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Avian studies and research opportunities in the Luquillo Experimental Forest: A tropical rain forest in Puerto Rico

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ABSTRACT

The Luquillo Experimental Forest (LEF) located on the Caribbean island of Puerto Rico has a rich history of ecological research, including a variety of avian studies, and is one of the most active ecological research sites in the Neotropics. The LEF spans an elevational range from 100 to 1075 m over which five life zones and four forest types are found in a warm, humid subtropical climate. A total of 23 bird species breeds here and another 76 species, mostly migrants, are known to occur. The food web of the forest in the lower elevations is especially well studied, which allows an assessment of the role of birds in the food web. The LEF is noted for its high densities of *Eleutherodactylus* frogs and *Anolis* lizards, which may depress insect densities thereby contributing to the low species richness and densities of most insectivorous birds. The signature species of the forest is the endangered Puerto Rican Parrot (*Amazona vittata*) that has been the focus of intensive long-term research and recovery efforts, which have spawned research on associated species, including long-term studies on the Pearly-eyed Thrasher (*Margarops fuscatus*) and botfly (*Philornis* spp.) ectoparasitism. Given the frequency of hurricane disturbance to the LEF and studies providing baseline for comparisons, research has made major contributions to an understanding of the effects of hurricanes on forest ecosystems including bird populations and their resources. We summarize these and other studies from the LEF to characterize the avifauna and its environment while noting studies with management implications and identify opportunities for future ornithological studies.

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1. Introduction

Situated in the eastern-most island of the Greater Antilles, the U.S. territory of Puerto Rico hosts the only tropical rain forest in the U.S. Forest Service's system of experimental and national forests. The Luquillo Experimental Forest (LEF), also previously known as the Caribbean National Forest and now the El Yunque National Forest, has a long and rich history of tropical research, which provides a wealth of research opportunities (Brown et al., 1983; Harris et al., in press; Weaver, in press). Forestry research in Puerto Rico was stimulated in 1939 with the establishment of the Tropical Forest Experiment Station (now International Institute of Tropical Forestry), which by 1982 produced 1357 titles pertaining to forestry research conducted on the island, most from the LEF (Mosquera and Feheley, 1983). In 1963, ecological research in the LEF received a boost from the U.S. Department of Energy, which supported ecosystem studies associated with a radiation experiment in the LEF's El Verde rain forest, resulting in a classic study of a tropical rain forest (Odum and Pigeon, 1970). This work stimulated food web studies at El Verde conducted by University of Puerto Rico ecologists and others, and culminated in a comprehensive study of the forest food web, the first for a tropical rain forest (Reagan and Waide, 1996). Building on these studies, researchers in the LEF obtained funding through the Long-term Ecological Research (LTER) program of the National Science Foundation in 1988, which focuses research on a disturbance ecology theme and continues, having produced over 930 publications pertaining to the LEF (http://luq.lternet.edu). Thus, as a result of these and other studies, the LEF has become one of the leading sites for tropical research, providing a substantial body of knowledge on which to base future studies.

The earliest studies of birds in Puerto Rico and the LEF focused on taxonomy and distribution based on specimens obtained by collectors (Biaggi, 1983; Wiley, 1996). Continuing the collecting tradition in his 1911–1912 surveys of the island's birds and their diets, Alexander Wetmore spent approximately two weeks in the Luquillo Mountains (Wetmore, 1916). It was not until the 1950s, however, that studies of avian natural history and breeding biology were initiated in the LEF when Rodríguez-Vidal (1959) studied the declining Puerto Rican Parrot population (see Appendix A for scientific names). More parrot studies and management efforts there followed in the 1970s as summarized by Snyder et al. (1987). Studies on other bird species and the avifauna in general were initiated

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in the 1960s when avian seasonality, distribution, and population densities were investigated (Recher and Recher, 1966; Recher, 1970) and compared with diversity and density in the Guánica dry forest in southern Puerto Rico (Kepler and Kepler, 1970). Also during this period, the life history and biology of the Puerto Rican Tody was studied in the forest (Kepler, 1977). These and other avian studies in the LEF were summarized by Waide (1996) in his characterization of the avifauna of the lowland forest of the LEF as part of his assessment of the role of birds in the food web. More recently, Arendt (2006) summarized more than 25 years of his long-term breeding and ecological studies of the Pearly-eyed Thrasher in the LEF and elsewhere. These and other ornithological studies from the LEF provide the basis for our review in this paper. Here we characterize the avifauna of the LEF by first describing the avifauna and its functional role in the food web and then discuss various topics including habitat specialization, long-term studies, the role of predation, population changes, challenges of a wet forest, and the effects of hurricanes on bird populations. As we review these topics we note the management findings or implications where applicable and identify topics requiring additional research. Finally, we end with a summary of some of the types of research needed to understand and potentially mitigate the effects of global and local environmental changes on the LEF's avifauna.

2. Site description

The LEF was proclaimed in 1956 from forested lands of the Caribbean National Forest, which had been established on Spanish Crown lands protected since 1860 and acquired by the U.S. in 1898 (for site description see Brown et al., 1983; Scatena http://luq.lternet.edu). At the time of its acquisition, the Forest comprised 5018 ha and has increased since 1930 to its present size of 11,332 ha (Fig. 1). The LEF encompasses most of the Luquillo Mountains, which range in elevation from 100 to 1075 m above sea level. The topography is deeply dissected with steep upper slopes, which serve as catchments for the headwaters of six major rivers. Associated with the steep topographic relief are climatic gradients, as illustrated by temperature which differs by 7 °C for mean maximum values between low and high elevation sites, but annually varies little with elevation for mean monthly temperatures (3–3.5 °C). The prevailing easterly trade winds drop rain as they rise over the mountains causing mean annual rainfall to generally increase with elevation up to 700 m and then decrease to the higher elevations. Annual rainfall ranges on average from about 245 cm/yr in the lowlands to 400 cm/yr at higher elevations. Rainfall occurs in every month of the year and usually there is a drier period from February to April, although mean annual rainfall varies considerably. Overall, the LEF can be described as having a warm and humid subtropical climate.

Associated with the LEF's variation in topography, soils, and climatic conditions are five life zones and four forest types. The life zones include subtropical moist forest, subtropical wet forest, subtropical rain forest, lower montane rain forest, and lower montane wet forest (Ewel and Whitmore, 1973), with the latter covering the largest proportion of the LEF (Fig. 1). The forest types are generally stratified by elevation (Fig. 1) and include the tabonuco, colorado, palm, and elfin forests (Wadsworth, 1951). The tabonuco forest, named for the predominate tabonuco tree (*Dacryodes excelsa* Vahl.), occurs in the lowlands below 600 m most commonly in the subtropical moist and wet forests and occupies approximately 70% of the LEF. Above 600 m at the average cloud condensation level is the colorado forest type, which covers 17% of the LEF and is named for the predominate palo colorado tree (*Cyrilla racemiflora* L.). Above 750 m on peaks and ridges is the elfin forest (2% of the LEF) with short, gnarled, and epiphyte-covered trees. Interspersed between elfin and Colorado forest types is the palm forest or palm brake, which covers 11% of the LEF and is limited to steep slopes and saturated soils. The sierra palm (*Prestoea acuminate var. montana* [Graham] Nicholson) is the predominate tree in the palm forest where it grows in almost pure stands.

The LEF has been disturbed by humans almost everywhere below 670 m, with relatively little human disturbance (e.g., some scattered cutting for charcoal) at higher elevations, with the exception of communication towers and access roads to the East and El Yunque peaks. On the western side of the forest from about 600–670 m there was some farming and tree thinning until about 50 years ago. Below 600 m the human disturbance included logging, charcoal production, coffee cultivation, and farming of diverse crops, all of which ceased in the 1930s. Despite the absence of human disturbance in the forest for over 70 years, the human impact of the past is still evident in the tree species composition despite damage from hurricanes in 1989 and 1998 (e.g., Zimmerman et al., 1995; Thompson et al., 2002).

3. The avifauna

Puerto Rico hosts 276 bird species of which 142 species breed, including 16 endemic species and 36 exotic species (Raffaele, 1989). In comparison, the LEF has 99 species including 23 species that breed, of which 12 are endemic (Appendix A). Of the breeding species, two are migratory (Black-whiskered Vireo and Black Swift) and are mostly absent from the island from September to February. No endemic species are confined to the LEF, although the relict population of the Puerto Rican Parrot was restricted to the LEF until recent re-introductions in the north central region of the island. The endemic Elfin-woods Warbler was first discovered in the mountains of the LEF (Kepler and Parkes, 1972) and later populations were found and studied to the west in the Maricao Commonwealth Forest (Cruz and Delannoy, 1984a,b). Although 34 Nearctic-Neotropical migrant species, mostly warblers and vireos, have been recorded from the forest, most are uncommon winter residents with low densities (Wunderle and Waide, 1993; Waide, 1996). Despite the abundance and variety of naturalized exotic finches and psittacines in anthropogenically disturbed habitats on the forest's periphery (Vázquez Plass, 2008), exotics rarely the forest. The LEF has three federally listed endangered species including the Puerto Rican Parrot and the island subspecies of Sharp-shinned and Broad-winged hawk. Two species known from the forest have become extinct on Puerto Rico in historic times including an endemic parakeet (*Aratinga maugei*), which disappeared in the late nineteenth century (Snyder et al., 1987), and the White-necked Crow (*Corvus leucognaphalus*), which was last seen in the LEF in 1963 (Raffaele, 1989). The Limpkin (*Aramus guarauna*) likely occurred in the LEF and was last known from the island in 1959 (Raffaele, 1989).

As with other Caribbean forests, the LEF has low avian species richness of resident species when compared with the continental tropics. This reduced species richness reflects the poor colonization abilities of many continental species resulting in a non-random subset of the continental avifauna on islands (e.g., MacArthur and Wilson, 1969; MacArthur et al., 1972). Those species that do colonize islands tend to become generalists and utilize the resources that several species might use under the competitive conditions of species-rich continental communities (e.g., MacArthur and Wilson, 1969). In addition, the high frequency of hurricanes in the Caribbean may further select for ecological generalists (Walker et al., 1991). These behavioral and ecological correlates of low species richness are believed to be important factors structuring the avian community in the LEF's tabonuco forest (Waide, 1996) and in the other forest types.

