Habitat Linkages and the Conservation of Tropical Biodiversity as Indicated by Seasonal Migrations of Three-Wattled Bellbirds

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Abstract: *Using radiotelemetry, we discovered that the Three-wattled Bellbird (*Procnias tricarunculata*), one of Central America's largest frugivorous birds, has the most complex migratory pattern yet recorded for a tropical species. The annual migration cycle included 2- to 5-month stopovers in four distinct life zones: two middle-elevation and two lowland sites separated by as much as 200 km. We captured and radio-tagged bellbirds during 4 years between July and September in middle-elevation forest fragments of the Pacific slope, 6 km from Monteverde in the Tilaran mountain range of north-central Costa Rica. These habitats, which exist almost exclusively as small, isolated fragments on private farms, are poorly represented (<2%) in Costa Rica's system of protected areas. During September and October, the bellbirds migrated from this site to the northeast into the lowland Atlantic forest of southeastern Nicaragua and northeastern Costa Rica. In Costa Rica these habitats have been heavily fragmented. In Nicaragua they remain intact but are highly threatened. In November and December, the bellbirds migrated from these Atlantic forests to heavily modified, little-protected forests along the Pacific coast of southwestern Costa Rica, where they remained until March. Here, most individuals utilized forest remnants and second growth on private property. In March the Bellbirds moved from the coastal areas to middle-elevation (1000–1800 m) moist forest on the Atlantic slope of the Tilaran mountains sites, where they bred. In June and July, they left the breeding area and moved back across the continental divide of the Tilaran Mountains to return to the middle-elevation Pacific slopes where they had been captured. Our findings demonstrate the complicated ecological integration of geographically dispersed tropical ecosystems and the need for comprehensive conservation strategies that include representation of the full array of regional habitats and a greater emphasis on maintaining connectivity. The bellbird's migratory pattern reveals serious inadequacies in protected-area networks of Costa Rica, a country that is considered to have one of the best systems of national parks and reserves in the Neotropics.*

Conexiones de Hábitat y la Conservación de la Biodiversidad Tropical Indicada por Migraciones Estacionales de *Procnias tricarunculata*

Resumen: *Utilizando radiotelemetría, descubrimos que* Procnias tricarunculata*, una de las aves frugívoras más grandes de Centroamérica, tiene el patrón migratorio más complejo registrado para una especie tropical. El ciclo de migración anual incluyó escalas de 2 - 5 meses en cuatro zonas de vida distintas: dos sitios de elevación media y dos sitios bajos, separados hasta por 200 km. Capturamos y radio-marcamos individuos de* Procnias tricarunculata *entre julio y septiembre en fragmentos de bosque de elevación media en la vertiente del Pacífico, a 6 km de Monteverde en la sierra Tilaran en el norte-centro de Costa Rica. Estos hábitats, que existen casi exclusivamente como pequeños fragmentos aislados en ranchos privados, están pobremente representados (<2%) en el sistema de áreas protegidas de Costa Rica. Durante septiembre y octubre, las aves migraron de este sitio al noreste hacia el bosque bajo del Atlántico del sureste de Nicaragua y noreste de Costa*

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Rica. En Costa Rica, estos hábitats están excesivamente fragmentados. En Nicaragua permanecen intactos pero están muy amenazados. En noviembre y diciembre, las aves migraron de estos bosques del Atlántico a bosques muy modificados y poco protegidos a lo largo de la costa del Pacífico en el suroeste de Costa Rica, donde permanecieron hasta marzo. Aquí, la mayoría de los individuos utilizaron remanentes de bosques y vegetación secundaria en propiedades privadas. En marzo, las aves se desplazaron de las áreas costeras a bosques húmedos de elevación media (1000–1800 m) en la vertiente Atlántica de las montañas Tilaran, donde se reprodujeron. En junio y julio, abandonaron el área de reproducción y atravesaron las montañas Tilaran para volver a las laderas de elevación media donde habían sido capturadas. Nuestros hallazgos demuestran la complicada integración ecológica de ecosistemas tropicales geográficamente dispersos y la necesidad de estrategias de conservación integrales que incluyan la representación del total de hábitats regionales y un mayor énfasis en el mantenimiento de la conectividad. El patrón migratorio de Procnias tricarunculata *revela serias falencias en las redes de áreas protegidas de Costa Rica, considerado como un país que tiene uno de los mejores sistemas de parques nacionales y reservas en los neotrópicos.*

Introduction

National systems of protected natural areas in Neotropical countries have, for the most part, been implemented haphazardly and without the input of ecological data to ensure that they have been properly designed to support that region's rich biodiversity (Powell et al. 2000). To date, the potential design flaws have not manifested themselves because protected areas tend to be in more remote areas, where they remain in contact with intact, or partially intact, natural habitats. However, the rapid rates of deforestation in this region (World Resources Institute 1988; Sanchez-Azofeifa et al. 1999) will soon eliminate or seriously degrade these de facto reserves. Before deforestation exhausts remaining unprotected habitat, every effort must be made to ensure that the designated protected areas in the Neotropics can maintain that region's biodiversity.

