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Adaptations of an Avian Supertramp: Distribution, Ecology, and Life History of the Pearly-Eyed Thrasher (*Margarops fuscatus*)

Wayne J. Arendt



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Cover photograph: Male pearly-eyed thrasher (*Margarops fuscatus*) singing from its favorite song perch in an avocado tree. Photo taken by Jerry Bauer in May 2006 from the second-story balcony of the author's home in Pitahaya Ward in northeastern Puerto Rico.

Abstract

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The pearly-eyed thrasher is a major nest predator and competitor for nest sites of the endangered Puerto Rican Parrot. In all aspects of its distribution and ecology, *Margarops fuscatus* is a classic example of an avian “supertramp.” It is a pugnacious, highly vagile species, i.e., a good disperser, with a propensity to fill vacant or underexploited niches at all elevations by adopting generalized nesting and foraging strategies, as well as a varied diet. Having evolved superior colonizing traits at the expense of strong competitive characters, it is confined to about 80 generally small, often disturbed, species-poor islands and habitats throughout the Caribbean. The pearly-eye’s future depends on its ability to adapt to the ever-changing conditions in the region’s natural and anthropogenic environments.

Keywords: *Amazona vittata*, life history, *Margarops fuscatus*, pearly-eyed thrasher, Puerto Rican parrot, supertramp.

Preface

This volume attempts to explain the current distribution of West Indian birds from an ecological perspective rather than from a physical or geological standpoint. Its primary objective is to present to the reader, for the first time, indepth information on the life history of a unique and widely distributed Caribbean mimid, one which exemplifies many of the ecological and reproductive traits recognized more than three decades ago by the human physiologist and avian ecologist Dr. Jared M. Diamond of the University of California in Los Angeles.

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Chapter 1: Introduction

Study Area and Methods

Data presented in this volume were obtained from 1978 to 2005. I assist in the efforts to restore the critically endangered Puerto Rican parrot (*Amazona vittata*), now limited to the Sierra de Luquillo Mountains (fig. 1.1), mostly within the confines of the Luquillo Experimental Forest (fig. 1.2). The Luquillo Experimental Forest is also known as the Caribbean National Forest, or simply “El Yunque,” the Spanish vernacular for a blacksmith’s anvil, which the Sierra de Luquillo reportedly resembles. I undertook this long-term study of the pearly-eyed thrasher because it is the Puerto Rican parrot’s principal nest predator and competitor for nest sites. The following section describes the thrasher study area



Figure 1.1—Overview of the Sierra de Luquillo Mountains located in eastern Puerto Rico, an island mostly forested prior to European colonization. This picture is part of a landsat thematic mapper satellite image captured in 1985 showing the Luquillo Experimental Forest and the area to its east. (Photo courtesy of Dr. Eileen Helmer and Olga Ramos of the USDA Forest Service, International Institute of Tropical Forestry’s Global Imaging System/Geographic Positioning System Laboratory. The satellite image and its full description are available at the following Web site: <http://luq.lternet.edu/data/spat-asc.html#satellite>.)



Figure 1.2—The 28 000-ha Luquillo Experimental Forest (*noms. alt.* Caribbean National Forest and “El Yunque”) located in northeastern Puerto Rico. The Taino Indians, early inhabitants of the area, revered the mountains believing they were the home of the “*espiritu benefactor*” (or benefactor spirit) who would bless them if they paid homage to him, usually through sacrifices. The word Luquillo is believed to be a corruption and contraction of “Yukaju” (the mythological benefactor spirit of the Taino Indians inhabiting Haiti, and the root word from which the Yokahú observation tower located at km 9 along highway 191 in the Luquillo Experimental Forest was named). “Yukaju” was used together with “Yuku,” resulting in the more simple term “Yukiyu.” The contemporary word “Luquillo” was adopted by the Spanish who thought that Yukiyu referred to a crazy Taino Chieftain who incessantly attacked the Spanish inhabitants of the area. “Loco” (or “loquillo”) in Spanish means crazy, from which was eventually derived the word “Luquillo,” which in addition to referring to the forest, is also a small nearby coastal city (preceding information taken, with permission, from Domínguez-Cristóbal 2000). (Photo courtesy of Gerald P. Bauer.)

and the methods used to obtain the data. One analysis covers a period of 32 years (1973–2005), another through 2004, and many more that include every year over a 21-year period from 1979 to 2000 (several figures); in other analyses, however, some years are excluded, e.g., 1983, 1984, and 1989 owing to incomplete data sets. Likewise, some analyses include shorter periods, e.g., 12 years—1979–91 (thrasher survival—a limitation of the model), 18 years—1979–97 (return rates), and 19 years—1979–98 (various egg-laying and recycling data sets).

Methods used will be summarized chapter by chapter. To ensure consistency and standardization in citing references pertaining to Caribbean birds, I followed as closely as possible the format used by J.W. Wiley (2000) in his comprehensive bibliography of West Indian ornithology.

Before presenting methodology summaries, I will first describe my long-term, life-history nest-box study (1979 to present), the software packages used to perform numerous parametric and nonparametric statistical tests, and those in the graphic display of the results, which include data gathered between 1979 and 2005.

Nest-Box Study

The pearly-eyed thrasher is a nonobligate, secondary cavity nester (Arendt 2004a). Although it often constructs its bulky open-cup nest on heavily foliated tree limbs and within bamboo thickets and vine entanglements, it readily takes to existing cavities. However, it does not excavate its own cavity. Nor does it lay its clutch of one to four pale bluish-green eggs directly on the interior cavity substrate as do primary cavity nesters, most of which have unpigmented eggs (Arendt 2004b). Instead, the pearly-eye builds a definitive stick nest lined with aerial or, less often, terrestrial rootlets within natural cavities or, as in this study, within nest boxes (fig. 1.3). In December, 1978, within the Luquillo Experimental Forest, I began monitoring 30 to 40 (avg. = 34 per year) modified wood-duck (*Aix sponsa*) nest boxes (fig. 1.4) known as “Kepler Boxes,” first used by C.B. Kepler as part of another

The pearly-eyed thrasher is a nonobligate, secondary cavity nester.



Figure 1.3—The pearly-eye’s typical three-egg clutch laid in a bulky stick nest lined with aerial rootlets and placed within a Kepler box (gray shadow surrounding the nest). Even in the rain forest, not all pearly-eyes nested in cavities. Favorite noncavity nest sites included bamboo thickets, vine entanglements, and other vegetation associations with dense foliage to ensure that nests were not only hidden but also sheltered from the persistent heavy rains.



Figure 1.4—Full view of the Kepler nest-box design used in this study. (see “Study Area and Methods” for a more detailed description of box placement and maintenance, and Snyder et al. 1987 for box specifications).

study related to the Puerto Rican Parrot. Boxes were numbered to enhance quality control of the data. Aboveground box height was irrelevant because breeders would readily accept boxes placed as low as 2 m and at any height above the forest floor, even in the upper story canopies of emergent trees. Because of rat predation, sheet metal was often nailed to the roof and walls of the box to reduce the rat’s traction and lower the probability of predation. With the invasion of the forest by the Africanized honeybee (*Apis mellifera scutellata*) in the mid-1990s, usurpation of nest boxes by swarming bees increased dramatically (Arendt 2000). By using both attractant and repellent baits as well as a viscous glue coating on the upper inner surfaces of boxes, the installation of bee traps helped to reduce the number and severity of invasions but did not successfully deter the ever more frequent swarms. Each box was placed about 0.1 km apart at elevations ranging from about 600 to 900 m primarily in palo colorado forest (fig. 1.5; see also Ewel and Whitmore 1973, Wadsworth 1951 for a description of the forest, including the four major forest types).



Figure 1.5—The colorado forest type. Classified as lower montane wet forest and located between roughly 600 and 900 m, colorado forest encompasses 3318 ha, or about 30 percent of the entire forest, and is the pearly-eyed thrasher's prime habitat in the Sierra de Luquillo. The large palo colorado tree (*Cyrilla racemiflora* L.) shown in the foreground rarely exceeds heights of 18 m but may reach almost 3 m in diameter and can survive more than a thousand years (Weaver 1986). It is a favorite of cavity-nesters such as the Puerto Rican parrot (*Amazona vittata*) and the pearly-eyed thrasher because its heartwood decays, forming natural cavities, over which the parrot and thrasher vie for use as nest sites.

Box locations have been permanently recorded by using geographic information system (GIS) and global positioning system (GPS) technology (Trimble Pro XL[®]).¹ Nest-box data were differentially corrected and plotted by using ArcView[®] software and overlaid on a forest map.

Nest boxes were monitored every 2 to 4 days throughout the nesting period, and daily at critical times, e.g., egg-laying, hatching, and fledging periods. During the nonbreeding season, each box was checked every 1 to 2 weeks for signs of activity. In several analyses throughout this document, data were collected from known-aged pearly-eyed thrashers (individuals that hatched in nest boxes) and “minimum-aged” individuals (determined by tallying the number of years after banding). For example, an unknown-aged (unbanded) thrasher that was banded and then bred in a nest box at the onset of the study (1979) was considered a minimum-aged 1-year-old as it generally takes about 9 months for first-time breeders to nest. Each succeeding year, the minimum age of that breeder was incremented by 1.

Natural Habitat Disturbances

The effects of Hurricanes Hugo (1989) and Georges (1998) on much of the forest and its vegetation will be felt for decades. Fortunately, however, their impacts were less severe in the areas harboring thrasher nest-box trees included in this study. Most nest-box trees were located in the Icacos Valley (fig. 1.6) along a south-facing slope that, in general, did not suffer extensive damage from high winds and water-induced damage such as erosion, landslides, and occasional uprooting. Only three nest-box trees toppled during Hurricane Hugo, and an additional two nest boxes blew down. As a result of a more direct hit and the heavier rains associated with Hurricane Georges, six nest-box trees toppled owing to high winds (n = four boxes) and landslides (n = two boxes). In addition to the 6 boxes downed with their respective trees, 4 more boxes were destroyed as a direct result of Hurricane Georges. After each hurricane, boxes were replaced either in their previous trees, or as in the instances of felled trees, within 10 m of their previous locations.

To study various aspects of the pearly-eye’s life history, my assistants and I constructed observation blinds made of easily sewn and portable burlap (fig. 1.7), camouflaged canvas, fiberglass, and even palm fronds, which were used for the roof and walls. Bundled tightly together, palm fronds not only hid the observer from view, but also were adequate in keeping the observer

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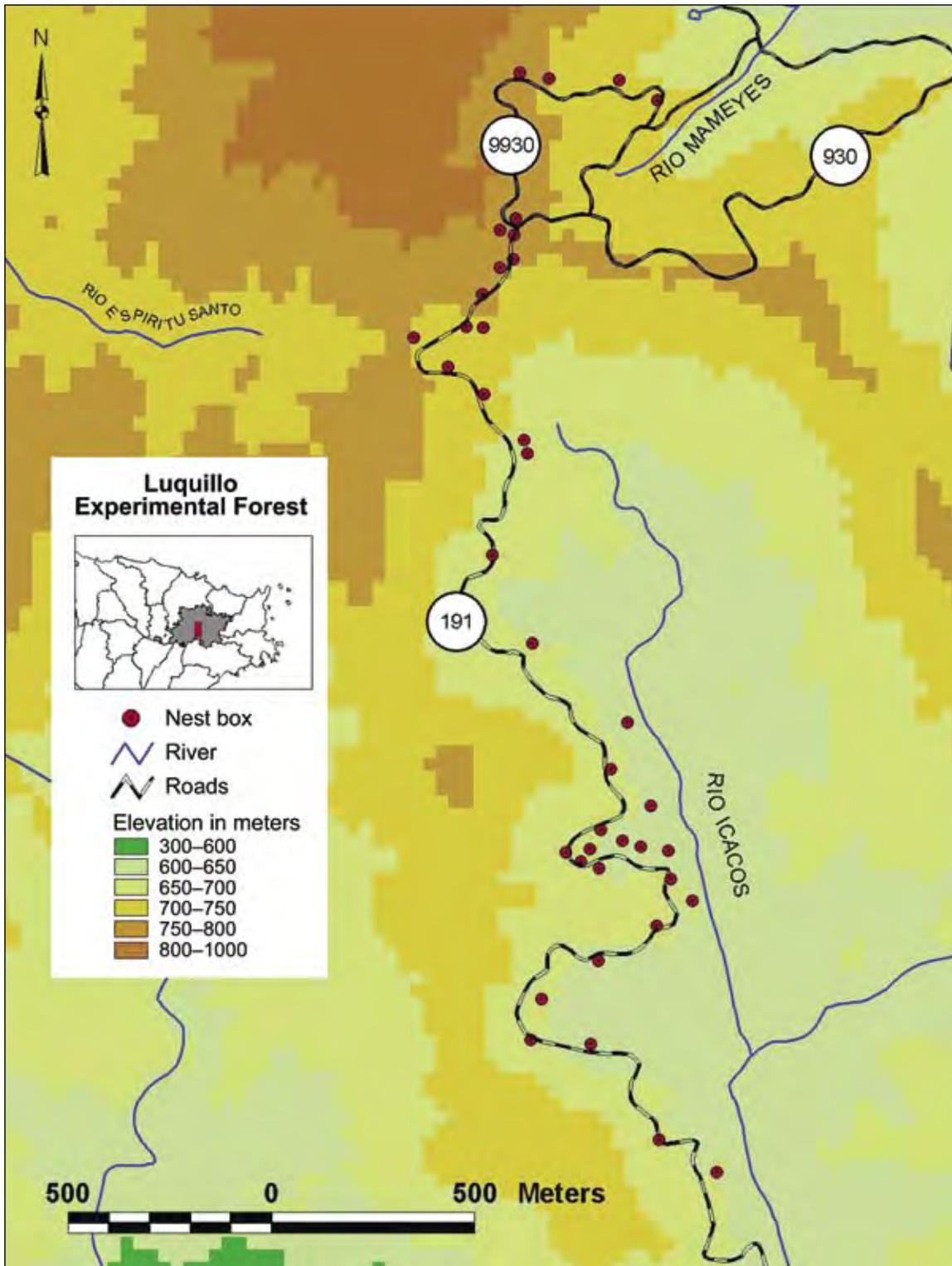


Figure 1.6—Pearly-eyed thrasher research areas within the Luquillo Experimental Forest. Delineated are the main study sites and the dispersion of nest boxes along PR Hwy. 191 in the Icacos Valley, PR auxiliary 9930 (Loop Road), and PR auxiliary 930 (Molindero Loop). One box (not shown) was located near Quebrada Juan Diego at an elevation of 460 m at km 9.8 along PR Hwy 191. Map courtesy of Carlos Rodríguez of the USDA Forest Service, International Institute of Tropical Forestry's Global Imaging System/Geographic Positioning System Laboratory.



Figure 1.7—Nest-monitoring observation blind (or “hide”). In the background, the author has just placed a mounted thrasher on the roof of a nest box during the nonbreeding season to determine if the pearly-eye is territorial year-round, which it is. Mist and low clouds moving through caused the haze noticeable in the background. (December 1979 photo courtesy of Gerald P. Bauer.)

(relatively) dry during even heavy downpours. Blinds were placed on the ground or in trees at distances of 3 to 30 m from nest boxes to observe thrasher behavior and activities such as (a) incubation and brooding schedules, (b) fledging, (c) rates of feeding and fecal sac removal, and (d) regurgitation of pellets containing the seeds of fruits and bones of animals too large to digest.

Adults were captured in traps attached to nest-box entrances during the breeding season, and in mist-nets outside of the reproductive period. Eggs and chicks were weighed and measured by using digital and dial calipers accurate to 0.01 and 0.02 mm, respectively, and 50- to 300-g spring scales with increments of

0.5, 1, and 2 g (see also Arendt, 2005). Adults were also measured by using the same calipers and 300-g spring scales with 2-g increments (measurement techniques followed Baldwin et al. 1931, Pettingill 1970, Pyle et al. 1987).

For almost 10 years, my wife, Angela, and I conducted the bulk of the field-work. Then, beginning in 1987, after receiving adequate training in the use of the previously described equipment, parrot project volunteers and one to three field technicians began assisting in the collection of nest-box data. After 1990, most of the field data were collected by Roberto Díaz (1991 to 1997), Morris S. Ford (1997 to 2002), and Matthew Anderson (2002 to present). During the 1990s, I periodically assisted in collecting the data when circumstances required my participation, e.g., posthurricane bird-population and habitat assessments.

The Effects of Dipteran Ectoparasitism

Some of the information in the following paragraphs is taken from Arendt (2000). It merits repeating to ensure that the reader has an adequate introduction to *Philornis* ectoparasitism in Puerto Rico (see also Delannoy and Cruz 1991, Rivera Irizarry 1990) and within the Sierra de Luquillo because it is such an integral part of the forest ecosystem and this research.

The genus *Philornis* includes more than 50 species of parasitic flies that have radiated widely throughout the Neotropics, showing a wide host specificity and parasitizing more than 100 species of birds (for examples, see Couri 1999, Dodge and Aitken 1968, LaRue 1987, Teixeira 1999). Within the Luquillo Experimental Forest, philornid botflies (fig. 1.8) parasitize more than 20 avian species in diverse taxa including Falconiformes, Columbiformes, Psittaciformes, Cuculiformes, and several species of Passeriformes (Snyder et al. 1987; Pérez-Rivera 1993, in litt.; and pers. observ.).

Adult *Philornis* botflies (Diptera: Muscidae) resemble the common housefly (*Musca domestica* L.) in appearance, and both have a lapping proboscis. Body shape and wing venation are typically muscid. Wings are hyaline (transparent and colorless). Philornid botflies are identified by the prominent r-m and m-m (radial and medial) cross veins in their wings. Adults have black abdomens and red heads. Females have a fleshy telescopic ovipositor and average body length (9.17 mm) smaller than males (10.65 mm). Females can also be distinguished from males by the yellowish pleural (lateral) areas of their legs and their wider interorbital spaces, which are golden rather than silver as in males (Arendt 1983, LaRue 1987). LaRue (1987) found that adults were mostly crepuscular (active at twilight); and, although they extended their proboscises to honey water, adults did so more frequently when parrot and thrasher excrement was provided.

***Philornis*
ectoparasitism
is an integral part
of this research.**

Female flies in the genus *Philornis* may be oviparous or viviparous, depending on their adaptive reproductive strategies (see detailed discussion in Couri 1999, Skidmore 1985, Teixeira 1999). Although to date in this forest, there is only circumstantial evidence, e.g., females with fleshy telescopic ovipositors, complex structural design of the egg encasement (fig. 1.9), sperm in the spermatheca, and chorionated (protective membrane) eggs in the median oviduct ready to be laid (LaRue 1987; and pers. obs.), it is believed that these botflies lay their eggs topically on their hosts.

To my knowledge (and corroborated by J.E. Loye 1998, pers. comm.), no one

has yet documented in the literature seeing philornid botfly eggs on nestling birds, although I, as well as others, have observed the eggs of blowflies (Calliphoridae) laid on moribund thrasher nestlings that exhibit rapidly falling body temperatures and soon succumb to the effects of philornid ectoparasitism. The telltale raised bumps on the integument of recently hatched nestlings suggest that female botflies are depositing eggs topically on the hosts; the eggs most likely hatch quickly following deposition, and the larvae burrow into the skin almost immediately after hatching. Citing Arendt (1985b), Couri (1999) and Teixeira (1999) concluded that because so many larvae infest ventral areas of pearly-eye nestlings, it is more probable that the adults lay their eggs in the nest and the larvae then climb up onto the host. This hypothesis does not, however, account for the primarily dorsal larval implantation sites on young, especially recently hatched, nestlings (Arendt 1985a). Moreover, in 1987, from within a tree blind with a thrasher box



Figure 1.8—Adult *Philornis* botfly (Diptera: Muscidae). Although they resemble the common housefly (*Musca domestica*), philornid botflies can be identified by the prominent r-m and m-m (radial and medial) wing cross veins, which are visible in the photograph.

