Journal of Field Ornithology

J. Field Ornithol. 83(2):107–121, 2012 DOI: 10.1111/j.1557-9263.2012.00361.x

Avian research in the Caribbean: past contributions and current priorities

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Received 6 December 2011; accepted 12 February 2012

ABSTRACT. The islands of the Caribbean contain habitat of critical importance to a large number of endemic and resident birds, as well as many overwintering Neotropical migrants, and they rank as a globally outstanding conservation priority ecoregion and biodiversity hotspot. Considerable research from the region has focused on the ecology of permanent resident species, and these studies have had particular significance for threatened species management, especially parrot biology and conservation, but also for tropical community ecology in general. Work by ornithologists in the Caribbean has been instrumental in improving our understanding of the ecology of overwintering Neotropical migrants and in developing long-term monitoring programs. Although Caribbean-based studies of birds have resulted in significant contributions in many important areas of ecological research, there is a great need for additional research. Especially needed are studies with application to the management of resident species, and studies of how bird populations may be affected by pathogens, parasites, plants, and other types of biotic interactions. Studies focusing on how bird species and populations are affected by global climate change, and cumulative, landscape-level changes in land use are also needed. Along with additional research, scientists have an important role to play in building capacity to prepare the next generation of biologists in the region who will need to address mounting challenges related to biodiversity protection. As with many conservation efforts, funding is a critical need for almost all organizations and agencies involved in research, conservation action, and capacity building in the West Indies.

RESUMEN. **La investigación ornitológica en el Caribe: contribuciones pasadas y prioridades actuales**

Las islas del Caribe contienen hábitat de importancia crítica para un gran número de aves endémicas y residentes, así como muchos migrantes Neotropicales durante el invierno, y figuran como una ecorregión prioritaria para la conservación y de importancia para la biodiversidad a nivel mundial. Muchas investigaciones en la región se han concentrado en la ecología de las especies residentes permanentes, y estos estudios han tenido un significado particular para la gestión de especies amenazadas, especialmente en cuanto a la biología y conservación de loros, pero también para la ecología de comunidades tropicales en general. El trabajo de ornitólogos en el Caribe ha sido instrumental en mejorar nuestro conocimiento de la ecología de las aves migratorias Neotropicales durante el invierno y en el desarrollo de programas de monitoreo a largo plazo. Aunque los estudios de aves basadas en el Caribe han hecho contribuciones significativas en muchas áreas importantes de investigación ecológica, hay una gran necesidad de investigación adicional. Se necesitan en especial estudios con aplicación a la gestión de las especies residentes, e investigaciones de cómo las poblaciones de aves pueden ser afectadas por las interacciones con patógenos, parásitos, plantas, y otros tipos de interacciones bióticas. Estudios enfocados en cómo las especies y poblaciones de aves son afectadas por el cambio climático global y por cambios cumulativos a nivel del paisaje en el uso de la tierra también son necesarios. Además de realizar mas investigaciones, los científicos tienen un papel importante que desempeñar en capacitar la próxima generación de biólogos de la región, en prepararlos para enfrentar los crecientes desafíos relacionados con la protección de la biodiversidad. Al igual que muchos esfuerzos de conservación, el financiamiento es una necesidad crítica para casi todas las organizaciones y agencias involucradas en la investigación, acción conservacionista y capacitación en las Indias Occidentales.

Key words: biodiversity, capacity building, endemic birds, Greater Antilles, Neotropical migrants, West Indies

The islands of the Caribbean contain habitat of critical importance to a large number of resident bird species as well as many wintering Neotropical migrants. In the Caribbean, the Greater Antillean islands of Cuba, Jamaica, Hispaniola, and Puerto Rico encompass nearly 90% of the land area, and contain the greatest biological diversity in the region (FAO 1991, Keith et al. 2003). The Bahamas, Turks and Caicos, Bermuda, and the Lesser Antilles are also home to many bird species, including some endemics. Of the ~770 bird species found on Caribbean islands, 148 are endemic to the region, and 105 are confined to a single island

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(BirdLife International 2008). In the region, 54 species are threatened with extinction, and 12 are considered Critically Endangered (BirdLife International 2008). In addition, many migratory species visit the Caribbean, with some populations wintering either primarily or exclusively in the region (Faaborg and Terborgh 1980). Global biodiversity assessments recognize the importance of the region (Myers 1988, Stattersfield et al. 1998, Mittermeier et al. 1999, WCPA Caribbean 2003) and rank the Caribbean as a globally outstanding conservation priority ecoregion and biodiversity hotspot, distinguished by high terrestrial endemism and little pristine vegetation.

