family of hummingbirds, which are a monophyletic group (Sibley and Ahlquist 1990), the patterns associated with these factors could be investigated. We think that monitoring areas of high diversity for a taxonomic family provides important information such as general habitat requirements for that family. Changing diversity patterns at these sites can also help identify species that might be encountering population threats elsewhere and thus help focus attention. We suggest that it is important to focus monitoring efforts at the family level, in addition to the species level. For as the name implies, the family is the evolutionary reproductive unit required for sustainability.

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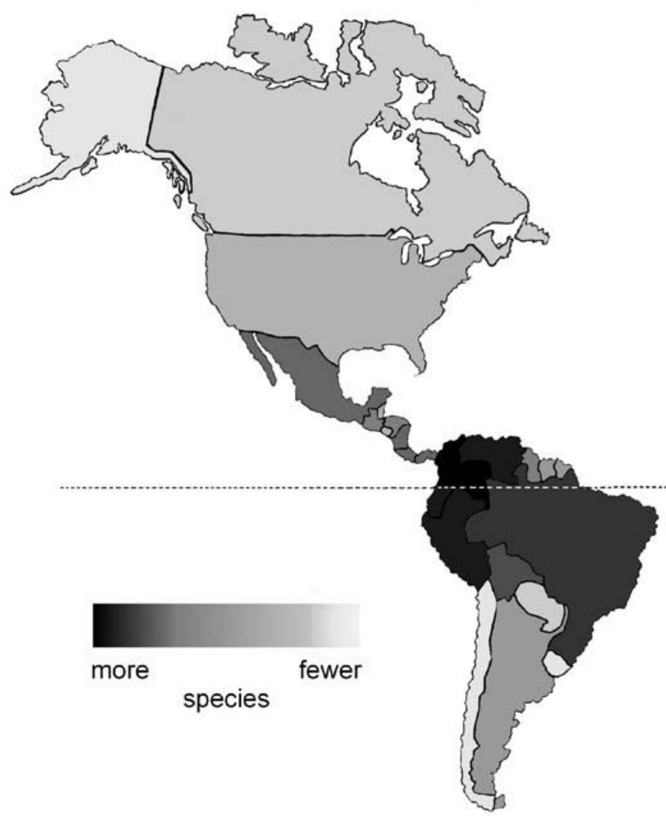

Figure 5—Map of hummingbird richness for North, Central, and South America by country.

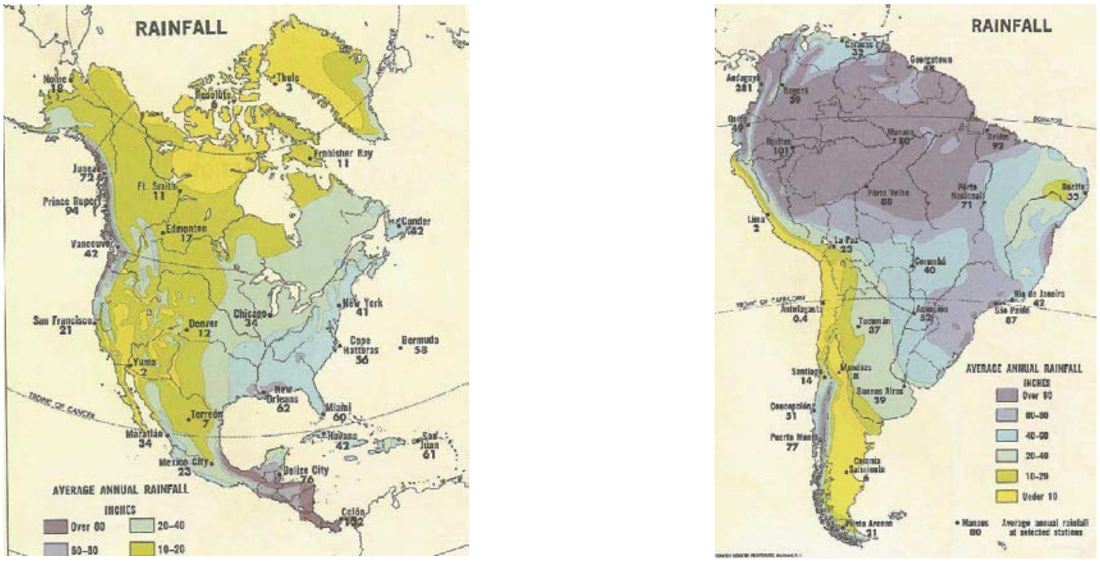

Figure 6—Maps of average annual rainfall for North, Central, and South America (Hamond 1971).

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