Implications of Intratropical Migration on Reserve Design: A Case Study Using *Pharomachrus mocinno*

GEORGE V. N. POWELL* AND ROBIN BJORK†‡

*RARE Center for Tropical Conservation, Apartado 56–5655, Monteverde, Puntarenas, Costa Rica, email gpowell@huracan.cr

†National Audubon Society, 115 Indian Mound Trail, Tavernier, FL 33070, U.S.A.

Abstract: *As habitat loss continues, natural protected areas will become islands in human-modified landscapes; maintenance of functional communities and ecosystems will depend on properly designed protected areas. We demonstrate that incorporating regional habitat linkages that allow for seasonal migrations of intratropical resident species must be a major design criterion for establishing protected areas. Using radiotelemetry, we monitored the seasonal movements of one such migrant, the Resplendent Quetzal (Pharomachrus mocinno), a large, frugivorous bird, one of many tropical residents known to migrate altitudinally within Mesoamerica. Based on three years of data we determined that quetzals followed a complicated local migration that linked four montane life zones. Using this species as an indicator revealed that the configuration of the Monteverde reserve complex in the Tilaran Mountains in west-central Costa Rica lacked sufficient habitat distribution to conserve montane biodiversity. On the basis of these results, we propose that the three-step process proposed by Soulé and Simberloff (1986) for estimating minimum sizes of reserves be amended to include a fourth step: The critical habitats used throughout the annual cycles of target or keystone species must be identified and adequately protected. Natural protected areas can be considered adequately designed only when sufficient area with a full complement of ecologically linked habitats is included.*

Las concecuencias de la migración intratropical para el diseño de reservas: un caso de estudio usando *Pharomachrus mocinno*

Resumen: *A medida que la pérdida de hábitat continúa, las áreas naturales protegidas se irán transformando en islas dentro de paisajes modificados por las actividades humanas; el mantenimiento de comunidades y ecosistemas funcionales dependerá de áreas protegidas correctamente diseñadas. En el presente estudio demostramos que la incorporación las conecciones entre hábitats de una misma región que permitan las migraciones estacionales de especies residentes intratropicales debe ser un criterio de diseño de gran importancia para el establecimiento de áreas protegidas. Por medio del uso de radiotelemetría, supervisamos los movimientos estacionales de uno de tales migrantes, el Quetzal Resplandeciente (Pharomarchrus mocinno), un ave frugívora grande y uno de los tantos residentes tropicales que migran en forma altitudinal dentro de Mesoamérica. En base a tres años de datos determinamos que los quetzales siguieron una migración local complicada que conectó cuatro biomas montaños. El uso de esta especie como indicador, reveló que la configuración del complejo de reservas de Monterverde en las Montañas Tilaran, en el centro-oeste de Costa Rica carecía de una distribución de hábitat suficiente para conservar la biodiversidad montana. Sobre la base estos resultados, proponemos que el proceso en tres etapas para estimar los tamaños mínimos de las reservas propuesto por Soulé y Simberloff (1986) sea modificado de tal forma que incluya una cuarta etapa: los hábitats críticos usados a lo largo de los ciclos anuales de las especies clave deben ser identificados y protegidos adecuadamente. Las áreas naturales protegidas sólo pueden ser consideradas como diseñadas adecuadamente cuando se incluya un área suficiente que comprenda un complemento de los hábitats conectados ecológicamente.*

354

Introduction

Concern for the loss of biodiversity due to anthropogenic modifications of natural landscapes has generated debate over the design of protected natural areas that will eventually serve as refugia for most ecosystems. Initial arguments calling for a few large (May 1975; Wilson & Willis 1975) or numerous small reserves (Gilpin & Diamond 1980; Higgs & Usher 1980; Quinn & Harrison 1988) have given way to more sophisticated theoretical designs (Boecklen & Gotelli 1984; Soulé & Simberloss 1986; Burkey 1989; Schonewald-Cox & Bayless 1992). Soulé and Simberloff (1986) proposed a three-step process for estimating minimum sizes of reserves. That process included (1) identifying target or keystone species, (2) determining the minimum population sizes needed for the survival of these species, and (3) using their population densities to estimate area needed.

A common characteristic of these design criteria remains the treatment of organisms as sedentary, or restricted to a single home range, when considering their habitat requirements. In tropical environments, many species have been identified as seasonal migrants within the tropics, though the details of their migrations are rarely known (Stiles 1983; Stiles 1985; Levey 1988; Loiselle & Blake 1991). For example, Stiles (1983) reported that about half of the avian species of Costa Rica migrate seasonally; many of these migrations are intratropical.

