Herpetological Conservation and Biology 4(1):120-131
Submitted: 12 April 2008; Accepted: 27 January 2009

THE AMPHIBIANS AND REPTILES OF PARQUE NACIONAL CARARA, A TRANSITIONAL HERPETOFAUNAL ASSEMBLAGE IN COSTA RICA

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***Abstract*.—Parque Nacional Carara is located midway along the Pacific versant of Costa Rica in the transition zone between dry tropical forest to the north and wet tropical forest to the south. We documented patterns of biodiversity among three sites within Parque Nacional Carara and compared the park's overall herpetofaunal community to those found in the dry tropical forest to the north and to the tropical rainforest to the south. We documented 39 amphibian and 65 reptile species for Carara. Within Carara, the lowland region contained the highest species richness. The park contained both dry and wet forest species, but the wet forest assemblage of both amphibians and reptiles dominated the area. Our analysis of the fauna's generic origins showed that the park contained a transitional assemblage corresponding to neither the southwestern nor the northwestern faunal area. Because Carara is the only large protected area in this region, its importance to the preservation of this unique faunal assemblage is paramount.**

Key Words.—alpha diversity; amphibians; beta diversity; Costa Rica; Parque Nacional Carara, reptiles; transition zone

INTRODUCTION

The herpetofauna of Costa Rica is one of the best known and most studied in the Neotropics with over 400 documented species of amphibians and reptiles (Savage 2002). This body of knowledge arose from herpetofaunal surveys that document species occurrence in a wide variety of habitats and geographic localities, including Pacific and Caribbean lowland rainforests (Donnelly 1994; Guyer 1994; McDiarmid and Savage 2005), tropical dry forests (Sasa and Solórzano 1995), and cloud forests (Hayes et al. 1989). However, the herpetofauna of Costa Rica's Central Pacific coast remains virtually undocumented. This area is of particular interest to biodiversity scientists as it is a transition zone between the tropical dry forest in the northwest and the lowland rainforest of the Osa Peninsula to the southwest.

Transitional zones occur at the boundary of two discrete biomes or habitat types and can be narrow and sudden, or more gradual across the landscape (Williams 1996). Often, these areas have physical and climatic attributes intermediate to the adjacent habitats (Brown and Lomolino 1998). As a result, assemblages in transitional zones are often a blend of those found in the adjacent areas (Brown and Lomolino 1998). However, if the transition zone also contains endemic species, its species richness may surpass that of the adjacent areas (Ramanamanjato et al. 2002). Additionally, these zones can be important centers of speciation and contribute to creation and maintenance of biodiversity in tropical forests (Smith et al. 1997). Transition zones thus have high conservation value, both in their own right and as connections between ecosystems (Ramanamanjato et al. 2002). An increased understanding of the patterns and processes that form transition zones is important to the explanation of local and regional diversity patterns (Gosz 1992).

Parque Nacional Carara (PN Carara) stands as the largest tract of forest and the only significant protected area within the central Pacific transitional zone. It is located almost equidistant from Parque Nacional Santa Rosa (PN Santa Rosa), a typical tropical dry forest site to the north, and Rincón de Osa, a lowland wet rainforest site to the south. Furthermore, the Tárcoles River, which forms the northern border of PN Carara, is an important border on a regional scale which separates dry and wet forest forms in several groups, including: vegetation (Gomez 1986), insects (Kohlmann and Wilkinson 2007), birds (Stiles and Skutch 1989), and amphibians and reptiles (Savage 2002). A comprehensive list of the herpetofauna of PN Carara would document the species assemblage found in a central pacific transitional zone site and help elucidate the relationship of the local herpetofauna to that of the adjacent forest types. The objectives of the present study were to: (1) present a list of the amphibians and reptiles found in PN Carara based on our surveys using multiple methods; (2) compare herpetofaunal diversity among three sites surveyed within PN Carara; and (3) compare the herpetofauna of

