6

Birds — Update 2014

Bruce E. Young

Although the pace of research on birds in Monteverde may have slowed during the 14 years since the last synopsis (Young and McDonald 2000), researchers continue to make important contributions to tropical avian biology and other scientific disciplines. Elevational gradients and migrations of birds along them still inspire research in Monteverde, where field study at varying elevations is facilitated by the steep topography and easy access. These gradients are also useful for studying biotic responses to climate change, a growing threat to biodiversity, especially in the tropics (Colwell et al. 2008). Ornithologists completed two new autecological studies and finished two long-term studies initiated in the 20th century, continuing a long and valuable tradition in Monteverde. Other scientists tackled new research topics in bird-army ant interactions and behavior. Finally, careful observation continues to extend our knowledge of natural history, such of the first nest description for Silvery-fronted Tapaculo (*Scytalopus argentifrons*; Young and Zuchowski 2003) and an observation of a Slaty-backed Nightingale Thrush (*Catharus frantzii*) foraging on a frog (Acosta and Morún 2014). The following summarizes the major findings of the 27 publications that encompass this new research.

Elevational Gradients, Migration, and Conservation

New research has shed light on the remarkable biotic turnovers associated with elevational gradients that characterize Monteverde and many tropical mountain slopes. A new statistical analysis revealed that the beta diversity (the increase in species richness across habitats) of birds on the Pacific slope of Monteverde is twice as high as that at the same elevations on temperate mountains (Jankowski et al. 2009). Moisture gradients, rather than elevation per se, best explained the rapid species turnover. The Caribbean slope of Monteverde, with a less dramatic moisture gradient, has substantially lower beta diversity than that of the Pacific slope, where a rain shadow accentuates moisture differences. One mechanism leading to narrow ranges of Monteverde birds appears to be behavior. A series of song playback experiments demonstrated that congeneric species that replace each other along elevational gradients

show interspecific territorial behavior toward one other (Jankowski et al. 2010).

How does abundance correlate with range size in birds occupying Monteverde's different elevational zones? An extensive analysis using both mist-net and point count data revealed that species occupying fewer sites also tend to be less abundant in those sites than those occupying more sites (Jankowsli and Rabenold 2007). At a broader scale, species with larger range sizes occupied more habitat zones in Monteverde than those with smaller range sizes. Species endemic to Costa Rica and western Panama tended to occur at the highest elevations and have lower abundance. These results highlight the conservation challenges posed by this and other endemic highland avifaunas: most species are relatively rare at both geographical and local scales.

Seasonal migration across elevational gradients continues to attract scientific attention. A study of eight large frugivorous bird species, including guans, trogons, toucans, and cotingas, confirmed the results of earlier studies on seasonal movements (Chaves-Campos 2004). The birds generally nest at higher elevations and move to lower elevations when not breeding, although some individuals remain at high elevations year round. This pattern may be partially explained by seasonal changes in fruit abundance and precipitation, but additional factors may also be involved. A separate study of vegetation seasonality did not detect a link between vegetation changes and the migration of one of the species that Chaves-Campos studied, the Bare-necked Umbrellabird (*Cephalopterus glabricollis*; Papes et al. 2012)

Radio-tracking of two of these large, migrant frugivores, the Bare-necked Umbrellabird and Three-wattled Bellbird (*Procnias tricarunculatus*), revealed more details about the annual movements of the two species. These species are important from a conservation standpoint because both are categorized as threatened on the IUCN Red List of Threatened Species. The Bare-necked Umbrellabird appears to make a straightforward migration between breeding areas at 800-1400 m, and lower elevations (600-800 m) during the nonbreeding season (Chaves-Campos et al. 2003). The bellbird, on the other hand, makes a spectacular four-part migration that spans 200 km (Powell and Bjork 2004). Radio-collared individuals migrated from Monteverde to the Caribbean lowlands of northwestern Costa Rica and southeastern Nicaragua during the period of September to December, then flew to southeastern Costa Rica where they remained until March. Then they migrated to their breeding area at 1000-1800 m on the Caribbean slope of Monteverde. Finally, in June and July, the birds migrated back across the continental divide to mid-elevation Pacific slopes in Monteverde, where they remained until September. The migrations of bellbirds and umbrellabirds highlight pressing conservation needs. Although the breeding areas of both are well protected in Monteverde, each spends significant periods of time in unprotected habitats. Umbrellabirds descend to the lowest elevation where intact forest remains on the Caribbean slope of Monteverde. Loss of lowland habitat may be a limitation for the Monteverde population as this species is known to occur at much lower elevations elsewhere in Costa Rica where lowland forests persist. Bellbirds are also vulnerable because they spend at least half of their annual cycle on unprotected lands.