These seasonal movements create ecological linkages among the diverse array of communities or life zones, occurring in altitudinal bands, that typify Neotropical montane ecosystems (Holdrige 1967). Several researchers have concluded, based on seasonal differences in distributions and abundances of species, that seasonal mobility must be a primary consideration in the design of protected natural areas lest they fail to protect critical habitat for many of the species they aim to conserve (Wheelwright 1983; Levey 1988; Stiles 1988; Stiles & Clark 1989; Loiselle & Blake 1992; Woinarski et al. 1992). Their conclusions, however, have been based on census data that by their nature are inferential regarding the significance of the movements at the population level. A rigorous test of the hypothesis requires that a representative sample of individuals be monitored to determine the extent to which the total population is dependent on seasonal movements. Toward this end, we monitored seasonal movements of the Resplendent Quetzal (*Pharomachrus mocinno*), a large, frugivorous bird (Skutch 1944; Bowes & Allen 1969; La Bastille 1983; Wheelwright 1983; Wheelwright et al. 1984; Avila & Hernandez 1990) that has been identified as an altitudinal migrant (Wheelwright 1983; Loiselle et al. 1989) and used as an indicator of reserve capacity to protect montane biodiversity in a montane reserve in Costa Rica. In this regard, the quetzal served as a mobile link species (Soulé & Kohm 1989) and an indicator of habitat heterogeneity (Noss 1990), elucidating patterns that are likely important to other altitudinal migrant species.

Study Area and Methods

The Resplendent Quetzal's distribution consists of disjunct populations in montane areas from southern Mexico through western Panama (La Bastille 1983). We collected habitat use data from the quetzal population that breeds in the Monteverde reserve complex (hereafter referred to as reserve complex) and nearby farms in the Tilaran mountain range of west-central Costa Rica (Fig. 1). The reserve complex consists of two privately-owned protected natural areas, the Monteverde Cloud Forest Preserve and the Children's International Rainforest. The reserve complex totals more than 20,000 ha and extends from 1500 meters elevation on the Pacific slope, across the Continental Divide at about 1800 meters, and down to 800 meters elevation on the Atlantic side.

The montane region of Costa Rica runs the length of the country, with only slight breaks that separate the mountains into four ranges: Guanacaste, Tilaran, Central, and Talamanca. In these mountains, the combination of topographic relief and seasonal trade winds from the east produces a pronounced moisture gradient and highly diversified vegetational communities or life zones (Holdridge 1967). On the Atlantic side, communities are arranged in relatively broad altitudinal belts that receive high rainfall most of the year. On the Pacific slope, they exist as narrow belts with increasingly extended dry seasons (up to six months) at the base of the mountain.

To identify the forest habitats that are necessary for the survival of quetzals, we used radiotelemetry to track them throughout their annual cycle. Radio transmitters (Holohil Systems Ltd., Ontario, Canada) with batteries that lasted about 13 months, were placed on the quetzals with a harness in the form of a backpack. The harness was composed of straps of lightweight teflon ribbon that ran from the forward end of the transmitter, crossing on the breast, passing under the wings, and attaching to the end of the transmitter on the lower back. The harness was custom-fit for each bird, and the straps were sewn together at the rear attachment with cotton thread. The entire apparatus weighed 6 grams, or about 3% of an average individual's body mass.

We used two methods to capture the quetzals: nest traps and mist nets placed in front of fruiting trees. The nest trap, a modified version of Jackson's (1991) trap, consisted of a mist-net bag attached to a small aluminum hoop (0.4 m in diameter) mounted on an extendable
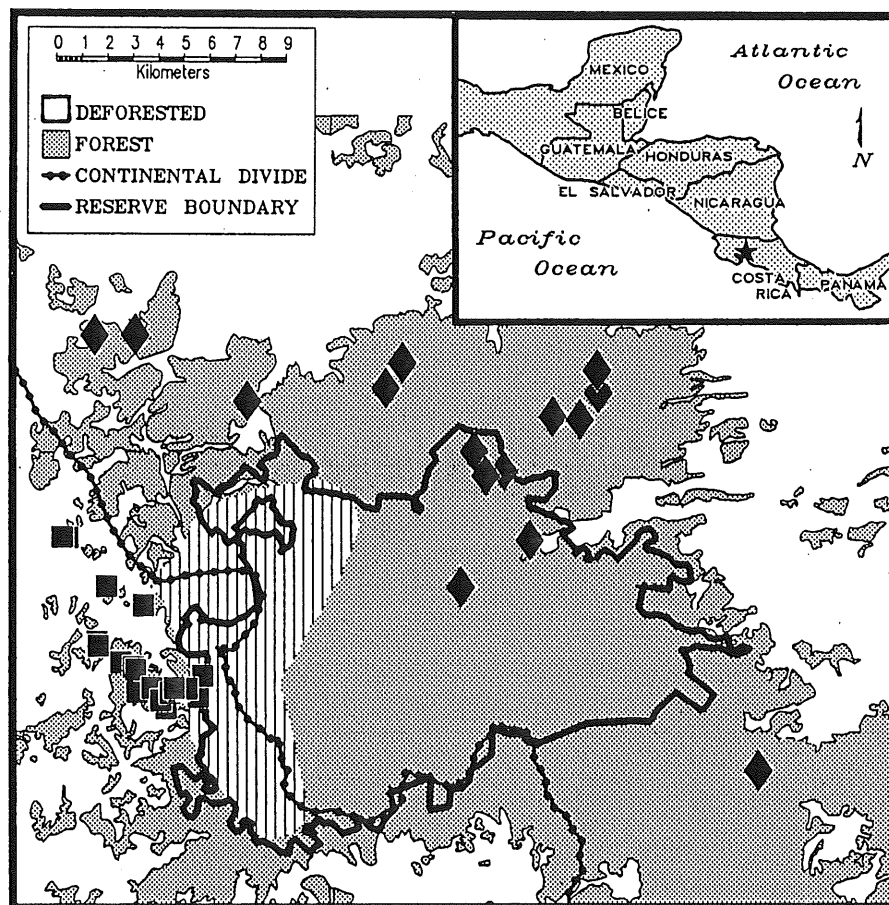
Figure 1. Distribution of individual radio-tagged Resplendent Quetzals in west-central Costa Rica during their two-parted migration from the breeding area (vertical lines) to the Pacific slope (squares) and about three months later to the Atlantic slope (diamonds).