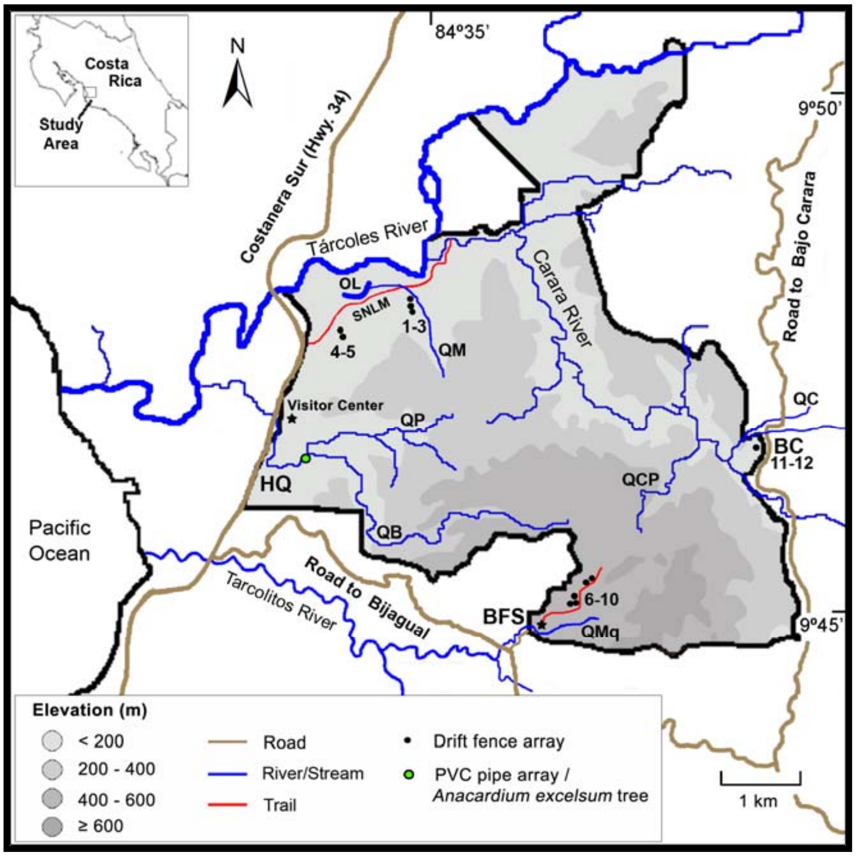

FIGURE 1. Map of Parque Nacional Carara, Costa Rica. The location of study sites, drift fence arrays, water bodies, trails and roads are provided. See text for details. Three surveyed sites are labeled: BC – Bajo Carara, BFS – Bijagual Field Station, HQ – Headquarters. Drift fence arrays are shown as black circles and have been labeled by groups according to their number: 1-3, 4-5, 6-10 and 11-12. Other Abbreviations include: OL – Oxbow Lagoon, QB – Quebrada Bonita, QC – Quebrada Chanchos, QCP – Quebrada Cinco Pasos, QM – Quebrada Mona, QMq – Quebrada Máquina, QP – Quebrada Patos, SNLM – Sendero Natural Laguna Meandrica.

PN Carara to that of the tropical dry forests to the north and lowland wet forests to the south in order to examine patterns of diversity in the Central Pacific transition zone.

MATERIALS AND METHODS

Study site.—Parque Nacional Carara (9° 45’ 22”N, 84° 36’ 27”W), is a 5,242 ha natural area that is 40 km southwest of Orotina, along Costa Rica’s central Pacific coast. Lying in both Puntarenas and San José provinces, PN Carara is bordered to the north by the Tárcoles River and to the west by the Costanera Sur highway (Hwy. 34, Fig. 1). Carara is 95% forested and contains several habitat types including: swamps, oxbows, and primary, gallery and secondary forests (Boza 1984). Carara was created in 1978 as a biological reserve from lands that were formerly a part of the massive rural estate, Hacienda Coyolar (Vargas Ulate 1992). In 1980, the area of the reserve lost approximately 2,900 ha for a settlement for rural laborers.

Carara remained a biological reserve until 1998 when, to better serve the needs of the ever increasing number of tourists, Carara became a national park. The majority of the park consists of primary forest, characterized by trees and other vegetation typical of both the tropical dry forest and lowland wet forest (Vargas Ulate 1992). PN Carara contains tropical moist forest, tropical wet forest, and tropical wet forest premontane belt transition (Tosi 1969). Elevation within the park ranges from 30 to 636 m. Mean precipitation generally varies between 2000 and 3000 mm rainfall yearly with distinct wet (May – November) and dry (December – April) seasons (Boza 1984; Barrantes 1985). The annual mean temperature is 27.8° C (Vargas Ulate 1992).

We focused our sampling efforts in areas of the park that captured a variety of habitats found in low-, mid-, and high-elevations. The lowland area (abbreviated HQ), included the park’s headquarters and visitor center, all public trails, the seasonally flooded forest of the Tárcoles floodplain, an oxbow lagoon, three streams (Quebrada Bonita, Quebrada Pizote and Quebrada

TABLE 1. Latitude and longitude of important amphibian and reptile sampling points within Parque Nacional Carara, Costa Rica. All points were taken using Datum WGS84. For a graphical depiction of these points, see Fig. 1.

Site Description	Latitude	Longitude
Drift Fence Array 1	9° 47’ 59.3”N	84° 35’ 13.2”W
Drift Fence Array 2	9° 47’ 55.7”N	84° 35’ 12.6”W
Drift Fence Array 3	9° 47’ 52.4”N	84° 35’ 11.8”W
Drift Fence Array 4	9° 47’ 40.9”N	84° 35’ 52.7”W
Drift Fence Array 5	9° 47’ 38.8”N	84° 35’ 51.5”W
Drift Fence Array 6	9° 45’ 4.9”N	84° 33’ 41.6”W
Drift Fence Array 7	9° 45’ 5.5”N	84° 33’ 37.7”W
Drift Fence Array 8	9° 45’ 8.5”N	84° 33’ 38.3”W
Drift Fence Array 9	9° 45’ 16.4”N	84° 33’ 32.2”W
Drift Fence Array 10	9° 45’ 19.0”N	84° 33’ 28.4”W
PVC Pipe Array	9° 46’ 25.7”N	84° 36’ 10.3”W
HQ	9° 46’ 22.6”N	84° 36’ 27.6”W
Visitor Center	9° 46’ 51.7”N	84° 36’ 22.0”W
Quebrada Bonita at Quebrada Patos	9° 46’ 28.5”N	84° 36’ 7.0”W
Sendero Natural Laguna Meandrica	9° 47’ 34.6”N	84° 36’ 8.3”W
Oxbow Lagoon	9° 47’ 52.0”N	84° 35’ 43.5”W
Bijagual Field Station	9° 44’ 49.4”N	84° 33’ 57.5”W
Bajo Carara Guardhouse	9° 46’ 36.7”N	84° 31’ 45.5”W
Pond at Bajo Carara	9° 46’ 46.0”N	84° 31’ 52.6”W

Mona), and the canopy of one *Anacardium excelsum* tree (Fig. 1). The elevation for these areas ranged from 30 – 50 m and was approximately 14% wetlands, 85% forests, and 1% developed. The mid elevation area (330 m elevation) was at the Bajo Carara Field Station (BC), a park guardhouse on the eastern border of the park (Fig. 1). Bajo Carara was next to the Río Carara between a mosaic of cultivated lands outside the park’s boundaries and primary and gallery forest within the park. We focused sampling efforts at BC on the Rio Carara and its associated gallery forest as well as two streams, Quebrada Chanchos and Quebrada Cinco Pasos. The sampled areas were ~ 95% forest, 5% wetlands, and < 1% developed. The high elevation site (630 m) included habitat around the Bijagual Field Station (BFS; Fig. 1). The BFS area comprised a narrow strip of forest surrounded by farmland and pasture with one stream, Quebrada Máquina (called Quebrada Tarcolitos downstream of the park). Most (> 95%) of the land area within the park was forest. Due to the increased slope at this site there is only a small wetland area (approximately 1%) around the guardhouse and a small area cleared for the guardhouse itself (< 5%). Most of the terrestrial habitat surrounding the park is farmland or pasture.