Costa Rica has been exemplary in the creation of a large system of protected natural areas, with strict protected areas now covering about 12% of its surface area (Boza 1993). The system has grown opportunistically, however, without the benefit of principles of landscape ecology or conservation biology to guide its design. For example, there has been little regard for representation of habitat types in protected areas (Powell et al. 2000) or concern for whether enough of each habitat type is conserved (Powell et al. 2002), particularly for species characterized by large home ranges such as jaguars (*Panthera onca*; Crawshaw & Quigley 1991). Furthermore, conservation efforts have failed to account for the mobility of species in tropical environments, particularly with respect to seasonal migrations that occur within the tropics (Stiles 1983, 1985; Levey 1988; Loiselle & Blake 1991). All these factors result in tropical ecosystems being tightly linked and interdependent.

The object of our study was to assess the adequacy of the design of the Costa Rican system of protected areas with respect to its avifauna by monitoring habitat use by one of the country's larger frugivorous species, the Three-wattled Bellbird (*Procnias tricarunculata*; hereafter bellbird). The bellbird is a Central American endemic that breeds in middle-elevation montane moist forests between southern Honduras and western Panama (Stiles & Skutch 1989). Because breeding areas are restricted to middle elevations (1000–1800 m), their populations are isolated by the geographic separation of mountain massifs that are approximately centrally located along the isthmus except for a small, remnant population in the higher elevations near the tip of the Azuero Peninsula in Panama (Ridgely 1976). Bellbirds have been known to be elevational migrants (Wetmore 1972; Stiles & Skutch 1989), but the details of their migrations and habitat requirements were unknown prior to this study. Our goal was to determine whether Costa Rica's system of protected natural areas included representation of habitats in an appropriate spatial distribution that fulfilled the requisites for sustaining a viable population of bellbirds in this country.

Methods

Monitoring Bellbirds

We radio tagged bellbirds between the end of July and beginning of September 1991 through 1994 in forest fragments on the Pacific slopes of the Tilaran Mountains, approximately 4 km west of the Monteverde reserve complex. The birds were captured with mist nets that were placed in and just below the forest canopy after the breeding season.

With the capture of the first individuals, we discovered it was necessary to anesthetize the birds to prevent them from going into shock while being handled. We used a mixture of 100 mg/kg of ketamine and xylasine through an intramuscular injection in the breast muscle to anesthetize the birds for about 1 hour. After processing, we placed the sedated individual in a covered cardboard box and allowed it to fully recover before release. The box was opened about 2 hours after the anesthetic had been

applied, allowing the individual to fly away without further handling. We made an effort to radio tag a sample of adult males, subadult males (males acquire adult plumage at 6–7 years of age; G.V.N.P. and D. Hamilton, personal observation), and females.

The most successful harness arrangement was a 6-g transmitter/harness package that produced a signal for an average of 13 months (Powell & Bjork 1994). The radiotransmitters (Holohil Systems, Inc.) were placed on the bellbirds with a Teflon harness in the form of a specialized backpack. We ensured that the harness did not interfere with the individual's capacity to process the large fruits of the Lauraceae family, which are their primary food source during most of the year. The transmitter signals could be detected at distances of up to 1 km within the forest and up to 15 km on mountain tops or by fixed-wing aircraft.

We checked all birds with radiotransmitters on a daily basis while they remained within a 10-km radius of their capture area and plotted their use of habitat on 1:10,000-scale maps derived from low-level aerial photographs. When birds disappeared from the capture area, we used aerial surveillance to relocate them. Initially, flights were restricted to the described range of the species (Stiles & Skutch 1989), but when signals were not detected in those areas in 1992–1993, flights were extended to cover all of Nicaragua, Costa Rica, and the western half of Panama until the birds were finally located in an unexpected area. Thereafter, whenever we could not find the majority of birds, we continued to check throughout the area previous years had delineated, though less frequently, in attempts to locate the missing individuals. The only time we did not use this search pattern was during the breeding season and when birds were being captured. During the breeding season, we limited our searches to the breeding area throughout Costa Rica and western Panama to determine whether missing birds were breeding elsewhere within their range, which was the case with one female. We did not search during the capture period because transmitter batteries were over 12 months old and thus unreliable. During monitoring flights, we precisely located detected birds with a global positioning system (GPS). When the bellbirds were away from the Tilaran Mountains, we made aerial flights as frequently as bimonthly (in 1993) and as infrequently as once every 3 months in other years. Only two flights were made in the pilot year of 1991. Whenever possible, individuals we located while in the air were visited on the ground to collect data on their diet.

Assessing Habitat Status and Protection

Habitats used by the bellbirds were classified with respect to life zone (Holdridge 1967; Bolaños & Watson 1993) and status (primary, intervened, or secondary). We assessed the status of habitats within the Tilaran Mountains on the basis of 1985 aerial photography that was digitized and updated through extensive field observations. We classified the habitat status of areas used by bellbirds elsewhere in Costa Rica and Nicaragua based on forest coverage that we digitized from 1:200,000-scale maps produced by the Costa Rican Forest Service from 1989 Landsat satellite imagery. Protection status of the different life zones was taken from the results of a gap analysis for Costa Rica (Powell et al. 2000).