The early history of research and bird monitoring in the Caribbean basin followed a similar pattern on different islands (Latta et al. 2003a). Most work prior to the 1970s was limited to species lists and natural history observations, and these were usually published as notes, included in checklists, or summarized in bird guides and special publications. A number of annotated checklists were published that summarized the basic biology of birds, including occurrence, distribution, breeding periods, and habitat use (Keith 1997, Bradley 2000, Keith et al. 2003, Buckley et al. 2009). These were followed by summaries of the distribution and status of birds including compendiums of seabird breeding sites (Bradley and Norton 2009) and important bird areas (BirdLife International 2008) that were developed for conservation planning purposes. Although previous papers have included summaries of advances within narrowly defined research themes such as Neotropical migratory bird ecology (Holmes 2007, 2011, Faaborg et al. 2010b) or biogeographic patterns of bird distribution (Ricklefs 2011), a comprehensive summary of ornithological research in the region has never been published.

My objective was to fill that void and explain how studies of the ecology and evolution of birds in the Caribbean islands have contributed to the broader field of ornithology. Although much work from the region has focused on the ecology of resident species, particularly important studies have focused on management of threatened species, parrot biology and conservation, and tropical community ecology. Theoretical studies by ornithologists working in the Caribbean have also been instrumental in advancing our understanding of the ecology of overwintering Neotropical migrants, developing long-term monitoring programs, and understanding how evolutionary and ecological processes, including biotic interactions, generate biological diversity. Below I address each of these areas of research. My review is not intended to be encyclopedic, and my focus is on key papers that have made the most significant contributions to ornithology. In addition, I suggest areas of research where ornithologists in the Caribbean can make important contributions, and conclude with ideas on how the research community can help advance conservation efforts.

RESEARCH CONTRIBUTIONS

Threatened species management. Early studies of the ecology of Caribbean birds often focused on endemic species, including Kepler's (1977) monograph on todies and Short's (1974) study of West Indian woodpeckers. Other work focused on the ecology of threatened species and provided the basis for management and conservation activities. Many studies were conducted in Puerto Rico where an unfortunate wealth of threatened species coincided with funding availability and legal mandates for action. Species of particular concern included Puerto Rican Nightjars (*Caprimulgus noctitherus*) threatened by deforestation and habitat change (Kepler and Kepler 1973, Vilella and Zwank 1993, Vilella 2008), and Yellow-shouldered Blackbirds (*Agelaius xanthomus*) that were endangered primarily because of brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*; Post and Wiley 1977, Post 1981, Wiley et al. 1991), as were Puerto Rican Vireos (*Vireo latimeri*; Woodworth 1997, Woodworth et al. 1998).

Elsewhere, Staus (1998) studied West Indian Whistling-Ducks (*Dendrocygna arborea*) in the Bahamas, and emphasized the importance of protected wetlands to their conservation. This work was instrumental in the establishment of a West Indian Whistling-Duck conservation program focused on community education and protection of coastal wetlands (Sutton et al. 2004). Another declining coastal species, the White-crowned Pigeon (*Columba leucocephala*), was studied in Puerto Rico, leading to an impressive monograph (Wiley and Wiley 1979b). A study of Caribbean Flamingos (*Phoenicopterus ruber*) by Allen (1956) led to conservation efforts on

Great Inagua in the Bahamas, as well as similar efforts in Cuba, Bonaire, and elsewhere. Efforts to conserve flamingos continue through broad census and monitoring programs (Wiley and Wiley 1979a, Paulino et al. 2010).

Other studies have also had important management and conservation implications, including studies of Montserrat Orioles (*Icterus oberi*), a species that faces unique threats from volcanic activity (Hilton et al. 2003, Dalsgaard et al. 2007), as well as two Hispaniolan species, Ridgway's Hawks (*Buteo ridgwayi*; Wiley and Wiley 1981), and White-necked Crows (*Corvus leucognaphalus*; Wiley 2006), that are threatened by hunting and habitat loss. Also on Hispaniola, Latta et al. (2000) examined the nesting and foraging habitats of Hispaniolan Crossbills (*Loxia megaplaga*), emphasizing the need to control wildfires affecting mature pine forests. Similarly, Hayes et al. (2004) noted the importance of mature stands of Caribbean pines (*Pinus caribaea*) for conserving the remaining population of Bahama Nuthatches (*Sitta pusilla*).