Sampling.—Our work at Carara took place in both the rainy and dry seasons from 1999-2001 and encompassed about 288 total days of fieldwork. We used several collecting methods to sample the herpetofauna at Carara including diurnal and nocturnal visual encounter surveys (VES; Crump and Scott 1994), drift fence arrays with pitfall and funnel traps (Corn 1994), PVC pipes for hylid frogs (Moulton et al. 1996; Boughton et al. 2000), canopy ascents using standard techniques (Dial and Tobin 1994; Laman 1995), leaf-litter plots (Scott 1976), and opportunistic collecting on roads and areas of travel in between sampling sites.

Visual Encounter Searches varied depending on the habitat sampled, time of day, and personal present. Typically, VES searches had at least two people and lasted for about 45 min at a particular location. In forested areas, we did not perform VES surveys on specific transects; instead we conducted them haphazardly to maximize the number of amphibians and reptiles observed. Along creeks however, VES transects ranged from 274 m to several kilometers of stream. We spent 507.88 person-hours conducting VES at PN Carara, with most (61.0%) of the VES hours occurring at HQ. At HQ, we made 79 diurnal and 27 nocturnal searches over 310 person-hours. We centered our searches at HQ on several areas including: Quebrada Bonita, Quebrada Patos, Sendero Natural Laguna Meandrica, Quebrada Mona and the areas surrounding the park headquarters and the visitor center (Fig. 1). At BC, we searched areas including Quebrada Chanchos, Rio Carara, Quebrada Cinco Pasos and various trails within the park over 11 days during January 2001 (Fig. 1). We employed 82.83 person-hours of VES surveys of which 40 were diurnal and 48 were nocturnal. Finally, at BFS we surveyed several areas over 115.05 person–hours. Of those hours, 55.6% were diurnal and 44.4% nocturnal. Areas searched included Quebrada Máquina, the area surrounding the BFS and the trail entering the park which starts at the BFS (Fig. 1).

Drift fence arrays had a ‘Y’ configuration (Corn 1994) with 15 m drift fences constructed from aluminum flashing, polystyrene sheeting (Malone and Laurencio 2004), or silt fencing (Enge 1997). Each drift fence had four pitfall traps and six funnel traps. Pitfall traps consisted of 20 L buckets buried at the end of each fence and in the center of the array. We drilled a series of small holes in the bottom of each pitfall to allow water to drain from traps. Otherwise, we bailed water from open pitfall traps each day. We constructed funnel traps using 1/8” wire mesh and fashioned in the shape of a 22.9 cm x 44.5 cm Gee Minnow Trap (Wildco, Buffalo, New York) . We placed funnel traps about 7.5 m from each bucket on both sides of each arm of drift fence arrays. We placed a piece of plastic over funnel traps to serve as shade cover. For drift fence sampling, we opened traps for about 10 days/month.

We erected five drift fence arrays (three aluminum and two polystyrene) in the lowland (HQ) region (see Table 1 and Fig. 1 for drift fence locations and GPS coordinates). Two of the five (spaced about 50-100 m apart) were placed along the edge of an unnamed creek near the entrance of the park trail. The remaining three arrays were located about 30 m south of Quebrada Mona and these were about 1.29 km from the previous two arrays. These two areas were chosen as they represented characteristics typical of lowland forest. We opened drift fences at HQ 47 days between 1999 and 2000 for a total of 2,101 trap nights.

Two drift fences made of silt fencing were established in BC. We constructed drift fences just behind the guardhouse on the border of disturbed forest (Fig. 1). BC was the least sampled of all three regions of the park and drift fences were opened for about two weeks in January 2001 for a total of 112 trap nights.

Finally, we established five drift fences (three aluminum and two polystyrene) at BFS (Fig. 1). Spacing between arrays was similar to that described above for arrays placed at HQ. We placed arrays at BFS along slopes within forest at two premontane forest sites and opened them beginning summer 1999 and then intermittently through 2001 for a total of 386 trap nights. Sampling at BFS consisted of approximately 10 continuous day sampling periods each month.

We utilized PVC pipes to sample hylid frogs at one site along Quebrada Bonita at HQ (Table 1, Fig. 1). We placed PVC pipes in a 25 X 25 m grid spanning across Quebrada Bonita and its north and south banks. Five rows of 5 bundles were evenly spaced to create a 5 X 5 grid. At each grid point, we placed bundles of 1 m sections of 2.54, 5.08, and 6.35 cm diameter pipe into the ground, and an adjoining bundle of 60 cm pipes of the same sizes, fitted with end caps, were hung from vegetation approximately 2 m above the ground. Pipes were placed at the site in November 1999 and checked about once/month until May 2000.

We used single rope techniques to ascend and sample possible amphibians and reptiles living in the canopy. We placed four, 0.5 m long, 2.54 cm diameter PVC pipes, fitted with end caps and three funnel traps on branches about 35 m above the ground in the lower reaches of the canopy of an *Anacardium excelsum* tree. PVC pipe traps were hung across branches using rope and funnel traps were affixed to branches using rope. We ran traps at least once/month from summer 1999 through May 2000 providing about 77 trap days in the canopy. Four 15 x 15 m leaf-litter plots were sampled at HQ. These were sampled only once during the study. Last, we collected specimens opportunistically and via road cruising when traveling between the Tárcoles River, HQ and BFS (Costanera Sur [Hwy. 34] and road to Bijagual, Fig. 1). Additional anecdotal observations were made during fieldwork on the ecology of *Smilisca* spp. at Quebrada Bonita (Malone 2004, 2006).