pole that was placed in front of the entrance to the nest cavity after a quetzal entered the cavity to feed its young. When the quetzal exited the cavity, it was entrapped in the mist-net bag. Captured quetzals were weighed, fitted with transmitters, and released within 45–60 minutes. Initially, we placed transmitters on two individuals and observed them for one month for signs of problems with their flight or feeding that might be attributed to the radio-tagging. After concluding that the birds continued to feed and fly without observable disturbance from the transmitters, we continued radio-tagging efforts.

Movements of the quetzals were monitored using a portable receiver and hand-held directional "H" antenna, which gave us a ground detection range of 1–2 km. Our observation protocol was designed to collect data on two scales of movement: local or micro and long-distance or migratory. We used vector-based geographical information processing (GIS) software, CAMRIS (Ecological Consulting, Inc., Portland, Oregon), to record the birds' movements with respect to the distribution of the reserve complex and forest habitats. We digitized topography from 1:50,000–scale topo-

graphic quadrangles (obtained from Instituto Geográfico National, San José, Costa Rica), the protected area (boundary delineations provided by the Monteverde Conservation League, Apartado 10581–1000, San José, Costa Rica), and forest distribution from 1:30,000–scale low-level aerial photographs taken in 1983 (obtained from Instituto Geográfico National). The distribution of life zones was digitized from 1:250,000–scale maps prepared by Bolaños and Watson (1993). We surveyed existing trail systems and roads in the study area and entered those data into the GIS.

We checked all radio-tagged individuals on a daily basis to verify their presence in the local area. After these checks, two individuals were selected, based on days lapsed since previous observation, and observed for 3–4 hours each to collect local movement data. Birds were followed and visually observed as continuously as possible; locality data were recorded at five-minute intervals. Locations of birds under observation were plotted (±25 m) in the field on detailed maps produced from the GIS, and subsequently the data were loaded into the GIS. During these observations, habitat use, food selection, and social interactions were col-

lected. For the broad-scale analysis of seasonal migration presented in this report, the location of each radio-tagged individual was plotted by approximating the center of habitat used during each phase of the migration.

Results

Twenty-one individuals were radio-tagged over three years. Four individuals were recaptured once, and two individuals were recaptured on all three years, bringing the total to 29 transmitters placed on quetzals over the three-year period. Premature failure of four transmitters during the first year, five during the second, and one during the third prevented us from obtaining complete movement records on those individuals. All but five of the birds, however, had already moved off their breeding ranges before their transmitters failed, and in all cases we were able to monitor the presence and absence on their breeding home ranges by using the transmitter as a visual marker.

With the radio-tagged birds, we were able to follow the quetzals' migrations precisely, which took them from their nesting habitat into forest habitats lower in elevation on both the Pacific and Atlantic slopes (Fig. 1).

They first moved from their breeding area, located between 1500 and 1800 meters in elevation on both slopes, down the Pacific slope, and they remained for three to four months (July–October) outside the protected area in small forest fragments (Fig. 1). They then moved to locations on the Atlantic slope for two to three months (November–January, Fig. 1). They returned to their breeding areas in January. These movements were largely consistent among years, with minor differences in timing and distribution as detailed below.