Not only is the LEF's avifauna depauperate in terms of number of species, but the abundance of individual species (i.e., rank-order

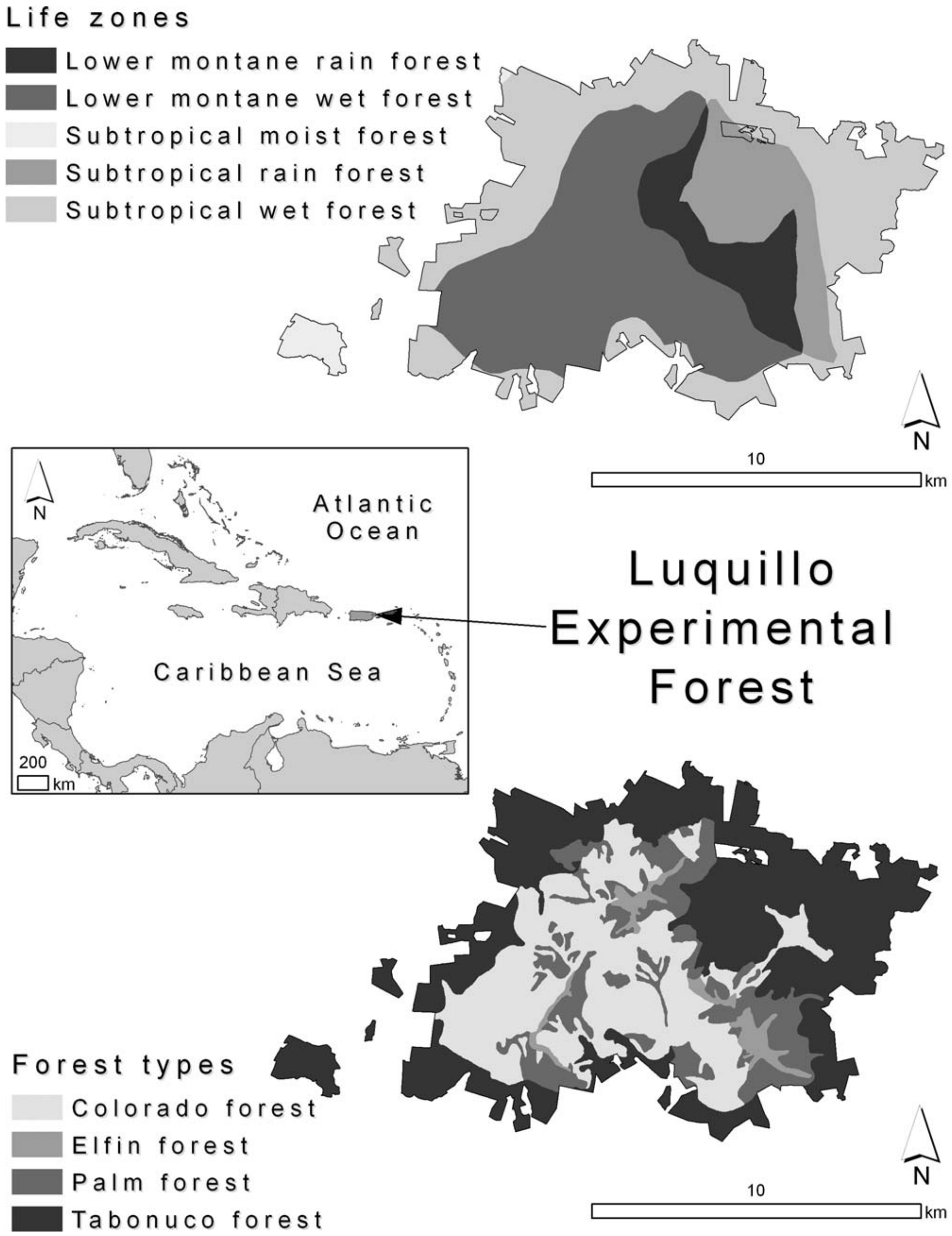

Fig. 1. Map showing the position of Puerto Rico in the Caribbean and the Luquillo Experimental Forest (LEF) or El Yunque National Forest in eastern Puerto Rico. The upper map shows the five Holdridge life zones in the LEF after Ewel and Whitmore (1973). The lower map shows the four major forest types of the LEF after Wadsworth (1951).

abundance distribution) differs markedly from tropical continental bird communities by having a few very abundant species and relatively few rare species (i.e., low species diversity, H') in contrast to mainland communities. For example, Waide (1996) found that Bananaquits constituted 50% of point count detections in the tabonuco forest as also found in other forest types of the LEF (Snyder et al., 1987). Similarly, mist net captures at El Verde were dominated by a few very common species (i.e., Ruddy Quail-Dove, Puerto Rican Tody, Bananaquit) and very few rare species (Wunderle et al., 1987; Waide, 1996) in contrast to continental tropical forests where rare species constitute a disproportionate number of the species in understory mist net samples (Karr et al., 1990).

4. Functional roles and birds in the food web

The role of birds in the food web of the tabonuco forest at El Verde differs markedly from their role in mainland tropical bird communities (Waide, 1996). For example, the high density (33 individuals/ha) and large average body weight (50.9 g) of birds in El Verde contributes to the higher biomass of birds per hectare (1.68 kg) than found in continental bird communities. Moreover, energy flows through the El Verde avifauna at a rate (307,899 kcal/ha per year) that is at least twice as high as that found in temperate forests. Waide notes that the most important trophic role of birds in El Verde is that of a predator, especially at the upper-level, where birds are important top predators (e.g., Red-tailed Hawk, Puerto Rican Screech-Owl, Puerto Rican Lizard-Cuckoo, Pearly-eyed Thrasher). As lower-level predators (e.g., Puerto Rican Tody), however, birds are relatively unimportant in contrast to frogs and lizards as predators on insects. Thus, Waide concludes that any top down control that birds might exert in El Verde is through predation on frogs and lizards.

The guild signature of the bird community in the tabonuco forest at El Verde is skewed towards frugivores, in contrast to bird communities in continental Neotropical forests where insectivores constitute the most speciose guild (Waide, 1996). The high proportion of species that consumes fruit in the tabonuco forest, and the LEF in general, is not surprising, given that 74% of the species of trees and shrubs in Puerto Rico have fleshy exocarps or arils and are adapted for seed dispersal by animals (Flores and Schemske, 1984). Although bats may also consume some of these fruits, birds are believed to play the predominant role in seed dispersal in the forest (Waide, 1996) given their abundance relative to frugivorous bats, which are uncommon at El Verde (Willig and Gannon, 1996). The importance of avian seed dispersal in the LEF was demonstrated by Shiels and Walker (2003) who found that placing perches (i.e., dead shrubs) on open landslides increased the numbers of bird-dispersed forest seeds in plots beneath the introduced perches relative to control plots. Except for this study and that of Carlo et al. (2003), few studies have examined avian frugivory and seed dispersal in Puerto Rico; although some of the species of fruits consumed by birds and the frugivorous species in the LEF have been summarized (Snyder et al., 1987; Waide, 1996).

The role of birds as pollinators in the LEF is poorly known, although the forest's very wet conditions suggest that wind pollination may be ineffective relative to insect or avian pollination (Waide, 1996). This contention is supported by the observation that more elfin forest plants are pollinated by insects and birds than wind, although fruit set here is low for both syndromes (Neveling, 1971). The only avian pollination study conducted in the LEF found that three species – Green Mango, Puerto Rican Emerald, and Bananaquit – visited flowers of *Tabebuia rigida* (Hernández-Prieto, 1986). However in this instance, only Green Mangos pollinated the flowers, as the latter two species were nectar robbers and consumed nectar from holes pierced at the base of the corolla. The effect of avian nectar robbers on pollination has not been studied in the LEF, but the impact is likely great given the abundance of Bananaquits. In the tabonuco forest, Puerto Rican Emeralds feed heavily on flowers of the dominant understory shrub, *Palicourea riparia* Benth. (Waide, 1996) and Green Mangos were captured only when *Heliconia* was flowering (Wunderle et al., 1987). Patterns documented by Kodric-Brown et al. (1984) in their study on the ecology of avian nectarivores in western Puerto Rico may be relevant to the LEF.

For insectivorous birds, the LEF is an especially challenging environment given the extremely wet, foggy conditions at high elevations and the potential for competition for arthropod prey from the forest's exceptionally high frog and lizard densities, especially in the lowlands. In tabonuco forest for example, the population density of the predominant frog, *Eleutherodactylus coqui*, is one of the highest densities known for any amphibian (Stewart and Woolbright, 1996). Similarly for *Anolis* lizards, the density of *A. stratulus* in the tabonuco forest canopy is one of the highest densities known for a lizard species (Reagan, 1996). Given this superabundance of frogs and lizards it should not be surprising that the herpetofauna exerts substantial top down pressure on arthropod densities (Reagan and Waide, 1996). Evidence that *Anolis* lizards in the LEF can depress arthropod densities was provided by Dial and Roughgarden (1995) who excluded lizards from canopy trees in the tabonuco forest for 6 months and monitored the arthropod response. In their experiment, lizard removal had a strong positive effect on some canopy-dwelling arthropods > 2 mm, but not all large taxa increased, and arthropods < 2 mm decreased in abundance. Similarly, in both small and large scale experiments in the tabonuco understory where *E. coqui* was removed the arthropod abundance on plants was higher in removal sites than control sites, although leaf litter abundance of arthropods was unchanged (Beard et al., 2003). Thus both the anole and coqui removal experiments demonstrate that the herpetofauna may have top-down effects on populations of some arthropods in the LEF.

Given the high herpetofauna densities and demonstrated top-down effects of the two most abundant herp species on certain arthropod prey in the LEF it is not surprising that species richness of avian insectivores is low as well as are most of their population densities in the LEF. Waide (1996) lists only four resident insectivores from the tabonuco forest, and with the exception of the Puerto Rican Tody, all are rare (Puerto Rican Flycatcher, Puerto Rican Vireo, Elfin-woods Warbler). The tody is the most abundant insectivore in the LEF (Kepler, 1977; Waide, 1996). Its ability to obtain most of its arthropod prey by sallying upward to the undersides of leaves (Kepler, 1977) where arthropod prey, perhaps inaccessible to frogs and lizards, may contribute to its abundance. Also, todies nest in burrows excavated in exposed banks where they have high nest success (62% of nests fledge at least one young) relative to the low nesting success of open cup nesters (Kepler, 1977; Latta et al., 1995). Low densities characterize the Nearctic-Neotropical migrants, most of which are insectivorous and overwinter in the LEF (Waide, 1996). These migrant densities are especially low relative to other Caribbean forests (Wunderle and Waide, 1993). An exception, however, is the Black-throated Blue Warbler, which is relatively abundant in parts of the LEF, and this is attributable to the species' consumption of fruit (Wunderle, 1995a).