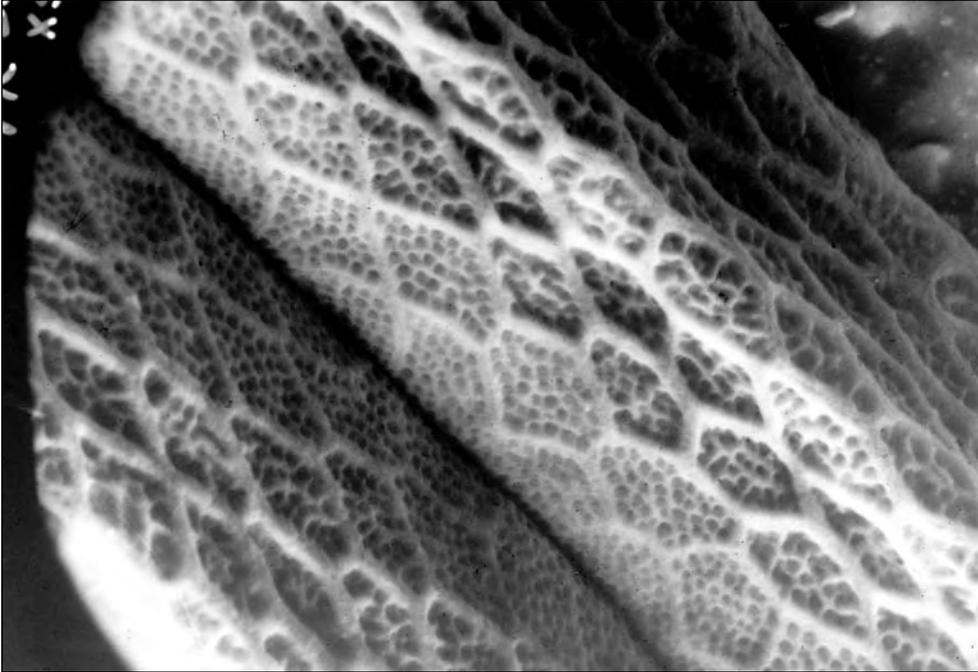


Figure 1.9—Scanning electron microscope image of a philornid botfly egg. Although it remains unknown whether or not the philornid flies inhabiting the Sierra de Luquillo are oviparous or viviparous (J.E. Loye 1998, pers. comm.), the intricate honeycomb-within-honeycomb pattern of the respiratory pores and structural supports shown in this picture, which no doubt greatly strengthens the egg and increases its resistance to being crushed, lends support to the notion that the fly has adopted an oviparous deposition strategy. Eggs laid typically must be resilient and able to withstand external pressures such as the nestling pressing itself up against the wooden wall of the nest box or even brushing up against its siblings. (Photo courtesy of Robin Kennedy, University of Missouri-Columbia.)

mounted on one side, and through one-way glass, I observed adult philornid females buzzing over nestlings and alighting on their heads and dorsal areas. Unfortunately, no female was observed ovipositing, and the blind, box, and glass were destroyed soon thereafter in a windstorm, curtailing further observations. However, more recently, A.L. Rivera (2004, pers. comm.) and others have captured on video philornid flies entering Puerto Rican parrot nest cavities and alighting on the heads and dorsal areas of parrot chicks, thus strengthening the possibility of a topical (vs. nest) deposition of eggs. Clearly, much more research into the ecology of the ectoparasite is needed before definitive statements can be made regarding its egg/larvae deposition strategy.

Philornid botfly larvae infesting pearly-eyed thrashers, both nestlings and adults, live subcutaneously for about a week, situated in furuncles (cavernous lesions with cornified epithelial walls) with their caudal spiracles visible through the dermal openings (fig. 1.10). Botfly larvae are maggot-like in general appearance. The anterior end tapers to a rounded head segment, and the much broader posterior end is obliquely truncate. Larvae are off-white to dark brown. They consist of 12 segments and range in length from about 1 to 20 mm, with a width

of 1.3 to 6 mm. Paired anterior and posterior respiratory spiracles are present on the 2nd and 12th segments, respectively. Rear-facing and sharply pointed cuticular spines cover portions of the thoracic and abdominal segments and are used to anchor the larvae within the furuncle, thus making extraction by a preening bird much more difficult. The heavily sclerotized cephalopharyngeal skeleton of the first instar larvae is probably a secondary adaptation for cutting through the host's integument (Nielsen 1911, Skidmore 1985). The puparial cuticular bands and caudal spiracles are the best taxonomic characters for the genus (Dodge and Aitken 1968).

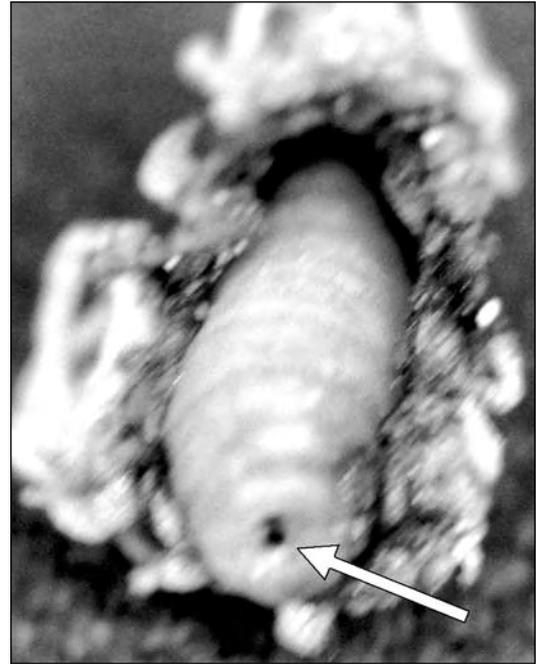


Figure 1.10—Philornid botfly larva. Before evacuation and pupation, infesting larvae live subcutaneously in both nestlings and adults for about a week, situated in furuncles (cavernous lesions with cornified epithelial walls). Paired posterior respiratory spiracles are visible in the photo.

Larval implantation follows the advancement of the breeding season and the ontogeny and pteryiae development of the nestlings.

Larval implantation strategies follow the advancement of the breeding season and the ontogeny and pteryiae development of the thrasher nestlings. Early in the season, larvae usually appear first in dorsal areas of young, unfeathered nestlings (fig. 1.11), usually commencing in anterior (coronal and nuchal) areas, and then along the capital tract beginning in the interscapular region. Larvae infest axillary and pelvic areas generally only after the remigial, humeral, and caudal feather tracts had begun to develop. Infesting larvae then concentrate ventrolaterally in older chicks to take advantage of the nutrient-rich blood supplied to the developing feathers of the ventrolateral and humeral tracts (fig. 1.12). Later in the season, however, owing to the exponential growth of the philornid population, there are so many flies vying for implantation sites that space is critically limited. As a result, early-season site specificity is abandoned and eggs are laid virtually over the host's entire body, commonly observed even in recently hatched nestlings. Larval saturation is conducive to the host's early demise because the period of most rapid growth in thrasher nestlings is within the first 1.5 weeks after hatching. Even if a heavily infested nestling survives, it is often critically compromised as evidenced in the nestling in figure 1.12. Soon after the larva that was implanted in its left auditory canal evacuated, the nestling's external auditory orifice sealed



Figure 1.11—Four-day-old, still unfeathered pearly-eye nestling heavily infested with philornid larvae. Late in the breeding season, owing to the exponential growth of the botfly population, there are so many female flies vying for implantation sites that space becomes critically limited. As a result, the early-season site specificity (dorsal—nucal and coronal—implantations in young nestlings) is augmented by eggs being laid virtually over the host's entire body as shown in this nestling hatched in June 1982.



Figure 1.12—Ten-day-old pearly-eye nestling infested with philornid larvae. Once the host's feather development was well under way, larval implantation sites tended to shift from dorsal to ventral surfaces, especially in the throat and inferior neck areas, and along the ventrolateral feather tracts. Note the large larva protruding from the bird's left auditory meatus.

over completely and it is assumed that this individual was left hearing impaired as a result of the ectoparasitism. In addition to its hearing problems, this nestling was unable to respire or feed normally owing to the numerous larvae implanted near its trachea and esophagus. As the larvae grew, they obstructed the passage of air and food.

The shift from dorsal sites in younger nestlings to ventral sites in older nestlings has been reported in another passerine, namely the redwing, *Turdus iliacus* (Bakkal 1980). Although nutrient-rich feather tracts and other trunk sites are preferred (Arendt 1985b: table 5), botfly maggots sometimes infest the host's legs and feet, including footpads and intertarsal joints (fig. 1.13), especially when the more "preferred" corporal and brachial areas are saturated with larvae, particularly late in the breeding season. Heavy larval infestations in and around intertarsal joints sometimes had a crippling effect on the host. In one instance

in 1982, a nestling thrasher having suffered from more than 20 larval implants on its legs could not stand firmly, and consequently did not fledge. It remained in the nest box 42 days before succumbing to what appeared to be malnutrition. The adults eventually stopped feeding the physically impaired chick. A similar instance involving a nestling of the critically endangered Puerto Rican parrot occurred in 1984. The nestling did not fledge because it was unable to climb up and out of its nest cavity owing to 12 philornid larvae infesting both tibiotarsi (Snyder et al. 1987).

Dissection of larval-infested thrasher nestlings that succumbed to philornid ectoparasitism suggested that the larvae were feeding on proximate subcutaneous blood supplies (fig. 1.14). Therefore, the pathenogenesis of the philornid myiasis was also investigated as part of this research (Uhazy and Arendt 1986). These



Figure 1.13—Pearly-eye nestling infested with botfly larvae implanted in appendicular extremes. Late in the breeding season when the “preferred” corporal and brachial implantation sites were saturated, infesting larvae then became more concentrated along the tibiotarsi, tarsometatarsi, and footpads, where they were able to take advantage of the proximity of underlying blood supplies.

Larvae feed on rich adipose tissues as well as erythrocytes, mononuclear cells, necrotic cellular debris, and body fluids.

investigations confirmed that larvae feed on their host’s rich adipose (“fatty”) tissues forming the base of the ventrolateral feather tracts, as well as erythrocytes, mononuclear cells, necrotic cellular debris, and body fluids (fig. 1.15). At pupation, via modified salivary glands, the larvae secrete a frothy cocoon (fig. 1.16) that anchors the puparia to twigs (fig. 1.17) under the female-warmed nest cup, which also assures relative safety from the brooding bird (see Couri 1984, 1985, 1991, 1999; LaRue 1987; Teixeira 1999; Uhazy and Arendt 1986 for a more detailed history of the taxonomy and ecology of philornid botflies).

The prevalence (proportion of nestlings infested), incidence (total number of infesting larvae), and larval implantation sites were recorded on diagrams of thrasher nestlings and in field notebooks, noting the age, size, and feather development of each chick and the age (instar) and size of each larva.

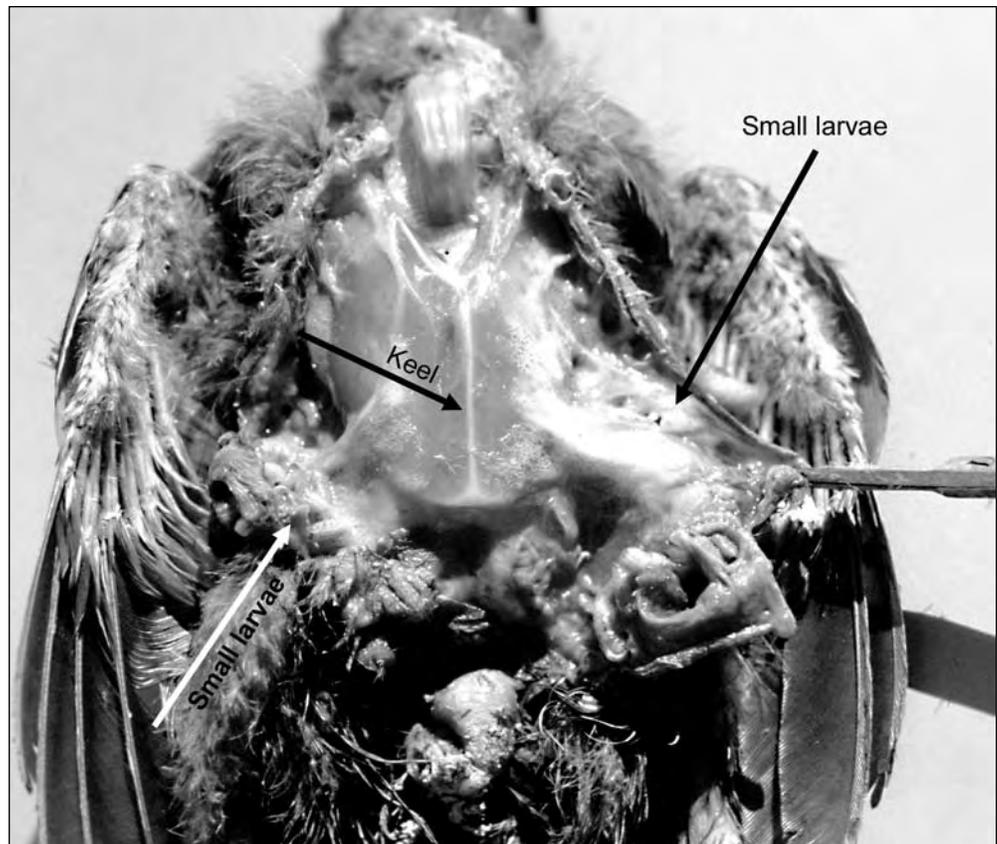


Figure 1.14—Dissected pearly-eye nestling. Thrasher nestlings that succumbed to the effects of philornid ectoparasitism were taken to the laboratory and necropsied to further study the effects of avian myiasis. Several small, first-instar larvae are shown here implanted along the nutrient-rich ventrolateral feather tracts. Note the protruding keel of the sternum, demonstrating the malnourishment of this individual as a result of its heavy infestation of botfly larvae.

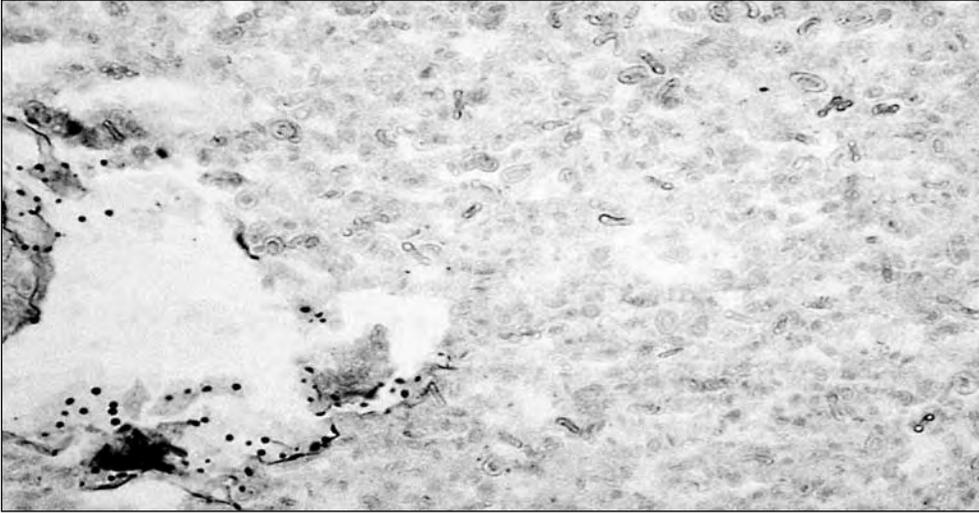


Figure 1.15—Photomicrograph of the cross section of a philornid larva showing the alimentary tract. Red blood cells (ghost-like circular to subcircular structures), mononuclear cells, and cellular debris are often found within the peritrophic membrane. The black dots represent pycnotic nuclei associated with degenerated necrotic cells (standard histological stain Haematoxylin and Eosin, at 610 power magnification) (Photo courtesy of Leslie S. Uhazy).

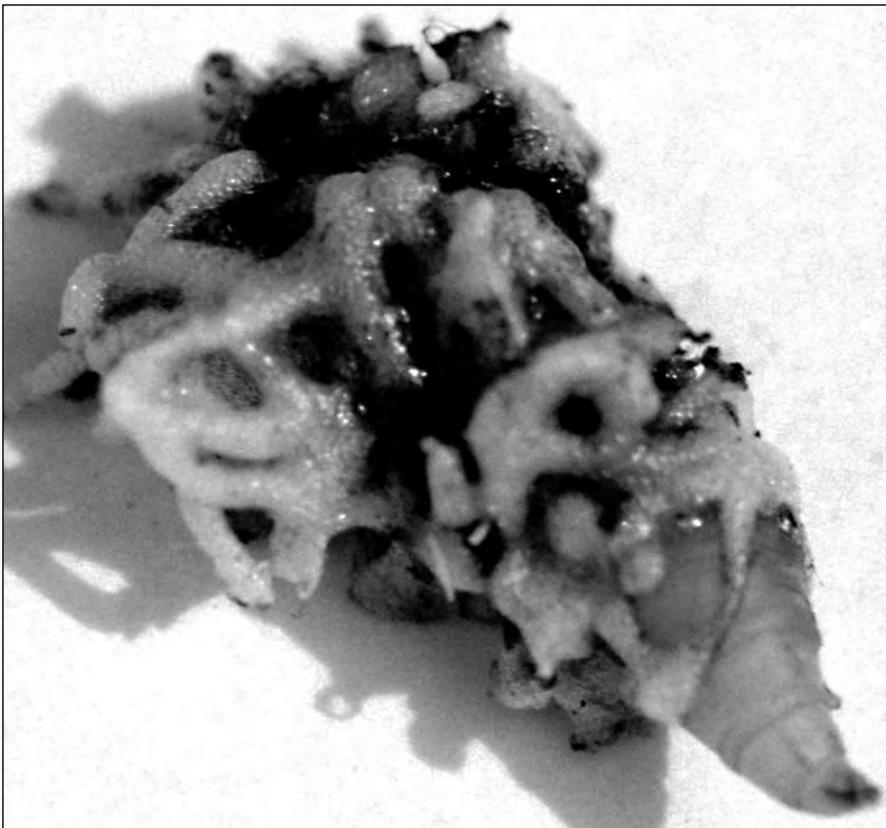


Figure 1.16—Philornid botfly maggot and cocoon. This maggot is secreting its frothy cocoon via modified salivary glands. The cocoon will soon adhere to twigs just below the thrasher's nest cup (Arendt 1983). At pupation, the larval hindgut is purged, and the dense, black fluid smells strongly of ammonia; the elongated salivary glands lose their white color and thereafter appear translucent (LaRue 1987).

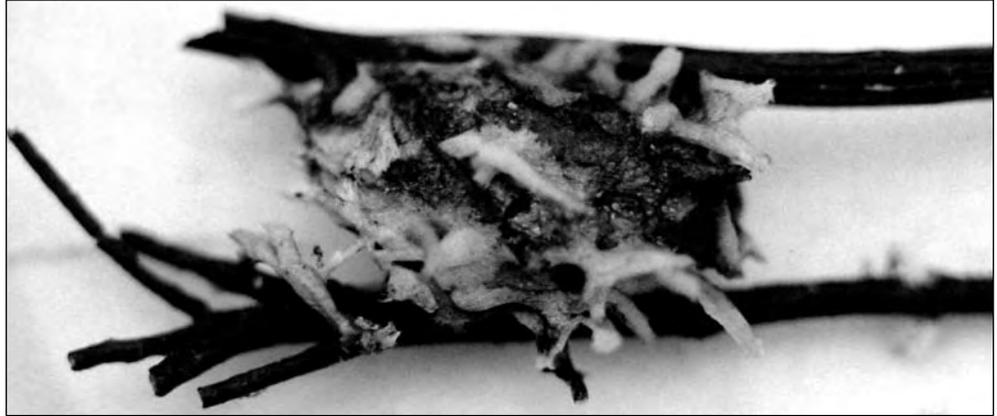


Figure 1.17—Philornid puparium. Although viscous during construction of the cocoon, the glue-like adhesive rapidly dries, cementing the puparium to the nest-cup twigs. Adult botflies emerged from their puparia after about 2 weeks (14 to 17 days).

Supplemental Nest Sites and Thrasher Densities

Installation of artificial nest boxes is often used to achieve, maintain, and enhance forest-bird biodiversity and density (Blem and Blem 1991, Fleming and Petit 1986, Twedt and Henne-Kerr 2001). Therefore, nest boxes are an integral part of the ever-growing arsenal of tools and techniques used by conservation biologists to manage forest-bird populations. Placement of artificial nest boxes in certain habitats such as small forest fragments can augment avian populations to desired levels, sometimes comparable to those in nearby natural forest stands (Báldi 1991). However, at the other end of the conservation spectrum, the occupancy of surplus nest sites by “undesirable” or “pest” species such as the house sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*), which often results in the complete competitive exclusion of all other potential nesters, poses a potential threat to populations of several beneficial (and often already threatened or endangered) cavity-nesting birds, for whom the boxes were originally designed. Because the pearly-eye is often considered a “pest” species, a few concerned people have asked if supplemental nest boxes might have dangerously elevated this forest’s population of the pearly-eyed thrasher, and if the research results from this study may be biased as a consequence of supplemental nest sites and an artificially elevated population?

