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RAPTOR DENSITIES ALONG THE PARAGUAY RIVER: SEASONAL, GEOGRAPHICAL AND TIME OF DAY VARIATION

FLOYD E. HAYES¹

*Museo Nacional de Historia Natural del Paraguay, Sucursal 19, Ciudad Universitaria,
San Lorenzo, Paraguay*

ABSTRACT.—Nineteen species of diurnal raptors were recorded during four censuses from ships along 859 km of the Paraguay River in June, August and October 1988 and January 1989. Seasonal, geographical and time of day variation in linear densities was documented for several of the common species. Most species of non-migratory hunting raptors were most common in June; they may have been exploiting prey concentrated in emergent vegetation when the river was flooded. The Lesser Yellow-headed Vulture (*Cathartes burrovianus*) appeared to be most abundant when water levels were low. Both the Lesser Yellow-headed Vulture and Snail Kite (*Rostrhamus sociabilis*) were more common farther north where marshes were more extensive; the Black Vulture (*Coragyps atratus*) was more common farther south where human habitations were more prevalent. Both the Snail Kite and Crested Caracara (*Polyborus plancus*) were most active in the early morning whereas the Lesser Yellow-headed and Black Vultures were more active at midday.

Densidades poblacionales de aves raptoras a lo largo del río Paraguay: variaciones con la estación, la geografía y la hora del día

EXTRACTO.—Se registraron 19 especies de rapaces diurnas, durante cuatro censos desde barcos, a lo largo de 859 km del río Paraguay durante los meses de junio, agosto y octubre de 1988, y enero de 1989. Se documentó la variación de densidades lineales para algunas especies de rapaces comunes durante diferentes épocas, regiones geográficas y períodos del día. La mayoría de las especies de rapaces cazadoras no-migratorias fue más común en junio; pudiera ser que las rapaces estuvieran explotando presas concentradas en la vegetación emergente cuando el río estaba desbordado. El *Cathartes burrovianus* parecía ser más común cuando los niveles de agua estaban bajos. El *C. burrovianus* y el *Rostrhamus sociabilis* (caracolero) eran más comunes hacia el norte donde los esteros son más extensos; el *Coragyps atratus* resultó ser más común hacia el sur donde los asentamientos humanos prevalecen. El *R. sociabilis* y el *Polyborus plancus* estuvieron más activos temprano por la mañana, mientras que el *C. burrovianus* y el *C. atratus* desplegaron mayor actividad al medio día.

[Traducción de S. Soret]

Few studies have attempted to determine raptor densities in specific areas of South America (e.g., Wilson 1983, Albuquerque 1986, Thiollay 1989a, 1989b). In view of the accelerating rate of habitat destruction on the continent, information on raptor populations is urgently needed in order to monitor

the long-term responses of raptor populations to changing environmental conditions and to design protected areas large enough to maintain viable populations.

The status and distribution of raptors in the Republic of Paraguay, a land-locked country in south-central South America, have been summarized recently by Contreras et al. (1987). However, most of their data were obtained from published records and

¹ Present address: Department of Natural Sciences, Loma Linda University, Loma Linda, CA 92350.