Parrot biology and conservation. Because of their charismatic nature and their often threatened population status, psittacids have been the focus of numerous studies in the Caribbean. Eleven of the surviving parrot species in the West Indies are endemics, and all are of conservation concern. Gnam (1991) studied the breeding biology of Bahama Parrots (*Amazona leucocephala bahamensis*), and other investigators have examined the distribution, abundance, and threats facing several other parrot species in the Lesser Antilles (Gochfeld 1974) and Greater Antilles (Wiley 1991). Puerto Rican Parrots (*Amazona vittata*) have been the focus of considerable research and management efforts. A classic monograph on the species (Snyder et al. 1987) was followed by a study by Beissinger et al. (2008) focusing on the relative importance of genetic, demographic, environmental, and catastrophic processes in maintaining a population bottleneck. In addition, efforts to reintroduce Puerto Rican Parrots have led to the development of methods for captive-rearing, nest-site management, and relocation (Snyder et al. 1987, Brock and White 1992, Collazo et al. 2000, 2003, White and Vilella 2004, White et al. 2005, Koenig et al. 2007). At the interface between research and conservation, White et al. (2011) described how local residents could become involved in research to help conserve Hispaniolan Parrots (*Amazona ventralis*). In addition, Butler (1992) described innovative methods for conserving parrots in the Lesser Antilles. Now exported worldwide, Butler's (1992) pride program identifies endangered birds as unique symbols of nationhood, changing human attitudes and ultimately leading to increases in parrot populations.

Tropical community ecology. As suggested above, studies conducted in the Caribbean have generated a rich literature on avian brood parasites. This is in part a response to the arrival of Shiny Cowbirds in the Caribbean and their exploitation of the island avifaunas (Cruz et al. 1985, Wiley 1985, 1988, Post et al. 1993). Comparing host responses to brood parasitism in areas with a long history of parasite–host interaction to those in areas where cowbirds recently arrived, Cruz and Wiley (1989) found changes in nest placement, nest defense, and productivity, as well as differences in egg acceptance and rejection by hosts. In addition, Cruz et al. (2008) examined how these behaviors changed over time with increased exposure to cowbirds.

Classic studies of community assemblages were conducted in Jamaica (Diamond 1974, Cruz 1974), Grand Bahama Island (Emlen 1977), and Cuba (Acosta Cruz and Mugica Valdés 1988). The low species richness of birds on Caribbean islands allowed detailed studies of hummingbird-plant webs (Lack 1976, Dalsgaard et al. 2008, 2009), and of a tropical forest food web in the Luquillo Experimental Forest (Puerto Rico), with the latter resulting in the most complete summary of the role of birds in a tropical forest food web (Waide 1984). More recently, Arendt (2006) studied Pearly-eyed Thrashers (*Margarops fuscatus*) and argued that they are preeminent avian "supertramps." With generalized nesting and foraging strategies, these thrashers are able to adapt to the ever-changing conditions in the region's natural and anthropogenic environments, and they now occur on often disturbed, species-poor islands and habitats throughout the Caribbean. In another important study, Mugica Valdés et al. (2006) examined the ecology and conservation status of wetland birds in Cuba, and described strategies for conserving the birds and their wetland habitats.

Studies conducted in the Caribbean have also contributed to our understanding of the effects

of hurricanes on birds (Wunderle 1995b, 1999). The greatest impacts occur after a hurricane, with nectarivores and frugivores affected by interrupted food supplies, and highland birds impacted by relatively slow plant regrowth at higher, cooler elevations (Waide 1991, Askins and Ewert 1991, Wunderle et al. 1992, Wiley and Wunderle 1993, Wunderle 2005).

A number of important studies in the Caribbean have addressed the impacts of anthropogenic habitats on tropical birds, especially their responses to monocultures and forests dominated by introduced tree species (Cruz 1987, 1988). Other investigators have compared avian communities in native forests to those found in Caribbean pine plantations (Collazo and Bonilla Martinez 1988), sun and shade coffee plantations (Wunderle and Latta 1996), and several agricultural habitats in Jamaica, including coffee and citrus (Johnson 2000, Johnson et al. 2006). The results of these studies suggest that arboreal agricultural habitats (e.g., coffee, citrus, and cacao) can play a role in the conservation of generalist, insectivorous birds, and that plantations may aid efforts to reforest abandoned agricultural fields. Studies on Hispaniola, and later Jamaica, were among the first to reveal the value of shade grown coffee plantations as bird habitat (Wunderle and Latta 1996, 1998, 2000, Johnson 2000), and follow-up studies in Jamaica were the first to show that birds can control coffee borers (*Hypothenemus hampei*), an important coffee pest (Kellermann et al. 2008), and to place a monetary value on the ecosystem services provided by birds in coffee plantations (Johnson et al. 2009, 2010).