Thrasher densities are higher in my study area than in some other sections of the forest and within the other three forest types (see chapter 8). However, my study area is in prime thrasher habitat, where a high population density is expected, regardless of the presence or absence of supplemental nest sites. But, to test the relevance of this finding, thrasher populations on other islands were surveyed comparing different habitat types (see chapter 4). Both mist-net and

audio-visual (pointcount) census results revealed that thrasher numbers in the Luquillo Experimental Forest, and even in my study area, are not as high as on some other islands where no supplemental nest sites have been provided. In fact, pearly-eyed thrasher numbers in colorado forest, particularly within my Icacos Valley study site, declined significantly during the first 6 years following Hurricanes Hugo (Arendt 2000: fig. 2) and Georges. The same pattern was observed in tabonuco forest within the Puerto Rican parrot’s primary nesting valley during the first 6 years following Hurricane Georges (fig. 1.18). Furthermore, dipteran ectoparasitism is so intense within the study area that, after May of each breeding season, often 100 percent of the infested nestlings die before fledging. Thus the forest thrasher population is not being saturated with new potential breeders as has been suggested by some. As further examples, not a single thrasher-box nestling fledged during the 1998 breeding season owing to exceptionally heavy botfly infestations that year. Likewise, only four thrasher-box nestlings fledged during the 1999 breeding season owing to very limited breeding and heavy philornid ectoparasitism resulting from the effects of Hurricane Georges the previous year. Lastly, during a three-season span (2000–2002), owing to a series of egg experiments conducted by University of California Berkeley collaborators, only

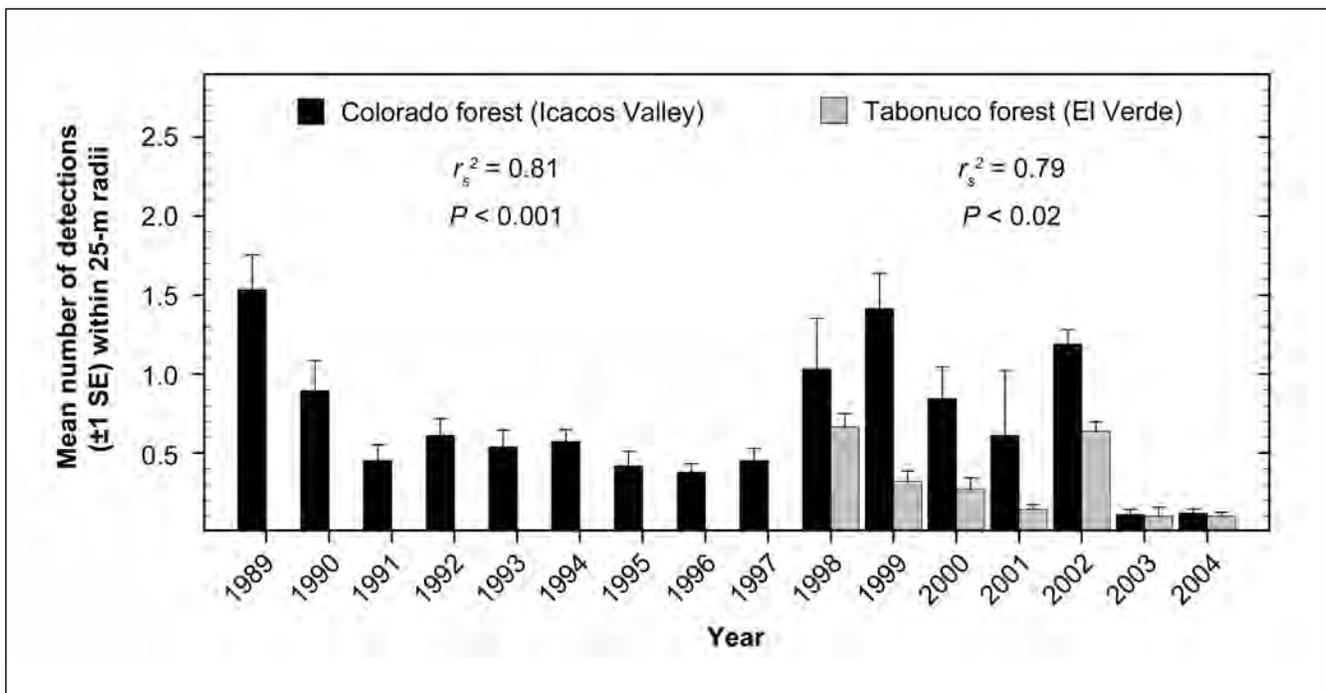


Figure 1.18—Population dynamics of the pearly-eyed thrasher between 1989 and 2004 in the Icacos Valley study area within its preferred palo colorado (*Cyrilla racemiflora* L.) forest habitat, and in tabonuco (*Dacryodes excelsa* Vahl.) forest within the main nesting valley of the critically endangered Puerto Rican parrot. In both forest types during this 15-year period, pearly-eyes reacted as do supertramps in general by increasing in number immediately following two major habitat disturbances, one each in September of 1989 and 1998, but then their numbers dwindled in both areas between disturbances. Note also the continued significant downward trend in thrasher populations in both areas during this period.

45 young pearly-eyes fledged from nest boxes. Thus, over a 5-year period, thrasher nest boxes produced only 49 fledglings (about 10 per year); certainly not enough to deleteriously impact the forest (see additional effects of ectoparasitism in chapters 6 and 7).

On a closely related subject, to assuage any anxieties among readers that I am significantly increasing the population of parasitic botflies in my study area as a consequence of producing more thrasher nestlings each season, I simply point out that I have, on numerous occasions over the past two decades, found comparable parasite loads on nestling pearly-eyes from natural cavities and open-cup nests in areas of the forest far removed from the study area. Moreover, philornid botflies are known to parasitize some 100 species of forest birds throughout the Neotropics (LaRue 1987: app. 1), and at least 20 species within the Luquillo Experimental Forest (see chapter 6). Thus, unless a species is already stressed (e.g., Delannoy and Cruz 1991), no single species should be significantly affected by potentially small increases in the botfly population. Most importantly, however, as stated above, nestling mortality resulting from ectoparasitism is high throughout each breeding season, often with 100 percent mortality from May onward. Consequently, numerous nestling thrasher hosts die, often well before literally thousands of implanted larvae can develop sufficiently to successfully pupate.

A review of the literature on long-term, avian life-history studies (Newton 1989, Sorace et al. 1993, and others) revealed that some researchers supply hundreds (Báldi and Csörgő 1994, Potti and Montalvo 1991) and even more than a thousand artificial nest sites in their study areas (e.g., Sternberg's [1989] long-term study of the pied flycatcher [*Ficedula hypoleuca*]). I am confident that I have not significantly increased the Sierra de Luquillo thrasher or botfly population, or biased the research results by monitoring some 30 to 40 nest boxes per year. In reality, the botfly parasite and its thrasher host are acting as biological controls on each other's populations within the Luquillo Experimental Forest.

Effects of Artificial Nest Sites (Boxes) on Study Results

Within about the last decade, much concern has arisen about the use of artificial nest structures, generally nest boxes, in avian reproductive research. Some, e.g., Møller (1989, 1992; Møller et al. 1990), fear that nest-box study results will be biased at best, or even erroneous at worst, because birds in nest boxes are safer from predators than they would be in natural cavities. Also, researchers who routinely clean nest boxes before each subsequent breeding season may be removing large quantities of nest parasites that, if left in situ, could potentially affect the health and longevity of the adult birds and lower their reproductive success

The botfly parasite and its thrasher host are acting as biological controls on each other's populations within the Luquillo Experimental Forest.

by causing developmental retardation, illness, or even death of the young. These fears are justified in some instances (Kedra et al. 1996, Kruszewicz 1995), especially in areas where nest ectoparasites are abundant and known to significantly impact reproductive success (e.g., Merino and Potti 1995, Rendell and Verbeek 1996). However, many researchers have since shown that these biases and the parasites' impact on their hosts in relation to "clean" (previous nests removed) vs. "dirty" (previous nests left intact) nest boxes differ greatly from species to species and region to region (e.g., see Christe et al. 1994, Davis et al. 1994, Johnson 1996, Pacejka and Thompson 1996, Purcell et al. 1997, Thompson and Neill 1991).

In this study of the pearly-eyed thrasher, the previously mentioned biases are not relevant. Regarding the reduced predation assumption, over the past 21 years, the deaths of adult thrashers and reproductive losses within nest boxes have been substantial. Loss of breeding adults and nest contents have been caused by a diverse group of nest predators, competitors for nest sites, and ectoparasites, e.g., Puerto Rican screech-owls (*Megascops nudipes*) (fig. 1.19), black



Figure 1.19—Puerto Rican screech-owl (*Megascops nudipes*) nesting in a thrasher box. This endemic owl is common in the Luquillo Experimental Forest. Owls prospecting for roosts and nest sites often eat the adult thrashers (usually females) and their young before usurping the box. Here, an incubating female is startled by the author during a routine nest inspection.

rats (*Rattus rattus*), other thrashers, philornid botflies (*Philornis* spp.) and, more recently, honey bees *Apis mellifera ligustica* and *A. m. scutellata* (Arendt 2000). Moreover, as in other parts of the forest, losses increased following major habitat disturbances, namely Hurricane Hugo (1989), a class 4 hurricane (Arendt 2000) and Hurricane Georges (1998), a strong class 3 hurricane.

As for the concern about the removal of previous nesting material reducing the potential impact of ectoparasitism on subsequent nestings, to minimize as much as possible any potential nest-site manipulation biases, I did not clean old nest material from boxes, either within, or between, breeding seasons. I allowed thrasher nest pairs to make the choice of building over old nests or removing previously used nesting materials. Such behavior differed among nest pairs. Many males (first) and females (later) simply threw in small sticks and twigs forming a platform over old nest materials, upon which they built new nest cups. Others hollowed out depressions in the old nest substrates, which often consisted of a compacted mud-like surface composed of discarded seeds, frog, bird, and lizard skeletons, etc., all glued together by the nestlings' excrement. The pairs (most often the females) would then construct open-cup nests in the excavated hollows. If the "ownership" of a box was not certain, prospecting individuals would sneak in and remove nest materials. Finally, some pairs actually pitched out old nests in their entirety before constructing new platforms and nest cups, especially if previous nests were elevated to the point that they were close to the entrance hole. I have observed similar behavior by thrasher nest pairs constructing open-cup nests and nests within natural cavities in areas of the forest free of nest boxes and in other forests and diverse habitats on other islands.

Lack of Experimentation in This Study

I am often asked why I conducted so few experiments while conducting thrasher research over so many years, as, after all, nest-box studies are conducive to the scientific experimental design with its quantitative and controlled manipulation of the variables, which is preferred by most researchers over the more traditional "field" studies, which are mostly limited to observations. Early on, I did attempt a few experimental studies such as clutch size manipulations and supplemental food provisioning to answer some of the more interesting biological and ecological questions about clutch and egg size, parental and offspring fitness, chick growth and development, and so on. Unfortunately, however, in this rain-forest population of the pearly-eyed thrasher, even over a 21-year period, the numbers of unparasitized nests and nestlings were so few that sample sizes in the various experimental categories were never large enough for statistical comparisons, thus

rendering experiments impractical, at least in the nestling stage. However, some experimentation while nests were still in the egg stage was possible. Consequently, just prior to the 2000 breeding season, cooperative studies into the theory behind, and mechanisms (e.g., microbial pathogens) influencing, the onset of incubation in birds in general, and the pearly-eye in particular, began with researchers from the University of California at Berkeley (Cook et al. 2003, 2005).

Banding

Numbered U.S. Geological Service Biological Resources Division (formerly U.S. Fish and Wildlife Service) metal leg bands and two to five uniquely coded, colored leg bands were attached to adult and nestling thrashers for future identification. Over the 21-year period, 1,363 nestlings and 247 adult breeders (9 months and older) were banded. Many more nestlings were hatched and handled, but not all of them were given metal leg bands because of anticipated prefledging mortality resulting from heavy infestations of botfly larvae.

Over the 21-year period, 1,363 nestlings and 247 adult breeders were banded.

Statistical Analyses and Graphics Software Programs

With the exception of chapter 5 (see below), all statistical analyses were conducted by using SigmaStat[®] version 2 (Fox et al. 1995) for Windows 95[®] and SYSTAT[®] version 9 for Windows 98[®] (SPSS 1998a, 1998b) statistical software packages for personal computers. A 95 percent confidence level ($\alpha = 0.05$) was maintained in all of the analyses (except chapter 5, see below).

During exploratory analyses, all variables used in the statistical analyses were checked for normality (Kolmogorov-Smirnov test with Lilliefors' correction) and equal variance (Levene Median Test). Deviations from Gaussian expectations for skewness and kurtosis, as well as the adherence to the assumptions underlying regression statistics, were examined by using various descriptive statistical procedures in the STATS module, and PLOT (probability plot), STEM (stem-and-leaf diagrams), and RESIDS (residuals) commands in SYGRAPH. However, throughout this volume, most graphs were made by using SigmaPlot[®] (SPSS, Inc., formerly Jandell Scientific), whereas free-hand line drawings (fig. 4.1 in chapter 4) were produced with an ACECAD[®] model ACECAT II graphics tablet.

Owing to the complex nature of the geographical, environmental, biological, and ecological variables and multiple interactions among them and those of the pearly-eye's morphological characters, a special, more indepth statistical analysis was conducted by Dr. Michael R. Willig, a professor and biostatistical and environmental consultant at Texas Tech University, Lubbock, Texas. All of his statistical analyses were conducted by using SPSS (1990).

Unless otherwise specified, significance was recognized at five levels. Letters and symbols within brackets correspond to those appearing in figure 5.2 in chapter 5. “NS” denotes nonsignificance.

1. [NS] $P > 0.10$
2. [@] $0.10 > P > 0.05$
3. [*] $0.05 \geq P > 0.01$
4. [**] $0.01 > P > 0.001$
5. [***] $0.001 > P$

Program ONEWAY was used to conduct a priori (SNK tests) and a posteriori analyses of univariate characters; in these cases, equality of variances was not assumed. Pearson Product Moment Correlation (PPMC) was used to compare the pearly-eye’s morphological data with geographical information such as latitude and landmass. Program MANOVA was used to conduct multivariate analyses of variance (MANOVA), whereas Datadesk (Data Description 1995) was used to generate Principal Components Analyses (PCA) based on variance-covariance matrices.

MANOVA and MANCOVA testing allowed for the determination and assessment of group differences in morphology with respect to combinations of dependent and independent variables. Through PCA, covarying patterns of variation in morphometric data are summarized to produce independent composite variables that are interpreted as size (PC1) and shape (PC2) axes (Bookstein et al. 1985, Pimentel 1979). The first axis is usually a unipolar size axis and is therefore a multivariate measure of size. All original morphological variables are positively correlated to the axis, and the correlations are more or less of the same magnitude. The first axis usually explains a substantial proportion of the variation in the original morphological data set and, oftentimes, the first two axes explain most of the variation.

Museum specimens and free-flying thrashers were measured and included in the various analyses. However, at no time were field and museum specimen data mixed. Some studies have shown that mensural variation in the population is often far greater than pre- vs. postmortem differences (Herremans 1985). Yet, several other studies (Bjordal 1984, Haftorn 1982, Winker 1993, and their respective references) have shown that the discordance in pre- and postmortem data can significantly affect analyses and results.

Four data sets were used in the morphometrics analyses: (1) ELEVCOMP (elevational comparison); (2) MUSEUMPET (pearly-eye museum specimens); (3) ELYUNQUE (live-caught pearly-eyes from the nest-box study); and (4) FIELDPET (all other live-caught pearly-eyes from around the Caribbean).

For each of the four data sets, the general analytical strategy was to conduct multivariate analyses to assess hypotheses of group differences in morphology with respect to season (see the 4 [“ELEVCOMP,” “MUSEUMPET,” “ELYUNQUE,” “FIELDPET”] analytical rationales below), sex (gender), SBTH (presence or absence of the scaly-breasted thrasher), or elevation (in meters), as appropriate. A suite of univariate tests on analogous treatment groups, modified by Bonferroni’s Sequential Adjustment, was used to determine the robustness of multivariate conclusions with regard to deviations from assumptions. In the case of multivariate significance, significant characters after adjustment by Bonferroni’s method (Beal and Khamis 1991) identify the univariate characters that strongly contribute to those differences. A priori and a posteriori contrasts were conducted in univariate settings as appropriate. When covariates were measured as well, corresponding MANCOVAs and ANCOVAs were conducted. To visualize differences in multivariate space for each of the four data sets, the PCA on log-transformed characters was conducted with groups defined by combinations of levels of treatment factors from the multivariate analyses. For heuristic purposes, if a treatment was significant in MANOVAs, differences between pairs of groups were interpreted as significant if confidence ellipses (1 standard error = \pm SE) did not overlap.

“ELEVCOMP” (elevational comparison) data set analytical rationale—

Two general approaches were undertaken to assess the effects of elevation (Mona, Guánica, El Yunque mid elevation, and El Yunque high elevation) and season (March to October vs. November to February) on morphological variation in the Pearly-eyed thrasher. In the first approach, an explicitly multivariate procedure was performed by using a two-way MANOVA based on culmen length from the feathered base (exposed culmen), tarsus, wing, and body mass (in lieu of “weight”—see Chardine 1986). Two characters (bill length from nares and tail) were deleted from these analyses because they had missing values for individuals at elevation = 1 (Mona Island), and would have prevented analyses of morphological differentiation that included that elevation. Because of concerns about conforming to the assumptions of MANOVA, and because an analysis based on all characters was desirable, a univariate approach was undertaken as well. In the second approach, univariate analyses were conducted by using separate two-way ANOVAs based on each of the six morphological characters separately, followed by Bonferroni’s Sequential Adjustment on the p-values for the treatment groups (cells based on combinations of elevation and season). If at least one character was significant after Bonferroni’s Sequential Adjustment, then a multivariate difference owing to treatment levels could be inferred. Moreover, the contribution

of each morphological character to overall differences was deduced based on the significance of those characters after adjustment. A priori and a posteriori analyses identified the level at which differences became significant owing to treatment effects. The PCA on log-transformed characters was used to graphically visualize the extent to which discrete groups of individuals corresponded to categories based on season and elevation.

“MUSEUMPET” (pearly-eye museum specimens) analytical rationale—

Both univariate and multivariate approaches were undertaken to assess the effects of season (March–June vs. July–October vs. November–February), sex, and SBTH on a suite of morphometric characters, i.e., exposed culmen, bill length from nares, tarsus, wing, and tail. In both cases, analyses were conducted **before** (MANOVA and ANOVAs) and **after** (MANCOVA and ANCOVAs) controlling for the effects of covariates, i.e., SPPNET (mist-netted, potential competitors in the immediate area), SPPISLA (island-wide, potential avian competitors), elevation (m), latitude (°N), and area (km²). Rationale for use of Bonferroni’s Sequential Adjustment of univariate results to corroborate multivariate analyses appears above in the “ELEVCOMP analytical rationale” section. The PCA on log-transformed characters was used to graphically visualize the extent to which discrete groups of individuals corresponded to categories based on season, sex, and SBTH.

“ELYUNQUE” (live-caught pearly-eyes from the nest-box study) analytical rationale—

After controlling for the effect of age, both univariate and multivariate approaches were undertaken to assess the effects of season and sex on morphometric variation in a suite of characters (length of exposed culmen, bill length from the nares, tarsus, wing, tail, body mass, and primary 9). Statistical analyses were performed on log-transformed data so that they corresponded to results from the PCA. The PCA was used to graphically visualize the extent to which discrete groups of individuals corresponded to categories based on season and sex. Rationale for use of Bonferroni’s Sequential Adjustment of univariate results to corroborate multivariate analyses appears above in the “ELEVCOMP analytical rationale” section.

“FIELDPET” (all other live-caught pearly-eyes from around the Caribbean) analytical rationale—

Both univariate and multivariate approaches were undertaken to assess the effects of season (March–October vs. November–February) and SBTH on morphometric

variation in the same set of morphometric characters named in “MUSEUM-PET” above. The rationale behind the use of Bonferroni’s Sequential Adjustment of univariate results to corroborate multivariate analyses appears under “ELEV-COMP analytical rationale.” The PCA on log-transformed characters was used to graphically visualize the extent to which discrete groups of individuals corresponded to categories based on season and SBTH.

Chapter-Specific Information

Chapter 1—

Species-specific information on the distribution and ecology of 224 species of landbirds inhabiting islands in the Greater Caribbean Basin rests on field data gathered over almost 30 years, augmented by information obtained from hundreds of published references. Nonetheless, pertinent information is incomplete for some species and must await the continued efforts of others in the field. Recent taxonomical classifications have altered the total number (224) of species under discussion but have not affected my major results and conclusions.

Chapter 2—

Background information on the supertramp theory was obtained through interviews with Dr. Jared Diamond and extensive literature reviews, and by literature searches of computerized biological databases. I used Citation Index to determine who was citing supertramp-related publications written by Jared Diamond, and to determine in what context and how broad an audience he had captured.

Species analyses—In my analyses of the West Indian avifauna, I incorporated the results of almost 30 years of research in the region (1976–2005). The information I present includes a synthesis of thousands of observations, numerous census results (e.g., Arendt 1990, 1995; Arendt et al. 1999; Faaborg and Arendt 1985; Faaborg et al. 2004), and unpublished data and field notes summarizing the distribution, abundance, and habitats of landbirds on several islands throughout the Caribbean. In addition, I spent almost 2 years reviewing standard reference texts (e.g., AOU 1998, Clements 2000), field guides (e.g., Bond 1979a, Evans 1990, Raffaele 1983, Raffaele et al. 1998), and the many publications on West Indian birds written by museum researchers, field ornithologists, regional experts, and early (1700–1800s) historians and naturalists (see Wiley 2000) to determine the range and habitat(s) of each species. Because most reference texts do not include habitat use, I continue to correspond with numerous local and regional authorities, many of whom have reviewed appendix 1 (see “Acknowledgments”).

Information on the distribution and ecology of 224 species of landbirds inhabiting islands in the Greater Caribbean Basin rests on field data gathered over almost 30 years.