Climate Change

Ongoing climate change threatens species and ecosystems worldwide. Sensitivity of Monteverde habitats to climate and dramatic climate differences over small spatial scales combine to make the area ideal for studying the effects of climate change on natural systems. Careful monitoring of the breeding birds in a small study plot near the entrance of the Monteverde Cloud Forest Preserve revealed that lower elevation species were colonizing and that higher elevation species were declining (Pounds et al. 1999). Annual colonizations were closely tied to the annual number of precipitation-free days, which result from increasing temperatures that raise cloud-bank levels.

A subsequent study modeled the effects of future climates on the community of montane birds. Using data on current population sizes, fine spatial-scale models predicted the decline of nearly half of 77 species currently occurring in the higher elevation forests of Monteverde during the next 100 years (Gasner et al. 2010).

More sobering was the finding that seven of the eight species predicted to become extirpated in the region already have small ranges restricted to Costa Rican and western Panamanian highlands.

Birds and Army Ants

A new area of study for Monteverde is the interaction between birds and army ants. The bird-army ant relationship is well known in tropical lowland forests, where several specialist species forage on insects and other invertebrates as they flee advancing army ant foraging raids. Recent observations in Monteverde reveal that a surprising diversity of montane birds also follow army ants when they swarm. During two months of opportunistic observations at 1200-1650 m elevation, researchers identified 41 bird species attending army ant raids (Kumar and O'Donnell 2007). Neither the diversity nor the abundance of ant-following birds was influenced by elevation, but both factors were affected by forest patch size. More bird species and more individuals followed army ants in continuous forest than in small forest fragments. More extensive observations showed that resident species are more likely to follow raids than long-distance migrants, and eight resident species regularly visit army ant bivouacs to determine when raids begin (O'Donnell et al. 2010). Although no montane species rely on army ants as extensively as some lowland specialists, attending army ant raids is an important foraging activity for several montane bird species.

Autecological Studies

A major contribution of ornithological research in Monteverde has been a series of autecological studies that provide detailed aspects of the life cycle and behavior or montane tropical birds (Young and McDonald 2000). Over the last 14 years, new results became available from two of those studies, on Brown Jays (*Cyanocorax morio*) and Long-tailed Manakins (*Chiroxiphia linearis*), while researchers initiated studies of two additional species, the Black-Breasted Wood-Quail (*Odontophorus leucolaemus*) and Slate-throated Redstart (*Myioborus miniatus*). In an epilogue to a long-term study of Long-tailed Manakins, a genetic study found little differentiation between manakins in Monteverde and those in Santa Rosa National Park, 115 km away in the Pacific lowlands (McDonald 2003). Although gene flow appears to be greater up from Santa Rosa to Monteverde than in the reverse direction, the intense sexual selection on this lek-breeding species appears to be insufficient to create significant genetic isolation to lead to speciation.

Brown Jays are known for their cooperative breeding system in which multiple females and males contribute to the rearing of young. Use of multi-locus DNA fingerprinting has shown that virtually all chicks in a nest are the offspring of a single primary female breeder that is able to suppress breeding by other females in her group (Williams 2004). Males have much less skewed breeding success, with multiple paternity occurring in 33-40% of nests, and extra-group paternity occurring in at least 20% of nests. Group size is important in determining the breeding success of a group. Larger groups are better able to defend territories with isolated nesting trees, which are key to preventing nest predation, the leading cause of nest failure (Williams and Hale 2006). Increased nesting success and post-fledging survival were also correlated with group size. The benefit to non-reproductive helpers in a group appears to be access to future breeding opportunities. Observation of marked individuals showed that breeding females and their social mates maintain their bond across years and have higher nest attendance and nestling feeding rates than helpers (Williams and Hale 2007). Compared to other New World jays, however, social mates invested relatively less in nesting activities, suggesting that mate guarding may not be an effective strategy (Williams and Hale 2008).

The Slate-throated Redstart is a common resident in all but the highest elevation forests in Monteverde, calling attention to itself with its constantly flashing white outer tail feathers. A set of ingenious experiments and observations confirmed a hypothesis that the adaptive value of this plumage coloration is to startle invertebrate prey during flush-pursuit foraging. Individuals that had their white outer tail feathers experimentally blackened foraged with only one-third the success of controls in which inner, black tail feathers where colored with a black marker (Mumme 2002). Further tail-coloring experiments that mimicked the natural

variation in the extent of white tail feathers in geographic subspecies of the Slate-throated Redstart ranging from Mexico to Bolivia suggested that white tail feathers are adaptive for increasing foraging success, but the extent of white is constrained by regional habitat characteristics (Mumme et al. 2006).