Results

Forty-eight individuals were radio tagged during the four capture seasons. In the 1991 pilot year, 5 individuals were radio tagged but 2 had experimental transmitters that lasted only 3 months. The 3 remaining individuals had 12-month transmitters. In the following year, 1992, we captured 43 bellbirds during 17 days of netting (631 net hours). Fifteen of these were fitted with radiotransmitters (6 adult males, 5 subadult males, and 4 females). In 1993, 46 individuals were captured during 32 days of netting (996 net hours). Nineteen of these were radio tagged (9 adult males, 6 subadult males, and 4 females). Nine of these individuals, all males, received transmitters with a 6-month battery life but stronger signals that made them easier to locate. Finally, in September of 1994, 12 individuals were captured during a reduced schedule of mist-netting (230 net hours). Nine of these individuals were radio tagged (6 females, 2 adult males, and 1 subadult male). With the exception of the 3- and 6- month transmitters, all transmitters were programmed to last about 12 months. Thus, signals located during a given year were those of individuals that had been radio tagged at the beginning of that field season.

During the pilot year (1991–1992), which was primarily intended to test techniques for capture and transmitter attachment, all radiotagged individuals left the capture area between late September and mid-November. Because Stiles and Skutch (1989) suggested that the birds migrated to the Atlantic slope, aerial flights focused on that area but failed to detect any radiotagged individuals. Two overflights of northeastern Costa Rica located one individual 33 km north-northwest of the banding area. A second was detected across the Nicaraguan border 93 km to the northeast (Table 1; Fig. 1). The exact location of the latter was not determined because we were unable to secure permission to fly over Nicaragua during the rest of that year. No further attempts were made to locate the radiotagged birds until the following August, when two of the three individuals with long-lived transmitters were relocated at the capture site (Table 1).

In 1992–1993, the birds again left the capture area between late September and late October, presumably to migrate to Nicaragua, where they had been detected the year before. Due to a lack of funding, however, we were unable to search for the birds in southeastern Nicaragua

Table 1. Sex, age, transmitter battery life, and locations where radiotagged individuals were detected.[a]

Transmitter ID and year	*Sex and age[b]*	*Transmitter life (months)*	*Pacific mid-elevation (capture site) Jul.–Sep./Oct.*	*Atlantic lowlands Sep.–Nov./Dec.*	*Pacific lowlands Dec.–Mar.*	*Atlantic mid-elevation (breeding area) Mar.–Jul.*	*Pacific mid-elevation Jul.–Sep./Oct.*
1991–1992, pilot year							
A	m, a	12	X	X	no data	no data	
B	m, a	12	X		no data	no data	X
C	m, a	12	X	X	no data	no data	X
1992–1993							
905	f, a	12	X	no data	X	X	X
919	f, a	12	X	no data		X (Braulio Carillo)	
925	f, a	12	X	no data		X	X
923	f, a	12	X	no data		died	
909	m, a	12	X	no data		X	X
930	m, a	12	X	no data	X	X	X
912	m, a	12	X	no data		X	X
944	m, a	died	X	no data			
890	m, a	12	X	no data	X	X	X
921	m, a	12	X	no data		X	X
946	m, sub	12	X	no data	X (Panama)	X	
933	m, sub	12	X	no data			X
939	m, sub	12	X	no data			X
941	m, sub	12	X	no data		X	X
915	m, sub	12	X	no data			
1993–1994							
974	f, a	12	X	X	X	X	X
963	f, a	12	X				
959	f, a	12	X	X		X	X
965	f, a	12	X	X			X
998	m, a	6	X	X	radio dead		
990	m, a	12	X				
931	m, a	6	X	X		battery dead	
908	m, a	6	X	X	X	X	
955	m, a	6	X	X	X	battery dead	
947	m, a	6	X	X		battery dead	
936	m, a	6	X	X		battery dead	
976	m, a	12	X	X	X	X	X
971	m, a	12	X	X	X	X	X
917	m, sub	6	X	X		battery dead	
927	m, sub	6	X	X	X	battery dead	
937	m, sub	6	X	X	X	battery dead	
984	m, sub	12	X			X	X
903	m, sub	6	X			battery dead	
900	m, sub	6	X	X	X	battery dead	
1994–1995							
916	f, a	12	X	X	X		
910	f, a	12	X	X			
905	f, a	12	X	X	X	X	
941	f, a	12	X	X		X	
913	f, a	12	X				
872	f, a	12	X	X	X	X	
908	m, a	12	X	X			
923	m, a	12	X	X			
971 (from 1993)	m, a	12	X		X	battery dead	
961	m, sub	12	X				

[a] *No data denote times when financial limitations prevented data collection.*
[b] *Abbreviations: m, male; f, female; a, adult; sub, subadult.*

until late November, when a single very limited overflight failed to locate any signals. In extensive searching throughout Nicaragua in January, we again failed to locate any radiotagged birds. A single juvenile male was located in the highlands of western Panama in late December. The remaining birds were not located until March, when we extended our search to include the Pacific coast of Costa Rica, an area outside the published range of the species (Stiles & Skutch 1989). We located three individuals (two males and one female) along the southwestern