Investigators conducting studies in the Caribbean have also examined how species and communities respond to variation in landscape characteristics. Tossas (2002) analyzed source and sink dynamics of Puerto Rican Vireos, and Acevedo and Restrepo (2008) showed how changes in land cover and land use across Puerto Rico influenced the large-scale organization of bird assemblages. In Jamaica, Kennedy et al. (2010) found that species richness, community composition, and abundance were matrix-dependent, with agricultural landscapes supporting greater avian diversity and more intact community assemblages than either peri-urban or bauxite-mined landscapes. Kennedy et al. (2011) found that within-patch vegetation structure and the matrix type between patches were more important than patch area and patch isolation in determining local colonization and extinction probabilities. Together, these studies reinforce the importance of differentiating among land cover and land uses in fragmentation research and management. Lessons from landscape-level studies have been invoked in proposed conservation measures for threatened Bicknell's Thrushes (*Catharus bicknelli*); Kerchner et al. (2009) modeled benefits of a voluntary incentive program for landowners in the Dominican Republic where changes in land use would yield a cost-effective network of protected habitat that would sustain overwintering thrush populations.

Ecology of Neotropical migratory birds. Beginning in the mid-1970s, the ecology of Neotropical migrants overwintering in the Caribbean attracted increased attention (Keast and Morton 1980). The results of early studies on overwintering ecology were summarized by Holmes (2007, 2011) and Faaborg et al. (2010b), with these studies generally focusing on habitat specific demographics and the site fidelity of warblers (Holmes et al. 1989, 1996, Wunderle 1995a, Marra et al. 1998, Wunderle and Latta 2000, Marra and Holmes 2001, Latta and Faaborg 2001, 2002). These studies often documented strong winter territoriality, generally with nonoverlapping territories (Holmes et al. 1989, Wunderle 1995a, Wunderle and Latta 2000, Latta and Faaborg 2001, 2002), differences in sex and age ratios among habitats resulting from dominance interactions (Holmes et al. 1989, Parrish and Sherry 1994, Wunderle 1995a, Marra 2000, Wunderle and Latta 2000, Marra and Holmes 2001, Latta and Faaborg 2002), and site faithfulness between winters (Holmes et al. 1989, Marra and Holmes 2001, Latta and Faaborg 2001). Researchers developed models to determine when during the annual cycle populations of migratory passerine birds might be limited (Sherry and Holmes 1995, 1996, Latta and Baltz 1997, Sherry et al. 2005), and hypothesized that winter food availability limits population sizes via habitat quality. Support for this hypothesis was provided by studies demonstrating the relationship between food availability and the physical condition of birds (Strong and Sherry 2000, Latta and Faaborg 2001, Studds and Marra 2005, Brown and Sherry 2006a, Diggs et al. 2011), decreased rates of site persistence in habitats with reduced food

resources (Johnson and Sherry 2001, Latta and Faaborg 2002), and linkages of both population responses and individual condition of nonbreeding birds to prevailing ecological conditions across divergent habitats (Latta and Faaborg 2002). The results of other studies suggested a relationship between rainfall or local moisture levels and habitat quality (Latta and Faaborg 2001, Studds and Marra 2007).

Other investigators focused more on carry-over effects, especially the impacts of winter habitat quality on later reproductive success. Marra and Holberton (1998) and Reudink et al. (2009) showed that nonbreeding season events could have fitness consequences during both the nonbreeding and subsequent breeding season, and that these seasonal interactions can play an important role in regulating populations (Runge and Marra 2005). For example, compared to those in optimal habitats, American Redstarts *(Setophaga ruticilla*) in suboptimal habitats had elevated corticosterone levels (Marra and Holberton 1998), lost mass over winter (Marra and Holmes 2001), departed later on spring migration (Marra et al. 1998, Studds and Marra 2005), and had lower annual survival (Johnson et al. 2006). These effects carry over to the breeding grounds with redstarts from suboptimal habitats arriving in poorer condition, settling on territories later, and fledging fewer young (Marra et al. 1998, Norris et al. 2004). Stable-hydrogen isotope ratios have also been used to show that habitat use during the first overwintering period plays a role in determining the direction and distance traveled during the first spring migration (Studds et al. 2008), further extending the role of carry-over effects to natal dispersal patterns.