Breeding in the Slate-throated Redstart is typical for Monteverde birds, spanning the late dry and early wet seasons from late May to early June during a five-year observation period (Mumme 2010). Females incubate clutches that average 2.9 eggs, but both parents feed young. Fledging occurred at an average age of 11 days, and parents subsequently provisioned fledglings for an additional four weeks. Nesting success was 40%, with predation the cause of 85% of nest failures (Mumme 2010).

Black-Breasted Wood-Quail live year-round in coveys of an average of four individuals (range 2-9) at similar densities (about one covey per 3.3 ha) in both fragmented and intact forest (Hale 2006). This species also breeds at the dry-wet season transition. Larger coveys produce more offspring than small coveys, hinting that the species may have a cooperative breeding system (Hale 2006). Sampling of 50 individuals from Monteverde revealed nine polymorphic microsatellite loci, providing useful markers for future genetic studies of this and other *Odontophorus* species (Hale and Hughes 2003).

Behavior

Several lines of evidence now indicate that Three-wattled Bellbirds learn their songs, making this species the first sub-oscine passerine known to learn songs (Saranathan et al. 2007, Kroodsma et al. 2013). Song learning has previously been documented only in hummingbirds, parrots, and oscine passerines. First, variation in mitochondrial DNA sequences and nuclear microsatellite loci does not correspond with the three vocal dialects of the species, which occur in Nicaragua, Monteverde, and Talamanca in southern Costa Rica (Saranathan et al. 2007). In addition, Monteverde birds appear to be bilingual, using the Talamanca as well as Monteverde dialects; a captive male raised in isolation developed abnormal songs that more closely resembled birds that occurred nearby. The lengthy (six year) song development period also strengthens the argument that bellbirds learn their songs, as does the fact that adults continually relearn songs (Kroodsma et al. 2013).

Landscape Ecology

One novel study developed land-cover models of bird use of habitats in forest fragments in Coto Brus, in southern Costa Rica, and then tested the models' ability to predict bird diversity and abundance in Monteverde habitats at similar elevations and life zones, 230 km away (Lindell et al. 2006). The results were mixed. Coto Brus models for canopy insectivores, understory insectivores and non-insectivores, and edge non-insectivores were successful for characterizing abundance of Monteverde birds in these habitats. However, Coto Brus models for open-country birds did not predict abundances of open-country birds in Monteverde. None of the predictions for species richness developed from the Coto Brus data set were more accurate than null models at predicting species richness in Monteverde communities. These findings indicate that land cover models are best extrapolated over the region where parameters are measured.

On a finer spatial scale, one observer asked what influenced bird visits to *Sapium glandulosum* trees isolated in pastures. Fifty-two bird species visited focal trees, preferentially visiting larger, more isolated trees with higher epiphyte loads (Sheldon and Nadkarni 2013). Although epiphyte loads helped attract birds, most foraging activity was focused on the host tree itself. Visitation was not affected by the distance of trees from forest edges, suggesting that Monteverde pastures are small relative to distances birds are willing to travel for foraging opportunities.

Conclusions

Study of Monteverde's avifauna continues to provide new perspectives on tropical birds. Although the area will continue to provide ready access to protected study sites, the future is uncertain for some members of the bird community. Climate change threatens to reduce the diversity of endemic species, and the shortage of protected habitats outside of Monteverde may compromise the persistence of

some regional migrant species. Colonization by lowland species may serve to maintain species richness, consistent with observations of assemblages in which species richness remains despite declining temporal beta-diversity (Dornelas et al. 2014). The new body of research from Monteverde extends the outsized role that the region's avifauna has played in shaping our understanding of tropical avian biology.

Literature Cited

Acosta, V., and O. Morún. 2014. Predation of *Craugastor podiciferus* (Anura: Craugastoridae) by *Catharus frantzii* (Passeriformes: Turdidae) in a neotropical cloud forest. Boletín de la Asociación Herpetológica Española 25:1-2.

Chaves-Campos, J. 2004. Elevational movement of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitología Neotropical 15:433–435.

Chaves-Campos, J., J. E. Arévalo, and M. Araya. 2003. Altitudinal movements and conservation of Bare-necked Umbrellabird *Cephalopterus glabricollis* of the Tilarán Mountains, Costa Rica. Bird Conservation International 13:45-58.

Colwell, R.K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258-261.

Dornelas, M. N., J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science 344:296-299.

Gasner, M. R., J. E. Jankowski, A. L. Ciecka, K. O. Kyle, and K. N. Rabenold. 2010. Projecting the local impacts of climate change on a Central American montane avian community. Biological Conservation 143:1250–1258.

Hale, A. M. 2006. Group living in the Black-Breasted Wood-Quail and the use of playbacks as a survey technique. Condor 108:107–119.