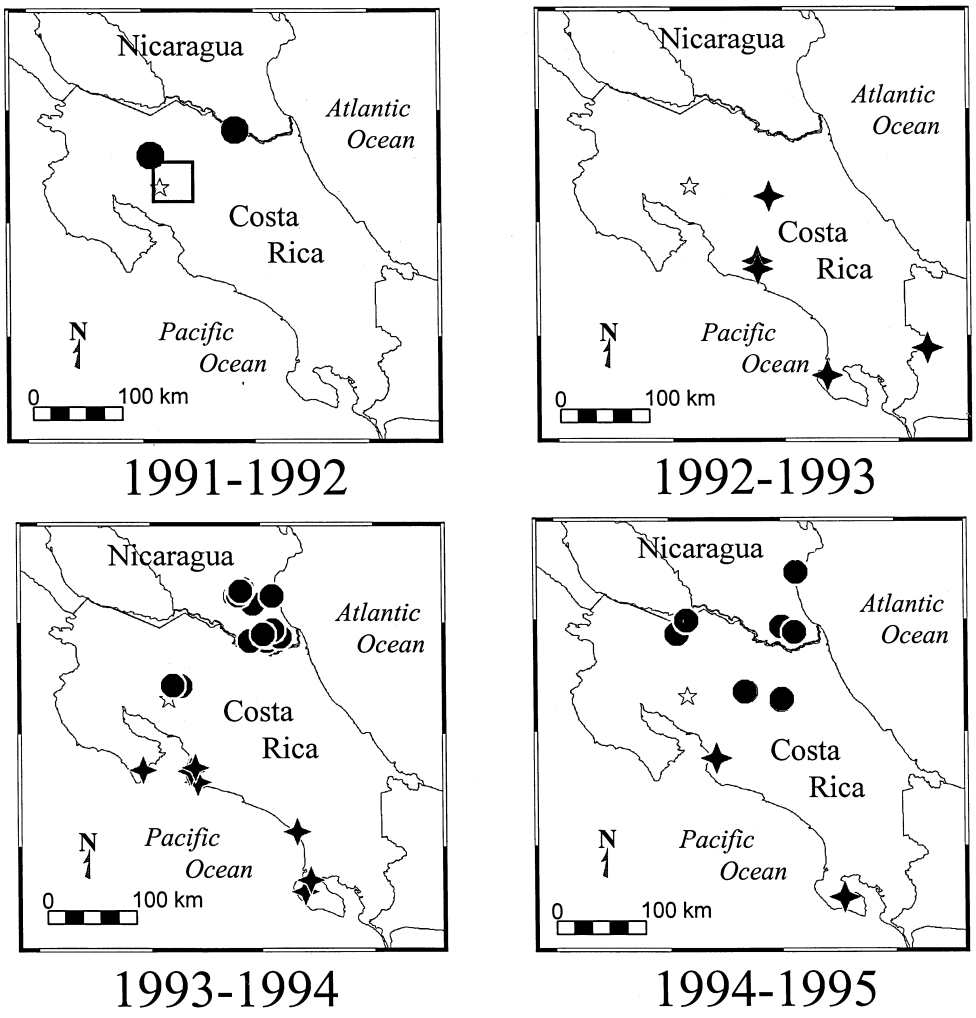

Figure 1. Locations of radiotagged bellbirds between September and November and December (circles) and between December and March (crosses) during each year of the 4-year study The star marks the Tilaran mountain range, where birds were captured and radio tagged during their postbreeding migration.

coast about 200 km south of their breeding area (Table 1; Fig. 1). We checked that area only after failing to locate the birds when searching throughout the Atlantic sides of Nicaragua, Costa Rica, and western Panama.

The next overflight 2 weeks later, 26 March, which coincided with the onset of breeding season, revealed that the 5 adult males (1 adult had been killed by a predator about a month after tagging), 1 subadult male, and 2 of the 3 females (1 female was predated soon thereafter) had returned to their breeding areas on the Atlantic slope of the Tilaran Mountains (Table 1; Fig. 2). The remaining female was located at 1000 m on the Atlantic slope of the Central mountain range, 93 km east of its capture site. The 3 remaining subadult males were relocated when they returned to the capture area between June and July. In June and July, the 5 adults and 1 female also moved from their Atlantic slope breeding areas to the Pacific slope near their previous year's capture site (Table 1; Fig. 2). The female in the Central Mountains disappeared from that area and was not detected again. Thus, 10 of the 13 individuals radio tagged in 1992 (excluding 2 that were known to have died) returned to the capture site in 1993.

In 1993–1994, aerial flights were made approximately biweekly, beginning in early September after the first individuals left the capture area. Between September and November, 14 of the 19 radiotagged individuals were located in southeastern Nicaragua, 100–120 km from the capture site, in the same general area as individuals had been detected in 1991–1992 (Table 1, Fig. 1). Two additional birds moved to the Atlantic side of the Tilaran Mountains, where they remained for several months. One was subsequently located in Nicaragua in December. In December, the birds began to disappear from Nicaragua. Eight were relocated along the Pacific coast of Costa Rica, where we had discovered birds the previous year (Table 1, Fig. 1). During March and early April flights, all radiotagged individuals disappeared from these sites, and 5 of the 8 individuals with 12-month transmitters (2 females, 2 adult males, and 1 sub-adult male) and 1 adult male with a 6-month transmitter were relocated in the breeding range adjacent to the capture site (Table 1, Fig. 2). Because 6 months had passed since the transmitters were installed, we assumed the remainder of the 6-month batteries were dead. In August, we accounted for only 2 of the 5 adult