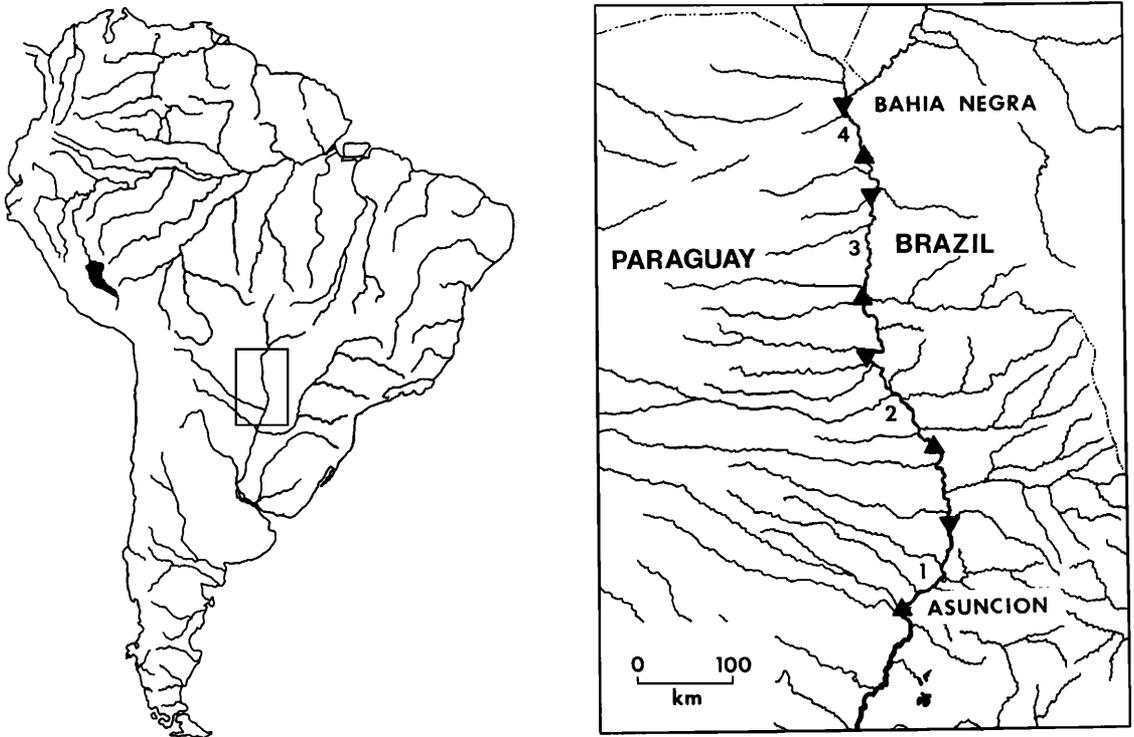


Figure 1. Major South American river systems, and Paraguay River (inset) showing the locations of geographical sectors 1-4.

museum specimens, with little information given on the actual abundance of raptors based on field work. Here I report data on raptor densities along the Paraguay River based on censuses conducted from ships during 1988 and 1989. I examine variation in raptor densities during different seasons, in different geographical areas and during different periods of the day, and discuss the factors that may cause variation.

STUDY AREA

Originating from surface waters in the Pantanal region of Brazil, the Paraguay River flows southward through central South America until it forms the La Plata River at its confluence with the Paraná River (Fig. 1). The La Plata River basin, which encompasses both the Paraguay and Paraná River basins, constitutes the largest and most important watershed of South America south of the Amazon River, draining an area of approximately 3 100 100 km² (Anonymous 1985). The Paraguay River is relatively shallow and sluggish. Its depth and width vary considerably; at a given locality, extremes in water levels during a single year may exceed 5 m and the width may vary from several hundred m to several km.

Compared with most river systems whose levels fluctuate directly with the quantity of precipitation, the Paraguay River is enigmatic; water levels are maximal during the dry winter months, from May to August, and are minimal during the rainy summer months, from November to February. This inversion of the typical pattern for rivers results partly from the seasonal pattern of rainfall at the river's sources, and partly from the inability of the river's drainage system to pass along immediately the large volumes of water it receives periodically in the form of precipitation (Anonymous 1985). Flooding of the river in 1988 reached unprecedented proportions along many sections of the river; it was the highest ever at Bahía Negra and the second highest at Asunción (Dirección de Hidrografía, unpubl. data).

The habitats along the margins of the Paraguay River comprise sandbars and mudflats when water levels are low, grassy marshes, brush-choked channels and ponds of variable sizes, wet or dry palm savannas, natural and man-made grasslands and subtropical riparian deciduous forest. As one proceeds northward from Asunción the river gradually narrows, becomes increasingly subdivided by channels, marshes bordering the river become more extensive and human habitations along the banks of the river become more widely spaced apart. Although human habitations are scattered along the entire length of the river, most of

Table 1. Dates, minutes of observation, kilometers surveyed, ship speed (km/hr) and water levels (cm) during four transects along the Paraguay River.

TRANSECT DATES	MIN OF OBS	KM SURVEYED	SHIP SPEED	WATER LEVELS ^a			
				ASUN- CIÓN	CONCEP- CIÓN	FUERTE OLIMPO	BAHÍA NEGRA
14-17 June 1988	580	138.2	14.3	706+	823+	958-	685-
09-11 Aug. 1988	680	159.8	14.1	739-	763-	823-	583-
25-28 Oct. 1988	780	195.0	15.0	425-	417-	432-	298-
24-27 Jan. 1989	870	185.6	12.8	260+	316+	346+	247+

^a Plus sign denotes rising water levels, minus sign denotes falling water levels. The zero mark is arbitrary at each site, hence comparisons between sites are relative rather than exact.

the habitat along the river's banks remains relatively undisturbed and the general appearance of the river remains rural except in small ports and in a few densely populated areas (e.g., Asunción, Concepción, Porto Murtiño and Bahía Negra).