Species-by-island matrix—I constructed a large matrix to delineate the range of each of the 224 resident landbirds, and to double-check the concordance of the various references, which often were contradictory to one another. My determination of the “true” range of each species was established by relying on (a) personal experience, (b) the most authoritative and complete reference texts, and (c) concurrence by several references for the current range of a given species. For example, many standard reference texts use broad statements, e.g., “throughout the Lesser Antilles...” Thus, I had to determine the specific and total number of islands on which each species is found.

Incidence functions—To construct Diamond’s (1975a) species incidence function curves for each species of Caribbean landbird, I conducted an extensive literature search to determine species richness (number of breeding species) for as many islands as possible for inclusion in the analyses. I obtained information pertaining to the number of breeding landbirds for 177 islands. To establish that the pearly-eye generally inhabits small islands, I consulted various reference texts, atlases, maps, and special reports to obtain the most recent estimations of the landmass (in square kilometers) of each of the 177 islands. It is noteworthy that the figures for total area (landmass) in appendix 2 differ greatly from one reference text to the next. Therefore, when possible, landmass figures in appendix 2 were taken from *World of Information* (1986).

While calculating “J” (the incidence of occurrence), I found that five categories (<12, 13 to 24, 25 to 36, 37 to 48, and >48 breeding species) best fit the data. Caribbean supertramps are found exclusively on small islands and, rarely, on larger islands in species-poor habitats. D-Tramps, besides colonizing small, species-poor islands in addition to large, species-rich islands, often are found on 80 to 100 percent of the islands in the various S-classes (determined by the number of breeding landbirds per island). C-Tramps are found on 40 to 60 percent of the islands in the different S-classes. B- and A-Tramps, although they do not generally colonize the small, species-poor islands, are often found on 40 to 60 percent of the larger, species-rich islands. High-S species are generally confined to 40 percent or fewer of the larger, species-rich islands.

Chapter 3—

To present a brief history of the origins, classification, and taxonomy of the pearly-eye and its congener, I performed numerous literature searches and visited several North American museums as well as the British Museum to speak with regional experts and to examine and measure specimens, including type specimens.

Chapter 4—

The background information for chapter 4 required years to compile. The historical accounts of the distribution and abundance of the pearly-eye presented in chapter 4 and appendix 3 are the results of numerous, extensive literature searches, personal observations, and correspondence with local and regional authorities. In gathering information on the distribution and ecology of mimids, numerous ornithological journals, reference texts, field guides, and life-history accounts were reviewed.

The sections on pearly-eye abundance in the Guánica Commonwealth Forest and Biosphere Reserve and abundance and density compensation on Mona Island were greatly enhanced by the timely completion of a comprehensive doctoral thesis written by Enrique Nicolás Hernández-Prieto (1993). Hernández-Prieto studied Mona's and Guánica's avian communities by using aural-visual census techniques. He compared avian species diversity and abundance, among many other parameters, on a year-round basis and over several years (1986–1990), and clearly demonstrated ecological release and density compensation on Mona Island.

Susúa pearly-eyed thrasher data were collected by Mark R. Ryan and his students from the University of Missouri-Columbia.

Census techniques—I obtained quantitative, regional distribution and abundance information on the pearly-eye by using a combination of three capture-recapture and standardized aural-visual census methods.

Mist-netting—Standardized mist-netting procedures followed Terborgh and Faaborg (1973): 16 contiguous nets, each made of 30- to 36-mm mesh and measuring 12 m long by 2.5 m high. Nets were operated from dawn to dusk for 3 consecutive days.

Variable-width line transects—I used Emlen's (1971) method to complement mist-net censuses. I established 1-km transects at least 100 m from edge in various habitats on several islands. By using this procedure, counts of all detections (visual and aural) were made to the limit of detectability. Counts were then tallied, and the count for each species was then multiplied by a conversion factor (coefficient of detectability), which represents the percentage of the population that is normally detected by these procedures.

Fixed-radius point counts—To compare results presented by others, I conducted fixed-radius point counts (Hutto et al. 1986) in Puerto Rico, Montserrat (Arendt 1990), and tiny Guana Island in the British Virgin

Islands (Arendt 1994). I established points every 100 m for a distance of 1 km in various habitats and at different elevations. All points were placed at least 50 m from edge. At each point, all detections (visual and aural) of birds ≤ 25 m were recorded. Difference in abundance results were tested statistically as recommended by Hutto et al. (1986) by using a Kruskal-Wallis one-way ANOVA on ranks procedure (e.g., chapter 4, table 4.3). In chapter 8, the abundance of six species of frugivorous species inhabiting three forest types (plantation, colorado, and cloud forest) was compared by using the mean number of detections per each of thirty 25-m-radius point counts per forest type. In total, 396 point counts (132 monthly counts \times 3 forest types) were conducted between January 1990 and December 2000—4 months (September through December 1989) following Hurricane Hugo were excluded to achieve a balanced design (12 months in each of 11 years). For comparisons of monthly averages between two paired years resulting in a significant difference between their medians, a Bonferroni all pair-wise multiple-comparison test was performed. Not only does the Bonferroni test for significant differences between all paired-year combinations, it also controls for the likelihood of committing Type I errors. That is, it minimizes the possibility of falsely declaring a significant difference between paired years simply by chance as a result of conducting several statistical comparisons (Rice 1989). Each Bonferroni test included 55 possible paired-year comparisons (1990 vs. 1991, 1990 vs. 1992...1999 vs. 2000).

Distance sampling (Buckland et al. 1993) was used to calculate the Centre Hills' (Montserrat) pearly-eyed thrasher population estimate reported in Arendt et al. (1999).

Categorical modeling—Categorical modeling was used to evaluate the ecological correlates related to the pearly-eye's distribution, abundance, and potential avian competitors. Categorical data modeling (Agresti 1990) is a statistical technique for fitting generalized linear models to categorical data, or data consisting of counts of observations classified according to one or more categories, e.g., contingency tables. The procedure involves fitting linear models to sample frequencies, and may be thought of as the analog of analysis-of-variance techniques for categorical dependent (response) variables.

Chapter 5—

For the analyses of the pearly-eye's nine morphological characters treated in chapter 5, thousands of measurements were taken by me, John Faaborg, and our associates on live birds from 34 islands from around the Caribbean (Arendt et al. 2004; see app. 2 for specific islands visited). In addition, I also made about

4,000 measurements on 584 specimens of pearly-eyes collected on some 40 islands and deposited in five North American museums (American and National Natural History Museums, Museum of Comparative Zoology at Harvard University, Natural Science Museum at Louisiana State University, including the Schwartz collection, and the Chicago Field Museum) and the British Museum at Tring. Owing to the complexity of the morphological data, a special, indepth statistical analysis was conducted by Dr. Michael R. Willig, a professor and biostatistical and environmental consultant at Texas Tech University, Lubbock, Texas. I extend to him my sincerest gratitude and indebtedness.

Measurement techniques follow those cited above as well as those presented in the North American Bird Banding Manual II prepared jointly by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service (Canadian Wildlife Service 1991).

Chapter 6—

Jolly-Seber Capture-Recapture Models (described below; see also Jolly [1965] and Seber [1982]) were used by Kate Dugger (Oregon State University, Corvallis) to analyze pearly-eyed thrasher survival data. The survival data used in the Jolly-Seber models include resident breeding adults (9 months or older) at thrasher nest boxes, captured between 1979 and 1991, and adult individuals of both sexes captured in mist nets periodically throughout their lives, but not included in the nest-box study. Dugger then compared survival results from the rain-forest thrasher population to those of a dry-forest thrasher population in southwestern Puerto Rico (see Faaborg and Arendt 1995).

Jolly-Seber capture-recapture models—The program JOLLY (ver. 01/24/91) offers five capture-recapture models for estimating rates of avian survival, each with its own unique set of parameters and underlying assumptions. All five models were explored to evaluate the “goodness of fit” of each model to the thrasher data (Pollock et al. 1985). The best fit was generated by model A, the standard Jolly-Seber model for open populations assuming births, deaths, emigration, and immigration in the sampled population. The close fit of model A to the thrasher survival data is evidenced by very small coefficients of variation (standard error divided by the square root of the mean) and the standard errors of the annual survival estimates. Both parameters suggest that these data meet all of the underlying assumptions of model A.

**Four thousand
measurements
were made on
584 specimens of
pearly-eyes collected
on some 40 islands.**

Nest-box observations—Once nestlings had fledged, nest boxes were visited on alternate days to monitor subsequent nestings. During such visits, it was possible to determine the location of postfledged young by listening for their food-begging calls, and to note the number of days since fledging, their distance from the nest box, and other site-related information, including behavior. Within the first 17 years of the study, 648 observations (about 50 per year) were made (some from observation blinds) involving recently-fledged young in the vicinity of their nest boxes. Length of parental care for a brood once fledged was determined, especially in relation to subsequent nesting efforts by the adults.

Biotelemetry studies—Over the course of the study, 24 fledglings were radio tagged: 5 in 1982, 11 in 1987, 6 in 1990, and 2 in 2000. Nestlings were fitted with low-drain, one-stage transmitters weighing 4 to 6 g. All but the 2000 season transmitters, which were collar mounts, were “back-pack” mounts (fig. 1.20). Transmitters plus harnesses averaged 5 percent ($SE = 0.34$; range: 3.3–7.7 percent) of the fledgling’s body mass (avg. = 104.4 g; $SE = 2.88$; range: 86.4–118 g). In 1987, an interscapular glue-mount technique was tested, but adults removed the transmitters and carried them 20 to 30 m from the nest box before discarding them.



Figure 1.20—A radioed pearly-eye nestling showing the trailing antenna and harness-mount transmitter design. Dummy transmitters were placed on nestlings about a week before fledging so the young could habituate to them, and also because adults occasionally removed both dummy and actual transmitters and carried them as far as 30 m from the nest boxes before discarding them. Although the transmitter shown here is still obviously burdensome, this nestling will reach its asymptotic body mass of about 100 g before fledging, at which time the transmitter, which weighs less than 5 g will be at the recommended ≤ 5 percent of the thrasher’s body mass.

Radio-tagged fledglings were tracked by using hand-held receiving systems and folding 3-element Yagi[®] antennas (from Wildlife Materials, Inc.). Encounters of radio-tagged young were recorded in field notebooks and on forest maps. An encounter consisted of either visual contact or electronic location (formation of minimum-area convex polygons) of radio-tagged fledglings via triangulation (for descriptions and evaluations of this technique, see Hupp and Ratti 1983, Kenwood 1987, Lee et al. 1985). Thrasher fledglings were tracked by following them on foot or by monitoring them from elevated sites, which included towers and vantage points on ridgetops throughout the forest (see Kenwood 1987 for further information on the telemetry techniques used in this study).

Recaptures and sightings of banded thrasher dispersers—To supplement the observational and biotelemetry studies, various analyses were performed on the dispersal data obtained from recaptures of banded pearly-eyes and sightings of banded thrasher dispersers.

Chapter 7—

Most of the data collected for the various topics covered in chapter 7 (return rates, site and mate tenacity, and numerous reproductive parameters) were collected as part of the nest-box study outlined above, and occasionally augmented by supplemental data from other areas of the forest and other islands. Under the discussion of the various egg fates, undoubtedly some addled (designated “infertile”) eggs contained embryos too small for detection without a microscope. Most embryos die at early stages of development (Beissinger et al. 2005).

Data analyses and their graphic presentations (with the exception of two graphs, explained below) are straightforward and self-explanatory. For example, I compared adult breeder return rates by using the parametric Student’s t-test when the assumptions of normality and equal variance were met. Otherwise, I used the nonparametric Mann-Whitney rank sum test (M-W R S). The two exceptions involve figures 7.4 and 7.6 (both include dates of egg deposition). Data were analyzed by using Julian dates (based on a 365-day calendar) for egg deposition, and then converted to the more conventional 12 months and 28 to 31 days, which are depicted on the ordinates in the two graphs.

Chapter 8—

The only methods used in chapter 8, other than literature searches and reliance on personal experience and fieldwork, involved the previously described audio-visual techniques used in conducting monthly point counts in three forest types within the Luquillo Experimental Forest.

The present-day distribution of West Indian birds is the result of regional geomorphic plate tectonics, climate, natural and human-induced vegetational changes.

Distribution of West Indian Landbirds

For centuries, ornithologists and ecologists have been fascinated with the distribution of landbirds among the literally thousands of islands and cays that make up the West Indian avifaunal region (boundary delineated by Bond 1934). How does one go about studying such an inviting, yet so complex and multifaceted, subject? First, we must identify the natural and anthropic mechanisms that influence insular bird distributions.

The present-day distribution of West Indian birds is the result of regional geomorphic plate tectonics, climate, natural and human-induced vegetational changes, in addition to all of the consequential selective pressures, physiological changes, and mutations within avian taxa that have taken place over several millennia as a result of these environmental and ecological influences. The processes that govern these events and organismic changes are dynamic by nature. Thus, landbird distributions have varied greatly over time and will continue to change at an even more accelerated pace in the future, commensurate with regional development, the ever-changing global environment, and the dynamic state of the diverse and unique ecosystems found among Caribbean islands.

In addition to the ultimate mechanisms shaping West Indian bird distributions, at least some of the contemporary distributions can be attributed to the varied, and often distinctive, life-history strategies previously recognized by Diamond (1974).

Subjectivity of West Indian Avifaunal Analyses

By design, the analysis of the West Indian avifauna following Diamond's classification scheme is subjective. Thus, the reader may question the placement of some of the species into their designated categories. Although someone may rightfully reassign some species to other categories, the overall results and conclusions will be little affected. Moreover, although I believe that some additional species may be considered supertramps, e.g., thick-billed vireo (*Vireo crassirostris*) and Caribbean elaenia (*Elaenia martinica*), their limited distributions and other species-specific characteristics suggest to me that they do not fit the supertramp mold as well as they might and, therefore, they were placed in other more appropriate categories. Even if more Caribbean supertramps are designated, it is highly unlikely that they will compete with the pearly-eyed thrasher (*Margarops fuscatus*) for the title of being the region's premier example.

Chapter 2: Supertramps in the West Indian Avifauna

What Is an Avian Supertramp?

After studying the distributional patterns of South Pacific birds (Diamond 1970a, 1970b; Diamond 1972), Jared M. Diamond (1974) identified two distinct and mutually exclusive competitive strategies in insular landbirds: colonizers and competitors. He noted that certain species, which he coined “tramp species,” are exceptional colonizers but poor competitors. The epitome of tramp species is the supertramp, i.e., a species that has developed superior colonizing traits at the expense of competitive characters. At the other extreme is what Diamond termed a high-S species, i.e., a species that has evolved strong competitive traits to establish itself and maintain its place in species-rich avian communities. Good competitors are generally K-selected,¹ sedentary, habitat specialists with limited geographic and ecological ranges. They are typically endemic and confined to larger, species-rich islands. In contrast, superior colonizers are generally r-selected² species that have evolved good dispersal abilities and a high reproductive potential featuring rapid and extended breeding and large clutch sizes (for further discussion, see Horn and Rubenstein 1986). Moreover, superior colonizers have the ability to fill vacant or underexploited niches (MacArthur 1968) and are capable of undergoing marked shifts in altitudinal range, habitat type, diet, foraging techniques, and morphology (Baldwin 1953; Diamond 1970a, 1978, 1979; Diamond and Case 1986; Diamond and Marshall 1977a, 1977b; Diamond et al. 1989; Grant 1972a, 1986; Keast 1970; MacArthur et al. 1972; Terborgh et al. 1978; Traylor 1950; Voous 1955). This ecological and morphological plasticity permits successful establishment and rapid population growth by colonizers in areas less suitable, and thus more sparsely populated by the more competitive species already established on an island (Abbott 1974a, 1981; Diamond 1970b). Having evolved a superior colonizing ability at the expense of a strong competitive ability, however, tramps are forced out of species-rich communities by more specialized K-selected competitors and diffuse (interspecific) competition (Schoener 1982). As a result, the extreme supertramps become vagile (highly mobile) species that are typically confined to small, remote, or recently disturbed islands or habitats with few competing species (Diamond 1974, 1975a, 1982; Diamond and Marshall 1977a, 1977b).

¹K-selected species are those with a superior competitive ability in stable predictable environments, in which rapid population growth is unimportant as the population is maintained at or near the carrying capacity of the habitat (Lincoln et al. 1983).

²The r-selected species are characteristic of variable or unpredictable environments; typically show rapid development, high innate capacity for increase (r), early reproduction, and small body size (Lincoln et al. 1983).

“Tramp species” are exceptional colonizers but poor competitors. The epitome of tramp species is the supertramp, i.e., a species that has developed superior colonizing traits at the expense of competitive characters.

Incidence Functions

To further quantify his theory of mutually exclusive competitive strategies in insular birds, while studying bird distribution in the Bismarck Archipelago in New Guinea, Diamond (1975a) noted differences in how the incidence of occurrence (J) of a particular species on an island was related to the number of breeding landbird species (S) on that island. He defined five species types based on their life-history traits, dispersal capabilities, and reproductive potentials. He placed each species in one of six distinct categories according to the shape of its incidence function: competitive high- S species and five categories of more generalist, K - and r -selected tramp species (A-tramps, B-tramps, C-tramps, D-tramps, and supertramps). A-tramps are most similar to high- S species, and thus tend to be K -selected specialists confined to very few islands, whereas D-tramps are most akin to supertramps, the champion r -selected opportunists.

Intertaxonomic Analogues of Avian Tramps

The discovery of tramp species among many nonavian taxa adds credence to Diamond's original concept. Tramp species have been described among terrestrial arthropods (Green 1979), land snails (Bauer and Bengtsson 1987), fresh-water invertebrates (Ball and Glucksman 1978), marine invertebrates (Green 1979), and zooplankton (Hayward and McGowan 1979). However, in communities of sessile marine organisms, especially where predator-prey relations appear to be more important than interspecific competition in determining colonization success and community structure, the tramp concept is less applicable (Keough 1984). Tramp species have been identified also in reptiles (Case et al. 1979) and mammals (Glazier 1980). All of these studies show that the traits of a tramp species include (1) superior dispersal ability, (2) high degree of plasticity and ability to broaden their ecological niches, (3) regional abundance, (4) competitive exclusion by superior resource exploiters, (5) the ability to inhabit marginal habitats, and (6) high reproductive potential.

The concept of tramp species has even been applied to plants. K -selected, late-successional plants are analogous to Diamond's competitive high- S species. Ruderals ("weedy" species that are often r -selected exotics confined to marginal habitats) are analogous to Diamond's supertramps. Fugitive species (often native pioneer species with life-history traits and dispersal abilities intermediate between those of high- S and supertramp species) were considered analogous to Diamond's A- through D-tramp species (Platt 1975). From a theoretical perspective, three primary reproductive strategies in plants are equated to the r - and K -selection continuum presented by MacArthur and Wilson (1967) and expanded by Pianka

(1970). C (competition)-selected plants have evolved to be highly competitive in productive, relatively undisturbed areas. S (stress)-selected plants, although having reduced vegetative and reproductive vigor, have evolved to endure continuously unproductive conditions arising from environmental stress, severe resource depletion by the vegetation, or the combined effect of the two. R (Ruderal)-selected plants are generally short-lived, prolific species that have evolved in severely disturbed but potentially productive environments (Grime 1977).

Species-Area Curves and Incidence Functions of West Indian Birds

A linear logarithmic relation exists between the numbers of most species of flora and fauna and island size (area). In general, island species' numbers represent an equilibrium between extinction and immigration, larger islands reaching equilibrium at more species because of larger populations, lower extinction rates, and greater habitat diversity (MacArthur and Wilson 1967, Schoener 1976). West Indian islands and their respective avifaunal populations (Slud 1976) are exemplary of this well-known species-area relationship (fig. 2.1). However, a recent study (Ricklefs and Lovette 1999) showed that bird species richness in the Lesser Antilles responds independently to both habitat diversity and area. These authors concluded that the species-area relationship is most likely generated by island-size-dependent extinction. Because many West Indian islands are small, the number of breeding landbird species on most islands is consequentially limited (fig. 2.2). Only on the larger islands of the Greater Antilles are there more than 50 species of resident landbirds.

Comparison of Pacific and Caribbean Island Landbirds

To illustrate the use of incidence functions in classifying island birds in terms of their competitive strategies, and to compare Pacific birds with Caribbean birds in terms of Diamond's classification scheme, I offer a classification of West Indian landbirds (Falconiformes, and Columbiformes through Passeriformes) (app. 1). Following the American Ornithologists' Union Checklist (AOU 1998), I categorized the region's 224³ landbird species into seven categories: Diamond's original six, plus an additional category of anomalous (introduced or aberrant) species, based on their (a) incidence of occurrence on islands with varying numbers of breeding species, (b) degree of endemism, (c) dispersal capabilities, and (d) habitat use (table 2.1 and app. 1).

³Although the total has changed following recent taxonomical revisions, the overall results and conclusions from the original analyses have not been significantly affected. Therefore, some genera and species changes have not been included in the text, tables, and figures.