Hale, A. M., and C. R.Hughes. 2003. Characterization of polymorphic microsatellite loci in a neotropical wood-quail, *Odontophorus leucolaemus*. Molecular Ecology Notes 3:508–510.

Hale, A. M., D. A. Williams, and K. N. Rabenold. 2003. Territoriality and neighbor assessment in Brown Jays (*Cyanocorax morio*) in Costa Rica. Auk 120:446-456.

Jankowski, J. E. and K. N. Rabenold. 2007. Endemism and local rarity in birds of neotropical montane rainforest. Biological Conservation 138:453–463.

Jankowski, J. E., A. L. Ciecka, N. Y. Meyer, and K. N. Rabenold. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. Journal of Animal Ecology 78:315–27.

Jankowski, J. E., S. K. Robinson, D. J. Levey. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. Ecology 91:1877–1884.

Kroodsma, D., D. Hamilton, J. E. Sánchez, E. Bruce, H. Fandiño-Mariño, D. W. Stemple, J. N. Trainer, and G. V. N. Powell. 2013. Behavioral evidence for song learning in the Suboscine bellbirds (*Procnias* spp; Cotingidae). Wilson Journal of Ornithology 125:1–14.

Kumar, A. and S. O'Donnell. 2007. Fragmentation and elevation effects on bird–army ant interactions in neotropical montane forest of Costa Rica. Journal of Tropical Ecology 23:581-590.

Lindell, C. A., W. H. Chomentowski, J. R. Zook, and S. A. Kaiser. 2006. Generalizability of Neotropical bird abundance and richness models. Animal Conservation, 9:445–455.

McDonald, D. B. 2003. Microsatelite DNA evidence for gene flow in neotropical lek-mating long-tailed manakins. Condor 105:580–586.

Mumme, R. L. 2002. Scare tactics in a Neotropical warbler: White tail feathers enhance flush-pursuit foraging performance in the Slate-throated Redstart (*Myioborus miniatus*). Auk 119:1024–1035.

Mumme, R. L. 2010. Breeding biology and nesting success of the Slate-throated Whitestart (*Myioborus miniatus*) in Monteverde, Costa Rica. Wilson Journal of Ornithology 122:29-38.

Mumme, R. L., M. L. Galatowitsch, P. G., Jab, T. M. Stawarczyk, and J. P. Cygan. 2006). Plumage-based foraging adaptation: An experimental test in the Slate-throated Redstart (*Myioborus miniatus*). Evolution 60:1086–1097.

O'Donnell, S., A. Kumar, and C. Logan. 2010. Army ant raid attendance and bivouac-checking behavior by Neotropical montane forest birds. Wilson Journal of Ornithology 122:503–512.

Papes, M., A. T. Peterson, and G. V. N. Powell. 2012. Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling. Journal of Biogeography 39:652–664.

Powell, G. V. N. and R. D. Bjork. 2004. Habitat linkages and the conservation of tropical biodiversity as indicated by seasonal migrations of Three-Wattled Bellbirds. Conservation Biology 18:500–509.

Saranathan, V., D. Hamilton, G. V. N. Powell, D. E. Kroodsma, and R. O. Prum. 2007. Genetic evidence supports song learning in the three-wattled bellbird *Procnias tricarunculata* (Cotingidae). Molecular Ecology 16:3689–702.

Sheldon, K. S. and N. M. Nadkarni. 2013. The use of pasture trees by birds in a tropical montane

landscape in Monteverde, Costa Rica. Journal of Tropical Ecology 29:459–462.
Williams, D. A. 2004. Female control of reproductive skew in cooperatively breeding brown jays (*Cyanocorax morio*). Behavioral Ecology and Sociobiology 55:370-380.
Williams, D. A. and A. M. Hale. 2006. Helper effects on offspring production in cooperatively breeding Brown Jays (*Cyanocorax morio*). Auk 123:847.
Williams, D. A. and A. M. Hale. 2007. Female-biased helping in a cooperatively breeding bird: Female benefits or male costs? Ethology, 113:534–542.
Williams, D. A. and A. M. Hale. 2008. Investment in nesting activities and patterns of extra- and within-group genetic paternity in a cooperatively breeding bird. Condor 110:13–23.
Young, B. E. and W. Zuchowski. 2003. First description of the nest of the Silvery-fronted Tapaculo, *Scytalopus argentifrons*. Wilson Bulletin 115:91-93.
Young, B. E. and D. B. McDonald. 2000. Birds. In Monteverde: Ecology and Conservation of a Tropical Rainforest, N. M. Nadkarni and N. T. Wheelwright (eds). Oxford University Press, New York, pp. 179-222.