In 1989, seven birds were radio-tagged. In late June, the birds began to move off the breeding area (Lower Montane Rain Forest Life Zone), and by July the six birds with functioning transmitters were doing all of their feeding between 1300 and 1400 meters elevation (Lower Montane Wet Forest Life Zone) on the Pacific slope; four of the six individuals were outside the boundaries of the reserve complex (Fig. 2). Five of the six individuals made occasional forays back to their home ranges or returned to roost there on a regular basis. In November, the three birds with functioning transmitters returned to their breeding home ranges for one to two weeks before all three birds left the area between November 17 and 20. On December 5 they
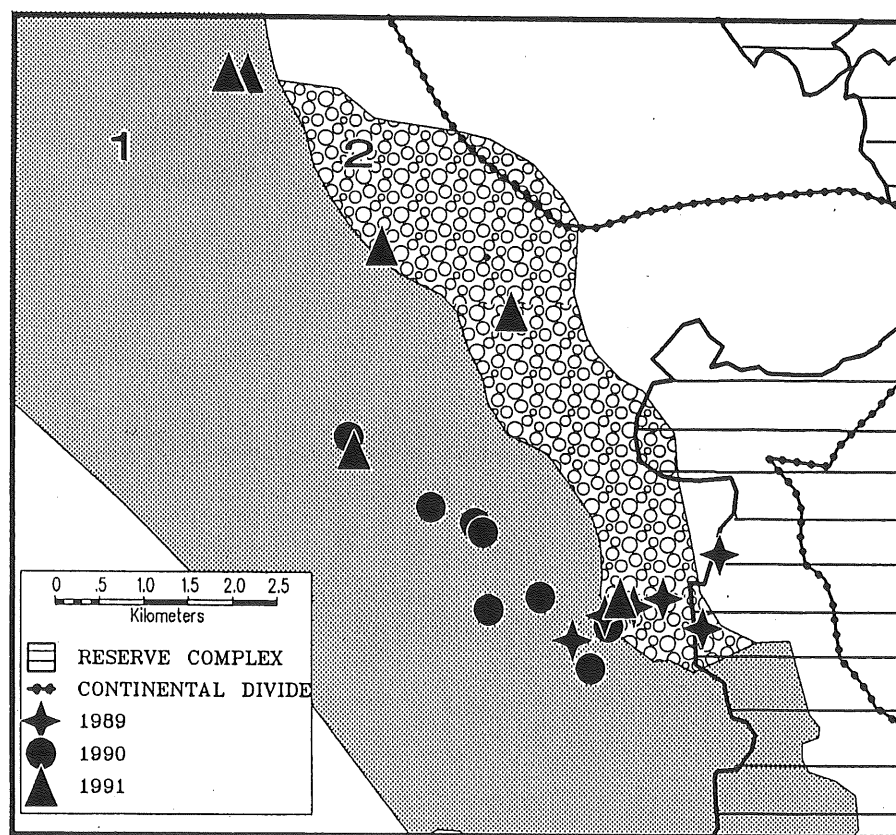

Figure 2. Distribution of radio-tagged Resplendent Quetzals in 1989, 1990, and 1991 on the Pacific slope during the first part of their migration. Life zones (Holdridge 1967), or habitats occurring in altitudinal bands, are numbered and represented by different patterns: (1) premontane wet, (2) lower montane wet.

were relocated by aerial reconnaissance between 700 and 1100 meters elevation (Premontane Rain Forest Life Zone) on the Atlantic slope 13–19 km northwest of their breeding sites; two of the three individuals were beyond the boundaries of the reserve complex (Fig. 3). Each remained on the Atlantic slope until mid-January. Extensive searching for the four individuals with malfunctioning transmitters on their breeding home ranges between November and January failed to detect them, indicating they had migrated as well. Between January 10 and February 13 all individuals (birds with functional and nonfunctional transmitters) were relocated on their respective breeding home ranges.

In 1990, 12 birds were radio-tagged (four of these were recaptures). The breeding season ended earlier than in 1989; eight birds with functioning transmitters moved down the Pacific slope in early June. This year they moved to sites lower in elevation at 1000 to 1200 meters, further from their breeding sites (1–4 km), and

into a different life zone (Premontane Wet Forest Life Zone) than in 1989 (Fig. 2). All eight birds foraged outside the boundaries of the reserve complex. Only one individual returned to its breeding home range during this period. By October, all seven birds with functioning transmitters had left the Pacific slope and were relocated on the Atlantic side between 550 and 1200 meters in elevation. Five of the seven birds were located outside of the reserve complex (Fig. 3; two individuals that were detected by air on the Atlantic slope outside the reserve complex but not subsequently pinpointed by ground check are not shown). All but one individual were relocated on their respective home ranges between mid-January and the end of February (the missing individual also disappeared from its Atlantic home range and was presumed dead).