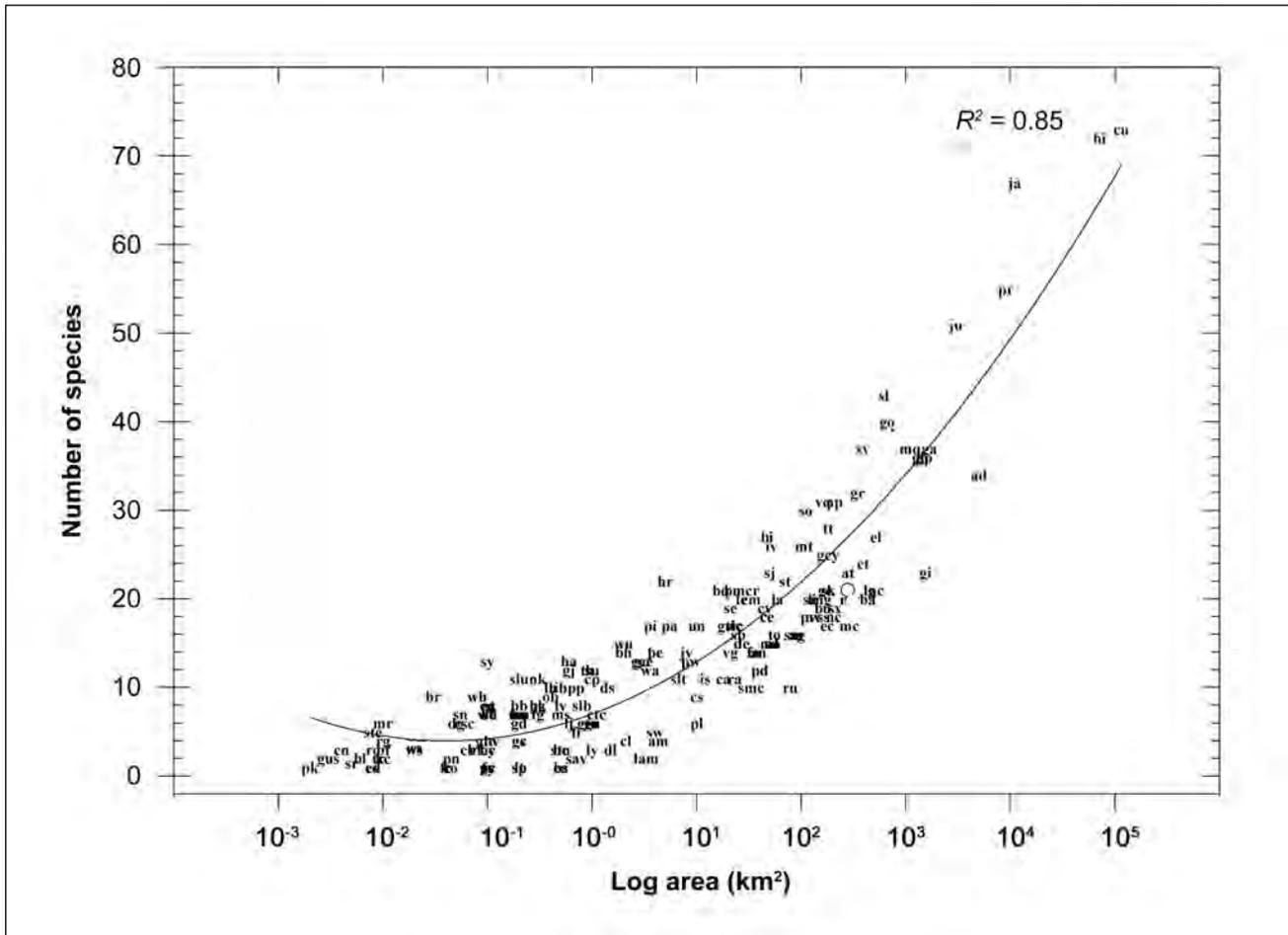


Figure 2.1—Species-area curve for West Indian landbirds. Note that several Bahamian islands fall well below the curve, most likely because they, like all of the islands in the Bahamian Archipelago, are very flat, with few habitat types (discussed in chapter 4). Island codes: ac (Acklins) ad (Andros) ag (Anguilla) am (Big Ambergris Cay) an (Anegada) at (Antigua) ba (Barbados) bb (Buck-BVI*) bc (Booby Cay) be (Beef) bf (Big Flat Cay) bh (Big Hans-Lollick) bi (Beata Island) bk (Buck-US) bl (Bellamy Cay) bm (Biminis) bq (Bequia) br (Bird Rock) bs (Big Sand Cay) bu (Barbuda) bv (Bovoni Cay) by (Bay Cay) ca (Catalina) cb (Cockroach-BVI) cc (Culebra) cg (Congo Cay) ci (Crooked) ck (Cockroach-USVI) cl (Castle) cm (Cayman Brac) cn (Cinnamon Cay) co (Cocoloba Cay) cp (Cooper) cr (Carriacou) cs (Cay Sal) csc (Cas Cay) ct (Cat) ctc (Cotton Cay) cu (Cuba) cv (Carval) cy (Cayemites) dc (Dutch Cap) de (la Desirade) dg (Dog) dl (Dellis Cay) do (Dominica) ds (Desecheo) dt (Dead Chest) ea (East Cay) ec (East Caicos) ed (East Seal Dog) el (Eleuthera) es (East Six Hill) eu (Eustatia) fc (French Cap) fg (Ft. George) fi (Fish Cay) fo (Fortune) fr (French Cay) ga (Great Abaco) gb (Grand Bahama) gbv (Green Cay-BVI) gc (Guana Cay) gce (Great Camanoe) gcy (Grand Cayman) gd (George Dog) ge (Great Exuma) gg (Great Dog) gi (Great Inagua) gj (Great St. James) gn (Ginger) go (Gonave) gp (Guadeloupe) gr (Grenada) gs (Grass Cay) gt (Grand Turk) gto (Great Tobago) gu (Guana) gus (Green Cay (USVI) gy (Gibbs Cay) ha (Hassel) hc (Henley Cay) hi (Hispaniola) hr (Harbour) ib (Inner Brass Cay) is (Îsles les Saintes) iv (Île-à-vache) ja (Jamaica) ju (Juventud) jv (Jost Van Dyke) kc (Kalkun Cay) la (Little Abaco) lam (Little Ambergris Cay) lc (Little Cayman) le (Little Exuma) lg (Long) lh (Little Hans-Lollick) li (Little Inagua) lj (Little Jost Van) lm (Little Camanoe) lt (Long Cay-T) lv (Lovango Cay) ly (Long Cay-C) mc (Middle Caicos) mg (Marie Galante) mn (Mingo Cay) mo (Mona) mq (Martinique) mr (Marina Cay) ms (Mosquito) mt (Montserrat) my (Mayaguana) nc (North Caicos) nk (Necker) no (Norman) np (New Providence) nv (Nevis) ob (Outer Brass Cay) pa (Parrot Cay) pc (Pear Cay) pd (Providencia) pe (Peter) pi (Pine Cay) pk (Perkins Cay) pl (Plana Cay) pn (Penniston Cay) pp (Prickly Pear) pr (Puerto Rico) pt (Patricia Cay) pv (Providenciales) pw (Plana Cay West) ra (Ragged Islands) rg (Ramgoat Cay) ro (Rotto Cay) ru (Rum Cay) sa (Saba Cay) sav (Savanna) sb (St. Barthelemy) sd (San Andrés) se (St. Eustatius) si (South Caicos) sj (St. John) sk (St. Kitts) sl (St. Lucia) slb (Salt Cay-BVI) slt (Salt Cay-T) slu (Salt Cay-USVI) sm (St. Martin) smc (Samana Cay) sn (Sandy Cay) so (Saona) sp (Sheep Cay) sr (Shark Rock) ss (San Salvador) st (St. Thomas) ste (Steven Cay) stu (Stubbs Cay) su (Scrub) sv (St. Vincent) sw (Swan) sx (St. Croix) sy (Saba Cay) th (Thatch Cay) to (Tortola) tr (Trunk Cay) tt (Tortue) tu (Turtle-dove Cay) un (Union) vg (Virgin Gorda) vq (Vieques) wa (Water Cay-C) wc (West Caicos) wd (West Dog) we (West Cay (USVI) wh (Whistling Cay) ws (West Seal Dog) wu (Water Cay-USVI) (*See app. 2 for Island political affiliates).

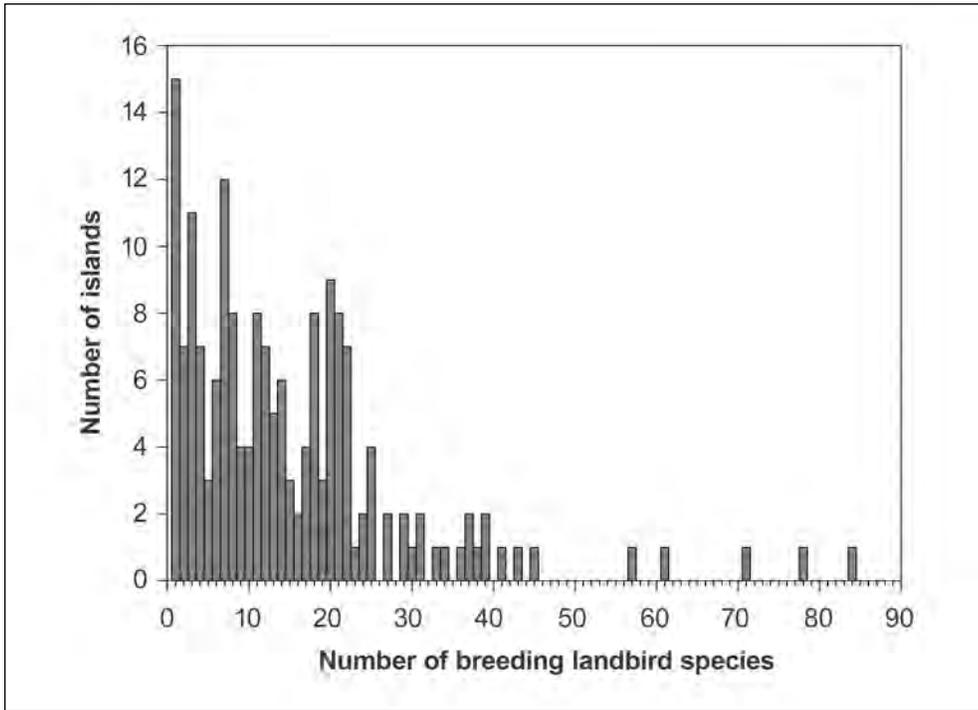


Figure 2.2—Frequency distributions of islands compared to the number of breeding landbird species on each. The high percentage of islands with fewer than five species reflects the large number of islets and cays included in the analysis. Several small- to medium-size islands in the Lesser Antilles account for the range from 10 to 25 resident breeding species. All five islands with more than 50 permanent resident species are among the larger islands found in the Greater Antilles.

Although West Indian birds reflect incidences of occurrence and distributional patterns similar to those in the Bismarck Archipelago (table 2.1), they show two striking differences at both extremes of the classification scheme. About one-third (37 percent) of the birds in the Bismarck Archipelago are high-S species (fig. 2.3), whereas more than half (59 percent) of the West Indian birds are high-S species, possibly because of the two archipelagoes’ disparate frequency distributions of island areas (J. Diamond 1994, in litt.). The Bismarck Archipelago has one giant island (New Britain) that is five times larger than any of the other islands. Moreover, New Ireland, the second largest island, is several times the area of the next largest island, followed by a graded distribution of islands from 2590 km² downwards. The West Indies differs in having several large islands. At the opposite extreme, whereas 9 percent of the Bismarck birds are supertramps, only one species (<1 percent) of the West Indian birds merits supertramp status (fig. 2.3). It is noteworthy, however, that after this analysis was completed and, following the passage of two severe hurricanes that greatly affected the Caribbean, the explosive and invasive nature of the Caribbean elaeenia (*Elaenia martinica*) observed on several islands and among several forest types within islands makes it a strong contender for supertramp status (see also Voous 1955).

Thirty-seven percent of the birds in the Bismarck Archipelago are high-S species, whereas more than half (59 percent) of the West Indian birds are high-S species.

Table 2.1—Distribution of birds in the West Indian and Bismarck Archipelagos following Diamond’s competitive strategy classification scheme

Incidence function category	Species	Islands	Degree of endemism		
			None	Subspecies	Species
			<i>Number</i>		
High-S	132 (52) ^a	1–6 (1–5)	0 (9)	50 (14)	82 (8)
A-Tramp	22 (26)	2–11 (3–9)	0 (8)	19 (14)	3 (1)
B-Tramp	19 (17)	4–14 (10–14)	0 (4)	15 (12)	4 (0)
C-Tramp	29 (19)	10–73 (15–19)	0 (8)	26 (10)	3 (0)
D-Tramp	16 (14)	23–148 (20–35)	3 (9)	13 (5)	3 (0)
Supertramp	1 (13)	80+ (2–33)	0 (2)	1 (8)	0 (1)
Anomalous ^b	5 (0)	1–5 (0)	0 (0)	5 (0)	0 (0)
Total	224 (141)^c	177 (50)	31 (40)	29 (63)	95 (10)

^aParenthetical numbers are from Diamond (1975a).

^bAnomalous species are those thought to be introduced by man, relict species that did not radiate following isolation resulting from past, dramatic climatic changes, or mainland species naturally occurring on landbridge or extralimital islands near continental source populations.

^cThe total number of species in columns 4 through 6 is 113 because an additional 28 species (for the correct total of 141) were categorized as “Semispecies” (allospecies of a superspecies) in Diamond’s analysis (1975a: table 1), but not treated in this comparison.

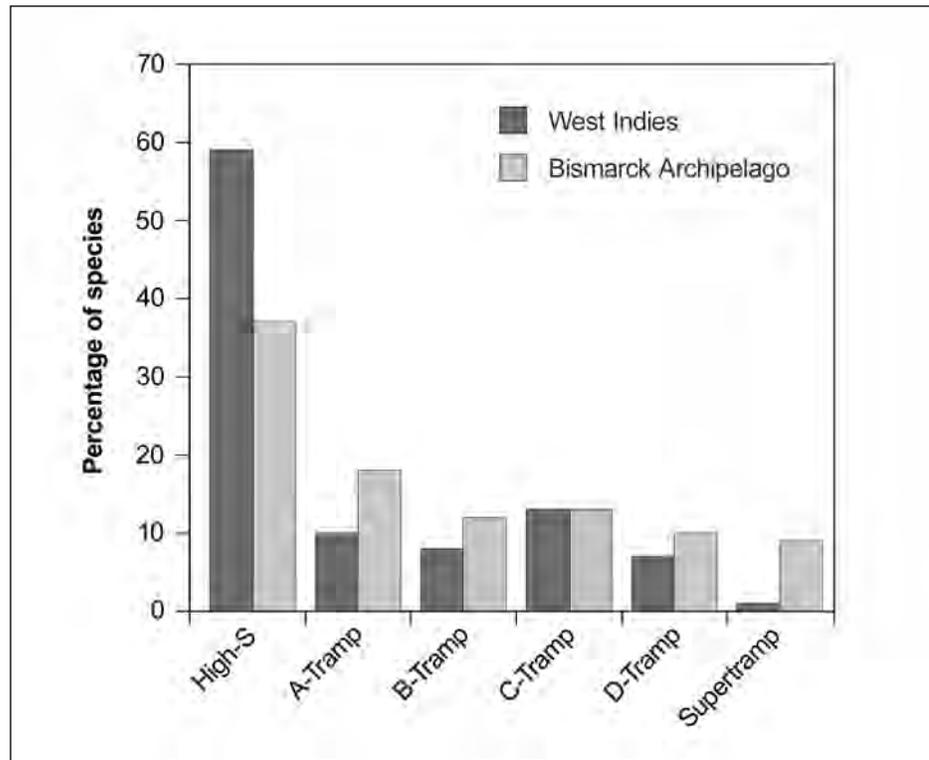


Figure 2.3—Comparison of West Indian birds with those of the Bismarck Archipelago by following Diamond’s (1975) competitive strategy scheme. Fifty Pacific islands and 141 avian species were included in Diamond’s analysis, whereas 177 Caribbean islands and 224 species were treated in this analysis. The y-axis constitutes the number of species in each of the six categories presented as a percentage of the total number of species. The two most obvious differences between these widely separated geographical regions are the disparate numbers of supertramps and the greater extent of endemism (reflected by the large number of High-S species) attained in the West Indies.

The above-noted differences between the Pacific and Caribbean landbird avifauna notwithstanding, the forms of the various incidence function curves for the 224 West Indian species combined are quite similar to those obtained by Diamond (1975a) for Pacific landbirds (fig. 2.4). As predicted by the supertramp theory, with one exception, the Caribbean’s single supertramp species is found on only the smallest species-poor islands in which suitable habitat is found, but its occurrence drops off precipitously as island size and species-richness increase. Although found on the relatively large island of Puerto Rico, the pearly-eyed thrasher (*Margarops fuscatus*) abounds only in species-poor habitats. The Caribbean’s wide ranging C- and D-tramps are found on 40 to 100 percent of all islands, regardless of the number of breeders. In contrast, B- and A-tramps, although occurring on all of the larger islands, are absent from smaller islands with fewer than 25 resident landbird species. High-S species are confined to the largest islands with more than 48 resident landbird species.

Species-Specific Incidence Functions

To further explain contemporary species’ distributions, incidence function curves for each of the 224 resident landbird species were plotted (fig. 2.5a–d). Criteria used to classify each species into Diamond’s six colonization categories included elevation, habitat and vegetation type, and structure (app. 1). It is not obvious

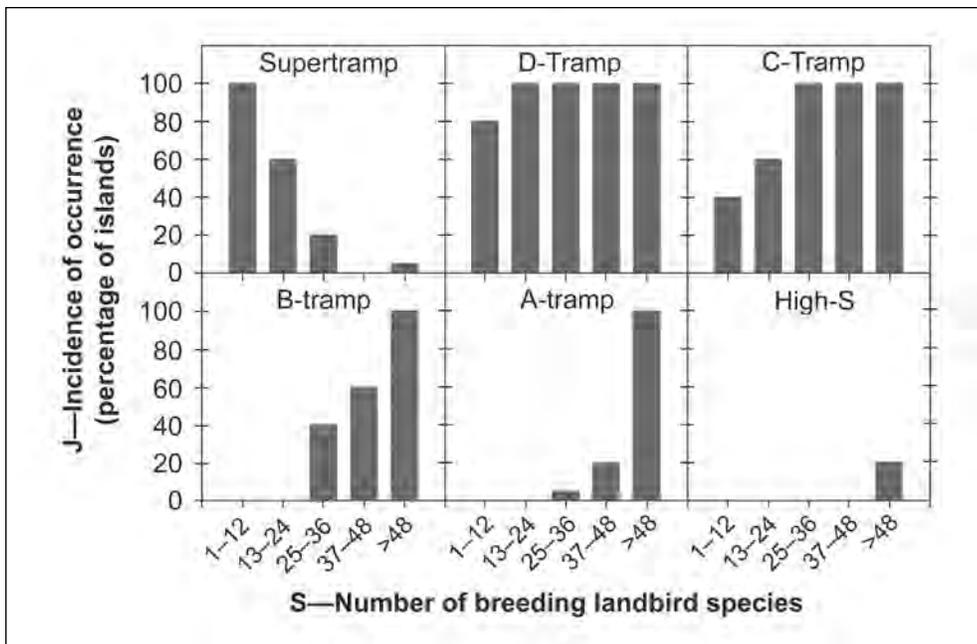


Figure 2.4—Incidence functions for all 224 species of West Indian landbirds combined. “J” is the incidence of occurrence, or the proportion (percentage) of islands on which a species is found plotted against “S,” the number of breeding landbirds per island (see “Study Area and Methods” for a more indepth description).

from the illustrations that there are any clearly defined patterns, e.g., certain taxa, range of body sizes, or ecological groups, that help to explain today's species' distributions within a competition vs. colonization context. For example, not all wide-ranging birds (colonizers) are large, highly mobile species such as raptors and pigeons found at widely ranging elevations or among several habitat types. Likewise, at the opposite extreme, not all high-S species (competitors) are limited to a single taxon or habitat type. Examples of species ranging from very small to very large occur at all elevations and among most habitats and within several vegetation associations, and thus are found in all of the six distribution categories (fig. 2.5a–d). As a further example, whereas some hummingbirds are high-S species confined to large, species-rich islands inhabiting single (or very few) habitats, others are C- and D-tramps found among several habitats along a wide range of island-sizes and geographical expanse. At the other extreme, although some large raptors are found over much of the region on islands of all sizes and among many habitats, others are high-S, habitat specialists confined to single islands and few habitats. Thus, it is safer to conclude that distribution, in all respects (e.g., geographical and ecological), is highly species dependent. Indeed, resulting from recent advances in molecular biology, by determining levels of mitochondrial DNA (mtDNA) divergence among populations of island birds, researchers (e.g., Lovette et al. 1999) are now able to trace not only the source islands for the various species but can also ascertain the chronological sequence of colonization for each species. They are finding that insular bird communities are composed of species with different invasion histories, and that community composition changes repeatedly over time. In effect, they are using a new tool to corroborate what ecologists and ornithologists have known for many years through direct observation.