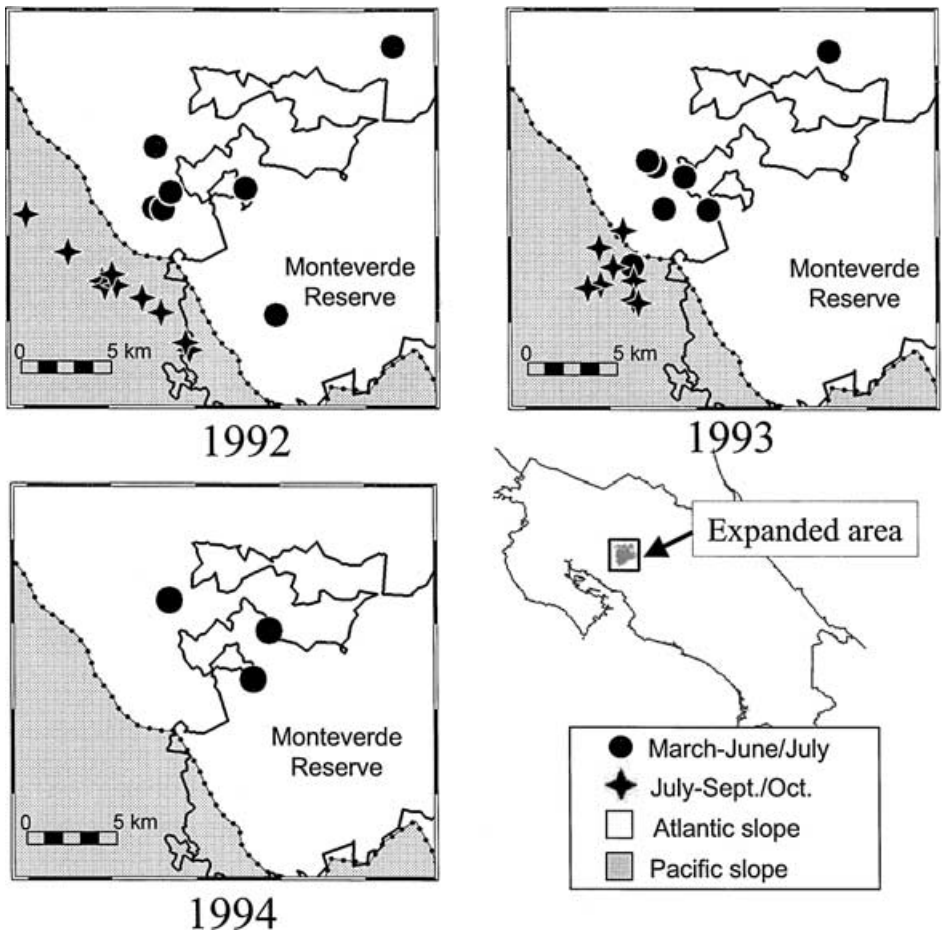

Figure 2. Locations of radiotagged bellbirds during breeding season (circles), primarily on the Atlantic slope, and postbreeding season (crosses), on the Pacific slope, during 3 years of the study. The map is an enlargement of Tilaran mountain range (box in orientation map at lower right).

males with long-term transmitters, 3 of the 4 females, and the 1 subadult male with a 12-month battery (Table 1).

In 1994–1995, aerial flights were again limited by the availability of funding, but flights every 2–3 months were sufficient to locate most of the individuals tagged that year. All radiotagged individuals had left the capture area by early October, and seven of nine had been located in southeastern Nicaragua and adjacent northeastern Costa Rica, the same area as in previous years. Again, as with the previous year, the birds left these locations sometime between late November and early January. Between late January and February, we relocated five individuals (three females, one male, and one radiotagged male from the previous year whose transmitter had an exceptionally long battery life of 17 months). Although repeated attempts were made to locate the missing individuals with flights throughout Costa Rica and portions of western Panama, none were relocated until the following breeding season in May of 1995, when three of the six females were found in the breeding area. By the end of breeding season in July, all the females had disappeared. None of these birds were detected in the capture area after the breeding season, as they had been in 3 previous years. We could not ascertain whether the transmitters had failed or whether the birds had failed to return to the capture area.

Status and Existing Protection of Habitats

The status and level of protection afforded to the four different geographic regions used by the bellbirds during their migratory cycle was highly variable. Two of these areas are within the Tilaran mountain range; therefore, protection of these habitats depends on their inclusion within the greater Monteverde reserve complex. The other two habitats are unconnected lowland sites, one on the Atlantic slope and the other on the Pacific slope. In the absence of ample ecological data, such as those represented here, these lowland sites would appear to be far removed from conservation issues related to the Tilaran Mountains.

The rainforest habitats used by the bellbirds during the breeding season, the premontane rainforest and lower montane rainforest life zones, are well represented in the Monteverde reserve (more than 150 km^2 protected; Fig. 3) and throughout Costa Rica (2750 km^2 protected; Fig. 4).

The habitats used by bellbirds on the Pacific slope of the Tilaran Mountains (July through September–October) are poorly represented in the Monteverde reserve complex (3 and 6 km^2, respectively; Fig. 3). Remaining samples of these habitats, the premontane wet forest and lower