In 1991, we expanded the area of capture to include breeding habitat approximately 10 km outside the reserve complex. Ten birds were radio-tagged (four of
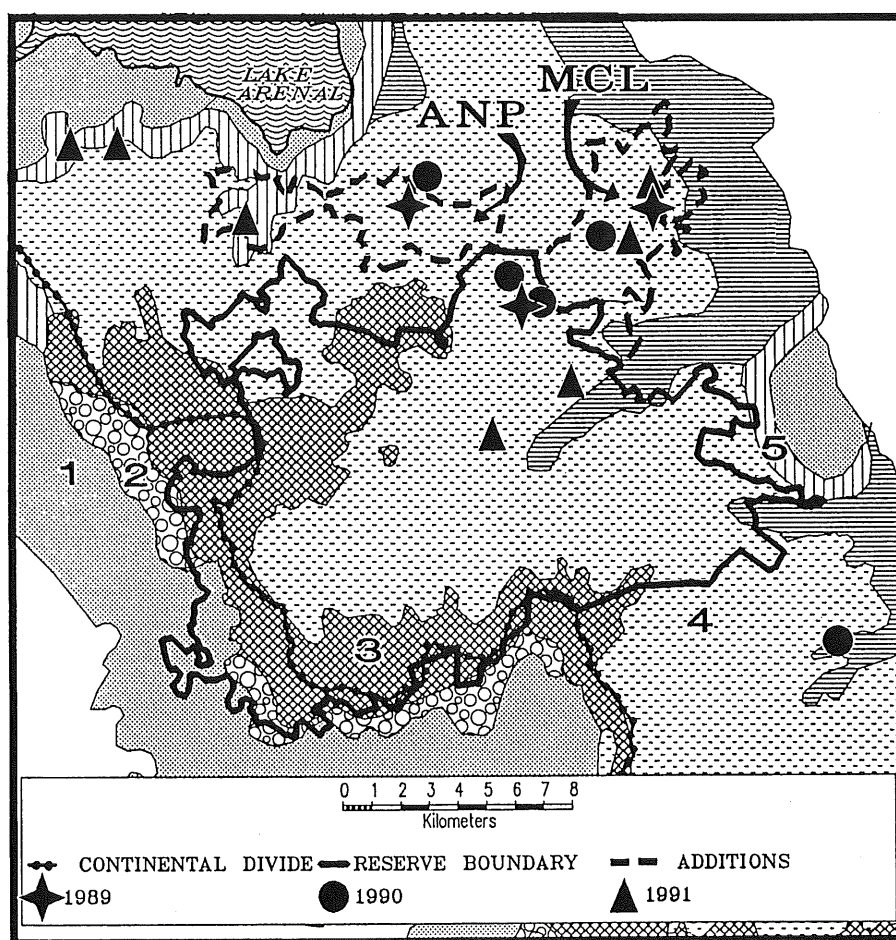

Figure 3. Distribution of radio-tagged Resplendent Quetzals in 1989, 1990, and 1991 on the Atlantic slope during the second part of migration. The quetzals' locations represent areas that they used for about three months. Life zones (Holdridge 1967), or habitats occurring in altitudinal bands, are numbered and represented by different patterns: (1) premontane wet; (2) lower montane wet; (3) lower montane rain; (4) premontane rain; and (5) premontane moist transition to rain MCL (Monteverde Conservation League) and ANP (Renal National Park) are reserve editions in the region.

these were recaptures). That year, the breeding season lasted into July, about a month longer than previous years, and the postbreeding season migration was more variable. In late July, three of the 10 individuals moved down the Pacific slope and within the Lower Montane Wet Forest Life Zone, three birds moved down into the Premontane Wet Forest Life Zone (Fig. 2), three birds remained on their breeding areas (Lower Montane Rain Forest Life Zone), and one bird moved directly to the Atlantic side (Premontane Rain Forest Life Zone), thereby skipping the Pacific phase of its migration. Between the end of August and beginning of September, five of the six birds that had moved down on the Pacific sites left those areas and moved across the Continental Divide into habitat of the Premontane Rain Forest Life Zone; the sixth transmitter failed (Fig. 3; one individual was located by air, but could not be pinpointed by ground checks). During the same period, two of the three individuals that had remained on their breeding ranges also migrated to the Premontane Rain Forest Life Zone. The remaining individual continued foraging on its breeding range until late December, when it left for an undiscovered location. As in the other years, all birds returned to their breeding ranges in January.

Discussion

At the outset of this study in 1989, the reserve complex extended onto both the Pacific and Atlantic slopes and, in the case of the latter, it reached as low as 800 meters elevation or within the elevational limits of the quetzals' migration on that slope. Based on the seasonal movements we recorded, however, the reserve failed to provide adequate habitat protection for the quetzal.

All the radio-tagged quetzals left the reserve complex during at least one of their migration phases. Between 65% and 100% of the study birds annually left the reserve complex during the first migratory phase. The two Pacific-slope life zones, Lower Montane Wet Forest and Premontane Wet Forest, that were used by quetzals during their first migratory phase have little representation in the reserve complex (300 and 600 ha, respectively; Fig. 2). These life zones support distinct floras (Sawyer & Lindsey 1971) and avifaunas (Fogden 1994), including seven species of Lauraceae that are unrepresented in the reserve complex (C. Guindon, personal communication). Fruits of these species constitute primary food resources for quetzals while they are in these areas (G. Powell & R. Bjork, unpublished data).