Some LEF omnivores such as the Puerto Rican Tanager and Puerto Rican Woodpecker also feed heavily on insects as well as consuming (in decreasing order of importance) fruits, seeds, lizards, and frogs, arachnids and other invertebrates (Wetmore, 1916; Waide, 1996). By feeding on insects in vine tangles and in suspended dead leaves (Waide, 1996) the tanager may obtain larger insects than normally consumed by arboreal herps and in sites inaccessible to most herps. An ability to obtain insect prey inaccessible to herps by excavating wood and their opportunistic consumption of fruit (Wetmore, 1916) relieves woodpeckers from competition with herps. Other omnivores rely primarily on fruit and supplement their diet with animal prey (Red-legged Thrushes, Black-whiskered Vireos, Pearly-eyed Thrashers, and Puerto Rican Bullfinches; Wetmore, 1916; Waide, 1996). Fruit also is an important component of nestling diet for species such as the Red-legged Thrush in which 44.4% of 1769 food deliveries to nestlings were of plant material (mostly *Cecropia* [*peltata* L.] *schreberiana* Miq., 50%; *Miconia* spp., 17%; and *Ficus americana* Aubl., 15%) and 54.6% were of animal prey (worms, insects, and lizards) during 1986–1994 on the grounds of the USFS's Catalina Service Center (A.I. Arendt, unpubl. data). Similarly, adult Pearly-eyed Thrashers feed on the fruits of 19 species of plants (Waide, 1996), although fruits of the sierra palm are a prime component (22% of the diet, Snyder et al., 1987; Arendt, 2000, 2006). Fruit also is important in the nestling thrasher diet (11 species, W.J. Arendt, unpubl. data).

Raptors play an important role as top-level predators in the LEF (Waide, 1996), especially the Red-tailed Hawk, which is the most important diurnal predator due to its abundance and generalist diet. Red-tails reach their highest density in the LEF's montane forests relative to lowland dry and moist forests (Santana C. and Temple, 1988; Rivera-Milán, 1995). The hawk's densities in the upper reaches of the LEF are greater than found in its continental North American range (Santana C. and Temple, 1988); and the maximum mean density of 1.7 pairs/km^2 from the high-elevation windward slopes on the northeast side of El Yunque represents its highest recorded density anywhere (Snyder et al., 1987). However, densities vary widely depending on wind-conditions and altitude and tend to be lower on the western side of the LEF (Snyder et al., 1987; Nimitz, 2005). Diet varies with elevation: lowland red-tails outside the LEF consume mostly mammals (e.g., small Indian mongoose, *Herpestes javanicus*; black rat, *Rattus rattus*; brown rat, *R. norvegicus*) in pasture-dominated habitats, in contrast to high elevation where they feed on amphibians, reptiles, and birds taken from the canopy (Santana C. and Temple, 1988). High elevation populations of red-tails in the LEF may represent “sinks” relative to lowland “source” populations, because of greater nestling mortality at high elevations due to frequent reduction in prey delivery rates by adults because of rain and fog (Santana C. and Temple, 1988). It is also likely that red-tail populations have been little affected by the island’s past forest loss because they use edge habitats of forest fragments in suburban and agricultural areas (Santana C. et al., 1986; Nimitz, 2005).

In contrast to Red-tailed Hawks, both Sharp-shinned and Broad-winged hawks require extensive forest (Raffaele, 1989) and are believed to have declined island wide, due to forest loss and hunting (Pérez-Rivera and Cotté-Santana, 1977; Wiley, 1985; Delannoy and Cruz, 1988), as well as recently in the LEF (see below). The recent rarity of the two species in the LEF, however, has made it difficult to study them there. Snyder et al. (1987), however, found 10 Sharp-shinned Hawk nests in the LEF and observed that the accipiter fed mostly on small birds ($\leq$30 g), as similarly found by Delannoy and Cruz (1999) in the western mountains of the island, where the smaller males consumed smaller (12.6 g) prey than females (45.2 g). The sharp-shin’s breeding biology has been more thoroughly studied in Maricao where Delannoy and Cruz (1988) found that fecundity and reproductive success were lower than reported from the continental U.S. Adult broad-wings in the LEF were observed bringing a mix of prey items to nests including centipedes, frogs, lizards, mice, rats, and small birds (Snyder et al., 1987). Breeding studies have not been conducted on broad-wings in the LEF, but studies in north central Puerto Rico indicate that broad-wings maintain small (relative to the continent; mean = 39.5 ha), clustered, non-overlapping home ranges, many of which were occupied in the following year (Delannoy and Tossas, 2000).

Although a variety of species besides raptors opportunistically consumes frogs and lizards in the LEF, the most specialized avian predators of herps are the Puerto Rican Screech-Owl and the Puerto Rican Lizard-Cuckoo (Waide, 1996). The screech-owl is abundant in the LEF and has the highest density of any raptor in the colorado forest (1.3 pair/ha^2) where the owl’s diet consists primarily of frogs followed by insects, lizards, and mice (Snyder et al., 1987). Although density estimates are unavailable, screech-owl density is probably greatest in tabonuco forest given the higher densities of frogs and lizards (Stewart and Woolbright, 1996; Reagan, 1996) and its acceptance of a wide range of cavities for nesting (Snyder et al., 1987). In contrast to screech-owls in eastern North American, Puerto Rican Screech-Owl abundance was not lower in fragmented forests in rural areas outside the LEF than in the extensive tabonuco forest of the LEF (Pardieck et al., 1996). In contrast to the screech-owl, the diurnal Puerto Rican Lizard-Cuckoo feeds heavily on *Anolis* lizards (Wetmore, 1916), which constituted 68% of 193 food items fed to nestling cuckoos, whereas frogs comprised only 14%, insects (16%), centipedes and arachnids, 1% each (A.I. Arendt, unpubl. data).

5. Habitat specialization

Given that island species tend to be habitat generalists it is not surprising that the extent of habitat specialization at various scales documented within the LEF tends to be limited. For example, as expected the number of breeding species decreases with elevation, although the change in species richness is relatively gradual and most species are found across a broad elevational range (Snyder et al., 1987; Pagán, 1995). For instance, despite its name, the Elfin-woods Warbler also occurs in the colorado forest where it obtains higher densities than in the elfin forest (Cruz and Delannoy, 1984a; Anadón-Irizarry, 2006; Arendt et al., in review). Overall, birds show relatively little habitat segregation among the native forest types or life zones within the LEF (Wiley and Bauer, 1985; Snyder et al., 1987; Pagán, 1995). In contrast, however, the migrant Black-throated Blue Warbler does show sexual habitat segregation related to successional stage and forest stature while overwintering in the forest (Wunderle, 1992, 1995a). Nonetheless, despite the tendency for most birds in the LEF to be habitat generalists, some species, especially frugivores, are rare or absent from the LEF’s monospecific plantations of exotic trees (mahogany, *Swietenia macrophylla; ×mahagoni* hybrid Stehle and Cusin, Caribbean pine, *Pinus elliottii* Engelm var. *Pinus caribaea* sensu *Small*), where fruiting understory plants are rare (Cruz, 1987, 1988).

Associated with the habitat generalist traits of the LEF’s avifauna is the frequent use of a wide breadth of vertical foliage layers by species in the tabonuco forest. For instance, Reagan et al. (1982) found that seven of ten species used all of the vertical space in El Verde. As expected, the species using the greatest diversity of foraging heights also tended to have broad diets (Waide, 1996). Species confined to one or only a few vertical strata include only the Ruddy Quail-Dove, which is strictly a terrestrial forager feeding on fruits and seeds, and Scaly-naped Pigeon and Black-whiskered Vireo, which are mostly confined to the upper canopy where they obtain fruit and insects (vireo). These patterns are consistent with those observed by MacArthur et al. (1966) who found that birds in seven Puerto Rican forests, including tabonuco forest, used a greater breadth of vertical layers than birds in temperate or tropical mainland forests. They concluded that the tendency for the island’s species to show less subdivision of vertical space was not a result of the structural traits of island forests, but rather a behavioral response to ecological release in depauperate island avifauna. Moreover, the ability to use a breadth of vertical strata is likely favored by frequent hurricanes, which may select for species that have the flexibility to shift among strata after storm damage (Waide, 1991; Wunderle, 1995b).

Although small openings in tropical forests provide structural heterogeneity, which contributes to avian composition and richness (Stiles, 1983), the effect of openings or treefall gaps on the avifauna in the LEF’s tabonuco forest appears to be minor in contrast to continental tropical forests, where gap specialists occur (Wunderle et al., 2005). Although gap specialists were not found in a tabonuco mist net study (Wunderle et al., 1987), which compared assemblages in a large gap (powerline corridor) with small treefall gaps and forest understory, the assemblages of species differed among the three habitats. Here the gap assemblages differed from the understory assemblage as a result of canopy dwellers that followed the canopy contour down to net level in the gap. Overall capture rates were highest in the large gap and small gaps and lowest in the forest understory. Capture rates in the large and small gaps were highest where a small stream was present, even in the absence of water during a dry period. Species such as Bananaquits, Puerto Rican Tody, Puerto Rican Emerald, Green Mango, and Louisiana Waterthrush were associated with the stream in the gaps, but not in the forest understory where the stream had no effect on capture rates. Thus differences in avian habitat use are evident at small spatial scales in the tabonuco forest, but no species are known to specialize on forest gaps there in contrast to the continental tropics. This difference was attributed by Wunderle et al. (1987) to the island generalist traits that preclude habitat specialization especially when gaps are typically small and rare in forests frequently affected by hurricanes (Odum, 1970; Doyle, 1981).

6. Long-term bird studies in the LEF

6.1. Puerto Rican Parrot

The Puerto Rican Parrot has been the focus of long-term research and recovery efforts in the LEF, which have stimulated associated studies including long-term Pearly-eyed Thrasher studies. Snyder et al. (1987) summarize the biology of the parrot, its environment, threats, and management efforts on its behalf in a monograph, which has become a classic study on the psittacine genus *Amazona*. Their work indicates that at the time of Columbus the parrot was widespread and abundant on Puerto Rico and satellite islands, but by the 1650s it began to decline as the human population increased. The parrot's decline in range and abundance continued and by the early 1940s it was confined to the Luquillo Mountains, where it breeds primarily in the colorado forest. Here the population continued its decline from about 2,000 parrots in 1937 to 200 in 1954 to 24 in 1968, and finally to a low of 13 birds in 1975 (Wadsworth, 1949; Rodríguez-Vidal, 1959; Snyder et al., 1987). Massive deforestation of the island along with harvest for food and pets, shooting to protect crops, and hurricanes contributed to the decline (Rodríguez-Vidal, 1959; Snyder et al., 1987).