We marked animals captured in pitfall arrays that were not collected for voucher specimens using toe or scale clips (Ferner 1979) to distinguish resampled from new individuals. Resampled individuals were released, but very few animals were recaptured in drift fence arrays. We collected voucher specimens for each species and these were deposited at the Museum of Zoology of the University of Costa Rica (UCR) and the Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University. Tissue samples from voucher specimens were deposited in the frozen tissue collection at Texas State University. We supplemented our survey data with existing specimen records from UCR, as well as photographic evidence collected by Jim Kavney of Hiss ‘N’ Things and verified by Alejandro Solórzano of the National Serpentarium.

***Faunal Comparisons*.—**Because of the heterogeneous nature of our sampling effort, we report qualitative estimates of species abundance following Rand and Myers (1990). These qualitative estimates were defined based on the probability of encountering an individual of a given species within the park. Four abundance categories (common, usual, infrequent, rare) were used as defined by Rand and Myers (1990). Common species are those that are conspicuous in the right habitat. Usual species are defined as those in which at least one individual can almost always be found if appropriate habitat is searched. Infrequent species are those that are encountered repeatedly, but not predictably. Rare species are those whom are seldom encountered. Rand and Myers (1990) add that rare species may be locally extinct; however some may also be abundant yet difficult to encounter. While not quantitative, these qualitative estimates provide a heuristic guide for more quantitative work that may occur at Carara in the future. Alpha and beta diversity values were computed to compare faunal composition for the three within-park sites as well as compare the overall faunal composition of PN Carara to published species lists from a representative tropical dry forest, Parque Nacional Santa forest, Parque Nacional Santa Rosa (Sasa and Solórzano 1995), and a tropical (lowland) wet forest, Rincón de Osa (McDiarmid and Savage 2005). We defined alpha

TABLE 2. Relative abundance of amphibian species found in Parque Nacional Carara, Costa Rica. Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen.

Taxon	Abundance		
	HQ	Bajo Carara	Bijagual
GYMNOPHIONA (1 species)			
Caecilidae (1)			
Dermophis parviceps			R
CAUDATA (3 species)			
Plethodontidae (3)			
Bolitoglossa (Bolitoglossa) lignicolor		R	
Oedipina (Oedopinola) alleni			R
Oedipina (Oedipina) pacificensis			R
ANURA (35 species)			
Microhylidae (1)			
Hypopachus variolosus	R		
Brachycephalidae (6)			
Craugastor (Craugastor) crassidigitus	R		R
Craugastor (Craugastor) fitzingeri	C	U	C
Craugastor (Craugastor) rugosus	U		
Craugastor (Craugastor) stejnegerianus	C	R	I
Diasporus diastema		R	I
Pristimantis (Hypodictyon) ridens		R	R
Leptodactylidae (5)			
Leptodactylus bolivianus	R		R
Leptodactylus fragilis	R		I
Leptodactylus melanonotus	I		
Leptodactylus savagei	I		I
Leptodactylus poecilochilus	U		
Bufonidae (4)			
Incilius aucoinea	R	R	U
Incilius coccifer	I		I
Rhaebo haematiticus		R	
Rhinella marina	C	I	C
Hylidae (11)			
Agalychnis callidryas	U	I	I
Dendropsophus ebraccatus	U		
Dendropsophus microcephala	U		
Hypsiboas rosenbergus	I	I	R
Scinax boulengeri	R		
Scinax elaeochroa	R		
Smilisca baudinii	R		
Smilisca phaeota	C	C	C
Smilisca sila		U	R
Smilisca sordida	C	U	C
Trachycephalus venulosus	R		
Dendrobatidae (1)			
Dendrobates auratus	C		
Centrolenidae (6)			
Centrolene prosoblepon		R	R
Cochranella albomaculata		R	R
Cochranella granulosa		R	
Hyalinobatrachium colymbiphyllum	I		
Hyalinobatrachium fleischmanni		R	I
Hyalinobatrachium valerioi	I	R	
Ranidae (1)			
Lithobates forreri	R		R

diversity as local species richness (i.e., the number of species at a particular location) and beta diversity as the difference in species between Parque Nacional Santa Rosa, Carara, and Rincón de Osa (Whittaker 1972). We calculated beta diversity using Jaccard's Similarity Index (Krebs 1989).

RESULTS

We documented 39 amphibian and 63 reptile species for PN Carara, including one caecilian, three salamanders, 35 anurans, one crocodilian, two turtles, 24 lizards and 36 snakes (Tables 2 and 3). Most species were not common and were classified as rare or infrequent based on the scheme of Rand and Myers (1990). The most common amphibian species were: *Dendrobates auratus*, *Smilisca phaeota*, and *Rhinella marina*. Reptile species considered common were: *Ctenosaura similis*, *Ameiva leptophrys*, and *Anolis cupreus*.

We captured two caecilians, 59 frogs, 112 lizards, and 13 snakes in drift-fence arrays over 2,599 trap-nights. Four species were documented based solely on drift-fence trapping: *Dermophis parviceps*, *Polychrus gutturosus*, *Mabuya unimarginata* and *Urotheca decipiens*. In drift-fence arrays, the most frequently captured amphibian was *Dendrobates auratus* (N = 32) followed by *Rhinella marina* (N = 8). The most commonly captured reptile was *Ameiva leptophrys* (N = 54), followed by *Anolis cupreus* (N = 14), *Sphenomorphus cherriei* and *Corytophanes cristatus* (N = 11 each). We caputered six individuals of three frog species in the PVC pipe array: four *Smilisca phaeota*, one *Scinax elaeochroa* and one *Trachycephalus venulosus.* During canopy sampling we captured one *Thecadactylus rapicauda* in a funnel trap, but had no captures in the canopy PVC pipes. We also observed several *Dendrobates auratus* froglets and 10-15 tadpoles in a water-filled tree hole about 30 m above the ground. We found one *Craugastor (Craugastor) stejnegerianus* in the leaf litter plots.