On the Atlantic slope, the reserve complex also apparently failed to incorporate sufficient habitat because in all years most individuals (65–75%) were located beyond the limits of the reserve complex (Fig. 3). In this case, the life zone classification did not differentiate the relatively narrow altitudinal band of habitat used by the quetzals from the rest of the Premontane Rain Forest Life Zone that extends from the Continental Divide down to about 600 meters and is well-represented within the reserve complex. The flora of the Atlantic zone used by the quetzals is only now being sampled by botanists, so its uniqueness and heterogeneity are largely unknown (W. Haber, personal communication).

Habitat Linkages and Design of Protected Natural Areas

The significance of ecological linkages is not a new concept for reserve design (Wheelwright 1983; Levey 1988; Stiles 1988; Stiles & Clark 1989; Loiselle & Blake 1992; Woinarski et al. 1992), but this study has identified the pattern of and extent to which a specific population is engaged in seasonal movements. The large proportion of the Monteverde quetzal population undertaking altitudinal migrations and the complexity of those migrations unequivocally demonstrate that annual habitat-use data must be incorporated into the design of montane protected natural areas if those areas are going to protect regional biodiversity.

The reserve complex, though relatively large in size (more than 20,000 ha), does not provide sufficient altitudinal relief to include the full range of habitats used by the quetzals. Additional studies (G. Powell, R. Bjork & C. Guindon, unpublished data) show that other avian species in the area, including Three-wattled Bellbirds (*Procnias tricarunculata*) and Mountain Robins (*Turdus plebejus*), exhibit similar migrations onto the Pacific slope during part of their annual cycle. These examples further reinforce the need to expand protection to include greater vertical range on the Pacific slope. Very likely, many other species that are believed to be altitudinal migrants but have not had their migratory pathways elucidated receive inadequate habitat protection as well (Stiles 1985, 1988; Levey 1988; Loiselle & Blake 1991, 1992).

The need for protected natural areas in the tropics to allow for seasonal movements of resident species is probably not limited to montane situations. Many lowland bird species, such as members of the Ciconiiformes (for example, Maguari Stork, *Ciconia maguari*; B. T. Thomas, personal communication) and Psittaciformes (for example, macaws, *Ara* sp.: Hilty & Brown 1986; Stiles & Skutch 1989), have extensive but largely undescribed seasonal migrations. In view of the probable universality of seasonal migrations in tropical ecosystems, we propose that the basic design strategy developed by Soulé and Simberloff (1986) be modified to take into account seasonal movements. That process, selecting the target or keystone species to be used for the analysis and determining minimum viable population size(s) and minimum habitat requirements, should be amended to include identification of all habitats required by the spe-

cies during its annual cycle. For this process, target species should be selected from those known or suspected to be seasonal migrants. Once the linkages are identified, the process should be repeated for each linked habitat with the original or additional target species to identify the minimum areas required to support viable populations of those species. Only when sufficient area of the full complement of ecologically linked habitats are included can the protected natural area be considered adequately designed. In cases where seasonal movements include dependencies on disjunct habitats, it may be necessary to propose a network of reserves that will protect the required habitats.

Addressing Design Deficiencies

The actual process of determining a sufficient area of linked habitats may differ from that of identifying linkages. While tracking seasonal migrants demonstrates ecological linkages among habitats and, consequently, the need to integrate them into protected natural areas, these migrants may not be appropriate target species (as used by Soulé & Simberloff 1986) for determining the minimum critical area of habitats that are linked. For example, in the case of the two Pacific slope life zones that are linked by Resplendent Quetzals, it may not be appropriate to use that species to set minimum spatial requirements for either zone because the migrating quetzals, which are nonbreeding and remain in the area for only a few months, are likely to have less extensive habitat needs than those of many permanent residents. Minimal spatial requirements of ecologically linked habitats must be quantified through the use of appropriate target species via separate applications of the process outlined by Soulé and Simberloff (1986) and amended above.

While the Resplendent Quetzal may not be an appropriate species to define minimum-area requirements that will adequately protect resident fauna and flora of the life zones it uses during the nonbreeding season, it is useful to evaluate the status of its protection because of its inordinate impact on human responses to conservation recommendations. Numerous protected areas, including the Monteverde reserve complex, and millions of dollars have already been dedicated, at least in part, to the conservation of the quetzal. Assessing the status of habitat protection for this species thus provides a measure of success of those efforts plus a strong incentive for further conservation action where protection is determined to be inadequate.

At the onset of our study, the habitats used during both Pacific and Atlantic slope migrations were poorly represented in the Monteverde reserve complex. Since that time, the status of habitat protection on the Atlantic slope has changed dramatically. When preliminary results of our study revealed the deficiencies in habitat

protection for quetzals, the Monteverde Conservation League and owners of the International Children's Rainforest (about two-thirds of the reserve complex) focused their reserve expansion priorities on purchasing Atlantic slope forest within the zone used by the species. By focusing on the quetzal as a symbol to solicit funds, they were able to expand the protected area to include 2300 ha of habitat in the lower portions of the Premontane Rain Forest Life Zone (Fig. 3). In addition, a small national park, Arenal National Park, (1900 ha) was established by the Costa Rican government in the area (Fig. 3). The continuing effort to consolidate those expansions into a wide band of Atlantic slope habitat should result in protection of sufficient habitat to support the quetzal population in the Tilaran Mountains during the second phase of its migration.