In response to the parrot's decline, Rodríguez-Vidal (1959) undertook basic studies and initiated recovery efforts for the parrot in the LEF. It was not until 1973, however, that intensive recovery efforts were initiated (Snyder et al., 1987). These efforts, which continue today include (1) provisioning of nest boxes and rehabilitating deficient nest cavities; (2) monitoring and guarding of nests to deter predation by black rats and Pearly-eyed Thrashers and preventing nestling mortality from parasitic botflies (*Philornis* spp.) and preventing bee colonization of cavities; and (3) captive breeding in two aviaries (in the LEF and in north-central PR) to provide a source of nestlings for fostering into wild nests as well as to provide birds for direct release in the wild (Snyder et al., 1987; White et al., 2005a). Although these efforts stopped the decline and prevented the parrot's loss from the LEF, and resulted in modest growth, the population remains in a bottleneck of 25–40 birds after more than 30 years of intensive management (for histories of parrot nests see Snyder et al., 1987; Wunderle et al., 2003).

Although several factors are believed to contribute to the maintenance of the parrot's population bottleneck in the LEF, only recently has the relative importance of these factors been quantitatively assessed. For example, an age-structured population model indicated that the estimated parrot population of 48 birds in 2000 had a 4.7% chance of extinction in 100 years under present management (Thompson Baranello, 2000; Thompson, 2004). Sensitivity analyses of Thompson's model indicated that the modeled population was most sensitive to mortality of breeding-aged parrots followed by fledging success. In contrast, Muiznieks (2003) using the program *Vortex* found that the basic scenario model projections over 100 years were of a declining population (stoc. $r = -0.066$) and that the persistence of the population was 0 and the mean time to extinction was 37.4 years. The only positive average stochastic growth rate found by Muiznieks occurred with low juvenile annual mortality (32%). The population grew only when productivity levels exceeded 2.5 young fledged per nest. Her analyses also indicated that productivity levels varied from 1.88 (1990–95) to 1.23 (1996–2002) young/nest resulting in a steady population decline and low likelihood of persistence (0–3%).

Beissinger et al. (2008) conducted a risk analysis and determined the relative importance of genetic, demographic, environmental, and catastrophic processes in maintaining the parrot population bottleneck from 1973 through 2000. During this period, annual population growth was slow and variable (1.0 ± 5.2 parrots per year or an average $\lambda = 1.05 \pm 0.19$) ranging from a low of 13 parrots in 1975 to a high of 40–42 in 1997–1998. Their analysis indicates that four primary factors were involved in maintaining the bottleneck, including reduced hatching success, failure of adults to breed, nest failure due to non-genetic causes, and reduced survival of adults and juveniles. Hatching success was low (76.8%), frequently changing after mate changes when it sometimes improved, suggesting inbreeding, which was indicated previously using DNA fingerprinting (Brock and White, 1992). Only an average of 34% of the population breeds annually, which is below the percentage of adults that should have reached the age of breeding (41–56%). This low breeding rate is believed to be due to environmental or behavioral factors and not due to a paucity of nest cavities or a skewed sex ratio. Nest failure rates due to non-genetic causes were low (29%) as a result of intensive nest guarding and management, which reduced losses to botfly ectoparasitism, predation, and wet cavities (Snyder et al., 1987; Lindsey, 1992; Vilella and Arnizaut, 1994; Vilella and García, 1995). Annual survival rates, at least for adults, have been high in the absence of hurricanes. The annual survival rate for juveniles (first year) is poorly known (Meyers et al., 1996). Estimates of 75% annual survival for juveniles were obtained by Snyder et al. (1987). However, more recent calculations by Collazo et al. (2000) indicate an annual survival rate of only 32.5% based on 15 radio-tagged juveniles studied by Lindsey et al. (1994).

Although the importance of various factors constraining the parrot's population growth has varied during the 30-year period of their study, Beissinger et al. (2008) found that certain factors had marked long-term influence on λ by use of life-stage simulation analysis (LSA). This analysis indicated that the 30-year population bottleneck was maintained primarily by periodic hurricanes that reduced adult survival and secondarily by the failure of adults to breed due to environmental and/or behavioral factors. Low hatching success, possibly as a result of inbreeding, had a much less significant effect on population growth even when production of young was included in the LSA. As a result of this analysis, Beissinger et al. (2008) recommended that (1) nest guarding be continued to minimize the loss of eggs or chicks to non-genetic causes; (2) additional populations be established elsewhere on the island (now underway) to minimize the risk of hurricane-caused extinction; and (3) determine and ameliorate the factors that cause the low proportion of breeders in the population.

Not only has the Puerto Rican Parrot recovery effort contributed to the general knowledge of factors contributing to population bottlenecks and psittacine biology and ecology, but it has pioneered in the development and refinement of methods with utility for other recovery efforts (Snyder et al., 1987; Arendt, 2000). Since publication of the parrot monograph, biologists have relied heavily on radio telemetry for tracking movements and survival of parrots in the LEF, which required an assessment of triangulation accuracy (Lindsey and Arendt, 1991a), preliminary home range studies (Lindsey et al., 1991b), an evaluation of various transmitter designs and attachments (Meyers, 1996a), and a colored leg banding technique for parrots (Meyers, 1995). Telemetry studies by White et al. (2005a) of captive-reared parrots released in the LEF indicated that first year survival of 34 parrots was 41% (C.I. = 22–61%). In their study, raptor predation accounted for 54% of the mortalities and, overall, 21% of the released parrots were lost to raptors. Raptor predation was attributed to Red-tailed Hawks, which are believed to have a substantial impact on the wild parrot population given their high densities, wide ranging abilities, extensive overlap of home ranges, and frequent interaction with parrots (Snyder et al., 1987; Nimitz, 2005). Initial post-release survival of the parrots was likely improved by rigorous pre-release training and acclimation (White et al., 2005a). Also, by releasing mixed age-class groups they potentially reduced the time to recruitment. These methods and recommendations have served as the basis for protocols for subsequent releases in the LEF as well as releases of captive-reared parrots now underway in the north-central region of the island, and will undoubtedly prove useful for releases of captive-reared birds elsewhere.

In addition, quantitative and descriptive studies have been conducted on nesting Puerto Rican Parrot behavior, especially parental attentiveness, at both successful and unsuccessful nests (Wilson, 1993; Wilson et al., 1995, 1997). These behavioral studies provide guidelines for identifying nesting problems that may be mitigated by intervention. The use of video cameras within nests has further enhanced monitoring effectiveness by enabling managers to spot potential problems quickly, thereby increasing the likelihood of successful intervention (White and Vilella, 2004). Also, biologists have refined methods for producing artificial nest cavities (White et al., 2005b), which have been used exclusively by nesting parrots since 2001. The parrot's use of artificial nests allowed White et al. (2006) to evaluate parrot artificial nest-site selection without the confounding effects of nest-cavity characteristics. Using a distribution-free statistical simulation they found that occupied nest sites differed from unoccupied nest sites in having greater visibility from the nest entrance, greater sierra palm density, and more westerly and leeward orientation of the nest entrance. These nest site attributes may facilitate predator detection and avoidance and therefore this "nest gestalt" should be replicated in the placement of artificial nest cavities to increase the likelihood of parrot use. Thus the Puerto Rican Parrot recovery effort has pioneered management procedures that will be useful in future recovery efforts elsewhere. Moreover, other studies stimulated by the parrot recovery efforts in the LEF (e.g., Pearly-eyed Thrasher and botfly parasitism) provide useful baseline for comparisons and utility for management elsewhere.

6.2. *Pearly-eyed Thrasher*

Studies of the Pearly-eyed Thrasher were initiated in the LEF over 30 years ago to determine the thrasher's role as a nest predator and competitor with the Puerto Rican Parrot. In addition, because the thrasher and the parrot share similar ecologies (feeding, roosting, nesting and breeding habitat, and food plants), life-history and reproductive traits (annual survival, timing and duration of the breeding season, clutch size, and asynchronous hatching), the thrasher has served as a valuable surrogate for studying many of the organisms stressing the parrots (Arendt, 1980, 1983, 1985a,b, 1993, 2000, 2006; Beissinger et al., 2005; Cook et al., 2003, 2004, 2005).

The open- and cavity-nesting traits (Arendt, 2004a), coupled with many other behavioral, developmental, and morphological adaptations, make the thrasher an excellent candidate for the Caribbean's premier avian supertramp (Arendt, 2006). It clearly demonstrates morphological plasticity, generalized nesting and foraging strategies, an inclusive diet and superior colonizing traits. It is pugnacious, highly vagile, a good disperser, and has the ability to fill vacant or underexploited niches at all elevations (Arendt, 1996, 1997). Even though the thrasher is a secondary cavity-nesting passerine, it practices iteroparity and has adopted other egg-laying and incubation strategies characteristic of small, open-cup nesters (Arendt, 2004a,b, 2005). It has also adopted an egg stage of minimum duration, allowing it to re-nest more quickly with each successive clutch. Thus, it is able to maximize reproductive yield, increase annual fecundity and, ultimately, its lifetime reproductive success (Arendt, 2006). Collectively, these attributes enhance thrasher numbers in the LEF and make it the parrot's prime nest predator and competitor for nest sites (Arendt, 2000).

Historically, thrasher research focused on the biological and environmental factors that affect thrasher and parrot reproductive success and survival. In both species, breeding is synchronized with production of sierra palm fruit (Snyder et al., 1987; Beltrán Salazar, 2004; Arendt, 2006). Reproductive success of both species is often greatly reduced as a result of the synergistic effects of a diverse group of predators, competitors and ectoparasites, namely, other thrashers, black rat, honeybee (*Apis mellifera ligustica* and *A. m. scutellata*) and botfly and Puerto Rican Screech-Owl (Arendt, 2000). Thrasher research not only summarizes the prevalence and intensity of nest predation and ectoparasitism, but also addresses the interaction between these two forms of biological control on predator–prey and parasite–host populations.

Thrasher studies confirmed that predation rates, nest-site competition, and the prevalence and intensity of botfly parasitism at thrasher nest boxes vary significantly among years and months, increase with the progression of the thrasher breeding season, and escalate following major habitat disturbance. At thrasher nest boxes, instances of predation, cavity takeovers, and the prevalence and intensity of botfly parasitism are highly correlated with each predator's, competitor's, and parasite's own breeding seasons. These breeding seasons span the entire reproductive period of both the thrasher and parrot, which increases the probability of substantially lowering their reproductive success. Thrasher and parrot reproductive success was also lowered with the arrival in 1994 of the Africanized honey-bee in the LEF, which aggressively colonizes nest cavities (Arendt, 2000).