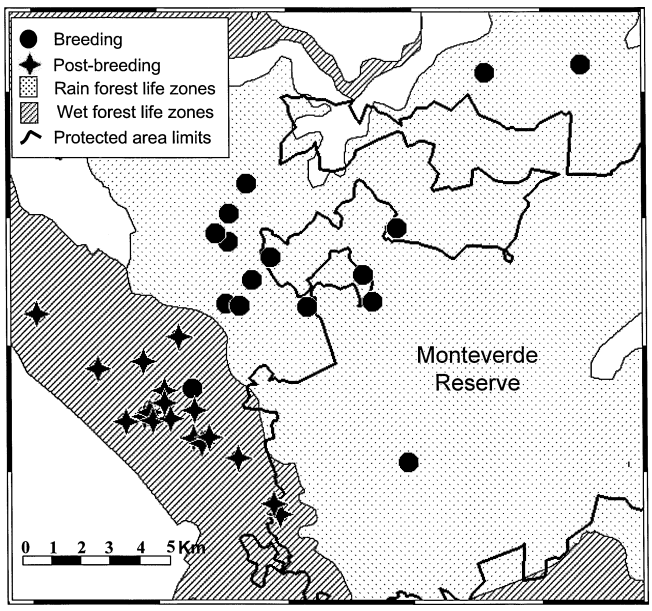

Figure 3. Distribution of the rainforest life zones (Atlantic slope, stippled) and wet forest life zones (Pacific slope, striped) in the Tilaran Mountains with respect to bellbird locations during the breeding season (March-June and July, circles) and postbreeding season (July-September/October, crosses).

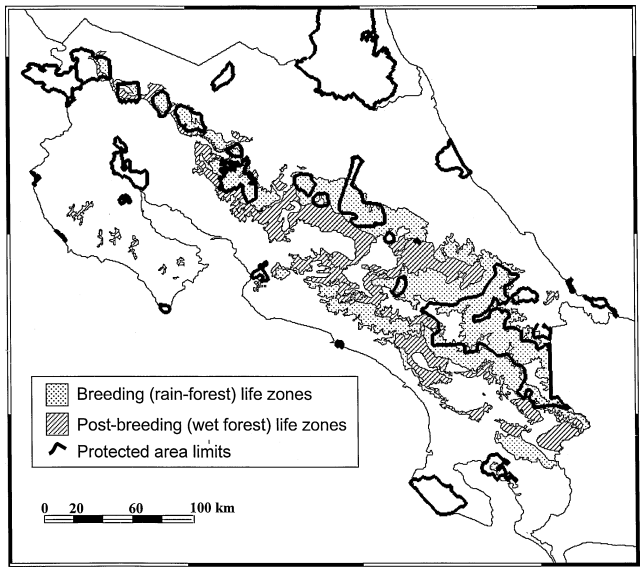

Figure 4. Distribution of the life zones used by bellbirds during breeding season (lower montane and premontane rain forest, stippled) and postbreeding season (lower montane and premontane wet forest, striped).

montane wet forest life zones, outside and adjacent to the reserve complex, are highly fragmented. About 75% of the premontane wet forest life zone has been deforested, with only about 7.5 km^2 remaining as forest fragments. The lower montane wet forest is in somewhat better condition, with 65% (11 km^2) still remaining in forest, though what remains is also highly fragmented and degraded. The poor representation of these two life zones in protected areas is characteristic throughout Costa Rica (Fig. 4). Only 39 km^2 of premontane wet forest and 81 km^2 of lower montane wet forest are protected in Costa Rica.

The two remaining habitats used by the bellbirds during their annual cycle are distant from the Tilaran Mountains and are in low-elevation habitats in opposite directions on opposite coasts. They also receive contrasting levels of legal protection. The lowland Atlantic area is still largely intact, and much of it falls within the Indio-Maiz Biological Reserve of Nicaragua (Fig. 5). This area of nearly one-quarter of a million hectares of virtually pristine tropical wet forest represents one of the most important blocks of that habitat still remaining in Central America. Although the area has been declared a reserve, it is currently under heavy pressure from development interests (N. Robertson, personal communication). Both international logging interests and local slash-and-burn agriculturists threaten the reserve.

The lowland moist forest life zone along the Pacific coast (Fig. 5.) is largely deforested, with only about 23% remaining in forest. Most of that forest is located in three national parks: Corcovado (43,900 ha), Carara (5200 ha), and Cabo Blanco (1400 ha). Although the bellbirds were on the Pacific coast, they tended to use second-growth habitat outside the protected areas, where they foraged heavily on fruit produced by vines (*Smilax* sp.).

Discussion

Annual Migratory Cycle of *Procnias tricarunculata*

The data collected from 4 years of study expanded the known habitat requirements of the Tilaran Bellbird population by two orders of magnitude, from about 400 to 36,000 km^2 and documented a complex migratory cycle comprising stops in four separate geographical regions separated by as much as 280 km.

During each of the 4 study years, the radiotagged individuals began leaving the Pacific slopes, where they had been captured, in September and had all departed by the end of October. Monitoring them with overflights revealed that they consistently moved in a northeasterly direction into tropical wet forest life zones of the lowland Atlantic zone of northeastern Costa Rica and adjacent southeastern Nicaragua (Fig. 5). The movements away from the Tilaran Mountains apparently occurred via direct extended flights, because surveillance flights determined that at least some individuals covered the 120 km distance between the Tilaran range and Nicaragua within 24 hours. They typically remained in the lowland Atlantic zone for up to several months.