Avian monitoring. Complementing field studies of overwintering migrants, investigators in the Caribbean region have led in the development of monitoring strategies and implementation of long-term avian monitoring programs. One of the longest bird monitoring programs in the hemisphere was initiated in 1973 at Guánica, Puerto Rico, and the results of this work have contributed to our understanding of the ecology of migrants during the nonbreeding season (Faaborg and Arendt 1989, Faaborg et al. 2000, Faaborg 2002, Dugger et al. 2004). In addition, lessons learned from this pioneering monitoring effort were critical in developing recommendations for other constant-effort monitoring programs in the Caribbean and Latin America (Rivera-Milán 1992, 1995a, b, 1997, Latta et al. 2003a, 2005, Faaborg et al. 2007). Monitoring programs have also contributed to our understanding of the impacts of stochastic events such as hurricanes (Waide 1991, Askins and Ewert 1991, Wunderle et al. 1992, Wiley and Wunderle 1993, Wunderle 2005) and volcanic eruptions (Dalsgaard et al. 2007) on avian populations, and more intensive, often species-specific, monitoring efforts have improved our understanding of the ecology and conservation (Townsend et al. 2010), and population trends (Rimmer et al. 2011) of threatened species such as Bicknell's Thrushes.

Generating biological diversity. Caribbean islands have also been important in attempts to better understand how ecological and evolutionary processes generate biological diversity. Studies conducted in the West Indies were central to debates in community ecology about factors influencing bird diversity on islands (MacArthur et al. 1966, Case et al. 1983, Ricklefs and Bermingham 2001, Ricklefs 2011). Lack (1976) used Jamaican birds to illustrate his theory of island biology, now discredited, that rested on the idea that habitats on an island determined the number of species present, with distance from the source of colonists playing little role. Ecological patterns of community structure included a search for "assembly rules" such that the composition of birds in foraging guilds was not random but repeatable, and that guilds on larger islands could become saturated (Terborgh and Faaborg 1973, Terborgh et al. 1978, Faaborg 1980). In addition, coexisting guild members were shown to consistently differ in body size by body weight ratios of 2.0 (Faaborg 1982, 1985, Case et al. 1983). These observations were used to argue that the overall arrangement of species on islands is nonrandom, and that these patterns are consistent with the hypothesis that competition is a driving force in structuring communities (Case et al. 1983).

Because of their small size, geographical isolation with defined boundaries, and simplified communities, islands have also been central to improving our understanding of the role of evolutionary processes in generating biological diversity (Ricklefs and Bermingham 2001, 2007, 2008, Ricklefs 2011). Although Caribbean birds are not as well known and have not been used as textbook examples of adaptive radiation, Burns

et al. (2002), in a study designed to identify the sister taxon of Darwin's finches, showed that their closest living relatives were largely Caribbean endemics. Caribbean birds also show a remarkable diversity of bill types and feeding behaviors similar to that observed among Darwin's finches. Studies conducted in the West Indies have also illustrated the importance of allopatry for speciation, with Townsend et al. (2007) and Sly et al. (2010, 2011) using phylogenetic techniques and a knowledge of geologic events to eliminate the possibility that sympatric speciation explained the presence of sister species on Hispaniola. The results of these studies also lend support to Diamond's (1977) assertion that avian speciation is unlikely to occur on single islands smaller than New Guinea. Nevertheless, Coyne and Price (2000) noted that the existence of endemic sister species of hummingbirds (Red-billed [*Trochilus polytmus*] and Black-billed [*T. scitulus*] streamertails) on Jamaica that may be evidence of sympatric speciation.

Finally, many of these concepts come together in the idea of the taxon cycle (Wilson 1961), an idea closely associated with West Indian birds (Ricklefs and Cox 1972). Studies of Caribbean birds suggest that species progress through cycles of geographic expansion via dispersal followed by adaptation to local environments (especially on the margins of their range), divergence and extinction of some populations, and greater ecological specialization of remaining populations, especially in forest-interior habitats (Ricklefs and Cox 1972). Some species may evolve secondary distributions and initiate new cycles of expansion to continue the cycle. Ricklefs and Bermingham (2001) used molecular phylogenetic analyses of small land birds in the Lesser Antilles to lend support for the taxon cycle concept, while rejecting MacArthur and Wilson's (1967) equilibrium theory of biogeography based on nonequilibrium patterns of colonization and extinction at evolutionary, rather than ecological, time scales. In recent years, molecular phylogenetic evidence has also been used to confirm the temporal sequence of distribution patterns representing phases of species expansion and contraction (Ricklefs and Bermingham 2004), and to further suggest that the cycles may be generated by coevolutionary relationships between species and their predators and pathogens (Ricklefs and Bermingham 2002, Losos and Ricklefs 2009, Ricklefs 2011).