METHODS

From June 1988 to January 1989, I conducted four separate raptor censuses along 859 km of the Paraguay River between Asunción and Bahía Negra (Table 1). While censusing raptors I scanned the forests and sky on both sides of the river by unaided eye or with 7 × 35 binoculars; during 10 min observation periods I counted all raptors seen within 500 m of an observation post situated 8-10 m above the river on the deck of one of the identical passenger ships *Presidente Stroessner* (subsequently renamed *Bahía Negra*) or *Presidente Carlos Antonio López*. The birds were identified by consulting Narosky and Yzurieta (1987). No counts were taken during periods of rain, within 30 min of sunrise or sunset or in areas densely populated by humans (Asunción, Concepción, Porto Murtiño and Bahía Negra). Ship speed (Table 1) was calculated by timing the interval between fixed markers. Because the ship often stopped to embark or unload passengers and supplies, I counted raptors only while the ship was cruising at full speed. Data on water levels were obtained from the Dirección de Hidrografía of the Armada Nacional, in Asunción (Table 1). The taxonomy of raptors follows Altman and Swift (1989).

Linear densities were calculated as the number of birds/10 km of river. To determine whether the densities of birds varied geographically, I compared counts along four different geographical sectors: (1) from Asunción, Dept. Central, to Rosario, Dept. San Pedro; (2) from Puerto Tacurú Pytá, Dept. San Pedro, to Puerto Itapucú Mí, Dept. Concepción; (3) from Puerto Valle Mí, Dept. Concepción, to Fuerte Olimpo, Dept. Alto Paraguay; and (4) from Puerto Mihanovick, Dept. Alto Paraguay, to Bahía Negra, Dept. Alto Paraguay (Fig. 1). I also compared the densities (or detectability) of raptors during six periods of the day: 0600-0800, 0800-1000, 1000-1200, 1200-1400, 1400-1600 and 1600-1800 H.

Kruskal-Wallis tests (H statistic; Zar 1984) were used to compare the density of each species during different seasons, in different geographical sectors and during dif-

ferent periods of the day. Chi-square tests (χ^2 statistic; Zar 1984) were used to compare the number of 10 min count periods in each sector during the four censuses and also the number of count periods in each time period during the four censuses. The binomial test (Zar 1984) was used to compare the maximum density of non-migratory hunting raptor species during different seasons. Species richness was calculated as the number of species recorded during each census. Species diversity during each census was computed using the Shannon diversity index (H' statistic; Zar 1984). The Kruskal-Wallis, chi-square and binomial tests were computed with Statistix software (Heisey and Nimis 1985), using two-tailed probabilities with $\alpha = 0.05$.

RESULTS

Seasonal Variation. Nineteen species of diurnal raptors were recorded during the study. Of these, the densities of seven species varied seasonally (Table 2). The Black Vulture (*Coragyps atratus*), usually the most common raptor, occurred in low densities during the August census. The Lesser Yellow-headed Vulture (*Cathartes burrovianus*) was least common in June and most common in January. The Osprey (*Pandion haliaetus*), a Nearctic migrant (Hayes et al. 1990), was fairly common in October and January and virtually absent during June and August. Although a permanent resident in Paraguay, the Snail Kite (*Rostrhamus sociabilis*) is partially migratory and occurred most commonly in October, when large numbers were migrating southward in loose flocks. The Savanna Hawk (*Heterospizias meridionalis*), Black-collared Hawk (*Busarellus nigricollis*) and Crested Caracara (*Polyborus plancus*) all occurred most commonly in June; Crested Caracaras were also common in October. Two species, the Great Black Hawk (*Buteogallus urubitinga*) and the Roadside Hawk (*Buteo magnirostris*), did not vary seasonally in abundance.

Table 2. Densities, species richness and species diversity of raptors along the Paraguay River during different seasons (1988–1989).