Competitors Versus Colonizers Among Taxonomic Groups

Although the incidence function curves for individual species are informative and helpful when comparing one or more species, it is difficult to see how the species are distributed among the seven competitive strategy categories and to discover possible trends. To facilitate the interpretation and evaluation of the individual species-specific incidence function curves, West Indian landbirds were placed in 32 broad taxonomic groups (hawks and columbids through finches) and sorted into Diamond's six competitive strategy categories (table 2.2). Not obvious from the illustrations, but immediately evident from the table, is the fact that most high-S through B-tramp species confined to single or few islands and one or

(text continues on page 47)

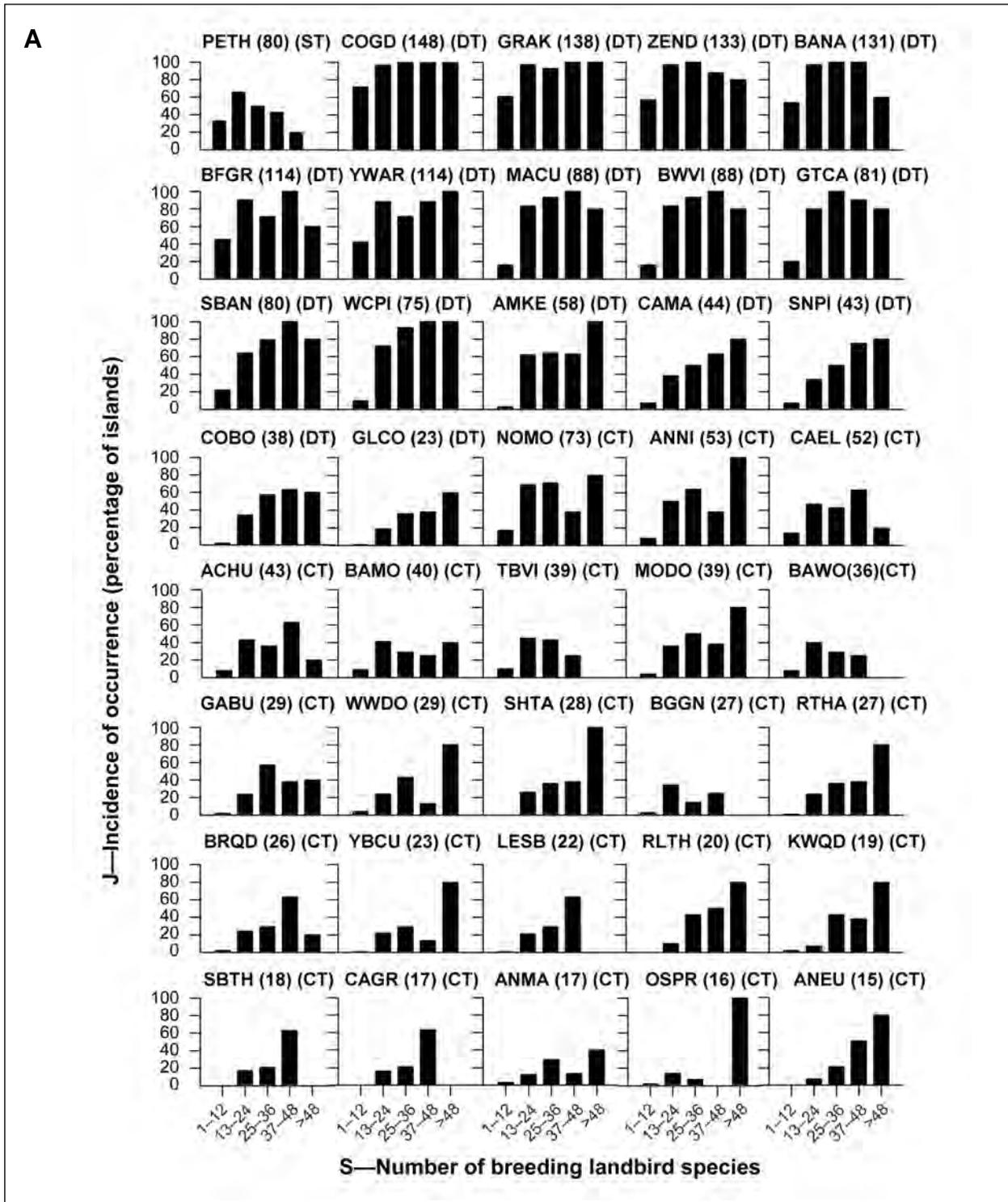


Figure 2.5 (A–D)—Incidence functions (J) for individual species of West Indian landbirds. Species names are coded (see app. 1). The number of islands on which each species is found is in parentheses following the species code. Histograms are arranged sequentially into seven categories (including anomalous species) from extreme colonizers to extreme competitors: Supertramps (ST), D-Tramps (DT), C-Tramps (CT), B-Tramps (BT), A-Tramps (AT), and High-S (HS) species. Histograms of anomalous species difficult to classify are included for illustrative purposes. Some High-S species such as the Hispaniolan endemics (e.g., RIHA, HIPT, GCPT, and PALM) appear to be better candidates for the A- and B-Tramp categories. This is due to their occurrence on nearby satellite islands (e.g., Saona, Beata, Cayemites, Ile-à-vache, Tortue, and Gonâve). Satellite islands act as land-bridge islands, thus confounding the classification results.

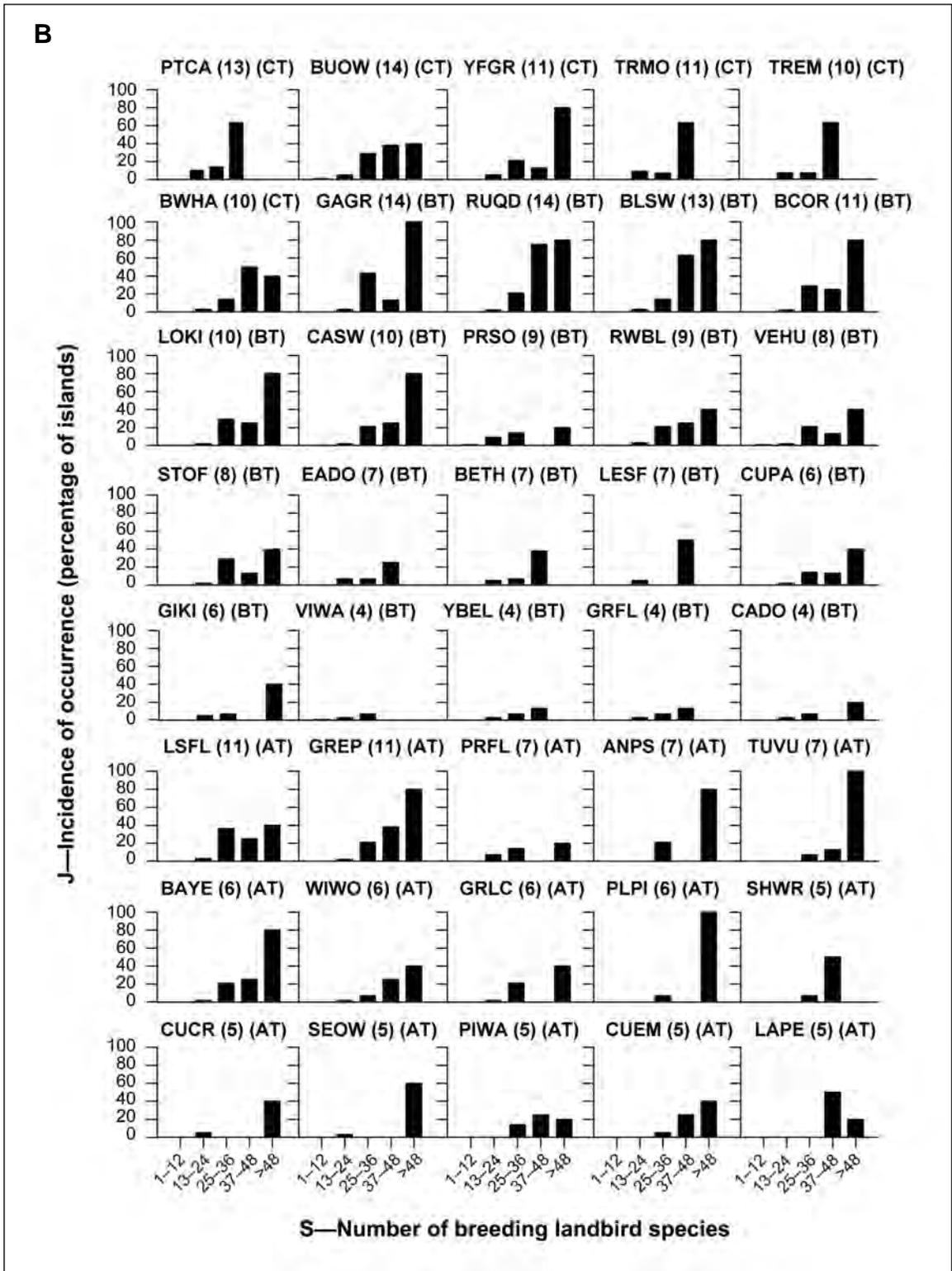


Figure 2.5—Incidence functions (J) for individual species of West Indian landbirds (continued).

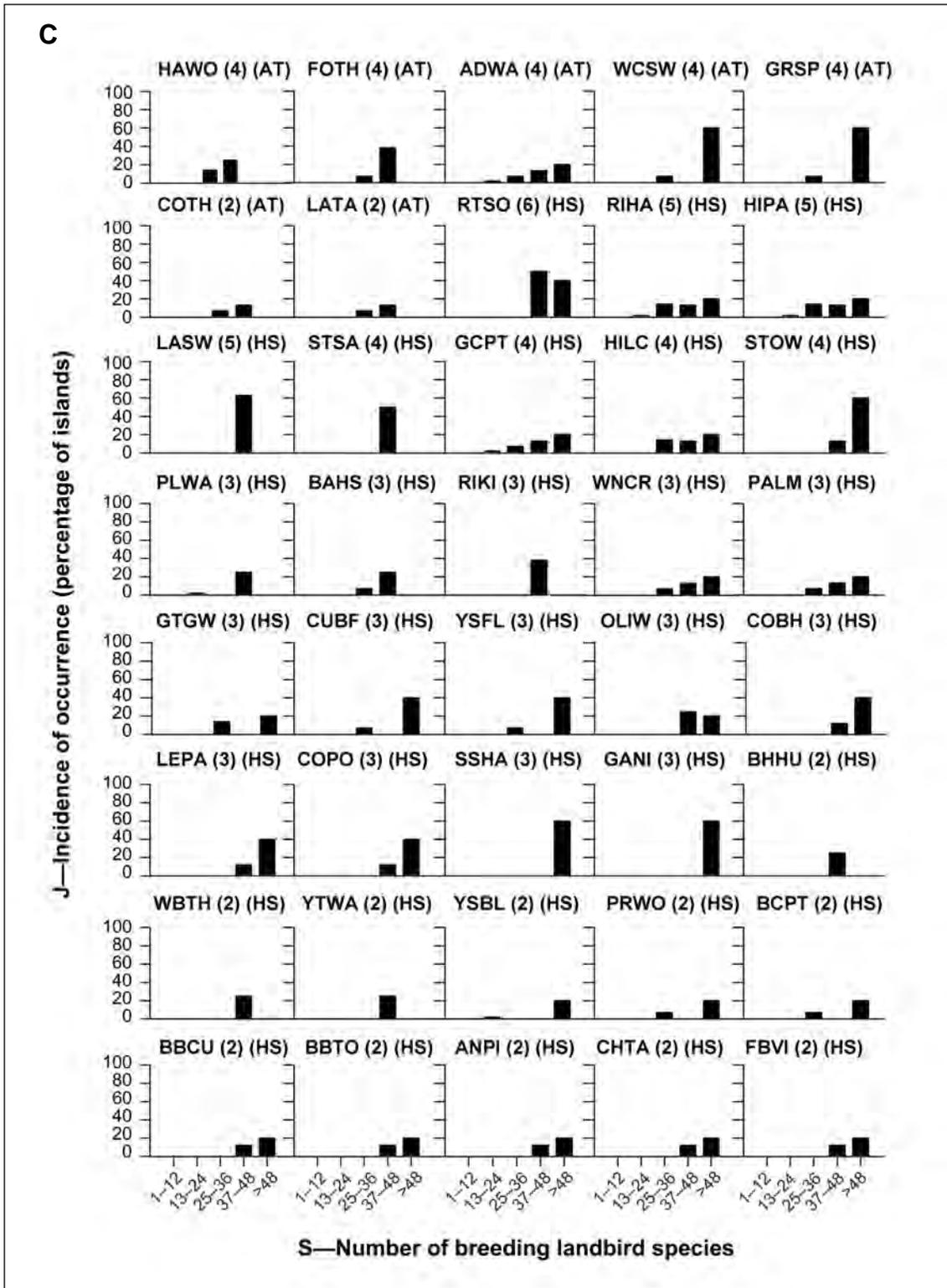


Figure 2.5—Incidence functions (J) for individual species of West Indian landbirds (continued).

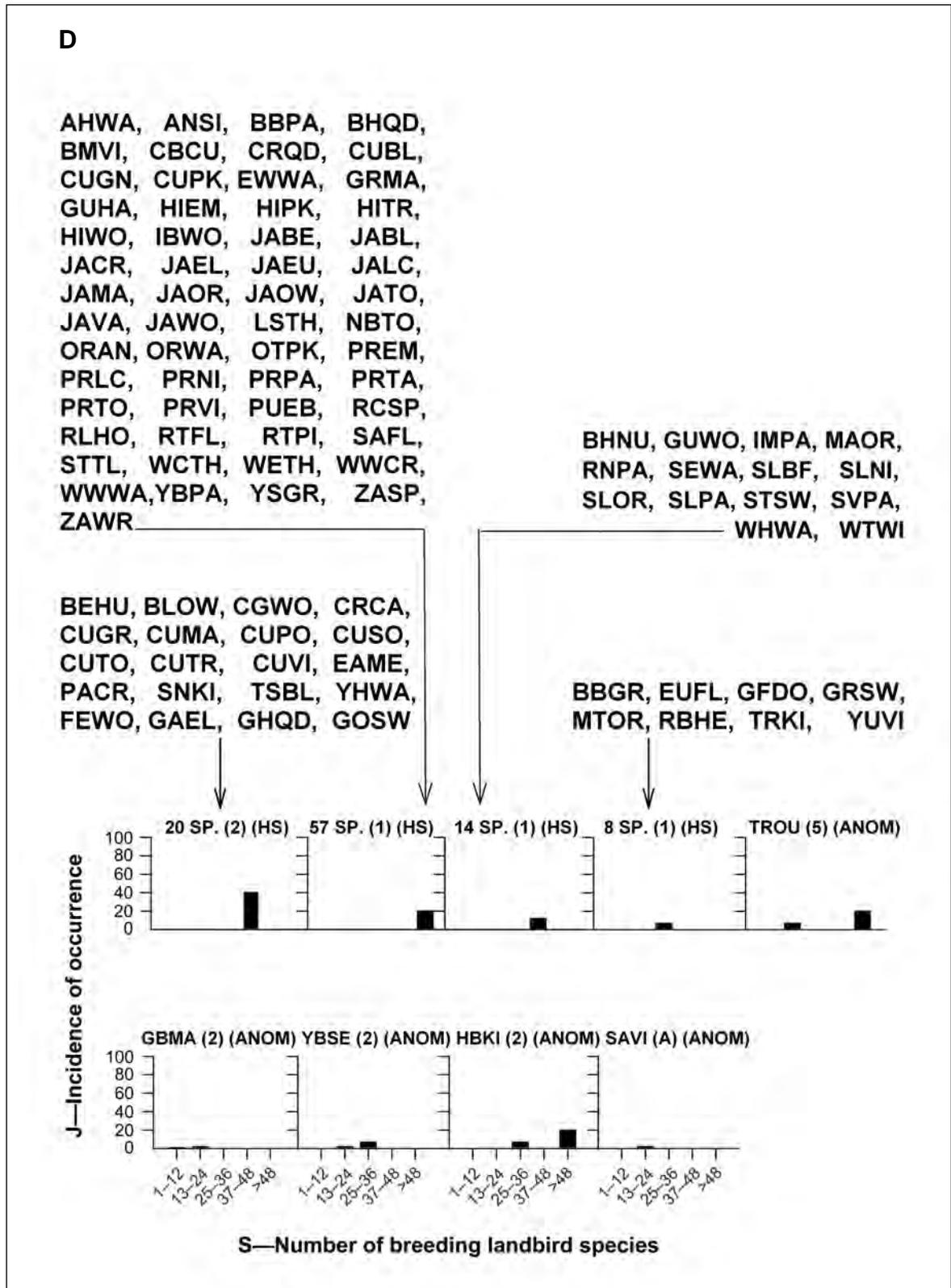


Figure 2.5—Incidence functions (J) for individual species of West Indian landbirds (continued).

Table 2.2—Generalized taxonomic groups of West Indian birds following Diamond’s (1975a) competitive strategy classification scheme (in order of decreasing competitiveness)

Taxonomic group	Number of species in respective categories						
	High-S	A-Tramp	B-Tramp	C-Tramp	D-Tramp	Supertramp	Anomalous ^a
Competitors:							
Parrots	11		1				
Woodpeckers	9	2					
Nightjars	6			1			
Todies	5						
Crows	3	1					
Trogons	2						
Becards	1						
Caracaras	1						
Honeycreepers	1						
Kingfishers	1						
Nuthatches	1						
Palmchats	1						
Wrens	1	1					
Gnatcatchers	1			1			
Kites	1						1
Vultures		1					
Colonizers:							
Tanagers	5	1		2			
Thrushes	5	2	1	1			
Swifts	3	2	1				
Finches	12	1		3	1		1
Warblers	11	3	1		1		
Blackbirds	9		3	1	1		1
Hummingbirds	8	1	1	4	1		1
Flycatchers	6	4	6	1	1		
Vireos	6			1	1		1
Cuckoos	5	1		1	2		
Owls	4	1	1	1	1		
Hawks	4			3	1		
Swallows	3		1		1		
Pigeons	5	1	3	4	4		
Bananaquits					1		
Thrashers	1			5		1	
Total	132	22	19	29	16	1	5

^aAnomalous species are those thought to be introduced by man, relict species that did not radiate following isolation resulting from past, dramatic climatic changes, or mainland species naturally occurring on landbridge and extralimital islands near continental source populations.

very few habitat types constitute more primitive and/or aberrant avian taxa. Even among the remaining primitive taxa with a broader distribution (i.e., including C- and D-tramps), most species (often at least half) are still classified as high-S to B-tramps. The fast flying, mobile columbids and more highly developed passerine groups are the best dispersers and thus are more evenly spread out among categories. The best colonizers (from owls onward) have at least as many dispersers (A- through supertramps) as specialists (high-S species). Flycatchers, pigeons, and thrashers

Caribbean mimids in general are tramp species. They constitute the only avian taxonomic group to decrease in species richness as island size increases.

have at least twice as many dispersers as specialists. Of all the groups, owing to their small size, high metabolism, and food specialization, probably the least likely to be considered good dispersers would be the hummingbirds. Yet, reminiscent of a few migratory species within north temperate genera (e.g., *Archilochus* and *Selasphorus*), almost as many Caribbean hummingbirds (seven species—not counting anomalous species) are dispersers as are specialists (eight species).

Caribbean mimids in general are tramp species. They constitute the only avian taxonomic group to decrease in species richness as island size increases (Terborgh 1973: fig. 6). Thrashers in particular constitute the only avian group in the West Indies whose members are primarily good to excellent colonizers (six of seven species). Other groups, e.g., pigeons and doves, include vagile species, but have similar (and usually many more) numbers of habitat specialists. Instead of being dubbed a supertramp, the ubiquitous bananaquit (*Coereba flaveola*) was classified as a D-Tramp. Although it is an excellent disperser and is found on 131 (about 75 percent) of the 177 islands analyzed, possibly because it is a food specialist (nectar robber), the bananaquit is absent from some of the region's smaller and larger islands. On Cuba, the region's largest island, there is a competing honey-creeper, which probably hinders the bananaquit's attempts to colonize.

The Pearly-Eyed Thrasher as a Classic Supertramp

From these analyses, the pearly-eyed thrasher (fig. 2.6) emerges as the only West Indian species that fits virtually all of the criteria of a supertramp. Two additional species, the Caribbean elaenia and thick-billed vireo (*Vireo crassirostris*), were strong candidates for the supertramp classification but were discarded because they have not dispersed throughout the region, although the elaenia continues to extend its range to the north and westward in the Greater Antilles (app. 1). The pearly-eyed thrasher, however, clearly satisfies the supertramp distributional requisite of generally being found only on small, species-poor islands throughout the region. It inhabits some 80 islands in both the Greater and Lesser Antilles, including islands in the extreme southern Caribbean Sea (apps. 1 and 2). And, until relatively recently, the pearly-eye was even found on extralimital islands off the north coast of Venezuela (see chapter 4, and app. 3). Although found on the large, species-rich island of Puerto Rico, the pearly-eye is scarce or absent in species-rich communities, but often super abundant (an example of density compensation⁴ in species-poor habitats where competitors are few or absent) (see also chapter 4). Diamond

⁴Density compensation is a higher abundance of insular species compensating for the absence of mainland species; it usually results in habitat expansions, wider ranges of vertical foraging strata, and decreased morphological variability, among other adaptations (MacArthur et al. 1972).