A search of voucher specimens present at the Museum of Natural History at the University of Costa Rica added one species, *Leptophis nebulosus*, known for the park yet not collected during out surveys. We added two additional species, *Sibon anthracops and Spillotes pullatus* to the species list by way of photographs taken by Jim Kavney of Hiss 'N' Things, Inc. during a trip to the area and verified by Alejandro Solórzano, curator of the National Serpentarium.

Within Park Site Comparison.—We documented similar alpha diversity at sites within PN Carara (Table 2). Twenty-seven amphibian species were found at HQ, 18 at BC, and 23 at BFS. Eight species co-occurred at all three sites, 13 species shared two sites and 17 species were found at only one. Of the latter, 12 were unique to HQ, two to BC, and three to BFS. Amphibian beta diversity was lowest between BC and BFS (JSI = 0.519) and highest between BC and HQ (JSI = 0.250; Table 4). The family Caeciliidae was only represented at BFS, and no Plethodontidae species were found at the lowland site. Two families (Microhylidae and Dendrobatidae) were found only at the lowland site.

We observed 55 reptile species at HQ, 27 at BC, and 29 at BFS (Table 3). Fourteen reptile species co-occurred at all three sites, 18 at two sites, and 32 species (primarily snakes) were found at only one site. Of those 32, 27 were unique to HQ, two to BC, and three to BFS. The reptile assemblages at BC and BFS were the most similar (JSI = 0.514; Table 4). Similarity values were lower between HQ and BC (JSI = 0.323) and between HQ and BFS (JSI = 0.333), illustrating the disparity between HQ and the other two sites with regard to reptile species. Six reptile families were restricted to the lowland area (Table 3). At all three sites, the majority of reptile species observed were in the family Colubridae.

Comparison with Dry and Wet Forest.—Amphibian alpha diversity at PN Carara (39 species) was greater than at the dry forest of PN Santa Rosa (18 species), and slightly less than the wet forest at Rincón de Osa (46 species; Table 5). Just over half the combined species at PN Carara and Rincón de Osa were shared between the two forest types (JSI = 0.574) and just over a quarter were shared (JSI = 0.273) between PN Carara and PN Santa Rosa. The amphibian faunas of PN Santa Rosa and Rincón de Osa, however, were very distinct (JSI = 0.125) with only seven species present at both sites.

Alpha diversity among the three forest types was more similar for reptiles than amphibians, with PN Carara found to contain 64 reptile species compared to 54 at PN Santa Rosa and 69 at Rincón de Osa (Table 5). Beta diversity values for reptiles showed the same pattern seen for the amphibian assemblages, with PN Carara sharing about 50% of the combined species with Rincón de Osa (JSI = 0.446) and 25% with PN Santa Rosa (JSI = 0.255). As with amphibians, the reptile assemblages of PN Santa Rosa and Rincón were very dissimilar (JSI = 0.108), sharing only 12 species.

DISCUSSION

Overall, PN Carara diversity was characterized by high alpha diversity in the lowland site, with fewer, but different, species found in the mid- and high-elevation sites. Differences in diversity among sites within PN Carara may be due to changes in elevation and associated changes in climate and vegetation. Additionally, the proximity of the BC and especially BFS to open farmlands and pasture could cause edge effects that affect the presence of some species at those

TABLE 3. Relative abundance of reptile species found in Parque Nacional Carara, Costa Rica. Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen. (*Continued on next page*).

Taxon	Abundance		
	HQ	**Bajo Carara**	**Bijagual**
CROCODYLIA (1 species)			
Crocodylidae (1)			
Crocodylus acutus	C (Rio Tárcoles)		
TESTUDINATA (2 species)			
Emydidae (1)			
Rhinoclemmys pulcherrima	R		
Kinosternidae (1)			
Kinosternon scorpioides	I		
SAURIA (26 species)			
Gekkonidae (7)			
Coleonyx mitratus	I		
Gonatodes albogularis	C	R	
Hemidactylus frenatus	U (Buildings)		
Hemidactylus garnoti	U (Buildings)		
Lepidoblepharis xanthostigma		R	R
Sphaerodactylus graptolaemus	R		R
Thecadactylus rapicauda	R	R	
Corytophanidae (2)			
Basiliscus basiliscus	U	R	I
Corytophanes cristatus	I	R	I
Gymnophthalmidae (1)			
Leposoma southi	R	U	R
Iguanidae (2)			
Ctenosaura similis	C		
Iguana iguana	I		
Polychrotidae (8)			
Anolis biporcatus	R	R	R
Anolis carpenteri	R		
Anolis capito			R
Anolis cupreus	C	R	U
Anolis limifrons		R	R
Anolis oxylophus		R	R
Anolis polylepis	C	R	R
Polychrus gutturosus	R		
Teiidae (3)			
Ameiva leptophrys	C	R	
Ameiva quadrilineata	R	R	
Aspidoscelis deppii	R		
Scincidae (2)			
Mabuya unimarginata	R		
Sphenomorphus cherriei	R	R	R
Xantusiidae (1)			
Lepidophyma reticulatum	R		
SERPENTES (36 species)			
Boidae (1)			
Boa constrictor	R		
Colubridae (31)			
Coniophanes fissidens	R		R
Dendrophidion percarinatum	R		R
Dendrophidion vinitor	R		R

* Voucher for this species occurs at UCR
** Identified from photo.

sites. Much of the observed difference in within-park assemblages was due to lowland species restricted to the HQ site (e.g., species in the families Microhylidae, Dendrobatidae and Iguanidae); Gymnophiona and Caudata being restricted to higher elevations, and the HQ site having greater alpha diversity in higher-order taxon groups shared with other sites. For instance, of the 11 hylid species found in PN Carara, four were found at all three sites, but of the remaining seven species, six were encountered only at HQ.