RESEARCH PRIORITIES

Although studies of Caribbean birds have made numerous important contributions, some areas of investigation have received less attention (Latta et al. 2003a, Faaborg et al. 2010a). Below I summarize some of the more critical needs.

Ecology of permanent resident species. Much of the work on West Indian birds has focused on several key threatened species or a few species of overwintering Neotropical migrants. As a result, little is known about the basic natural history of many species, including some of the most threatened endemics and most of the birds currently considered game species. However, this lack of information is not equally shared among all Caribbean islands; more is known, in general, about the natural history of birds in Puerto Rico, Cuba, and Jamaica than those on some of the smaller or more impoverished islands.

To effectively manage bird populations, we need species-specific studies to determine current distributions, habitat associations, timing of breeding, reproductive rates, and sex- and age-specific survival rates. In addition, few studies have used a multiscale perspective to determine how landscape-level habitat features may interact with nest-site, territory, habitat, and local patch effects to impact reproductive success and survival. Studies that include factors such as habitat patch size, proximity to edge, and characteristics of the matrix surrounding a patch have rarely been conducted in the Caribbean, despite their potential importance for understanding the ecology of many species.

Biotic interactions. Biotic interactions, such as host–pathogen, competitive bird–bird, and mutualistic bird–plant interactions, have not been well studied in Caribbean ecosystems. Although some work has been conducted on brood parasitism (Cruz and Wiley 1989), patterns of distribution of unique strains of avian malaria among hosts (Ricklefs et al. 2004, Ricklefs and Bermingham 2008), and relationships between overwintering migrants and permanent residents (Latta and Wunderle 1998, Johnson et al. 2005), few investigators have studied how biotic interactions affect population dynamics and the distribution of species. Failure to incorporate biotic interactions into ecological studies is currently viewed as a major reason why many models fail to fully describe bird

populations and their distribution (Kissling et al. 2012). Describing biotic interactions through, for example, network analyses, is not only useful for understanding distributional patterns, but for clarifying interdependencies between plants and their bird and insect pollinators, functional specialization, resilience, and stability (Dalsgaard et al. 2008, Kissling et al. 2012). Network analysis is also useful for evaluating and predicting ecosystem responses in the face of habitat change, species loss, and global climate change.

The Caribbean also offers opportunities for studies to improve our understanding of competitive relationships among and between resident and migratory species, and how habitats support overwintering migrants in addition to permanent residents. Recognizing that insects may control the size of bird populations, Greenberg (1995) proposed the "breeding currency hypothesis" to explain the apparent paradox of arthropod food sources for birds being at their lowest during the nonbreeding season when bird numbers peak. The hypothesis contrasts the abundance of large, high quality, soft-bodied arthropods that may limit numbers of permanent resident birds during reproduction, with the abundance of relatively low-quality, small insects that may maintain greater numbers of adult residents as well as overwintering migrants during the nonbreeding period. In the only test of the hypothesis, Johnson et al. (2005) found general support, but suggested that other factors are also operating because the ratio of migrants to residents was significantly higher than predicted in some habitats. Additional data are needed concerning how changes in bird distributions, and seasonal shifts in habitat or diet by permanent residents, may create ecological "vacancies" for overwintering migrants (Ricklefs 1992, Johnson et al. 2005). We also need a better understanding of how intratropical migrants such as some populations of Gray Kingbirds (*Tyrannus dominicensis*) and Black-whiskered Vireos (*Vireo altiloquus*) are integrated into breeding bird communities in the Caribbean (Johnson et al. 2005). In addition, we need to better understand how relationships between permanent residents and overwintering migrants may be affected by habitat alteration and changes in habitat quality.