SPECIES	BIRDS/10 KM				
	JUNE	AUG.	OCT.	JAN.	<i>H</i>
Black Vulture	8.25	1.94	8.97	11.10	11.76 ^a
Lesser Yellow-headed Vulture ^c	2.03	3.00	4.21	5.66	14.83 ^a
Osprey	0.07	0	1.13	0.86	25.51 ^b
Gray-headed Kite	0	0.13	0	0	—
Snail Kite	0.43	0.63	27.74	0.75	175.36 ^b
Mississippi Kite	0	0	0.15	0	—
Long-winged Harrier	0.07	0.06	0	0	—
Sharp-shinned Hawk	0	0	0	0.05	—
Crane Hawk ^d	0.22	0.06	+	0	—
Great Black Hawk	0.65	0.50	0.41	0.05	6.38
Savanna Hawk	1.30	0.63	0.31	0.27	16.88 ^a
Black-collared Hawk	0.80	0	0.15	0.16	14.41 ^a
Roadside Hawk	0.65	0.56	0.15	0.22	5.55
Crested Caracara	7.09	3.63	6.26	2.59	26.55 ^b
Yellow-headed Caracara	0.22	0	0.10	0.11	—
Laughing Falcon	0.22	0.13	0	0	—
American Kestrel	0.07	0	0	0	—
Peregrine Falcon	0	0	0	0.05	—
Unidentified	3.62	1.50	1.03	0.75	—
All raptors combined	25.69	12.77	50.62	22.63	—
Species richness	15	12	13	13	—
Species diversity	0.74	0.78	0.58	0.61	—

^a $P < 0.01$.

^b $P < 0.001$.

^c The Turkey Vulture was observed in small numbers (<5) during each census, but because of the difficulty in distinguishing it from the Lesser Yellow-headed Vulture, densities of both species are combined under the latter species.

^d Observed during the October census, but not during an actual 10 min count period.

The densities of 10 raptor species were too low to permit statistical comparisons (Table 2). These included the Turkey Vulture (*Cathartes aura*), Gray-headed Kite (*Leptodon cayanensis*), Mississippi Kite (*Ictinia mississippiensis*), Long-winged Harrier (*Circus buffoni*), Sharp-shinned Hawk (*Accipiter striatus*), Crane Hawk (*Geranoospiza caerulescens*), Yellow-headed Caracara (*Milvago chimachima*), Laughing Falcon (*Herpetotheres cachinnans*), American Kestrel (*Falco sparverius*) and Peregrine Falcon (*Falco peregrinus*). Of these, the Mississippi Kite and probably the Peregrine Falcon are Nearctic migrants (Hayes et al. 1990); all others are permanent residents (F.E. Hayes, unpubl. data). Although data from the Turkey Vulture were combined with the Lesser Yellow-headed Vulture (Tables 2–4), the numbers of the former species were so small that results for seasonal, geographical and time of day

variation in abundance of the Lesser Yellow-headed Vulture should not be affected.

Species richness was greatest in June, and species diversity was greatest during June and August (Table 1). Of the 12 species of non-migratory raptors which hunt live prey (excluding vultures, Nearctic migrants and the Snail Kite), the abundance of 10 was greatest during June; this was more than would be expected by chance (binomial test, $P < 0.001$). Furthermore, a Kruskal-Wallis test comparing the densities of all 12 species combined revealed significant differences in seasonal means, with the highest density in June ($H = 43.29$, $P < 0.001$; densities = 11.29 birds/10 km for June, 5.44 for August, 7.33 for October and 3.29 for January). Even when data were removed for the Crested Caracara, which accounted for 70.7% of the data, the density of non-migratory hunting raptors was still highest in June

Table 3. Mean number of birds per 10 min count along four geographical sectors of the Paraguay River. Data during all censuses are combined.

SPECIES	1	2	3	4	<i>H</i>
Black Vulture	1.60	2.76	1.36	0.10	7.85 ^a
Lesser Yellow-headed Vulture ^d	0.39	0.97	1.01	1.90	12.91 ^b
Osprey	0.09	0.11	0.19	0.10	3.62
Snail Kite	0.24	2.04	2.99	2.90	24.18 ^c
Great Black Hawk	0.05	0.10	0.13	0.00	2.95
Savanna Hawk	0.03	0.04	0.33	0.05	34.49 ^c
Black-collared Hawk	0.14	0.04	0.03	0.00	5.59
Roadside Hawk	0.09	0.05	0.07	0.05	0.47
Crested Caracara	1.10	1.23	1.08	0.85	2.25
Number of counts	74	99	98	20	

^a $P < 0.05$.