Although most individuals followed this pattern of movement from the middle-elevation Pacific slope to the

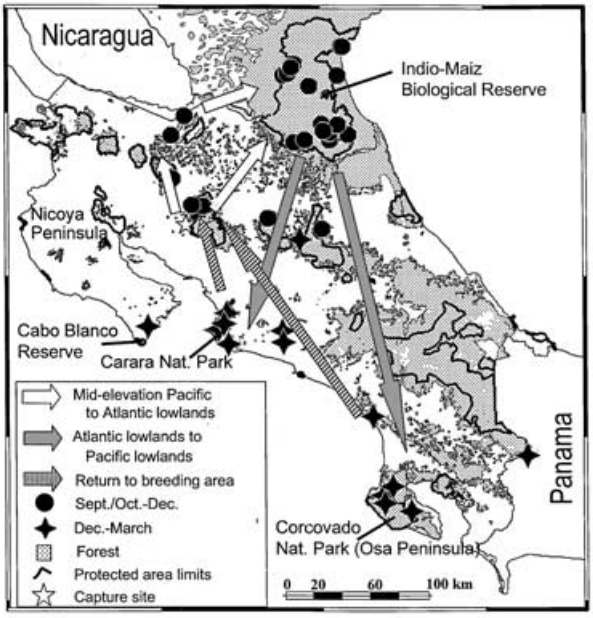

Figure 5. Distribution of forest in Costa Rica (1992) in relation to protected areas (dark outlines) and radio tagged bellbirds in September–December (circles) and December-March (crosses). Arrows show direction of movements between stopovers. Data from all years are combined. Star on lower left of breeding area denotes capture area.

Atlantic lowlands, there was at least one exception. In December of 1992, one individual, a subadult male, was discovered in western Panama at 1400 m elevation on the Pacific slope (Fig. 5), a distance of about 200 km from where it was radiotagged.

Between late November and February, the birds relocated to the Pacific lowlands of Costa Rica. At this time they settled in a 4000-km^2 section of the Pacific coast of Costa Rica between the tip of the Nicoya Peninsula (Cabo Blanco National Park) and the Osa Peninsula (Corcovado National Park), a distance of 150 to 280 km to the south and south-southwest of their sites in the Atlantic lowlands. The birds remained in these tropical wet and premontane wet forest life zones until March.

In March, adults moved back to the Tilaran Mountains, this time settling in middle-elevation sites (1000 and 1700 m), in the lower montane rainforest and premontane rainforest life zones, which occur primarily on the Atlantic slopes. These sites were 10–20 km from where the birds had been captured on the Pacific slope 8–9 months before. They bred in these largely intact forest habitats from March through late June or early July.

With the completion of breeding in July, the birds moved back across the continental divide, into the slightly drier lower montane wet and premontane wet forest life zones (1000 and 1300 m) on the Pacific slope (Fig. 3) where they had been captured. They remained in these Pacific-slope habitats for 3–4 months, feeding primarily on two forest species of Lauraceae (*Ocotea floribunda* and *Nectandra salicina*) that are restricted exclusively to this area (B. Haber, unpublished data).

Although the generalized migration pattern, utilizing four different geographic regions, appeared to be consistent for a majority of the radiotagged individuals, in all 4 years, all searches failed to locate some individuals. In large part, we attribute this to the logistical challenges of attempting to canvas 36,000 km^2 with limited funds for aerial surveys. However, our failure to locate some individuals also may reflect flexibility in the patterns of movements we recorded. Although all individuals consistently left each of the four stopovers reported in the annual cycle, they left at markedly different times, in some cases were discovered at intermediate locations for up to several months, or were not relocated until they appeared at a subsequent stopover site. In 1993–1994, for example, one individual remained on the lower Atlantic slope of the Tilaran Mountains (500 m) for several months before moving on to the Atlantic lowlands, where the remainder of the birds had been located. We visited that individual at the intermediate stopover on four occasions, and it was the only bellbird in the area. In 1992–1993 another individual moved south to a middle-elevation site in Panama rather than follow the pattern of moving to the Atlantic lowlands of Nicaragua. Extensive aerial searching failed to detect any other radiotagged individuals in that area. However, at least four additional calling males were recorded in the area. These examples of individuals moving independently of the majority of radiotagged individuals demonstrate flexibility in the species' movement patterns that could have important implications for the conservation of the species.

The individual variations in movements of bellbirds suggest that the species is to some degree flexible in its seasonal movements rather than having a set migration and that their movements may reflect tracking of temporary food resources (Levey & Stiles 1992; Levey 1994). Our data did not allow us to evaluate the flexibility of the migratory pattern beyond the fact that it was repeated during the 4 years. However, interannual variations in production of Lauraceae fruit in the Monteverde area (Wheelwright 1983) likely necessitate flexibility on the part of frugivorous birds, such as bellbirds, that depend on Lauraceae as their primary food source.

Status of the Three-Wattled Bellbird

Based on our findings and using the criteria of Soulé (1987), it is likely that sufficient breeding habitat is protected to maintain a viable population of Three-wattled Bellbirds in the Tilaran mountain range. The bellbird may be in a precarious position, however, unless there are increases in the protection of some habitats they use during their annual cycle.

The remaining middle-elevation premontane wet and lower montane wet forest habitats on the Pacific slopes of the Tilaran Mountains are probably already inadequate to support a viable population of bellbirds over the long term. The fragments that remain are being subjected to further fragmentation by a rapidly growing human population (responding to increasing ecotourism) and the degradation that accompanies fragmentation. In the Monteverde region, for example, forest fragments are a source of wood for landowners who use Lauraceae spp. as fence posts and lumber. In accordance with our results, organizations involved in conservation in the Tilaran Mountains should focus greater efforts on expanding protection of the Pacific-slope habitats, which currently have little representation in the Monteverde reserve complex or elsewhere in Costa Rica. Our concern over the conservation of the bellbird is consistent with data collected by M. P. L. Fogden (unpublished data), who has observed an 80% reduction in male bellbird calling rates in the Monteverde area during the breeding season since the early 1980s. In 1997–1999, a search was made throughout the region by G.V.N.P. and local biologists to locate alternative sites that might be used by the bellbirds during this period, but it failed to locate more than an occasional bellbird outside this area within the Tilaran range (D. DeRoser Hamilton, unpublished data).