Research into aspects of philornid botfly ecology and its harmful effects on thrasher reproduction and population dynamics began in 1978. Within their avian hosts, larval philornid botflies live subcutaneously within furuncles where they feed on their host's erythrocytes and other tissues before pupating (Arendt, 1985a,b, 2000). Infesting larvae significantly reduce the energy available for nestling growth and development (Uhazy and Arendt, 1986) and with high infestation rates cause nestling mortality. Given the prevalence of botfly parasitism in the LEF nestling mortality rates can be high. For example, over the first 17 years, Arendt (2000) found that botflies accounted for 56% of thrasher nestling mortalities whereas egg and chick losses from nest predators and competitors accounted for less than 10% of reproductive failures. Throughout the study, nestling survival has been significantly lowered as a result of botflies. In addition, moderately to heavily infested immature thrashers have a high risk of mortality after fledging (Arendt, 1983). Consequently, mortality due to botflies can be as high as 90% or higher in the first year of life (Arendt, 1985a,b). Nestling and fledgling mortality rates are even higher during breeding seasons immediately following major hurricanes (Arendt, 1992, 2000, 2006). Implications of botfly studies for the Puerto Rican Parrot and its management are summarized in Arendt (2000).

7. Predation on birds and their nests

In addition to studies on predation summarized in Snyder et al. (1987) and Arendt (2000, 2006), recent studies have provided additional information on the LEF's predators and their behavior. For example, the mongoose, as a ground forager, has not been viewed as a serious threat to most bird populations in the LEF (Snyder et al., 1987) as also supported by diet studies (Vilella, 1998) indicating that the most common prey in stomachs included *Anolis* lizards, centipedes, and cockroaches. However, mongooses accounted for 81% of tody nest losses in the LEF (Kepler, 1977) and they may be a threat to ground foraging birds, such as the Ruddy Quail-Dove (e.g., feathers of this species found in mongoose stomach, Vilella, 1998). In addition, fledgling parrots may be at risk to mongoose predation when they land on or near the ground (Snyder et al., 1987), as evidenced by fledgling remains and radio transmitters found in mongoose burrows (Engeman et al., 2006). Likewise, mongooses have been observed on several occasions preying on thrasher fledglings that had fallen to the forest floor, having been previously compromised by botfly larvae (Arendt, 2006). Given these concerns, Engeman et al. (2006) used tracking plates, monitoring blocks, and trapping to index abundance of mongooses as well as black rats and feral cats in parrot habitat and public use areas of the LEF. Their study demonstrated that mongooses were present in a greater portion of tracking plates within parrot habitat than in public-use sites. Also, they found that rat capture rates at all sites (42%) were among the highest reported anywhere. Thus Engeman et al. (2006) conclude that the abundance of exotic mammal predators in the parrot breeding areas poses more of a threat to parrots than previously recognized, especially given the evidence for mongoose predation on fledgling parrots. Given this threat, they advocate general control of mammalian predators at parrot breeding sites based on analyses that it is cost effective (Engeman et al., 2003). Left unanswered, however, are the questions of why and under what other circumstances are parrot fledglings on or near the ground and what management interventions might be applied to reduce the risk of a parrot's occurrence at ground level.

Snakes such as the Puerto Rican boa (*Epicrates inornatus*) may be important predators on birds and their nestlings at lower elevations of the LEF as evident from stomach contents indicating adult boas feed on birds, as well as a variety of other prey (Wiley, 2003). At least seven species of birds in the LEF have been found mobbing boas, suggesting that birds recognize boas as potential predators (Mercado et al., 2002). With the exception of the feather of a Puerto Rican Bullfinch in a fecal pellet, Wunderle et al. (2004) found no other prey items in their radio telemetry study of boa movements in the tabonuco forest. However, their study did identify the traits of trees used by boas—vines, canopy contact with neighboring trees, and large size. These traits correspond to traits of cavity trees in which nests of Black-billed Parrots (*Amazona agilis*) were most likely to fail, due to chick losses in Jamaica (Koenig, 2001). This evidence strongly implicated predation by the Jamaican boa (*E. subflavus*) and led to a review (Koenig et al., 2007) of snake predation on parrot nests and recommended management interventions to protect nests trees of endangered bird species. However, the Puerto Rican boa is not a likely threat to nesting parrots in the LEF because parrots currently breed in mid elevation where boas are rare and in only one instance has a boa been suspected of preying on a parrot nest there (Snyder et al., 1987). Nonetheless, boas do represent a threat to nesting parrots released in the karst regions of the island where boas are more abundant, including areas of current and potential releases (Trujillo, 2005).

Patterns of nest predation in relation to vegetation were studied in tabonuco and colorado forests by Latta et al. (1995) who used quail eggs set in artificial nests and Bananaquit nests (with the dome removed) placed on the ground and in shrubs. Despite predictions, they failed to find differences in nest predation rates between forest edge along roads (5–50 m) and forest interior (100–250 m) for either ground or elevated nests, presumably resulting from the creation of canopy openings and early successional vegetation in the forest matrix due to hurricane disturbance (~3.5 years previously). Results suggested that egg predation occurred most frequently in areas damaged by the hurricane, but differences in vegetation recovery affected probabilities of nest success. Damaged sites colonized by *Cecropia* [*peltata* L] *shreberiana* Miq. had lower predation rates possibly due to the open understory, which may have been unattractive to predators.

8. Bird population changes in the LEF

8.1. Sharp-shinned and Broad-winged Hawk

Population declines in both Broad-winged and Sharp-shinned Hawks have been documented over the last several decades in the LEF (Delannoy, 1997). For Broad-winged Hawks, surveys by Santana C. and Temple (1984) indicated 50–60 individuals, followed by estimates of 40–50 by Snyder et al. (1987), and then Delannoy's average count of only 22.2 in 1991–1992 indicating that broad-wings had declined by 50% in the LEF. Even more marked were the declines in Sharp-shinned Hawks in the LEF: from 60 individuals reported by Cruz and Delannoy (1986) to 3.7 individuals in 1991–1992 estimated by Delannoy (1997) indicating a decline of 93% in the LEF. Broad-winged Hawks are still detected occasionally in the LEF during parrot censuses (Thomas White, personal comm.) and in some recent Christmas bird counts (http://www.audubon.org/bird/cbc/hr/index.html for Fajardo; PRFA). However, Sharp-shinned Hawks have not been detected in recent years in the LEF (Thomas White, personal comm. and Christmas bird counts). Delannoy (1997) observed that the declines in these two raptor species occurred only in eastern Puerto Rico (LEF and Sierra de Cayey) as the populations in the west were stable. He attributes the decline of the two raptors in the east to multiple causes including Hurricane Hugo in 1989, *Philornis* botfly parasitism of nestlings, and the increase in Pearly-eyed Thrashers in the 1970s and 1980s, which may have increased predation on eggs and nestlings of the two raptor species. The thrasher is a predator on eggs and nestlings of many species (Snyder et al., 1987; Arendt, 2006) including Sharp-shinned Hawks (Delannoy, 1997). The risk of depredation may have increased only recently as the thrasher was believed to be rare in the LEF before the 1950s (Snyder et al., 1987; Arendt, 2006). Finally, botflies can reduce Sharp-shinned Hawk nestling survival, suggesting to Delannoy and Cruz (1991) that parasitism has an additive effect on overall mortality. Additional studies on these two raptor species are needed to determine the relative importance of these stresses so that management interventions may be implemented, although such studies may best be undertaken elsewhere on the island where populations of these raptors are more abundant than in the LEF.

8.2. Elfin-woods Warbler

Long-term monitoring (1989–2006) of the LEF's bird community took place monthly from 1989 to 2006, along several census routes dispersed among the four forest types. Point counts along these routes in the upper reaches of the forest indicate that the endemic Elfin-woods Warbler underwent a continuous, average rate of decline since 1989 of 0.002–0.01 individuals per ha/yr in elfin woodlands and 0.003–0.06 individuals per ha/yr in colorado forest (Arendt et al., in review). The elfin woodlands population showed a significant general declining trend from *ca.* 0.2 individuals per hectare in 1989 to *ca.* 0.02 individuals per hectare in 2006; and in Colorado forest from 1 individual to 0.2 individual during the same period. The cause of these declines is unknown and although we can not eliminate the possibility that the decline represents a local shift in the population from the census route to other montane areas of the forest, no concomitant increases were observed in other areas during the same period. For example, Waide (1995) reported the warbler rare in the areas of Mt. Britton and El Yunque Peak in surveys after Hurricane Hugo. Likewise, Anadón-Irizarry (2006) reported no detections from these two areas in surveys after Hurricanes Hugo and Georges. Arendt et al. (in review) suggests that the declines may result from hurricane damage to vegetation or its response. These declines are consistent with other declines reported elsewhere on the island (Arroyo-Vázquez, 1991) lending support to recommendations to reclassify the species from vulnerable to globally endangered and emphasizing the need for studies on the warbler's distribution, life history, survival and breeding biology in the LEF and elsewhere.

9. The challenges of a wet forest

The LEF's high annual rainfall and humidity, especially in the higher elevations, pose challenges for bird populations. As a possible response to the LEF's wet conditions, many species avoid breeding in the wettest months of the year and breed in March to June, coinciding with the drier months (Recher, 1970; Snyder et al., 1987; Waide, 1996) and thereby avoiding the peak period for tropical cyclones and botfly parasitism. Moreover, dry season breeding may be a response to food resource peaks that also occur at this time, such as the peak production of sierra palm fruits, which are important for parrots and thrashers (Snyder et al., 1987; Arendt, 2006), as well as peak flowering providing nectar for hummingbirds and Bananaquits. Nevertheless, wet conditions can contribute to egg and nestling mortality, as documented for parrots in wet cavities (Snyder et al., 1987), and botfly infestations of thrasher nestlings are lower in the drier months of the breeding season (Arendt, 1985b, 2006) and in drier habitats such as the Guánica dry forest (Arendt, 2006). Food delivery rates by parents to nestlings can also be impeded by rainfall and fog, contributing to nest failure in Red-tailed Hawks at high elevations (Santana C. and Temple, 1988). Rainfall extremes may also contribute to adult mortality as observed in Puerto Rican Parrots in which annual survival of breeders was reduced from normal rates in very wet and very dry years (Beissinger et al., 2008). In the latter instance, it is unknown if the reduced annual survival of parrots is due to the direct effects of the rainfall extremes, or indirect effects such as reduced food availability or increased predation risk.