^b $P < 0.01$.

^c $P < 0.001$.

^d See ^c in Table 2.

($H = 32.10$, $P < 0.001$; densities = 4.20 birds/10 km for June, 1.81 for August, 1.54 for October and 0.75 for January).

Geographical Variation. Because the number of 10 min count periods in each sector varied during the four censuses ($\chi^2 = 27.07$, $df = 9$, $P < 0.002$), tests for geographical variation in abundance were computed for each census and for all censuses combined. The abundance of four species varied geographically when data from all four censuses were combined. The Black Vulture was most common in sector 2 and least common in sector 4 (Table 3); however, no geographical variation in abundance occurred during any single census. Both the Lesser Yellow-headed Vulture and Snail Kite were scarce in the southern sectors and most abundant in the northern sectors (Table 3); during individual censuses significant geographical variation occurred only in October ($H = 7.81$, $P < 0.05$) for the Lesser Yellow-headed Vulture and during all but the January census for the Snail Kite (June, $H = 11.15$, $P < 0.01$; August, $H = 11.14$, $P < 0.01$; October, $H = 20.82$, $P < 0.001$). The Savanna Hawk was most common in the third sector and virtually absent elsewhere (Table 3); this was true during all but the January census (June, $H = 31.28$, $P < 0.001$; August, $H = 5.83$, $P = 0.05$; October, $H = 9.96$, $P < 0.05$). The other five species with sufficient data for analysis showed no geographical variation in abundance for any given census or when all data were combined (Table 3), except for the Crested Car-

acara, which was most common in sector 2 during October ($H = 13.10$, $P < 0.01$) but not during any other census.

Time of Day Variation. The number of 10 min count periods in each time period varied during the four censuses ($\chi^2 = 35.96$, $df = 15$, $P < 0.002$), hence tests for time of day variation in abundance were computed for each census and for all censuses combined. The abundance or detectability of birds during different periods of the day varied significantly for four species when all data for the four censuses were combined. Both species of vultures were detected most frequently during midday; the Black Vulture was commonest from 1000–1200 H and the Lesser Yellow-headed Vulture from 1200–1400 H (Table 4). The Black Vulture showed no time of day variation during any single census; the Lesser Yellow-headed Vulture was most common from 1200–1400 H during each census except in June, when no variation occurred (August, $H = 13.10$, $P < 0.05$; October, $H = 21.55$, $P < 0.001$; January, $H = 12.93$, $P < 0.05$). The abundance of the Snail Kite did not vary significantly when all data were combined, but during the October census, when it was most common, it was observed most frequently during the early morning hours, from 0600–1000 H (Table 4). The Crested Caracara was observed most frequently from 0800–1000 H when all data were combined (Table 4), but the only census with significant variation was in August ($H = 12.88$, $P < 0.05$).

Table 4. Mean number of birds per 10 min count during different periods of the day. Data during all censuses are combined unless noted otherwise.

SPECIES	0600-0800	0800-1000	1000-1200	1200-1400	1400-1600	1600-1800	<i>H</i>
Black Vulture	0.76	3.03	4.15	2.12	0.95	0.58	17.34 ^a
L. Y.-headed Vulture ^c	0.16	0.48	1.47	1.76	1.09	0.47	39.63 ^b
Osprey	0.16	0.20	0.09	0.09	0.13	0.13	2.22
Snail Kite	4.16	3.85	1.35	1.15	1.25	0.83	9.32
October census	10.30	10.76	5.71	4.11	5.85	2.50	17.77 ^a
Great Black Hawk	0.12	0.02	0.21	0.24	0.05	0.08	6.07
Savanna Hawk	0.24	0.08	0.09	0.24	0.16	0.11	7.55
Black-collared Hawk	0.04	0.05	0.00	0.18	0.05	0.06	7.50
Roadside Hawk	0.04	0.07	0.03	0.18	0.08	0.03	4.33
Crested Caracara	1.36	1.88	0.88	1.21	0.72	0.80	20.72 ^b
Number of counts	25	60	34	33	64	64	
October census	10	21	7	9	13	16	

^a $P < 0.01$.

^b $P < 0.001$.

^c See ^c in Table 2.