The situation on the Pacific slope remains unresolved and far more tenuous. Almost all land within the two life zones used by migrating quetzals is in private ownership, primarily in the form of small dairy farms (<50 ha), and is heavily fragmented. Based on 1980–1981 low-level aerial photographs that were field-updated to 1993, about 56% (1120 of 2000 ha) of the Lower Montane Wet Forest Life Zone and 25% (750 of 3000 ha) of the Premontane Wet Forest Life Zone remain forested (G. Powell & C. Guindon, unpublished data). While little outright clearing of remaining forest is occurring in this area, selective removal of trees, fire, wind, and intrusion by livestock continue to degrade remaining fragments.

It is difficult to estimate the minimum quantity of Pacific slope habitat that would be required to support the local quetzal population if the fragmented landscape was purchased and restored to pristine condition. No large blocks of forest currently exist, and even the forest fragments have been degraded. Our data from radio-tagged individuals revealed a dependency on a relatively small number of trees with fruit, but those trees were often spread out over distances of up to one kilometer. We cannot determine whether this pattern was an artifact of the fragmented landscape or whether it would persist in pristine conditions. Further confounding efforts to determine minimum habitat requirements for the quetzals is the fact that fruit production by Lauraceae in the Premontane and Lower Montane Wet Forest Life Zones is highly variable (Wheelwright 1986). For example, fruit was largely absent from the Lower Montane Wet Forest Life Zone during one of the three years (1990) of our study (G. Powell & R. Bjork, unpublished data), and the quetzals were dependent on the lower and more degraded Premontane Wet Forest Life Zone (Fig. 2).

In the face of these uncertainties, our predictions of the amount of habitat in each of the Pacific slope life zones that should be protected to support the Tilaran quetzal population must be speculative. We estimated

that population to be 100–150 nesting pairs (200–300 individuals), which falls within the range suggested by Soulé and Simberloff (1986). Based on monthly censuses of 30 forest fragments located in the Premontane and Lower Montane Forest Life Zones adjacent to the reserve complex during two migration seasons, the mean density of quetzals (using the highest number recorded in each fragment) was 0.44 individuals per hectare of forest patch (C. Guindon, unpublished data). Using a population size of 150 nesting pairs of quetzals, a minimum of 682 ha of forested area in each zone would be required to maintain the population. Based on forest coverage data presented above, we calculate that, as a minimum, virtually all of the remaining forest patches in the Premontane Wet Forest and at least half of the Lower Montane Wet Forest must be protected. Ideally, because the total distributions of these zones in the vicinity of the reserve complex are so limited, absolute protection should be given to the entire extension, thereby allowing natural forest regeneration and removing the human forces that continue to degrade habitat remnants. This action would cost millions of dollars, however, and would result in the displacement of thousands of people.

An alternative to complete protection is to focus on protecting a patchwork of interconnected forest fragments along streams and rivers and on steeper slopes, with selected purchases to tie the patchwork together (Powell & Bjork 1994). Even this minimum level of protection would require a major effort by conservationists because of continuing habitat degradation. Without this action, however, it seems likely that the quetzal population, as well as a myriad of other species unique to those life zones, will be extirpated from the area.

Two conservation priorities have resulted from our demonstration of ecological linkages among montane habitats. The first priority is to procure protection for our target species. Quetzals can survive the short-term bottleneck they currently face when using the Pacific-slope habitats during their first phase of migration only if enough habitat is maintained to support sufficient numbers of the trees they forage on. The second priority, which is more long term, is to protect sufficient quantities of linked habitats for the benefit of resident species that are restricted to those habitats. The quetzals depend, either directly or indirectly, on stable populations of an array of these species, from those that provide them food to those that are pollinators of the food species. Viable populations of these species must be protected for the long-term survival of the quetzal in the region.

We have attempted to quantify the level of risk for the quetzal population over the short term due to a lack of protection for linked habitats that presents an urgent conservation need. We propose that collaborative actions be taken with local conservation organizations and landowners to stabilize and restore those habitats. We have not attempted to quantify habitat requirements for the long-term viability of biodiversity in the habitats we found to be linked. A separate study, using appropriate target species, will be necessary to answer that question and thereby ultimately determine the long-term stability of the Resplendent Quetzal and other mobile-link species in the region.

Acknowledgments

Literature Cited

Avila, M. de L., and V. H. H. Hernández. 1990. Contribucion a la biologia y distribucion del quetzal *Pharomachrus mocinno mocinno* en la reserva "El Triunfo," Chiapas, Mexico. Master's Thesis. Universidad National Autonoma de Mexico, Mexico City, Mexico.