Temporal and seasonal sampling bias may also account for some differences in species diversity between sites. More species were found at HQ than at either other site, and the fewest number of species were recorded at BC. However, because of logistics, more person-days were spent sampling lowland areas (HQ)

TABLE 3. *Continued* Relative abundance of reptile species found in Parque Nacional Carara, Costa Rica. Abundance: C = common-can find many individuals; U = usual-can be found in appropriate habitat and season; I = infrequent-not predictable; R = rarely seen.

Taxon	Abundance		
	HQ	Bajo Carara	Bijagual
Drymobius margaritiferus	R		
Enuliophis sclateri		R	R
Geophis hoffmanni	R	R	
Hydromorphus concolor		R	
Imantodes cenchoa	I		
Imantodes gemnistratus	R	R	R
Imantodes inornatus	R		
Lampropeltis triangulum	R		
Leptodeira annulata	R		
Leptodeira septentrionalis	U	R	I
Leptophis ahaetulla	R	R	
Leptophis nebulosus	R*		
Masticophis mentovarius	R		
Mastigodryas melanolomus	R		R
Ninia maculata	R	R	R
Oxybelis aeneus	R	R	R
Oxyrhopus petola	R		
Pseustes poecilinotus	R		
Rhadinaea decorata	R	R	R
Sibon anthracops	R**		
Sibon dimidiatus	R		
Sibon nebulatus	I		R
Siphlophis compressus		R	R
Spilotes pullatus	R**		
Tantilla armillata	R		
Tantilla ruficeps		R	
Urotheca decipiens			R
Urotheca fulviceps			R
Elapidae (2)			
Micrurus alleni	R	R	R
Micrurus nigrocinctus	R		
Viperidae (2)			
Bothriechis schlegelii	R		R
Bothrops asper	C	U	I

* Voucher for this species occurs at UCR.

** Identified from photo.

than elsewhere, and a majority of the drift fence sampling (80.8%) and VES (61.0%) occurred there.
Conversely, BC had the lowest number of VES person-hours as well as drift fence array trap nights. Furthermore, sampling at BC occurred during the dry season (January 2001), possibly limiting the number of amphibians encountered, although several streams and a lagoon were surveyed. Differences in sampling effort probably most affected the capture of snake species, which are rare, secretive, and the hardest to sample.
This might help explain the higher number of snakes reported for the lowland (HQ) area.

Future sampling efforts at PN Carara would benefit from prolonged sampling at BC, especially during the rainy season. It is encouraging that even though BC had the lowest species richness of the three sites, we found 45 species in just 11 days. Moreover, five of PN Carara's species were only found at BC, suggesting that continued sampling there could add to the park's overall species list. A review of Savage's (2002) range maps provides a group of species that may be present in the park, yet not detected in our study. These include: *Centrolene ilex*, *Norops pentaprion*, *Gymnophthalmus speciosus*, *Ameiva undulata*, *Epicrates cenchria*, *Ungaliophis panamensis*, *Clelia clelia*, *Eurythrolamprus bizona* and *Stenorrhina dengenhardtii*. All of these species have ranges that incorporate areas surrounding but not within the park. This undoubtedly reflects the lack of previous sampling effort at PN Carara. Not surprisingly, most of these species are snakes, a group which is difficult to sample thoroughly. We expect most species not yet documented for Carara are snakes.

Comparison of Parque Nacional Carara to the Dry and Wet Forests.—Carara's amphibian and reptile assemblage was intermediate, in both species numbers and composition, between the dry forest to the north and the wet forest to the south. Although PN Carara contained herpetofaunal elements from both regions, the combination of species there was clearly distinct. Differences between PN Carara and PN Santa Rosa

TABLE 4. Comparison between amphibians and reptiles among three sites within Parque Nacional Carara, Costa Rica. The diagonal shows the total number of species at a locality (N) and the percentage of the overall assemblage found at that site. Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index. The top values are those for amphibians and the lower values are those for reptiles.

	HQ	Bajo Carara	Bijagual
Lowland HQ	**27 (69.2%)** **55 (87.3%)**	9 20	14 21
Bajo Carara	.250 .323	**18 (46.2%)** **27 (42.9%)**	14 19
Bijagual	.398 .333	.519 .514	**23 (59.0%)** **29 (46.0%)**

alpha and beta diversity for amphibians were due to a lack of salamanders and glass frogs (Centrolenidae) at PN Santa Rosa, as well as fewer hylid and brachycephalid species there. Differences in diversity components between PN Carara and Rincón de Osa were due primarily to fewer dendrobatid and colubrid species at PN Carara and the inclusion of dry forest species at PN Carara that were absent from Rincón de Osa.

A large number of dry-forest snake species at PN Santa Rosa explains the alpha diversity of reptiles at that site. The pattern of beta diversity we observed resulted from sets of species that were shared between PN Carara and PN Santa Rosa, and PN Carara and Rincón. Beta diversity was high between PN Santa Rosa and Rincón de Osa, and each of those sites shared very few species of either amphibians or reptiles. One interesting exception was the frog, *Engystomops pustulosus*, found in both northwest and southwest Costa Rica yet absent from the central Pacific coast. While this large gap in the species' distribution pattern is well documented (Savage 2002), non-presence at a site is difficult to prove with limited sampling effort. Our intensive efforts at PN Carara support the lack of *Engystomops* in central Costa Rica as a true distributional pattern and not an artifact of low sampling effort. Parque Nacional Carara shared roughly twice as many species of amphibians and reptiles with Rincón, making it more similar to the Pacific lowland rain forest than the tropical dry forest.