DISCUSSION

Seasonal Variation. Seasonal variation in the abundance of the Osprey and Snail Kite is apparently due to their migratory habits; the same should apply to the Mississippi Kite and Peregrine Falcon (Hayes et al. 1990). The greater abundance of the Savanna Hawk, Black-collared Hawk and Crested Caracara in June corresponded with the highest water levels along most sections of the Paraguay River. On 25 May and 2 June 1988, Vincent Roth (an arachnologist) and I observed from a rowboat large concentrations of insects, arachnids and two legless lizards trapped in emergent vegetation along the flooded Paraguay River at Asunción. The concentrations of invertebrates were the largest either of us had ever seen. The raptors may have been attracted to this ephemeral resource, which presumably also attracted small rodents, amphibians and other reptiles, along the river while the water level was rising. The greater abundance of non-migratory hunting raptors along the river in June and the greater species richness at this time support this hypothesis. In apparent contrast, the abundance of the Lesser Yellow-headed Vulture appeared to be negatively correlated with water levels, possibly because more carrion was exposed at lower water levels. The Black Vulture often appeared in flocks, especially near human dwellings; its occurrence was sporadic, hence conclusions about seasonal variation in abundance are unwarranted.

Two alternative explanations may account for the apparent increase in abundance of several raptor species along the river in June. The first may be due to the partial defoliation of trees at this time since June marks the onset of the austral winter. Defoliation of trees might increase the detectability of raptors by an observer. However, raptors typically perch on exposed limbs where they would be equally visible regardless of the quantity of foliage in the surrounding vegetation. Furthermore, the trees along the river's banks were still partially defoliated in August, when the quantity of non-migratory hunting raptors observed decreased. The second possible explanation may be that migrant birds from further south may have been concentrated along the river during the austral winter, some of which had already left by August. But because virtually nothing is known about seasonal movements of raptors in South America, this hypothesis cannot be evaluated at present. If this were the case, one would expect to observe a parallel increase in the densities of raptors in areas away from the river during the austral winter; this could be tested by conducting censuses elsewhere.

Seasonal variation in the abundance of raptors along the Paraguay River contrasts with that of waterbirds, most of which were most common during periods of low water. The differences in seasonal abundance between these two groups likely reflect differences in the abundance of preferred food resources and their respective foraging strategies. While

many raptors apparently exploit concentrations of terrestrial invertebrates and small vertebrates trapped in emergent vegetation during high water levels, waterbirds prefer to forage in shallow water and on mudflats where aquatic prey is concentrated and more easily accessible when water levels are low and more habitat is available.

Geographical Variation. The species with the most obvious geographical trends in abundance were the Lesser Yellow-headed Vulture and Snail Kite, both of which were most abundant farther north along the Paraguay River where marshes, their preferred habitat, are more extensive along the margins of the river. The Black Vulture, often associated with human dwellings, appeared to be more common farther south where human activity is more prevalent. I can offer no explanation for the greater abundance of the Savanna Hawk in sector 3.

Time of Day Variation. Time of day variation in abundance for several species of raptors suggests that certain species are more active, and hence more visible, along the river during certain periods of the day. Also, the time of day when activity is greatest apparently varies between species. The Snail Kite appeared to be most active in the early morning, the Crested Caracara during early morning and early afternoon, the Black Vulture during late morning, and the Lesser Yellow-headed Vulture during late morning and early afternoon. These differences presumably reflect differences in the foraging activities of each species. The activity of other raptor species may also vary during different periods of the day, but the data were too few to statistically detect such differences.

Implications for Census Methods. Although many methods have been devised to estimate raptor densities, the use of a ship along a river transect has seldom been employed (see Fuller and Mosher 1981). Most methods of censusing birds, including those along a linear transect, have been oriented toward estimating densities over a unit surface area, but because of the linear nature of rivers such a density measure would be meaningless. Shipboard censuses are the only practical method of estimating raptor densities along a river. Advantages include the ease with which birds may be viewed with unobstructed vision, the fairly constant and slow rate of travel and the long distance which may be sampled over an environmental gradient. A disadvantage is that species which are either smaller, seldom soar or seldom leave the forest canopy or understory are more dif-

ficult to detect, hence their calculated densities are conservative and relatively small compared to the more conspicuous species. To compensate one could conduct line transects by foot in forest along the river's edge.

In order to eliminate the biases of geographical and time of day variation when making seasonal comparisons of raptor densities along a linear transect, an equal amount of counts should be conducted for each geographical sector during a given census and also for each time period. Otherwise, complex interactions may occur between variables, as in this study, which may complicate the interpretation of results.

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