Availability of tropical wet forest habitat in southeastern Nicaragua (stopover from September through December) is not likely to limit bellbird population size if habitat protection in the Indio-Maiz Reserve is successfully implemented. However, the reserve is being challenged by logging and colonization. This reserve, which is vitally important in the conservation of a viable Atlantic lowland ecosystem in Central America, is also important—as the migrations of the bellbirds demonstrate—to the stability of other habitats that seem far removed from the Atlantic lowlands.

The Pacific coastal habitats of Costa Rica that were used by the bellbirds during their stopover between December and March are likely underrepresented in protected areas. Although several protected areas exist within this zone, the distribution of the radiotagged bellbirds tended to be in secondary habitat outside protected areas and distant from Corcovado National Park, the largest protected area in the region (Fig. 5). However, the propensity of bellbirds to use disturbed areas while in these drier habitats may buffer them from habitat limitations. At least in the short term, second-growth habitat in the Pacific lowlands has become relatively abundant in the face of a shrinking Costa Rican cattle industry.

Implications for Conservation Planners

Costa Rica's system of protected areas is considered one of the best in the tropical world. Our results suggest, however, that the patchwork of increasingly isolated parks and reserves may not adequately satisfy the habitat requirements of some species it is intended to protect.

Identifying the array of habitats required by Three-wattled Bellbirds during their annual cycle demonstrates the immense challenge of protecting tropical biodiversity. Previous studies in Costa Rica have revealed that elevational migrations by frugivorous and nectivorous species must be an important consideration in the design of protected areas, particularly for the Atlantic slopes of mountains that form the central spine of much of Central America (Wheelwright 1983; Stiles 1985; Loiselle & Blake 1991; Powell & Bjork 1994). Elevational transects, which initially existed only on the Atlantic slope of the Talamanca range, have subsequently been incorporated into protected areas of that slope in the Central, Tilaran, and Guanacaste mountain massifs. Only the Guanacaste Mountains have an elevational transect on the Pacific slope. Elsewhere, Pacific slope habitat is heavily fragmented.

Our results raise the issue of linkages among tropical habitats to another level. The bellbirds linked habitats on different slopes within mountain ranges. They also linked different lowland sites. Although we do not know to what extent the bellbirds can modify their seasonal migrations to alternative sites in response to habitat destruction, the data suggest that even if they have a large degree of site flexibility, they still require a wide range of habitat during their annual cycle (Table 1). Furthermore, if bellbirds are resource-flush specialists (after Levey 1994), they may require large areas in order to locate sites with elevated resources. Thus, although their flexibility in migratory pattern may allow them to locate alternatives as habitats are destroyed, the need for an array of such sites annually may still make them sensitive to habitat loss overall.

The bellbird is an extreme case but demonstrates that linkages among tropical habitats can be extensive and diverse. Our current research efforts with *Ara ambigua* and *Amazona farinosa* are revealing extensive seasonal movements by both species (movements repeated from year to year but with considerable variation, as in the case of the bellbirds). Similarly, extensive seasonal movements within lowland moist forests in Belize have recently been reported for *Ara macao (*B. Mallory, unpublished data), and Diamond and Bishop (1998) recorded extensive seasonal movements of canopy frugivores, particularly Columbidae and Psittacidae, in the Kikori region of New Guinea.

Efforts to conserve biodiversity should integrate the full array of regional habitats into a single regional protection strategy. For example, two of the four habitat types used extensively by bellbirds during their annual cycle are situated far beyond what would normally be considered relevant to the conservation of montane biodiversity. If these areas are not considered, management efforts will not be completely successful. Costa Rica's recently developed national conservation plan, which was developed

through a nation-wide biodiversity analysis, GRUAS (Garcia 1997), was a major step in that direction.

The situation with the bellbirds transcends current conservation paradigms, such as endemic bird areas (International Council for Bird Preservation 1992) and ecoregions (Olson & Dinerstein 1998), because these birds migrate among areas that extend beyond the boundaries of these priority-setting units. The complex seasonal pattern of habitat use exhibited by the Three-wattled Bellbird demonstrates the level of complexity of linkages that may exist among tropical habitats. Even if seasonal movements of this type are due to the bird's specializing in ephemeral resource flushes rather than following "hard-wired" patterns, they apparently still depend on widely dispersed, diverse habitats. Although greater flexibility in habitat use presumably allows greater flexibility in reserve networks designed to protect the minimum set of sites for migratory bellbirds, the stocasticity of these resource flushes compounds the challenge of designing a hard-wired system of protected areas that maintains sufficient habitat to ensure that resource flushes are available.

Given that the bellbird is only one of an unknown, but undoubtedly large, number of species that depend on multiple tropical habitats, protected areas cannot be considered in isolation but should be pieces of an integrated system. If conservation efforts are going to protect the diversity of species in the Neotropics, they will need to be expansive in focus. Failure to consider linkages among both adjacent and disjunct habitats will likely result in a significant loss of biodiversity.

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