***Faunal Zone Analysis*.**—It seems the transitional assemblage of PN Carara serves as a boundary for species from both faunal units. Six amphibian and five reptile species representative of the southwestern wet forest assemblage, for example, reach the northernmost known extent of their range at PN Carara. Additionally, one amphibian and three reptile species representative of the northwestern tropical dry forest assemblage, reach the southernmost known extent of their range at PN Carara (Savage 2002).

A review of Savage's (2002) herpetofaunal areas corroborates our results from the analysis of diversity components and further demonstrates the blending of herpetofaunas that created the transition assemblage at PN Carara. Geographically, PN Carara lies at the border of Savage's (2002) northwest and southwest faunal areas. Savage (2002) characterized the northwest faunal area by an equal proportion of Old Northern Element and Middle American Element genera (36:34%) and the southwest faunal area by similar proportion of Middle American to South American Element genera (37:33%). Of the 63 native genera found at PN Carara, 34.4% correspond to Old Northern Element, 40.6% to the Middle American Element and 23.4% to South American Element. Parque Nacional Carara's proportion of Old Northern Element to Middle American Element genera is 34:41%, and the proportion of Old Northern Element to South American Element genera is 41:23%. Therefore, PN Carara contains too high a proportion of Middle American genera to correspond to the northwestern fauna area, and relatively too few South American genera to correspond to the southwest faunal area. This unique combination of genera from all three faunal elements further supports the transitional nature of PN Carara's herpetofauna.

***Implications for conservation and future directions*.**—We have shown that Costa Rica's central Pacific coast contains a rich and unique herpetofaunal assemblage. While it contains elements of both the dry and wet forest, it stands apart from both. As such, the central Pacific coast transitional zone deserves preservation as a unique and different entity than that of the dry forest to the north and wet forest to the south. While we discovered no endemic species during this study, the possibility remains that endemic species are present at PN Carara masked as yet undiscovered cryptic species. It is conceivable that as genetic and ecological studies continue, species which we now consider widespread may indeed be local endemics. This would lead to new analyses of species richness and level of endemism for PN Carara and the central Pacific region

Table 5. Comparison between amphibians and reptiles among three localities along the Pacific coast of Costa Rica. The diagonal shows the total number of species at a locality (N). Figures above the diagonal represent number of species shared between sites (C). Below the diagonal is the Jaccard's Similarity Index. Data from Parque Nacional Santa Rosa is from Sasa and Solórzano (1995) and data from Rincón de Osa is from McDiarmid and Savage (2005). For each cell, top values represent amphibians, bottom values are those of reptiles.

	Santa Rosa	Carara	Rincón de Osa
Santa Rosa	**18** **54**	12 24	7 12
Carara	.273 .255	**39** **64**	31 41
Rincón de Osa	.125 .108	.574 .446	**46** **69**

as a whole.

Taken as a whole however, the herpetofaunal assemblage of PN Carara is unique in and of itself. As the largest tract of protected forest in a region mostly converted to farmland or pasture, PN Carara may be the last refuge for this transitional assemblage. In addition to regional protection, Carara is home to several species protected on the international level. One species, present at PN Carara, *Bolitoglosssa lignicolor*, is designated by the International Union for Conservation of Nature (IUCN) as vulnerable. An additional five species are protected through the Convention on International Trade in Endangered Species (CITES) including: *Dendrobates auratus*, *Iguana iguana*, *Boa constrictor*, *Micrurus nigrocinctus*, and *Crocodylus acutus*.

The emerging challenges to biodiversity resulting from climate change (Houghton et al. 2001) may have unique impacts at PN Carara given the transitional herpetofauna. These climatic changes may have unique consequences because these species are at the edge of their range and we might predict that they may have a higher probability of going locally extinct (Pounds et al. 1999, 2006). Additionally, climate change may create shifts in the distribution of species at Carara but how a transition zone assemblage would respond is unclear (Peterson et al. 2002; Parmesan and Yohe 2003; Root et al. 2003).

Although the herpetofauna of PN Carara is clearly transitional, it represents one locality along the central Pacific coast, and therefore it is difficult to comment on species diversity patterns and species turnover rates along the entire transition zone. Further work should focus on filling in knowledge gaps of species assemblages along the entire central Pacific coast of Costa Rica enabling a more enhanced understanding of the rate and pattern of turnover in herpetofaunal species along the entire Pacific coast. We hope this study will serve as a first step towards this goal as well as act as a catalyst for further research along Costa Rica's central Pacific coast.

Acknowledgements.— The authors would like to thank-Toby J. Hibbitts, Rachel Gallagher, Joel Johnson, Jacob Malcom, James R. Dixon, Mary Dixon, Robert Hibbitts, Thad Williams, Toby Ware, Julie Traweek and Kaylor Brenes for their help in the field and Federico Bolaños and Gerardo Chaves for their help at the UCR. We thank Laura Laurencio for help with the map and Lee A. Fitzgerald for reviewing earlier drafts of this manuscript.

This study was undertaken under the following permits: Resolución No. 237-97-OFAU, 237-98-OFAU, 019-2000-OFAU, and 342-2000-OFAU. Funding for this project was provided by a Youth Activity Grant from The Explorers Club to JHM, grants in herpetology from The East Texas Herpetological Society (DL and JHM), and Durman Esquivel, S. A. We give a special thanks to the PN Carara personnel who took us in and made us feel at home and to Dalia Edelman for her unwavering support.