Boecklen, W. J., and N. J. Gotelli. 1984. Island biogeographic theory and conservation practice: Species-area or specious-area relationships? Biological Conservation 29:63–80.

Bolaños, R. A., and V. Watson. 1993. Mapa Ecologico de Costa Rica. Tropical Science Center Publication, San José, Costa Rica.

Bowes, A. La Bastille, and D. G. Allen. 1969. Biology and conservation of the quetzal. Biological Conservation 1:297–306.

Burkey, T. V. 1989. Extinction in nature reserves: The effect of fragmentation and the importance of migration between reserve fragments. Oikos 55:75–81.

Fogden, T. V. 1994. An annotated checklist for the birds of Monteverde and Peñas Blancas. Fogden Press, Monteverde, Costa Rica.

Gilpin, M. E., and J. M. Diamond. 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature 285:567–568.

Higgs, A. J., and M. B. Usher. 1980. Should nature reserves be large or small? Nature 285:568–569.

Hilty, S. L., and W. L. Brown. 1986. Birds of Colombia. Princeton University Press, Princeton, New Jersey.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center Publication, San José, Costa Rica.

Jackson, A. J. 1991. A simple, effective net for capturing cavity roosting birds. North American Bird Bander 16:30–31.

La Bastille, A. 1983. *Pharomachrus mocinno* (Quetzal). Pages 599–601 in D. H. Janzen, editor. Costa Rican natural history. University of Chicago Press, Chicago, Illinois.

Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monograph 58:251–269.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193.

Loiselle, B. A., and J. G. Blake. 1992. Population variation in a tropical bird community: Implications for conservation. Bioscience 42:838–845.

Loiselle, B. A., J. G. Blake, T. C. Moermond, and D. J. Mason. 1989. Low elevation record for Resplendent Quetzals in Costa Rica. Journal of Field Ornithology 60:86–88.

May, R. M. 1975. Island biogeography and the design of wildlife preserves. Nature 254:177–178.

Noss, R.F. 1990. Indicators for monitoring biodiversity: A hierarchal approach. Conservation Biology 4:355–364.

Powell, G. V. N., and R. D. Bjork. 1994. Implications of altitudinal migration for conservation strategies to protect tropical biodiversity: A case study of the Quetzal *Pharomachrus mocinno* at Monteverde, Costa Rica. Bird Conservation International 4:243–255.

Quinn, J. F., and S. P. Harrison. 1988. Effects of habitat fragmentation and isolation on species richness: Evidence from biogeographic patterns. Oecologia 75:132–140.

Sawyer, J. O., and A. A. Lindsey. 1971. Vegetation of the life zones in Costa Rica. Monograph No. 2. Indiana Academy of Science, Indianapolis, Indiana.

Schonewald-Cox, C. M., and J. W. Bayless. 1992. The boundary model: A geographical analysis of design and conservation of nature reserves. Biological Conservation 37:305–323.

Skutch, A. F. 1944. Life history of the quetzal. Condor 46:213–235.

Soulé, M. E., and K. A. Kohm. 1989. The ecology of communities and small systems. Pages 21–29 in M. E. Soulé and K. A. Kohm, editors. Research priorities for conservation biology. Island Press, Washington, D.C.

Soulé, M. E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? Biological Conservation 35:19–40.

Stiles, F. G. 1983. Birds. Pages 502–530 in D. H. Janzen, editor. Costa Rican natural history. University of Chicago Press, Chicago, Illinois.

Stiles, F. G. 1985. Conservation of forest birds in Costa Rica: Problems and perspectives. Pages 141–168 in A. W. Diamond and T. E. Lovejoy, editors. Conservation of tropical birds. Technical Publication No. 4. International Council for Bird Preservation, Cambridge, England.

Stiles, F. G. 1988. Altitudinal movements of birds on the Caribbean slope of Costa Rica: Implications for conservation. Pages 243–258 in F. Almeda and C. M. Pringle, editors. Tropical rainforests: Diversity and conservation. Memoir No. 12. California Academy of Sciences, San Francisco, California.

Stiles, F. G., and D. A. Clark. 1989. Conservation of tropical rain forest birds: A case study from Costa Rica. American Birds 43:420–428.

Stiles, F. G., and A. F. Skutch. 1989. A field guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.

Wheelwright, N. T. 1983. Fruits and the ecology of Resplendent Quetzals. Auk 100:286–301.

Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: A survey of a Costa Rican Lower Montane Forest. Biotropica 16:173–192.

Wheelwright, N. T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. Pages 19–25 in A. Estrada, and T. H. Fleming, editors. Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody, and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts.

Woinarski, J. C. Z., P. J. Whitehead, D. M. J. S. Bowman, and J. Russell-Smith. 1992. Conservation of mobile species in a variable environment: The problem of reserve design in the Northern Territory, Australia. Global Ecology and Biogeography Letters 2:1–10.