The LEF's high annual rainfall may contribute directly to physiological stress in birds by increasing heat loss due to wetting of plumage (Lustick and Adams, 1977; Wilson et al., 2004), which is exacerbated by cool windy conditions at high elevation. The risk of energy shortage due to heat loss is greater for small birds given their greater surface-to-volume ratio and higher metabolic rates than large birds and their limited capacity for fat storage (Bucher and Worthington, 1982). Given these traits, the diminutive Puerto Rican Tody (5–7 g) would likely be energetically challenged by cooler temperatures and heavy rainfall, which also limits foraging time. Despite these energetic challenges the tody is found throughout the LEF's elevation gradient up into the elfin woods, albeit at lower densities than in the lowlands (Recher, 1970; Kepler, 1977; Waide, 1996). Oniki (1975) was the first to suggest that todies might have unusual thermoregulatory adaptations to mitigate energy shortages when she documented unusually low body temperatures in LEF todies. Subsequently, Merola-Zwartes and Ligon (2000) studied the ecological energetics of todies in the LEF and in the Guánica dry forest and uncovered some remarkable thermoregulatory adaptations enabling it to occupy diverse habitats despite the limitations of small body size.

Even though the tody's basal metabolic rate is high (BMR ∼33% higher than predicted by mass), it falls within the range for other small birds (Merola-Zwartes and Ligon, 2000). However, they found that todies are unusual in other aspects: (1) As found by Oniki (1975), the active-phase body temperature of todies (36.7 °C) is well below the avian norm of 40–41 °C. (2) Todies also exhibit heterothermy by allowing their body temperature to vary from 27.9 to 42.9 °C over an ambient range of 15–40 °C. At low ambient temperatures in the evening, some todies went into nocturnal hypothermia by dropping their body temperatures by 10–11 °C and yet still remained active and alert. (3) Climatic adaptation was evident in both BMR and body size. Tody BMRs in the LEF were significantly higher than in the hot dry forest at Guánica. Also, as per Bergman's Rule, todies in the LEF had larger body masses than those in Guánica, presumably as a heat loss adaptation. (4) BMR changed seasonally, with rates lowest when not breeding. (5) Some females went into torpor during the breeding season when exposed to low air temperatures (15 °C). The authors suggest that torpor in breeding females is a response to the stress of producing energetically expensive eggs. Todies are the only bird species for which torpor has been reported in only one sex. By allowing their body temperatures to fall, thereby minimizing heat loss, todies, despite their small size, can conserve energy allowing them to colonize a range of environments including the wetter and cooler habitats. Although not studied, similar adaptations might be expected in hummingbirds in the LEF.

The wet conditions of the rain forest create a challenging environment for maintaining the viability of unincubated eggs as demonstrated in a series of imaginative experiments using the LEF's elevational climate gradient (Beissinger et al., 2005; Cook et al., 2003, 2004, 2005). These experiments were designed to test the hypothesis that the onset of avian incubation in the tropics was constrained by the likelihood that viability (i.e., hatching success) of the earliest laid eggs in a clutch diminishes over time in the absence of incubation due to presumed effects of ambient temperature. This constraint to the onset of incubation may limit the ability of avian parents to influence the onset of development, hatching synchrony, and likelihood of brood reduction. An initial experiment by Beissinger et al. (2005) involved removing 382 freshly laid Pearly-eyed Thrasher eggs and placing them in holding boxes at three different elevations (lowland sites 6–20 m; mid-, 600 m; colorado-elfin forest, 810 m) for 3–7 days before returning them to nests to be incubated. Controls indicated that handling and transport had no effect on viability relative to unmanipulated naturally incubated thrasher eggs (85%). Hatching success was relatively high for eggs exposed for 1 day (79%), but declined sharply afterwards (3 days, 42%; 5 days, 12%; 7 days, 2%). Viability of experimental eggs exposed in the lowlands and colorado-elfin forest were similar, but viability of eggs at mid elevation was lower. Minimum temperature was important as hatching success was positively related to it, but only weakly related to mean temperature and percentage of time above developmental zero. Analyses indicated that exposure duration, treatment site, and maximum temperature were the only significant effects. Beissinger et al. (2005) concluded by cautioning that ambient temperature was not likely to be the sole cause of the mortality of unincubated eggs.

Subsequent experiments along the elevational gradient by Cook et al. (2003, 2004) indicated that trans-shell invasion by pathogenic bacteria and fungi also contribute to mortality of unincubated eggs, especially at high elevation. These experiments indicated that unincubated eggs exposed for 5 days at high elevation were invaded by microbes in 90% of thrasher eggs and 60% of domestic fowl eggs. In contrast, lowland microbial infection rates of exposed eggs were lower and slower (28% for thrashers; 25% for fowl). When exposed eggs were disinfected twice daily, the colorado-elfin site had relatively high viability (thrasher 43% cleaned vs. 0% not cleaned; domestic fowl, 78% cleaned vs. 22% not cleaned), whereas lowland eggs had low viability for both cleaned and uncleaned eggs (thrasher, 6% cleaned vs. 10% not cleaned; domestic fowl, 40% vs. 38% respectively). Only by experimentally controlling for microbial infections at the humid high elevation site could the effects of high ambient temperature be detected. Apparently, thrasher incubation reduced growth of pathogenic microbes, thereby reducing the opportunity for trans-shell infection (Cook et al., 2005). Thus incubation was especially important in deterring microbial growth in the humid high elevation site. Furthermore, microbial infection and ambient temperature act independently to reduce egg viability in unincubated eggs, suggesting that these two factors could affect the onset of incubation in a variety of environments.

10. Tropical cyclones and birds in the LEF

Tropical cyclones, including hurricanes and tropical storms, represent the predominant natural disturbance in the LEF (Scatena and Larsen, 1991; Scatena http://luq.lternet.edu). Approximately once every 10 years a hurricane passes sufficiently near the island to cause severe, but localized damage. Over the past several centuries, hurricanes have passed over the LEF causing widespread damage on an average of once every 50–60 years. For example, the forest's biota was severely affected when Hurricanes Hugo (September 1989) and

Georges (1998) passed over the LEF. In the interim between these severe storms the forest was also affected by hurricanes that passed nearby including Luis (1995), Marilyn (1995), Bertha (1996), and Hortense (1996).

Given the frequency of hurricane disturbance to the LEF and a rich history of ecological studies providing baseline for comparisons, LEF-based studies have made major contributions to our understanding of the effects of hurricanes on ecosystems and their biota. These studies indicate that the frequent occurrence of tropical cyclones can play an important role in determining the structure and composition of biotic communities (Wadsworth and Englerth, 1959; Odum, 1970; Doyle, 1981; Walker et al., 1991). Although direct effects of hurricanes are initially evident as structural damage to plants and mortality resulting from exposure to high winds and rainfall, it is the indirect effects that have the longest lasting impact on plant and animal populations (Walker et al., 1991; Wiley and Wunderle, 1993).

Direct mortality from hurricanes has rarely been documented for forest-dwelling birds, including those in the LEF (Wiley and Wunderle, 1993). However, the indirect effects of hurricanes on birds can be substantial as observed in the LEF and elsewhere. One of the more prevalent responses of land birds in the immediate aftermath of hurricanes is a diet-related population response: nectarivores and frugivore/granivores may decline drastically in contrast to insectivores and raptors (Wiley and Wunderle, 1993). This diet-related response following a storm suggests that the greatest effect of hurricanes on terrestrial bird populations occurs in its aftermath and not during the storm when bird mortality may result from high winds and rainfall. Declines in nectarivores and frugivore/granivores are expected, given that defoliating winds also remove flowers, fruits, and seeds. This was documented after Hurricane Hugo went across three phenology trails in the colorado forest in the LEF where 300 tagged trees and vines had been monitored for flowering and fruiting for 33 months prior to the storm's arrival (Wunderle, 1999). Not only did fruit abundance decline afterwards, but the annual cycle of fruiting by trees was disrupted for at least 27 months during which time fruiting was acyclic with little synchrony among species. In addition, fruit quality may decline shortly after a hurricane as found for sierra palm in which mean dry weight of pericarp decreased from pre-hurricane values (Thompson Baranello, 2000).

As a frugivore/seedeater, the Puerto Rican Parrot is especially sensitive to hurricane effects as evidenced by population declines associated with recent storms in the LEF (USFWS, 2008; Beissinger et al., 2008). For instance, population declines were registered in censuses following Hurricanes Hugo (49%) and Georges (10%). In addition, annual mortality of breeding parrots increased from a value of 12% over 27 years in the absence of hurricanes to 30% after Hugo and 50% after Georges. These declines are likely attributable in part to increased vulnerability to predation from Red-tailed Hawks, which appeared to be unaffected by the hurricanes (Boal et al., 2003) as also observed in other raptors elsewhere (Wiley and Wunderle, 1993). As the parrots responded to reduced food abundance and quality, irregular fruiting periods, and increased patchiness of food in the storms' aftermath (Wunderle, 1995b, 1999) the food-stressed parrots were likely more exposed to predation as they foraged in storm-damaged canopies with reduced cover. These factors may have also contributed to the decreased annual survival of Pearly-eyed Thrasher breeders after Hurricane Hugo (0.42 vs. 0.89 documented during a 10-year pre-hurricane period; Arendt, 2006). However, thrasher predation by red-tails is probably minimal, owing to the thrasher's tendency to forage within undamaged habitat refugia following hurricanes (Arendt, pers. obs.).

Not all post-hurricane bird population declines are attributable to mortality as many species shift locations in response to loss of substrates, cover, and resources. These population shifts can occur across a wide range of spatial and temporal scales depending on the extent and severity of storm damage and resource recovery times (Wunderle, 1995b). For example, two weeks after the passage of Hurricane Hugo, mist net capture rates were significantly higher than baseline capture rates in the tabonuco forest due to displaced canopy dwellers foraging near the ground. Although capture rates there returned to baseline levels 2 months after the storm as canopy dwellers dispersed, captures rates again increased after 3–4.5 months as fruit production peaked in pre-existing gaps. The influx of frugivores and omnivores (e.g., Pearly-eyed Thrashers, Puerto Rican Tanagers, Puerto Rican Spindalis) into the pre-existing gaps contrasted with low capture rates in nearby pre-existing understory sites without fruit, but with defoliated canopy. As light gaps present before the storm, pre-existing gaps had vegetation, which was able to quickly respond to increased light by producing fruit shortly after defoliation of surrounding canopies, in contrast to the understory where shade-adapted plants were initially light-shocked resulting in delayed fruiting. Thus even in the aftermath of a hurricane, early succession sites such as pre-existing gaps may serve as "keystone habitats" (sensu Levey, 1990) for frugivores in a time a of fruit scarcity.

Not only do some birds shift locations after hurricanes, but some also shifted their diets (Waide, 1991). In the LEF following Hurricane Hugo, a larger proportion of species fed on fruit after the storm than prior to it (59% vs. 34% of stomachs). Presumably this was a result of moving to fruit-rich early successional habitat patches. Taxa of insects consumed also changed after the storm with an increase in Coleoptera and a decrease in Hymonoptera and Araneidae in stomach samples. Insectivorous birds undoubtedly benefit from insect outbreaks in the aftermath of storms, when plants produce new leaves. As expected, given the flush of new leaves, 15 species of Lepidoptera larvae increased in abundance 7–9 months after Hurricane Hugo (Torres, 1992).