LITERATURE CITED

Barrantes, J.A., A. Liao, and A. Rosales. 1985. Atlas Climatológico de Costa Rica. Ministerio de Agricultura y Ganadería y Instituto Meteorológico Nacional, San José, Costa Rica.

Boza, M. 1984. Guía de los Parques Nacionales de Costa Rica. Fundación de Parques Nacionales, San Jose, Costa Rica.

Boughton, R.G., J. Staiger, and R. Franz. 2000. Use of PVC pipe refugia as a sampling technique for hylid treefrogs. American Midland Naturalist 144:168–177.

Brown, J.H., and M.V. Lomolino. 1998. Biogeography. 2nd Edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Corn, P.S. 1994. Straight-line drift fences and pitfall traps. Pp. 109–117 *In* Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians. Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). Smithsonian Institution Press, Washington, D.C., USA.

Crump, M., and N. Scott, Jr. 1994. Visual encounter surveys. Pp. 84–92 *In* Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians. Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). Smithsonian Institution Press, Washington, D.C., USA.

Dial, R., and S.C. Tobin. 1994. Description of arborist methods for forest canopy access and movement. Selbyana 15:24–37.

Donnelly, M.A. 1994. Amphibian diversity and natural history. Pp. 199–209 *In* La Selva: Ecology and History of a Neotropical Rain Forest. McDade, L.A., K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (Eds.). University of Chicago Press, Chicago, Illinois, USA.

Enge, K. 1997. Use of silt fencing and funnel traps for drift fencing. Herpetological Review 28:30–31.

Ferner, J.W. 1979. A review of marking techniques for amphibians and reptiles. SSAR Herpetological Circular 9. 42 p.

Gomez, L.D. 1986. Vegetación de Costa Rica. Editorial Universidad Estatal a Distancia, San José, Costa Rica.

Gosz, J.R. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. Pp. 55–75 *In* Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Hansen, A.J., and F. di Castri (Eds.). Springer, New York, New York, USA.

Guyer, C. 1994. The reptile fauna: diversity and ecology. Pp. 210–216 *In* La Selva: Ecology and History of a Neotropical Rain Forest. McDade, L.A., K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (Eds.). University of Chicago Press, Chicago, Illinois, USA.

Hayes, M.P., J.A Pounds, and W.W. Timmerman. 1989. An annotated list and guide to the amphibians and reptiles of Monteverde, Costa Rica. SSAR Herpetological Circulars 17. 70 p.

Houghton, J.T., Y. Ding, D.J. Griggs, N. noguer, P.J. van der Linden, D. Xiaosu, K. Maskell, and C.A. Johnson (eds). 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, United Kingdom.

Kohlmann, B., and M.J. Wilkinson. 2007. The Tárcoles Line: biogeographic effects of the Talamanca Range in lower Central America. Giornale Italiana Entomologia 12:1–30.

Krebs, C.J. 1989. Ecological Methodology. Harper-Collins, New York, New York, USA.

Laman, T.G. 1995. Safety recommendations for climbing rain forest trees with 'single rope technique'. Biotropica 27:406–409.

Malone, J.H. 2004. Reproduction in three species of *Smilisca* from Costa Rica. Journal of Herpetology 38:27–35.

Malone, J.H. 2006. Ecology of the basin construction reproductive mode in *Smilisca sordida*. Journal of Herpetology 40:230–239.

Malone, J.H., and D. Laurencio. 2004. The use of polystyrene for drift fence sampling in a tropical forest. Herpetological Review 35:142–143.

McDiarmid, R.W., and J.M. Savage. 2005. The herpetofauna of the Rincón area, Península de Osa, a Central American lowland evergreen forest site. Pp. 366–427 *In* Ecology and Evolution in the Tropics: A Herpetological Perspective. Donnelly, M.A., B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (Eds.). University of Chicago Press, Chicago, Illinois, USA.

Moulton, C.A., W.J. Fleming, and B.R. Nerney. 1996. The use of PVC pipes to capture hylid frogs. Herpetological Review 27:186–187.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Peterson, A.T., M.A. Ortega-Huerta, j. Bartley, V. Sanchez-Cordero, J. Soberon, R.H. Buddemeier, and D.R.B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626-629.

Pounds, J.A., M.P.L. Fogden, and J.H. Campbell. 1999. Biological responses to climate change on a tropical mountain. Nature 398:611-615.

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, S.R. Ron, G.A. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161-167.

Ramanamanjato, J., P.B. McIntyre, and R.A. Nussbaum. 2002. Reptile, amphibian, and lemur diversity of the Malahelo Forest, a biogeographical transition zone in southeast Madagascar. Biodiversity and Conservation 11:1791–1807.

Rand, A.S., and C.W. Myers. 1990. The herpetofauna of Barro Colorado Island, Panamá: an ecological summary. Pp. 386–409 *In* Four Neotropical Rainforests. Gentry, A.H. (Ed.). Yale University Press, New Haven, Connecticut, USA.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57-59.

Savage, J.M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.

Sasa, M., and A. Solórzano. 1995. The reptiles and amphibians of Santa Rosa National Park, Costa Rica, with comments about the herpetofauna of xerophytic areas. Herpetological Natural History 3:113–126.

Scott, N. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. Biotropica 8:41–58.

Smith, T.B., R.K. Wayne, D.J. Girman, and M.W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. Science 276:1855–1857.

Stiles, F.G., and A.F. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Tosi, J.A., Jr. 1969. Republica de Costa Rica: mapa ecológico. Map 1:750,000. Tropical Science Center, San Jose, Costa Rica.

Vargas Ulate, G. 1992. Cartografía Fitogeográfica de la Reserva Biológica de Carara. Editorial de la Universidad de Costa Rica, San José, Costa Rica.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:231–251.

Williams, P.H. 1996. Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. Proceedings of the Royal Society of London Series B 263:579–588.

Errata posted 10 August 2009. (corrected in text)

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