Habitat-specific survival of overwintering migrants. Most studies of the ecology of overwintering migrants in the Caribbean have been conducted at just a few sites in a few habitats. In addition, because most work has focused on just a few species, little is known about other overwintering migratory species, or whether models developed for the better-studied species apply to others. There is a need for a more widespread assessment of which species occupy which habitats, and a broader understanding of how variation in occupancy and survival across the entire wintering range impacts each species. Although most widespread natural habitats have received some attention from researchers, some habitat types are almost completely unstudied, including oil palms, cacao and other agricultural habitats other than coffee (but see Johnson et al. 2006), pastures and mesquite-dominated shrublands, grasslands, wetlands, lowland forests, and urban parks. Although wildlife managers may be most interested in knowing what levels of disturbance migratory birds will tolerate, with the exception of shade coffee (Wunderle and Latta 2000), few studies of survival have focused on anthropogenic habitats (but see Johnson et al. 2006) or the value of early successional habitats for migrants (but see Wunderle et al. 2010). Finally, as with studies conducted during the breeding season (see "Ecology of permanent resident species"), application of a multiscale perspective is required to fully understand the nonbreeding season ecology of migrants.

Temporal expansion of studies. Few studies of resident birds in the Caribbean have focused on their ecology outside of the breeding season, and few published studies of overwintering migrants encompass the entire nonbreeding season. In addition, use of stopover sites by passage migrants in the Caribbean is surprisingly understudied. Although shorebird counts have been conducted on a number of islands, few results of these counts appear to have been published (Wunderle et al. 1989, Collazo et al. 1995). We know from observational records that many landbird migrants use a wide variety of habitat types and even habitat fragments during migration, but little is known about the distribution or quality of these sites for migrants in the Caribbean, or whether there are concentrations of migrants at particular points during the migratory periods (but see Rodríguez et al. 1994, Rodríguez and Sánchez 1995, Latta and Brown 1999, McNair et al. 2002).

Citizen science projects such as eBird Caribbean (http://ebird.org/content/caribbean), Caribbean BirdWatch (http://conserveonline.org/workspaces/caribbeanbirdwatch), and the Caribbean Waterbird Census (http://www.scscb.org/) use simple monitoring or observational data to "visualize" migration of species on maps by plotting concentrations of birds at different sites and habitats during migrations. Such projects should contribute to our understanding of the location and use of stopover sites. However, we also need a better understanding of migrant ecology during the period of arrival and territory establishment. We do not know how territories are selected, how territorial individuals prepare behaviorally and physiologically for spring migration, or if they abandon territories to use different habitats during the spring fattening period prior to migration.

Finally, not all individuals or species are territorial during the nonbreeding period. We need a better understanding of what drives the movements of floaters during the nonbreeding period (but see Brown and Sherry 2008), the occurrence of altitudinal migration, and how wandering or seasonal movements influence survival.

Documenting population trends. Despite some prominent efforts described above, there has been insufficient monitoring to fully assess the status of vulnerable bird populations and their habitats in the Caribbean or to guide conservation strategies. Some highly threatened species such as the Puerto Rican Parrot are monitored regularly (Beissinger et al. 2008), and citizen-based efforts such as Caribbean BirdWatch, Caribbean Waterbird Census, and eBird Caribbean have been inaugurated, but long-term, locally intensive efforts (Latta et al. 2005) using mist nets are also needed. The long-term monitoring study described by Faaborg et al. (2007) has been invaluable for detecting population changes, but similar efforts are needed elsewhere. Constant-effort mist-netting in a variety of habitat types should be encouraged, but monitoring of birds in relatively unperturbed native habitats is preferred; population declines in habitats assumed to be optimal would best signal the need for management or conservation activities (Faaborg 2000). Such monitoring is needed to better understand population trends of both permanent resident and overwintering migratory birds, and patterns uncovered elsewhere will help determine if the decline in numbers of migrants at Guánica, Puerto Rico, are general or specific to that site.

We also need monitoring to document the spread of exotic diseases such as West Nile virus or avian influenza, and to understand the impact of disease and parasites on avian populations. Other than studies of avian malaria (Ricklefs and Fallon 2002, Ricklefs et al. 2004, Fallon et al. 2004, 2005, Latta and Ricklefs 2010), botfly infections (Arendt 1985a, b), and scaley-leg mites (Latta and O'Connor 2001, Latta 2003), few sampling efforts have focused on emerging diseases or parasites in the Caribbean (but see Dupuis et al. 2003, Komar et al. 2003), or on monitoring their impacts.