Hurricane effects may carry over into breeding seasons as observed in Puerto Rican Parrots and Pearly-eyed Thrashers (Arendt, 1993, 2006; Wunderle, 1999; Wunderle et al., 2003). The parrot's first post-hurricane breeding season was delayed by approximately a month and the thrasher's by almost 6 months. By reducing the number of clutches on average from 2.2 in non-hurricane years to <2 clutches, thrasher females ended the breeding season at the normal date (Arendt, 2006). Clutch sizes in the first post-hurricane breeding season, however, did not change from the mean values for parrots or thrashers (Wunderle et al., 2003; Arendt, 2006). Still, several female thrashers laid 1-egg clutches for the first time during this period, but not afterward. The delayed breeding was expected, given the storms' negative impact on fruit abundance and quality, especially fruits of sierra palm, which are important for both species (Snyder et al., 1987; Arendt, 2006). Finally, at least for thrashers, the incidence of nest failures increased due to increased predation or usurption of nest boxes by several predators and competitors, although for bees the increase in cavity invasions occurred 3–5 years after the storm (Arendt, 2000, 2006).

Not all hurricane effects on breeding were negative, as evident in the second post-hurricane breeding season for both thrashers and parrots. For example, thrashers in their second post-hurricane breeding season after Hurricane Hugo started breeding about 4 months earlier than normal and bred for almost an entire year, extending their breeding season by increasing the number of clutches above the mean for non-hurricane years (Arendt, 2006). Similarly, in the second breeding season following Hugo, parrots increased their breeding productivity with an increase in the number of pairs breeding despite a decline in population size, and breeders produced larger clutches and had greater fledging success (Vilella and García, 1995; Meyers et al., 1993; Wunderle et al., 2003). The enhanced reproduction following a hurricane may be due to increased food availability (Meyers et al., 1993) resulting from increased primary productivity and availability of more nutritious food supplies for several years (Scatena et al., 1996). This may be especially important for frugivores in which protein deficiencies may hinder breeding (Morton, 1973). Finally over the long-term, more nest cavities become available because hurricanes, by breaking branches from tree trunks, facilitate the process by which decay enters tree trunks and produces cavities (Snyder et al., 1987).

In the short-term, hurricanes may have negative population consequences for many birds, especially for species such as the parrot with a small population size, a restricted range, and slow population growth rate. In this instance, hurricane-induced mortality may drive a small population below the threshold for recovery. However, in the long-term the effects of hurricanes may be beneficial by increasing nutrient cycling and creating nest cavities (Meyers et al., 1993). Thus the challenge for the populations of many forest bird species is to be able to survive the short-term negative effects of hurricanes to enable them to take advantage of the delayed beneficial effects. For managers charged with the recovery of vulnerable species in hurricane regions, potential negative consequences during this bottleneck period in a hurricane's aftermath may be ameliorated by several management actions including encouragement of habitats (e.g., second growth habitats, lowland forests) and plant species (e.g., palms) that are resistant to storm damage and/or have high recovery rates (Wunderle and Wiley, 1996).

11. Future research opportunities

The LEF's elevational gradient, along which climate and biota vary provides a diversity of environments in which various aspects of avian biology and ecology can be profitably compared, in both descriptive (e.g., Kepler, 1977; Arendt, 2006) and experimental studies (e.g., Beissinger et al., 2005; Cook et al., 2003, 2004, 2005). Moreover, these comparisons can be expanded to other life zones, habitats, or habitat fragments outside of the LEF (e.g., Merola-Zwartes and Ligon, 2000; Arendt, 2006) or in the rural, suburban, or urban habitats near the LEF (Vázquez Plass, 2008). Little is known of how population regulation, demography, and mating systems vary among habitats in tropical birds (Stutchbury and Morton, 2001) and studies along gradients could prove useful in identifying factors underlying the maintenance and evolution of various behavioral, physiological, and ecological traits. Furthermore, the need for studies along elevational gradients takes on urgency as global warming causes upward shifts in elevation by organisms and places high elevation populations (e.g., Elfin-woods Warbler) at risk to habitat loss (Moritz et al., 2008).

The future for the Puerto Rican Parrot in the LEF remains precarious given that the population has continued in a prolonged bottleneck for over 30 years (USFWS, 2008; Beissinger et al., 2008). The mid elevation colorado forest of the LEF has been a refuge for the parrot, but it may not be the most optimal habitat for the species. Instead, it has been the only habitat where they persisted in the absence of human disturbance (Snyder et al., 1987). The colorado forest may have traditionally been a sink for the parrot population given the abundance and diversity of stresses facing the parrots there—botflies, bees, Red-tailed Hawks, Pearly-eyed Thrashers, rats, and reduced hatching success due to wet conditions. Movement of the parrots down into drier lowland habitats may prove beneficial, because of lower thrasher and hawk densities there (Snyder et al., 2007; Rivera-Milán, 1995; Trujillo, 2005). The cohort of old colorado trees, which provides nest cavities for the parrots, is susceptible to hurricane-induced mortality and is dying out (Weaver, 1986; Meyers, 1994, 1996b). It is likely, therefore, that parrots will be forced to breed in the tabonuco forest where suitable nest cavities are available (Meyers, 1996b; Thompson Baranello, 2000) or can be provided (White et al., 2005b, 2006). Although a move down into the tabonuco forest for breeding may relieve the parrots of some of the stresses currently encountered in the colorado forest, the population will face new limiting factors (e.g., boas and more bees competing for cavities) and greater interaction with people, especially given increased pressure for recreational access to the forest.

Determining the factor or factors that contribute to low breeding effort in the Puerto Rican Parrot, remains one of the highest research priorities for the recovery effort. As Beissinger et al. (2008) note, low breeding effort (mean of 34% of population per year) has constrained population growth over the entire 27-year study period. They suggest that the temporary burst in breeding after Hurricane Hugo suggests that breeding may be constrained by environmental factors rather than inbreeding avoidance. A suggested research approach would be to focus on nutritional effects through food supplementation as well as to examine the role of social facilitation of breeding. To test inbreeding avoidance hypotheses, uniquely color-banded individuals (Meyers, 1995) could have blood samples taken to allow the construction of pedigrees. It is possible that carefully designed experiments associated with releases of parrots elsewhere on the island could provide valuable insights into why so few parrots breed in the wild. Admittedly, answering the question will be difficult, but the payoff from any interventions that increase the proportion of breeders in the wild would have a large impact on population growth (Beissinger et al., 2008).

The Pearly-eyed Thrasher remains an important species for future studies especially given its role as a competitor and predator of the parrot and other species. If not a keystone species in the colorado forest, the thrasher is at least a key species in terms of its impacts on other members of the bird community, especially in the colorado forest where thrashers are most abundant, although its numbers have been declining even in this prime habitat (Arendt, 2006). As a predator/competitor, the thrasher may be responsible for locally depressing populations of some bird species, as suggested for the Sharp-shinned Hawk, Puerto Rican Parrot, White-necked Crow, and others (Snyder et al., 1987; Arendt, 2006). More intriguing is the possibility that thrashers may contribute to high botfly densities, which have a spillover effect on other species less resistant to botfly parasitism (Snyder et al., 1987). This may be aided by the fact that botflies parasitize at least 20 bird species in the LEF (Pérez-Rivera and Collazo Algarín, 1976; Snyder et al., 1987; Arendt, 2006), although many differ in their sensitivity and response to botfly parasitism (Snyder et al., 1987; Arendt, pers. obs.). Countering the possibility of a spillover effect is the finding that the botfly's population growth rate is logistic. Accordingly, nestling infestation rates as well as mortality resulting from parasitism rise steadily and sharply throughout the thrasher's nesting period (Arendt, 1985a,b). Not surprisingly, nestling mortality is often 100% from May onward. As a result, hundreds of nestling (and a few adult) thrasher hosts die well before their implanted botfly larvae can mature and pupate, thus eliminating those flies as a threat to the avian community. Yet, some botflies do successfully pupate from nestling thrashers, especially from first-hatched young in early broods of which 60% fledge (20% succumb to botflies) in contrast to later hatched nestlings in the clutch, most of which succumb to the larval infestations (Arendt, 1985b, 2006). Most importantly, however, species with populations already stressed by other factors such as the vacillations of climate, predation, disease, and competition may be especially vulnerable to botflies (see Delannoy and Cruz, 1991). Thus it is likely the thrasher plays a major role in regulating some bird populations (Arendt, 2006), through several means, although this needs further documentation.

The Pearly-eyed Thrasher is an especially tractable species for studies of breeding biology because it readily accepts nest boxes for breeding, which has facilitated long-term studies (Arendt, 2006) providing a baseline for comparison by future researchers. The evidence that the thrasher has become abundant in the LEF only recently (Snyder et al., 1987; Arendt, 1996, 1997, 2006) and the fact that botfly parasitism has a devastating impact on thrasher nestlings, suggest that the host-parasite contact is also a recent phenomenon. It is likely that there has been insufficient time for the thrasher host to adopt counteractive measures to the botfly. Future studies should test this hypothesis by evaluating the impact of botflies on nestling survival along with documenting any potential counteractive mechanisms adopted by nestlings. An approach to determine the physiological effects of botflies on thrasher nestlings would be to use fluctuating asymmetries, which quantify small, random deviations from symmetry of bilaterally symmetrical traits (Palmer and Strobeck, 1986a,b, 1992). It is still not known how variables such as rainfall, humidity, incident light, and densities of host populations affect the prevalence and intensity of botfly parasitism. An understanding of how these factors influence parasite-host interactions would be useful for predicting changes in parasitism rates with changing climate.

Throughout its history, organisms have colonized the LEF at rates that likely have increased since the arrival of the Amerindians. For instance, the LEF has been invaded by a variety of exotic organisms (e.g., black rats, European and Africanized honeybees, mongooses, and feral cats), whose impacts on the native biota are poorly known, although for some the consequences have been negative (Snyder et al., 1987; Arendt, 2000, 2006; Engeman et al., 2006). Similarly, we do not fully understand the consequences to the biota of population increases of native species, such as increases in thrashers (Snyder et al., 1987; Arendt, 1996, 1997, 2006). Even more poorly known are the effects of disease agents on the LEF's avifauna, such as West Nile virus, which was found in eastern Puerto Rico in 2003 (Dubuis et al., 2005), and shortly afterwards the virus was detected in parrots in the LEF's Luquillo aviary (Thomas White, personal comm.). Whether invasions of the LEF will be facilitated by the increasing suburbanization and urbanization along the forest's periphery (Thomlinson et al., 1996; Thomlinson and Rivera, 2000) is unknown. We find it noteworthy, however, that exotic bird species, especially psittacines common in the rural and suburban communities along the forest boundary, have yet to colonize the forest. Exotic bird species in the developed areas bordering the LEF might serve as a reservoir for diseases for forest birds, such as the parrot (for disease risk see Wilson et al., 1994). However, this possibility has not been studied. Finally, as globalization of commerce continues we expect that the number of exotic organisms colonizing the island will increase and some of these invaders may have deleterious consequences for vulnerable populations in the LEF.