Figure 2.6—The pearly-eyed thrasher (*Margarops fuscatus*): the Caribbean's prime example of an avian supertramp. It is found widely throughout the Greater Caribbean Basin on more than 80 islands and cays. Although restricted to small islands and species-depauperate communities, it occupies a full complement of habitats ranging from urban settings and coastal, littoral vegetation, to montane cloud forest. It is especially abundant in edge and disturbance-prone habitats. (Photo courtesy of Gerald P. Bauer.)

(1982) has documented a similar phenomenon among three archipelagoes in the Pacific Ocean. Supertramp species, confined to small islands in species-rich archipelagoes, expand to occupy larger islands in archipelagoes where the competitors are few or absent.

In summary, as with other mimids, the pearly-eye has evolved superior colonizing abilities and other life-history traits typical of all avian tramps. It is a strong flier, shows excellent dispersal among islands and habitats (see below and chapters 4 and 6), and is wide-ranging in the Caribbean region (AOU 1998, Bond 1979a, Evans 1990, Lack 1976, Raffaele et al. 1998). Within islands, it is often found at all elevations and in every major terrestrial habitat. It is omnivorous, exhibiting much variability in its diet and foraging techniques. It also shows morphological disparity among sexes and among individuals in allopatric (nonoverlapping) populations (chapter 5). Even more germane to the supertramp concept, the pearly-eye has evolved a reproductive strategy characterized by (1) extended breeding seasons, (2) multiple broods, (3) rapid recycling within breeding seasons, (4) asynchronous hatching, and (5) a highly adaptive resiliency to major habitat disturbances (chapter 7). Following natural disasters such as droughts and hurricanes, the pearly-eye can significantly alter its reproductive parameters. By adjusting its clutch size, and onset and length of breeding season, it compensates for the various physical and ecological stresses (e.g., damaged habitat and scarcity of adequate food resources) that severely lower the reproductive success of many other species. In addition to its superior reproductive performance, the pearly-eye often reaches high population densities in many, often disturbed or altered, habitats on several Caribbean islands (chapter 4).

Tramp Species Research

Previous authors have classified various species as supertramps usually on the basis of (a) incidence functions; (b) general impressions about their dispersal, colonization potential, and lack of competitive ability in species-rich communities; and (c) a few reproductive parameters, e.g., clutch size, length of nesting periods, and number of clutches per season (summarized by Diamond 1975a: 379–380). However, there have been no comprehensive studies of the ecology and life history of any supertramp species. By presenting the results of an ongoing (1979 to present) ecological study of the pearly-eyed thrasher, this report takes the first in-depth look at the life history and ecology of an avian supertramp.

Summary: Supertramps in the West Indian Avifauna

At least two distinctive competitive strategies exist among insular landbirds. Island birds tend to be either superior colonizers or strong competitors. Colonizers are generally r-selected species that have evolved good dispersal abilities and a high reproductive potential featuring rapid and extended breeding and large clutch sizes; they fill vacant or underexploited niches by making marked shifts in altitudinal range, habitat type, diet, foraging techniques, and morphology. However, colonizers are forced out of species-rich communities by more specialized K-selected competitors and diffuse competition. Supertramps are those species that have evolved extreme colonizing traits. They are highly vagile species that are typically confined to small, remote, or recently disturbed islands and habitats with few species. Tramp species have been described among terrestrial arthropods, land snails, freshwater and marine invertebrates, zooplankton, reptiles, mammals, and plants. In the Caribbean, the pearly-eyed thrasher best fits all the criteria of a true avian supertramp. It has evolved superior colonizing abilities, is a strong flier, shows excellent dispersal among islands and habitats, and is wide-ranging in the region. It is resident on some 80 islands and cays. Within islands, the pearly-eye is often found at all elevations and in every major terrestrial habitat type. It is omnivorous, exhibiting a diverse diet and numerous foraging techniques. It is long lived and shows morphological disparity among sexes and among individuals in allopatric populations. Most germane to the supertramp concept, the pearly-eye has evolved a reproductive strategy characterized by extended breeding seasons, multiple broods, rapid recycling within seasons, asynchronous hatching, and a highly adaptive resiliency to major habitat disturbances.

Chapter 3: Origins, Classification, and Taxonomy

Before presenting the available information on the origins, classification, and taxonomy of the pearly-eyed thrasher, a brief introduction to the possible mechanisms governing the current distribution of all West Indian birds is presented.

Colonization and Dispersal of West Indian Fauna

There are two main schools of thought regarding the mechanisms behind the origin, diversity, and distribution of the present-day West Indian fauna: (1) dispersal and (2) vicariance (allopatric speciation) (see Williams 1989 for a comprehensive review). These two partially conflicting theories notwithstanding, many biogeographers concur that the West Indian fauna, especially Greater Antillean species, are derived from North and Middle American taxa (Bond 1979b, 1982b; Darlington 1938; Pregill et al. 1994; Rosen 1976). For example, most West Indian bird genera arose from Middle American stock and are predominantly of tropical North American ancestry (Bond 1934, 1963a, 1966a, 1978a; Mayr 1946; S.L. Olson 1994, in litt.). Only two avian families with examples in South America, i.e., Trochilidae and Thraupidae, are represented by endemic genera (Bond 1979b).

Why should more ancestors of the West Indian fauna come from North and Middle America as opposed to South America? The Caribbean plate is known to be very old (more than 80 million years), and its history is as complex as it is ancient (Perfit and Williams 1989). Thus, to answer the question of the origins of West Indian progenitors, a plausible explanation is a geophysical theory based on plate tectonics and global shifts of prominent landmasses (continental drift) throughout Earth's early history. Rosen (1976) pointed out that the geophysical theory is "...strongly consistent with the distributional evidence." and West Indian islands were once "...part of an early lower Middle American archipelago that was later replaced by the tectonically and topographically similar, present-day, lower Middle American land." More recently, Perfit and Williams (1989) summarized the present state of geological knowledge of the Caribbean region in terms of four periods covering a large expanse of geological time, i.e., from the Late Cretaceous to the present. These authors showed the strengths and weaknesses of both major colonization hypotheses attempting to explain West Indian biogeography and concluded that caution and new evidence is needed for a more comprehensive knowledge of the region's biogeographical history. In support of the dispersal hypothesis, Donnelly (1989), using pelagic oceanic sedimentation records, showed that corridors or filter bridges (sensu Simpson 1940), so conducive for island-hopping organisms, existed as early as the early Miocene (see Keith et al. 2003 for a detailed summary of the Zoogeography of the region, including more recent studies).

There are two mechanisms behind the origin, diversity, and distribution of the present-day West Indian fauna, dispersal and vicariance.

History of Classification, Affiliations, and Distribution of the Mimidae

The pearly-eyed thrasher is a member of the avian family Mimidae. To put the pearly-eye in proper perspective, a brief discussion of the classification of the “mimic thrushes” follows.

The Mimidae (mockingbirds, thrashers, and allies) comprise a small family of New World birds, probably from Middle American stock (Bond 1978b, 1979b; Mayr 1946). For many years systematists thought mimids were most closely related to the thrushes and wrens and placed the group in an intermediate phylogenetic position between them, e.g., Lucas (1888 cited in Ridgway 1907). Sclater (1859) proposed that the genera *Margarops* and *Cichlherminia* be transitional from *Turdus* to the “mock-birds.” He noted that, like the turdid thrushes, species in the genera *Margarops* and *Cichlherminia* exhibit a well-developed first spurious primary and prominent scutella on the anterior crest of the tarsi. Some early authorities believed mimids are thrushes (e.g., Bonaparte 1850, Coues 1884, Gray 1869), and some more recent authors continued to place mimids with thrushes (e.g., Beecher 1953, Gulledge 1975, and Morioka 1967). Thereafter, the Mimidae were placed between the subfamily Turdinae (true thrushes) and Prunellidae (accentors) (AOU 1998). However, from a series of DNA-DNA hybridization tests, with substantiating results from morphological and serological evidence (Sibley and Ahlquist 1984) and analyses of nucleotide sequences (Barker et al. 2002; Ericson and Johansson 2003; Ericson et al. 2002a,b), mockingbirds were shown to be more closely related to starlings (Sturnidae) than to any other living taxon, and both groups have been placed by some authorities as sister tribes (Mimini and Sturnini) within the family Sturnidae, superfamily Muscipoidea, parvorder Passerida, and suborder Passeres (C.G. Sibley 1992, in litt.). The mimids’ next nearest relatives are members of the Turdidae, including typical thrushes, erithacinine chats, and muscicapine flycatchers (Sibley and Ahlquist 1984). These authors suggested that the sturnine-mimine dichotomy occurred in the late Oligocene or early Miocene, about 23 to 28 million years B.P. At that time, there were emergent land connections between Europe and North America, thus allowing the progenitor of the starlings and mockingbirds to spread over the Northern Hemisphere at a time when the increasingly severe boreal climate was pushing the two populations southward and out of contact.

Currently, most avian taxonomists recognize at least 11 extant genera and some 34 species of mimids (Clements 2000, Davis and Miller 1960). Most mimids are found in North America from Canada through the United States to Middle

America and the West Indies. Seven of North America's 10 genera and 17 species are found in Mexico, where mimids reach their greatest diversity. Only *Mimus* is found in South America (Howard and Moore 2003). *Nesomimus* (= *Mimus*) comprises four species of mockingbirds inhabiting various Galápagos islands. An 11th monotypic genus, *Donacobius*, *Donacobius atricapillus* (black-capped donacobius, or mockingthrush), was shown to be a wren (Clench et al. 1982) and was moved from Mimidae to the Troglodytidae (AOU 1998).

Systematists currently recognize 4 to 5 mimid genera and 9 to 11 species inhabiting the West Indies: (1) *Mimus* (mockingbirds, 4 species); (2) *Cinlocerthia* (tremblers—2 species now recognized by the AOU 1998 and Storer 1989. However, Hunt et al. (2001) proposed three distinct species, and Olson et al. (2005) suggest as many as four distinct trembler species on molecular genetic grounds); (3) *Ramphocinclus brachyurus* (white-breasted thrasher); and (4) *Margarops*—currently 2 species, the pearly-eyed thrasher and scaly-breasted thrasher; however, Hunt et al. (2001) found that “*Margarops fuscatus* displayed a moderate level of haplotype variation that lacked any apparent geographic pattern.” That is, *M. fuscatus* remains as one species. The same authors proposed two species of *M. fuscus* that also merit separation from the genus *Margarops* and potential replacement in a fifth genus, *Allenia*. With the exception of *Mimus* (widespread in North and South America), the remaining three genera are found only in the Caribbean region. *Cinlocerthia* and *Ramphocinclus* occur solely in the Lesser Antilles and historically, along with other avian genera such as *Todus*, *Priotelus*, *Dulus*, *Loxigilla*, *Spindalis*, *Euneornis*, *Teretistris*, and *Coccyzus* (formerly *Saurothera*), were believed to have originated in the southern region.

Origin of the Genus *Margarops*

The contemporary genus *Margarops* (Sclater 1859) is derived from the Greek *μάργαρας et οψ*, translated as “margaros” (S.L. Olson 2005, in litt.) or “pearl” and “ops” (eye) in English (Jobling 1991). The genus is presently known only from the greater Caribbean basin and comprises two species, the pearly-eyed thrasher (*Margarops fuscatus*) (= “fuscata,” Latin for dark; or, “fuscare” to darken) (fig. 2.6), and the scaly-breasted thrasher (*M. fuscus*) (“fuscus” also connotes dark or brown in Latin) (fig. 3.1). Neither *Margarops* species shows close affinities to continental (*Toxostoma* spp.) mimids (Bond 1963a, 1978a; S.L. Olson 1994, in litt.).

Historically, several avian taxonomists and paleontologists hypothesized that whereas some West Indian birds, e.g., many Jamaican species, are autochthons, i.e., endogenous to the region (Pregill and Olson 1981), both *Margarops* species derived from progenitors that arrived in the Caribbean region during the middle



Figure 3.1—Scaly-breasted thrasher (*Margarops fuscus*), the pearly-eye's only congener. Recent advances in molecular biology based on mitochondrial DNA and nuclear sequencing have prompted contemporary researchers to advocate that *M. fuscus* be returned to its former genus, *Allenia*.

Tertiary from Middle America (Bond 1978a), with *M. fuscus* preceding *M. fuscatus* (Bond 1934, 1970, 1979b). Bond (1934) postulated that during the Middle Tertiary, the West Indian landmass was much larger than it is currently, and probably was connected to Middle America. However, more recently, through mitochondrial DNA analyses, the three endemic Mimidae genera *Margarops*, *Ramphocinclus*, and *Cinlocerthia* are now thought to have originated 4 to 5 million years ago, i.e., as early as the beginning of the Pliocene (Ricklefs and Bermingham 1997), and may be the best plausible example of an autochthonous radiation in the Lesser Antilles (Hunt et al. 2001). These authors found that “Phylogenetic analyses of species-level Mimidae relationships based on mtDNA and nuclear sequences provide strong support for the monophyly and Antillean origin of a clade consisting of the tremblers, pearly-eyed thrasher, and scaly-breasted thrasher.” As examples, although now considered rare or vagrant on St. Vincent (Evans 1990, Raffaele et al. 1998), the scaly-breasted thrasher inhabited that island long enough for subspeciation (Kratler and Garrido 1996). Moreover, Hunt et al. (2001) concluded that “...the history of the endemic thrasher lineage in the West Indies extends back about 4 million years, and the three distinct clades of tremblers split about 2 million years ago.”

The Lesser Antillean Provenance is very distinct from that of the Greater Antilles, from which it is separated by the Anegada Channel. Cogently, the eggs of the *Margarops* species (along with those of *Cinlocerthia* and *Ramphocinclus*) are immaculate greenish blue like those of North and Middle American mimids (*Melanotis*, *Melanoptila*, and *Dumetella*), and unlike any mimid species currently inhabiting South America. Long before DNA-DNA hybridization analyses were

used to link mimids to starlings, Voous (1957), who also believed that *Margarops fuscatus* arose in the West Indies, made an insightful observation stating that he thought the song of the pearly-eye closely resembles that of the European starling, *Sturnus vulgaris* (see also Sibley and Ahlquist 1984, Sibley et al. 1988). The recent molecular results (Ericson and Johansson 2003, Hunt et al. 2001, Olson 2005) corroborate Voous' (1957) early hypothesis.

At the intraspecific level, very little mitochondrial differentiation was found between *M. fuscatus* populations on Puerto Rico, Barbuda, Montserrat, Guadeloupe, and Dominica (J.S. Hunt 2000, in litt.). This is less surprising, now that there is proof of interisland dispersal in the pearly-eye (e.g., Barbuda to Guadeloupe—see chapter 6).

Taxonomy of the Genus *Margarops*

As with mimids in general, confusion as to the true affinities of both *Margarops* species, i.e., whether they are thrashers or thrushes, was evident early in their classification. L.J.P. Vieillot (1807; corrected date 1808—Browning and Monroe 1991) collected the type specimen of the pearly-eyed thrasher in Puerto Rico and placed the species in the genus *Turdus*, naming it the pearly-eyed thrush *Turdus fuscatus* (The type remains in the Vieillot collection). More than 50 years later, Sclater (1859) assigned the pearly-eye to the present-day mimid genus *Margarops*. Before being transferred to the genus *Margarops*, the pearly-eyed “mocking thrush” (sensu Ridgway 1907) was placed in four separate genera with three distinct species names, e.g., the shrike-thrushes of the Australian region: *Coluricincla*, as *C. fusca* (Gould 1836); the New World mockingbirds: *Mimus*, as *M. fuscatus* (Bonaparte 1854); a defunct genus: *Cichlhalopia*, as *C. fuscatus* (Ridgway 1907); the forest thrushes: *Cichlherminia*, as *C. fuscata* (Newton and Newton 1859), and an additional defunct thrush genus: *Merula* (John Gould, *The Birds of Australia Supplement, 1851–1865*, as *M. fuscata* [Cassin 1861]). An overview of the history of the collection of specimens and taxonomic classification of the pearly-eyed thrasher is presented in table 3.1 (see Arendt 1993: 50–60, for a more detailed history).

Pearly-Eyed Thrasher

Distribution of taxonomically distinct species—

Two distinct species of the pearly-eyed thrasher were recognized by taxonomists for many years, a light-colored species inhabiting the Caribbean's northern (dry) islands (*M. fuscatus*) (Sclater 1859) and a darker species inhabiting the southern (humid) islands (*M. densirostris*) (Sclater 1859). The pearly-eye is a good example

Two distinct species of the pearly-eyed thrasher were recognized by taxonomists for many years.

Table 3.1—History of specimen collections and taxonomic classification^a of the pearly-eyed thrasher

Genus, species, and subspecies	Year	Taxonomist	Reference
<i>Turdus fuscatus</i>	1807	Vieillot	Histoire Naturelle des Oiseaux de l'Amérique Septentrionale, ii, p. 1, pl. 57 bis (Santo Domingo, Puerto Rico)
<i>Turdus densirostris</i>	1818	Vieillot	Nouveau Dictionnaire d' Histoire Naturelle, xx, p. 232 (Martinique)
<i>Colluricincla fusca</i>	1836	Gould	Proceedings of the Zoological Society of London 4, p. 6
<i>Mimus fuscatus</i>	1854	Bonaparte	Comptes Rendus, xxxviii, p. 2, footnote
<i>Cichlherminia densirostris</i>	1854	Bonaparte	Comptes Rendus, xxxviii, p. 2, footnote
<i>Cichlhalopia fuscatus</i>	1857	Bonaparte	Revue et Magasin de Zoologie Pure et Applique Series 2, vol. 9, p. 205
<i>Cichlherminia fuscata</i>	1859	Newton (A. & E.)	Ibis, pp. 141–142 (St. Croix, St. Thomas); pl. 12, fig. 8 (St. Croix)
<i>Margarops fuscatus</i>	1859	Sclater	Proceedings of the Zoological Society of London 27, p. 335 (monogr. St. Croix, St. Thomas)
<i>Margarops densirostris</i>	1859	Sclater	Proceedings of the Zoological Society of London 27, p. 336 (monogr. Guadeloupe, Martinique)
<i>Merula fuscata</i>	1861	Cassin	Proceedings of the Academy of Natural Sciences of Philadelphia 12, p. 376 (St. Thomas)
<i>Margarops f. bonariensis</i>	1948	Phelps and Phelps	Proceedings of the Biological Society of Washington 61, p. 171 (Fontein, Bonaire)

^aOnly major generic and species name changes are included, along with the respective years, taxonomists, reference sources, and occasional collection localities. For a more comprehensive summary of specimen collections and the numerous designations given by many early taxonomists, see Arendt (1993).

of Gloger's Rule, i.e., “The generalization that among warm-blooded animals those races living in warm and humid areas are more heavily pigmented than those in dry areas; pigments are typically black in warm humid environments...” (Lincoln et al. 1983); see Burt and Ichida (2004) for a causative mechanism, i.e., feather-degrading bacteria.

The species name *densirostris* is derived from Latin “densus” (thick or dense) and “rostris” (“billed”) (fig. 3.2). Today, one species and four subspecies of pearly-eye are generally recognized: (*M. f. fuscatus* (Greater Antilles and northern Leeward Islands); *M. f. densirostris* and *M. f. klinikowskii* (Lesser Antilles and southern Leeward Islands); and *M. f. bonariensis* (Bonaire and, previously, La Horquilla, Los Hermanos Islands, Venezuela) (Howard and Moore 2003, Meyer de Schauensee and Phelps, Jr. 1978, Phelps and Phelps 1948, Yopez Tamayo 1964). The subspecies, *M. f. klinikowskii* was named just recently. Garrido and Remsen (1996) proposed that the pearly-eyed thrasher population on St. Lucia warrants subspecific classification, basing their decision on morphological and plumage characteristics. St. Lucian pearly-eyes are definitely much larger and show distinct plumage differences from individuals inhabiting other islands (see chapter 5 for further discussion).



Figure 3.2—Pearly-eye profile emphasizing its formidable beak. Despite early taxonomists' reference specifically to *Margarops f. densirostris* as having a prominent bill, all four subspecies, including this Puerto Rican individual of *M. f. fuscatus*, possess quite an intimidating, predacious beak. The damage inflicted by the beak, in combination with its sharp, piercing claws, is what makes the pearly-eye such an intrepid predator (see chapter 8), and which has prompted such vernaculars as “insidious thrasher” (Snyder et al. 1987), “rapacious (or “predatory”) passerine” (several authors), and “intrepid poacher” (Seaman 1952).

Vernacular names—

Numerous vernaculars (local names) have been used to refer to *Margarops fuscatus* on various Caribbean Islands (table 3.2). No doubt, many more exist. Within the five major ethnic groups of the region (1) English; (2) Spanish; (3) French; (4) Dutch, including Papiamentu; and (5) Patois, including Creole, the most commonly used local names are, respectively, (1) thrush (used as a general descriptor); (2) zorzal (Spanish general translation of thrush, e.g., zorzal pardo—“brown thrush” in Puerto Rico); (3) moqueur (French general translation of thrush, e.g., le moqueur corossol—soursop bird in Guadeloupe); (4) witoogspotlijster (Dutch translation of white-eyed mockingbird); palabrua (Papiamentu translation of black magic bird); (5) grieve (pronounced grief), the general term used for thrush (e.g., grosse grieve, or “large thrush”) in the Patois and Creole dialects spoken in the French West Indies and Dominica, St. Lucia, and St. Vincent.