Climate change. Climate change, reflected in warming trends and more frequent extreme weather events, is affecting avian distributions and the timing of breeding and migration by birds around the world (Møller et al. 2010, Cox 2010). From a Caribbean perspective, only recently have a limited number of papers addressed climate change and birds, and these have focused primarily on how rainfall may affect habitat quality for overwintering migrants, thereby impacting spring departure schedules and breeding success through carry-over effects (Sillett et al. 2000, Smith et al. 2010, Wilson et al. 2011, Studds and Marra 2011). These studies have emphasized the need to understand within-season and annual variation in precipitation to model the impacts of climate change (Smith et al. 2010, Wilson et al. 2011). As Studds and Marra (2011) pointed out, migrants in the Caribbean may be informative in modeling impacts resulting from global climate change because they face both declining rainfall in the overwintering areas and increased temperatures on the breeding grounds. This approach, using events throughout the annual cycle to study population impacts and adaptive responses to climate change, is unique.

Other than these studies that focus on migrants and studies mentioned previously that have focused on the impacts of hurricanes, few authors have investigated how climate change may be affecting birds in the West Indies, or how weather patterns (especially rainfall) may affect reproduction and survival of resident species in the region (but see Faaborg and

Arendt 1989, Dugger et al. 2004). We need data to better understand interactions among climate change and global climate patterns such as the El Niño Southern Oscillation (ENSO) and La Niña events. Several global warming models are consistent in predicting increased summer droughts in the Caribbean basin over the next 50 yr (Neelin et al. 2006), and recent rainfall declines in the Bahamas (Martin and Weech 2001), Puerto Rico (Heartsill-Scalley et al. 2007), and Jamaica (Studds and Marra 2007) are consistent with the predictions of these models. The expected effects of these summer droughts include phenological disruptions, declines in food availability, and an increase in fire frequency (Weaver and Gonzalez 2005). Models to help evaluate how Caribbean birds might respond to these combined threats are needed, as is empirical data about bird condition and population trends. As previously mentioned, studies that use species interaction distribution models to better understand biotic interactions within guilds or across trophic levels at large spatial scales may be particularly informative with respect to the effects of a changing climate (Dalsgaard et al. 2008, Kissling et al. 2012).

BUILDING CAPACITY FOR RESEARCH AND CONSERVATION

To meet research needs, we must prioritize building capacity within indigenous conservation groups and among the next generation of biologists who will address the growing crisis in biodiversity protection. Although some islands such as Puerto Rico and Cuba have a number of excellent field biologists, many other countries have few, if any, trained research biologists to develop research or monitoring programs. Although excellent field assistants are available in most countries, managers are often dependent on outside researchers to design and direct research programs, and to interpret relevant research. Thus, building capacity, especially in terms of Ph.D.-level ornithologists with permanently supported positions, is a critical need in many countries across the region. This may be dependent on funding, but ornithologists based outside the region can have an important impact by collaborating with local organizations including universities, museums, governmental agencies, and nongovernmental conservation organizations. Such collaboration will result in studies more likely to reflect local needs and interests, and can also help build capacity. In addition, working with local citizens can provide them with a sense of ownership and personal investment in programs, and affirm the perception that some benefits will accrue to them for their efforts (White et al. 2011).

Funding is critical for almost all organizations and agencies involved in research, conservation action, and capacity building in the West Indies, and the funding devoted to these efforts can have important impacts. For example, Latta and Faaborg (2009) analyzed patterns of funding for research and monitoring using examples from Puerto Rico and the Dominican Republic, demonstrating that research has had an underappreciated effect on the development of conservation capacity and conservation efforts in host countries (e.g., Ewert et al. 2009). Investments in research contributed to an increase in the training of students and wildlife professionals, promoted conservation awareness, played an important role in the growth and professionalization of key environmental organizations, spawned a growing ecotourism industry for birdwatching, and drove planning and conservation efforts for birds in national parks.

Researchers in the tropics should also be encouraged to use protocols that provide the most information about all species of birds in their study areas (e.g., Latta et al. 2003b, Brown and Sherry 2006b). By broadening the scope of studies beyond a single focal species, additional opportunities are created for collaborations, student involvement, and generating results relevant to resource managers. With an awareness of unique histories and cultural and political traditions among islands, by partnering with local organizations and individuals, and with increased funding, ornithologists and conservationists working in the Caribbean region will have a greater chance of conserving Caribbean birds and their habitats in a challenging environment.

ACKNOWLEDGMENTS

I thank B. Dalsgaard, J. Faaborg, B. Mulvihill, C. Rimmer, T. W. Sherry, L. Sorenson, J. Wunderle, Jr., and two anonymous reviewers for their insightful comments on an early version of this manuscript. Their kind criticisms were greatly appreciated.

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