We expect that new species will colonize the LEF because of global climate change, which will likely alter the distribution of life zones and forest types within the forest. Associated with global warming in the Caribbean is the expectation that the region will become drier in the summer months (Neelin et al., 2006; Zhang et al., 2007). Already a decrease in annual rainfall has been demonstrated over a recent 15-year period in a tabonuco site in the LEF (Heartsill-Scalley et al., 2007). Not only would a drying trend facilitate changes in composition of species in the LEF, but it would likely cause changes in phenology of flowering and fruiting in plants and timing of breeding in many organisms. What the ecological consequences of these changes might be are unknown. In addition to a predicted drying trend associated with global warming is an expected increase in the frequency of the most powerful hurricanes (categories 4 and 5; Bender et al., 2010). Although research in the LEF has provided a basic understanding of how the forest ecosystem and biota respond to hurricane impacts (e.g., Walker et al., 1991) little is known how responses will vary with an increase in storm frequency. Yet, the hiatus between hurricanes may be important, as shown by Arendt (2006) indicating that thrasher reproduction and the response of their predators differed between Hurricanes Hugo (first major LEF strike in 57 years) and Georges, 9 years later. Thus studies in the LEF have the potential to serve as invaluable baseline for future research as the climate and biota change and urbanization proceeds on the island, especially in the vicinity of the forest.

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Appendix A.

Birds and their status, habitats, and abundance in the Luquillo Experimental Forest/El Yunque National Forest, Puerto Rico. The list is based on the original list in Wiley and Bauer (1985) as modified with recent observations by the authors, their field assistants, and biologists in the National Forest. Status code includes: introduced (I), endemic (E), nester (N), resident (R), transient or migrant (T), and transient that breeds in the forest (T*). Habitat code includes: edge between forest and non-forest (E), plantation (L), tabonuco forest (T), colorado forest (C), elfin forest (D), palm forest (P), and rivers, streams (R). Abundance code includes: common (C), uncommon (U), and rare (R).

Common name	Scientific name	Status	Habitat	Abundance
Snowy Egret	*Egretta thula*	N, T	R	R
Little Blue Heron	*Egretta caerulea*	N, T	R	U, R
Cattle Egret	*Bubulcus ibis*	N, T	E	R
Green Heron	*Butorides virescens*	N, T	T,C,R	R
Yellow-crowned Night-Heron	*Nyctanassa violacea*	N, T	T,R	U
Sharp-shinned Hawk	*Accipiter striatus*	R	T,C	R
Broad-winged Hawk	*Buteo platypterus*	R	T,C	U
Red-tailed Hawk	*Buteo jamaicensis*	R	T,C,P,D	C
American Kestrel	*Falco sparverius*	N, T	E	R
Merlin	*Falco columbarius*	T	T,C,P,D	U
Peregrine Falcon	*Falco peregrinus*	T	T,C,P,D	U
Spotted Sandpiper	*Actitis macularius*	T	T,C,P,R	U
Scaly-naped Pigeon	*Patagioenas squamosa*	R	T,C,P,D	C
White-crowned Pigeon	*Patagioenas leucocephala*	N, T	T,C	R
Plain Pigeon	*Patagioenas inornata*	N, T	T,C	R
White-winged Dove	*Zenaida asiatica*	T	E	R
Zenaida Dove	*Zenaida aurita*	R	E,L	C
Mourning Dove	*Zenaida macroura*	N, T	E	R
Common Gound-Dove	*Columbina passerina*	N, T	E	U
Ruddy Quail-Dove	*Geotrygon montana*	R	T,C,P,L	C
Orange-fronted Parakeet	*Aratinga canicularis*	I	E,L	U
White-winged Parakeet	*Brotogeris versicolurus*	I	E,L	U
Puerto Rican Parrot	*Amazona vittata*	R	T,C,P	R
Yellow-billed Cuckoo	*Coccyzus americanus*	T	E, L, T	R
Mangrove Cuckoo	*Coccyzus minor*	R	E,T,L	U
Puerto Rican Lizard-Cuckoo	*Coccyzus vieilloti*	R	E,L,T,C,P,D	C

Appendix A (*Continued*)

Common name	Scientific name	Status	Habitat	Abundance
Smooth-billed Ani	*Crotophaga ani*	R	E,L	U
Puerto Rican Screech-Owl	*Megascops nudipes*	R	L,T,C,P,D	C
Chuck-will's-widow	*Caprimulgus carolinensis*	T	T,C,P	R
Black Swift	*Cypseloides niger*	T*	T,C,P,D	C
Antillean Mango	*Anthracothorax dominicus*	R	E,L	R
Green Mango	*Anthracothorax viridis*	R	T,C	U
Green-throated Carib	*Eulampis holocericeus*	N, T	E, L, C	U
Antillean Crested Hummingbird	*Orthorhyncus cristatus*	N, T	E, L, T, C	R
Puerto Rican Emerald	*Clorostilbon maugaeus*	R	T,C,P,D	C
Puerto Rican Tody	*Todus mexicanus*	R	T,C,P,D	C
Belted Kingfisher	*Megaceryle alcyon*	T	T,R	R
Puerto Rican Woodpecker	*Melanerpes portoricensis*	R	L,T,C,P,D	C
Yellow-bellied Sapsucker	*Sphryapicu varius*	T	L,T,C,P,D	R
Western Wood-Pewee	*Contopus sordidulus*	T	E	R
Puerto Rican Flycatcher	*Myiarchus antillarum*	R	E,L	R
Gray Kingbird	*Tyrannus dominicensis*	R	E,L	U
Loggerhead Kingbird	*Tyrannus caudifasciastus*	R	E,L	R
White-eyed Vireo	*Vireo griseus*	T	L,E,T	R
Puerto Rican Vireo	*Vireo latimeri*	E	L,E	R
Yellow-throated Vireo	*Vireo flavifrons*	T	L,E	R
Red-eyed Vireo	*Vireo olivaceus*	T	L,E	R
Black-whiskered Vireo	*Vireo altiloquus*	T*	E,L,T,C	C
Caribbean Martin	*Progne dominicensis*	T	E,L,T,C,P,D	U
Cave Swallow	*Petrochelidon fulva*	N, T	E,C,T	U
Barn Swallow	*Hirundo rustica*	T	C,P,D	U
Bicknell's Thrush	*Catharus bicknelli*	T	E,L	R
Swainson's Thrush	*Catharus ustulatus*	T	E,L,T,C,P,D	R
Wood Thrush	*Hylocichla mustelina*	T	E,L	R
Red-legged Thrush	*Turdus plumbeus*	R	E,L,T,C	C
Gray Catbird	*Dumetella carolinensis*	T	T, C	R
Northern Mockingbird	*Mimus polyglottos*	R	E,L	U
Pearly-eyed Thrasher	*Margarops fuscatus*	R	L,T,C,P,D	C
Cedar Waxwing	*Bombycilla cedrorum*	T	L,T	R
Golden-winged Warbler	*Vermivora chrysoptera*	T	T,C	R
Northern Parula	*Parula americana*	T	E,L,T,C,P,D	C
Chestnut-sided Warbler	*Dendroica pensylvanica*	T	L,T,C	R
Magnolia Warbler	*Dendroica magnolia*	T	L,T,C	U
Cape May Warbler	*Dendroica tigrina*	T	L,T,C	U
Black-throated Blue Warbler	*Dendroica caerulescens*	T	L,T,C,P,D	C
Yellow-rumped Warbler	*Dendroica coronata*	T	L,T	R
Black-throated Green Warbler	*Dendroica virens*	T	L,T	R
Blackburnian Warbler	*Dendroica fusca*	T	L,T	R
Prairie Warbler	*Dendroica discolor*	T	E,L,T,C	C
Bay-breasted Warbler	*Dendroica castanea*	T	T	R
Blackpoll Warbler	*Dendroica striata*	T	E,L,T,C	U
Elfin-woods Warbler	*Dendroica angelae*	R	C,P,D,T	U
Black-and-white Warbler	*Mniotilta varia*	T	L,T,C,P,D	U
American Redstart	*Setophaga ruticilla*	T	L,T,C,P,D	C
Worm-eating Warbler	*Helmitheros vermivorum*	T	T,C,P	R
Ovenbird	*Seiurus aurocapilla*	T	L,T,C,P,D	U
Northern Waterthrush	*Seiurus noveboracensis*	T	T,C,P,R	U
Louisiana Waterthrush	*Seiurus motacilla*	T	E,T,C,P,R	C
Kentucky Warbler	*Oporornis formosus*	T	L,T	R
Common Yellowthroat	*Geothlypis trichas*	T	E,T,D	R
Hooded Warbler	*Wilsonia citrina*	T	L,T,C	R
Bananaquit	*Coereba flaveola*	R	L,T,C,P,D	C
Puerto Rican Tanager	*Nesospingus speculiferus*	E	T,C,P,D	C
Puerto Rican Spindalis	*Spindalis portoricensis*	E	L,T,C,P,D	C
Yellow-faced Grassquit	*Tiaris olivaceus*	R	L,E	U
Black-faced Grassquit	*Tiaris bicolor*	R	L,E	U
Puerto Rican Bullfinch	*Loxigilla portoricensis*	R	L,C,T,P,D	C
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	T	L	R
Indigo Bunting	*Passerina cyanea*	T	L,E	U
Greater Antillean Grackle	*Quiscalus niger*	R	E,L	R
Shiny Cowbird	*Molothrus bonariensis*	T	L,E	U
Greater Antillean Oriole	*Icterus dominicensis*	R	T,L,E	C
Venezuelan Troupial	*Icterus icterus*	I	E	R
Baltimore Oriole	*Icterus galbula*	T	L,E	R
Antillean Euphonia	*Euphonia musica*	R	T,C,P,D	C
Orange-cheeked Waxbill	*Estrilda melpoda*	I	E	U
Bronze Mannikin	*Lonchura cucullata*	I	E	U
Nutmeg Mannikin	*Lonchura punctulata*	I	E	R
Pin-tailed Whydah	*Vidua macroura*	I	E	U

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