Scaly-Breasted Thrasher

Taxonomy and distribution of distinct subspecies—

Like the pearly-eye, the affinities of its congener, the scaly-breasted thrasher (fig. 3.1), were obscure during the genesis of its discovery and classification. It, too, was thought to be a thrush (Ridgway 1907). Consequently, the scaly-breast was placed in several thrush genera (some of which remain in the present-day turdinae) and was assigned various species names before finally being classified as a mimid. P.L.S. Müller (1776) was the first to describe the scaly-breasted thrasher from a specimen collected in Martinique, placing the species together with the

Table 3.2—Most common vernacular names given to the pearly-eyed thrasher by people from five ethnic backgrounds scattered throughout the Caribbean

English ^a	Non-English ^a	Islands ^b	References ^c
Black magic bird (1, 3)	Palabrua (2)	4, 5, 8	7
Black thrasher (1, 3)	Zorzal negro (5)	2, 12	10, 14
Brown thrush	Grive brune (1, 4)	7, 9, 13, 16	1, 11
Drab, dull, or brown thrush	Zorzal pardo (5)	12	2
Jack bird (1, 3)	Pío-Juan, Pío-Hyab (5)	2, 12	2, 10
Large thrush	Grosse (grive) or grieve (1, 4)	7, 9, 13, 16	2, 9
Mango bird (1, 3)	Ave que come mangó (5)	11, 12	10
Mango bird (1, 3)	Le Moqueur que manage l' fruit (4)	7, 9	10
Palm thrush (1,3)	Zorzal de palmares (5)	12	14
Papaya bird ^d (1, 3)	Ave que come lechosa (5)	12	14
Paw-paw bird ^d (1, 3)	Ave que come lechosa (5)	2, 12, 14, 18	10, 14
(also paw-paw fruit thrush) ^d (1, 3)	Ave que come lechosa (5)	2, 12, 19	6
Pearly-eyed thrush (1, 3)	Zorzal con ojos de perla (5)	14	8
Soursop bird (1, 3)	Ave que come guanabana (5)	11, 12	10, 14
Soursop bird (1, 3)	Grise ^e (or Moqueur) corossol (2, 4)	2, 7, 12	9, 10, 11
Spanish mockingbird (3)	Chuchubi spanjo ^{f,g} (3)	4, 5, 8	7
Spanish mockingbird (3)	Tjutjubi spagnolf (var. spaño) (2)	4, 5	4, 7, 12
Strong beak	Boca dura (2, 5)	4, 5, 8	7
Thrasher (1, 3)	Louis jo (1)	11	10
Thrasher (1, 3)	Pie voleuse (1, 4)	13	10
Thrush and thrushee (1, 3)	Zorzal, Truche, Chucho (2, 4, 5)	1, 3, 10, 12, 15, 17, 19	2, 3, 5, 10, 11, 14
Wall-eyed (thrush) thrasher (1, 3)	Zorzal ojiblanco (5)	12, 19	5, 10
White-eyed mockingbird (3) (also, white-eyed mocking-thrush)	Witoogspotlijster ^{f,h} (2)	4	12, 13
White-throated fruit thrush (3)	Zorzal de las frutas con la garganta blanca (5)	6, 7, 9, 10, 16	6

^a Native language: (1) Creole: English and French Creole (including patois [pronounced “patwa”]) Antigua, Bahamas, Barbados, Barbuda, British Virgin Islands, Caicos Islands, Dominica, Jamaica, Montserrat, Nevis, St. Kitts, St. Lucia, St. Vincent and the Grenadines, Turks Islands, and U.S. Virgin Islands; (2) Dutch (including Papiamentu, the local dialect spoken on Aruba, Bonaire, and Curaçao) Saba, St. Eustatius, and St. Maarten; (3) English: Nevis, Puerto Rico (small percentage), St. Kitts, St. Lucia, St. Vincent and the Grenadines, Turks Islands, and U.S. Virgin Islands (St. Croix, St. John, St. Thomas); (4) French (Guadeloupe and its satellites, e.g., la Désirade and Marie Galante, Martinique, St. Barthélemy, and St. Martin); and (5) Spanish (also Spanish Creole), Cuba, Dominican Republic and Puerto Rico.

^b Island: (1) Antigua, (2) Bahamas, (3) Barbados, (4) Bonaire, (5) Curaçao, (6) Dominica, (7) Guadeloupe, (8) La Horquilla, (9) Martinique, (10) Montserrat, (11) Nevis, (12) Puerto Rico and Satellites, (13) St. Barthélemy, (14) St. Croix, (15) St. Eustatius, (16) St. Lucia, (17) St. Martin, (18) St. Thomas; (19) U.S. Virgin Islands.

^c References: (1) Bond 1979a; (2) Danforth 1926, 1930a, 1930b, 1931, 1934, 1935a, 1935b, 1935c, 1939a, 1939b, 1939c; (3) Feilden 1889; (4) Hartert 1893b; (5) Leopold 1963; (6) Maynard 1898–1903; (7) Meyer de Schauensee and Phelps 1978; (8) Newton and Newton 1859; (9) Noble 1916; (10) Raffaele et al. 1998; (11) Vieillot 1807; (12) Voous 1983; (13) University of the Virgin Islands 1988; (14) Wetmore 1916a, 1927.

^d Paw-paw (var. papaw) is synonymous with custard apple in North America; in the Caribbean, however, it is often used to refer to the papaya fruit; paw-paw is thought to have been derived from the Spanish word papaya.

^e Grise (= thrush); “corossol” in patois refers to the fruit of the soursop.

^f Translated by (the late) Frater Candidus van der Linden.

^g “Chuchubi” by itself is the vernacular for mockingbird, e.g., tropical mockingbird (*Mimus gilvus*).

^h Wit = white, oog = eye, spotlijster also denotes “mockingbird” (the late Frater Candidus van der Linden 1992, in litt.).

Old World flycatchers, Muscicapidae (*Muscicapa fusca*) (the type specimen is now in the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts). More than a century later, Cory (1891) assigned the scaly-breast to the monotypic genus *Allenia*, resulting in four separate species recognized between 1891 and 1945: *A. montana* (Cory 1891, Verrill 1892); *A. albiventris* and *A. apicalis* (Riley 1905a cited in Ridgway 1907); and *A. fusca* (Bangs 1930, Bangs and Penard 1921, Bond 1928b). A brief overview of the history of the collection of specimens, taxonomic classification, and distribution among islands is given in table 3.3 (for more detailed information, see Arendt 1993: 64–69). As with the pearly-eye, the plumage of the scaly-breast becomes progressively darker southward in the Lesser Antilles, the trend not appearing to be seasonal or sexual (Noble 1916). Almost 70 years after Cory (1891) assigned the scaly-breast to the genus *Allenia* and, following early authors, Bond (1959), among others, proposed that it be considered congeneric with *Margarops fuscatus*, and assigned a fifth species name, viz., *M. fuscus*. In describing the geographical variation of the scaly-breasted

Table 3.3—History of the collection of specimens and taxonomic classification^a of the scaly-breasted thrasher

Genus, species, and subspecies	Year	Taxonomist	Reference
<i>Muscicapa fusca</i>	?	Daubenton	Enlarged plate 586, fig. 2 (Martinique) (plate cited in Bangs and Penard 1921)
<i>Muscicapa fusca</i>	1776	P.L.S. Müller	Natursystems Supplements, p. 170 (Martinique)
<i>Turdus apicalis</i>	1854	Lichtenstein	Nom. Av. Museum Berol., p. 27 (cited in Ridgway 1907)
<i>Margarops montanus</i>	1859	Sclater	Proceedings of the Zoological Society of London 2, p. 336 (Guadeloupe, monogr.)
<i>Margarops montanus</i>	1880	Lister	Ibis Series 4: 38-44
<i>Cichlherminia montana</i>	1881	Sharpe	Catalog of the Birds of the British Museum VI, p. 330 (Lesser Antilles monogr.) (cited in Ridgway 1907)
<i>Margarops albiventris</i>	1887	Lawrence	Annals of the New York Academy of Science IV, p. 23 (Grenada) (cited in Ridgway 1907)
<i>Margarops albiventris</i>	1888a	Cory	Auk V, p. 157 (Grenada)
<i>Margarops rufus</i>	1888b	Cory	Auk V, p. 47 (Dominica)
<i>Allenia montana</i>	1891	Cory	Auk 8, pp. 46-47 (Antigua, St. Eustatius)
<i>Margarops albiventris</i>	1902	Wells	Auk xix, p. 349 (Carriacou; from St. Vincent hurricane of 1898)
<i>Allenia albiventris</i>	1905b	Riley	Smithsonian Miscellaneous Collections 47, p. 288 (Barbuda and Antigua)
<i>Allenia apicalis</i>	1905	Riley	Proceedings of the Biological Society of Washington 18, p. 186 (cited in Ridgway 1907)
<i>Allenia fusca</i>	1921	Bangs and Penard	Bulletin of the Museum of Comparative Zoology 64, p. 395
<i>Allenia fusca</i>	1945	Bond	Check-list, 2 nd ed., Academy of Natural Sciences of Philadelphia
<i>Allenia fusca</i>	1961	Deignan	Type specimens of birds in the U.S. National Museum

^aOnly major generic and species name changes are included, along with the respective years, taxonomists, reference sources, and occasional collection localities. For a more comprehensive summary of specimen collections and the numerous designations given by many early taxonomists, see Arendt (1993).

thrasher, Buden (1993) assigned three new subspecies. Despite the current practice of placing the scaly-breast in the genus *Margarops*, some contemporary taxonomists (e.g., Howard and Moore 2003) continue to place the species in the monotypic genus *Allenia*. Indeed, based on the results of genetic testing, Hunt et al. (2001) not only reject the monophyly of the genus *Margarops*, they also propose distinct southern (St. Lucia and Martinique) and northern (Dominica to Montserrat) mtDNA lineages of the scaly-breasted thrasher, i.e., two clades, which translates into two separate species.

Vernacular names—

Possibly owing to the scaly-breast's more restricted range, not as many vernacular names have been published for it as for the pearly-eye (table 3.4). In the more northern portions of its range, the scaly-breast is referred to locally as the black-billed thrush or simply “thrush” on St. Martin, St. Eustatius, St. Kitts, Nevis, Antigua, and Montserrat (Danforth 1930b, 1934, 1936a, 1939b, 1939c). In the more southern Leeward Islands, it is known as the spotted thrush, e.g., on Carriacou (Wells 1902). A few variations of “grieve” are used to describe *M. fuscus* in the French Departments (e.g., Guadeloupe, Martinique, and respective satellites) and on former French and English colonies (e.g., St. Lucia, Dominica, and St. Vincent). On these islands, the scaly-breast is known as the “grevotte,” “grivotte,” “grive (variation of “grieve”) fine” (small thrush), “grive cendree” (gray or ashy thrush), and “spotted grieve” (Danforth 1935b, Devas 1970, Noble 1916).

Table 3.4—Most common vernacular names given to the scaly-breasted thrasher by people from five ethnic backgrounds scattered throughout the Caribbean

English ^a	Non-English ^a	Islands ^b	References ^c
Black-billed thrush (1, 3)	Zorzal de pico negro (5)	7, 8, 9, 10, 11, 14	1, 5
Spotted thrush (1, 3)	Zorzal manchado (5)	2	7
Ash-colored thrush ^d (1)	Grieve cendree (1)	5	4
Thrush, small thrush	(Spotted) grieve, grivotte, grive fine (1, 4)	1, 6, 10, 12, 13, 14	1, 2, 5, 6
Thrush, small thrush	Moqueur grivotte, grive fine (1, 4)	5, 6	5
Mountain fruit thrush (3)	Le Moqueur de l' montagne que manage l' fruit (1, 4)	3, 4, 5, 6, 12, 14	3
Lawrence's fruit thrush (3) (also Cory's fruit thrush) (3)	Le Moqueur de Lawrence que manage l' fruit (1, 4)	4, 12	3

^aNative language: (1) Creole (also English and French patois), (2) Dutch (also Papiamentu), (3) English, (4) French, and (5) Spanish (also Spanish patois).

^bIslands: (1) Antigua, (2) Carriacou, (3) Dominica, (4) Grenada, (5) Guadeloupe, (6) Martinique, (7) Montserrat, (8) Nevis, (9) Saba, (10) St. Eustatius, (11) St. Kitts, (12) St. Lucia, (13) St. Martin (also Maartin), (14) St. Vincent.

^cReferences: (1) Danforth 1930a, 1930b, 1934, 1935a, 1935b, 1935c, 1936, 1939a, 1939b, 1939c; (2) Lawrence 1879b; (3) Maynard 1898–1903; (4) Noble 1916; (5) Raffaele et al. 1998; (6) Sclater 1871; (7) Wells 1902.

^dThe patois vernacular “Grieve cendree” (Ash-colored thrush) pertains not to the scaly-breasted thrasher but rather to the gray trembler (*Cinlocerthia gutturalis*) (reclassified by Storer 1989).

Summary: Origins, Classification, and Taxonomy

Four genera and nine species of the exclusively New World avian subfamily Miminae (mockingbirds, thrashers, and allies) are found in the West Indies: *Mimus* (mockingbirds: four species), *Cinclocerthia* (tremblers: two to four species are recognized by different taxonomists), *Ramphocinclus* (white-breasted thrasher), and *Margarops* (two species). Only two genera, *Cinclocerthia* and *Ramphocinclus*, occur solely in the Lesser Antilles.

Historically, systematists thought mimids were most closely related to the thrushes and wrens. However, recent genetic research using mitochondrial DNA sequencing has shown that Lesser Antillean mimids in the genera *Margarops*, *Ramphocinclus*, and *Cinclocerthia* form a single set of lineages (or clade), along with the gray catbird (*Dumetella carolinensis*) of North America. Neither *Margarops* species shows close affinities to continental mimids. Moreover, recent evidence suggests instead an autochthonous radiation in the Lesser Antilles by both species. The most recent DNA-derived evidence even brings into question the phylogenetic relatedness and, thus, the congeneric classification of the two *Margarops* species.

For many years, taxonomists recognized two distinct species of the pearly-eyed thrasher: a light-colored species inhabiting the Caribbean's northern low and dry islands (*Margarops fuscatus*), and a darker species inhabiting the southern high relief and humid islands (*M. densirostris*). Today, one species and four subspecies of pearly-eye are generally recognized: *M. f. fuscatus* (Greater Antilles and northern Leeward Islands); *M. f. densirostris* and *M. f. klinikowskii* (southern Leeward Islands); and *M. f. bonariensis* (Bonaire and, previously, La Horquilla Island, Los Hermanos Archipelago, Venezuela).

Neither *Margarops* species shows close affinities to continental mimids. Recent evidence suggests instead an autochthonous radiation in the Lesser Antilles by both species.

Chapter 4: Distribution and Abundance

Although confined to species-poor islands and habitats, a supertramp, by definition, possesses the ability to disperse over a wide geographic area. That the pearly-eyed thrasher (*Margarops fuscatus*) is the West Indies' premier avian supertramp becomes obvious when its distribution and abundance are considered. However, no species' current distribution or abundance is static, but rather is in a constant state of flux. In this chapter, the pearly-eye's current and historical ranges are presented, followed by various examples of documented, historical and present-day range and abundance contractions and expansions. Some of the environmental factors and ecological correlates influencing its distribution and abundance are also discussed.

Current Range

Margarops fuscatus inhabits some 80 islands and cays throughout the Greater Caribbean Basin, from Rum Cay and San Salvador in the Southern Bahamas south to Bonaire, Netherlands Antilles, over a north-south geographical range of almost 3000 km (apps. 1, 2, and 3). The Bahamian Archipelago is the major island group in the northwestern extreme of the pearly-eye's range. It encompasses about 30 major islands and thousands of smaller cays, and has a combined landmass of 13 864 km² (World of Information 1986). Elevations seldom exceed 5 to 10 m, except for a few ridges and hills that reach 30 to 60 m; the highest (67 m) is Mount Alvernia on Cat Island (Buden 1987a, 1987c). Although the pearly-eyed thrasher inhabits many of the smaller, species-poor islands and cays of the Southern Bahamas, it is curiously absent on the small islands and cays in the Cay Sal Bank and Ragged Islands, none of which has more than 11 landbird species (Buden 1987c, Buden and Schwartz 1986). Lack of habitat is no doubt a major factor explaining the pearly-eye's absence on some of the smaller islets and cays, which are no more than barren rocks jutting out of the sea. Still, some of the larger cays and islets are scrub covered or even partially wooded, a few with patches of mangrove forest (Buden 1987c). Intuitively, one would think that pearly-eyes would have colonized these islands. It is possible that, historically, the thrasher did in fact inhabit at least some of the larger islets and cays, but there is no such evidence today.

Little San Salvador (24°34' N. 75°56' W.) is a small, uninhabited island in the northern Bahamas located about 15 km east of the southern tip of Eleuthera and 20 km west of the northwestern tip of Cat Island. It has about eight species of resident landbirds (Norton 1993) and is less than 200 km northwest of San Salvador (= Watling Island), a potential source island on which the pearly-eye is a common resident (Murphy et al. 1998), and from which it could readily receive dispersing individuals. Yet, there are no reports of the pearly-eye from Little San Salvador

***Margarops fuscatus* inhabits some 80 islands and cays over a north-south geographical range of almost 3000 km.**

Island, although ornithologists have visited it as recently as 1981 (Norton 1993). Little San Salvador, however, is inhabited by the Bahama mockingbird (*Mimus gundlachi*), a potential confamilial competitor that may be keeping the pearly-eye from successfully colonizing the island.

The pearly-eye is sparsely distributed among the Turks and Caicos Islands (combined landmass of 430 km²). Buden (1987c) suggested that the pearly-eye is possibly a recent invader to the Turks Bank, where it has been observed only on Grand Turk.

With the exception of Puerto Rico, pearly-eyes are noticeably absent from the larger, species-rich islands of the Greater Antilles such as Cuba, Hispaniola, and Jamaica, inhabiting only species-poor satellite islands in the region. Among the much smaller, species-poor Leeward and Windward Islands of the Lesser Antilles, pearly-eyes are more evenly distributed. They inhabit numerous islands, islets, and cays throughout the area but are absent from presumably habitable islands of the southernmost Lesser Antilles, e.g., St. Vincent, the Grenadines, and Grenada (Evans 1990, Raffaele et al. 1998).

Historical Range

The present-day distribution of the pearly-eyed thrasher is well known. But, has its geographical range changed significantly over time? One must seek answers to these questions from a paleogeological perspective. A complete prehistorical account of the radiation of the genus *Margarops* throughout the Caribbean is impossible, owing largely to the dearth of paleontological records (Olson 1978, Pregill et al. 1994). However, a few discoveries of prehistoric bones of both *Margarops* species from the late Quaternary derived from cultural (archaeological) excavations as well as paleontological sites (mostly owl pellets deposited in limestone caves and sinkholes) shed some light on the history of the genus in the region (see also the discussion based on results from genetic studies in chapter 3). Dating back some 2000+ years, the first evidence of the prehistoric occurrence of both species currently constituting the genus *Margarops* in the Caribbean comes from an archaeological site (recently destroyed by volcanism) located near Trant's Bay, Montserrat, in the Lesser Antilles (Steadman et al. 1984b). The bones at the Trant's archeological site represent the first prehistoric record for *M. fuscus* anywhere in the Caribbean, and the first regional record for *M. fuscatus*. Moreover, this may also constitute the first prehistoric record for *M. fuscatus* in the Caribbean, as the two previous reports by Wetmore (1922, 1937) of fossils from the Bahamas and Puerto Rico thought to pertain to the pearly-eye have been shown to be erroneous. Instead, the bones discovered in the Greater Antilles are

First evidence of the prehistoric occurrence of both species of *Margarops* comes from an archaeological site located near Trant's Bay, Montserrat, in the Lesser Antilles.

now thought to pertain to the Bahama mockingbird and a large species of *Turdus* thrush (Olson and Hilgartner 1982, Olson in Snyder et al. 1987: 199–200). These results led Snyder et al. (1987: 200) to question an early arrival of the pearly-eye in Puerto Rico, citing the intriguing absence of pearly-eyed thrasher bones in cave deposits and failure by early ornithologists to report the species even after extensive fieldwork throughout the island. However, the fact that fossilized bones of the pearly-eye have been found in late Holocene deposits from the Burma Quarry, Antigua, Lesser Antilles (Pregill et al. 1988, Steadman et al. 1984a), does at least suggest that the species could have inhabited nearby Puerto Rico much earlier than previously thought.

Bones of the pearly-eyed thrasher from the late Quaternary have been found on Anguilla, St. Eustatius, Barbuda, Antigua, and Montserrat, whereas bones of the scaly-breasted thrasher, corresponding to the same period, have been found only in Barbuda and Montserrat (Pregill et al. 1994; and app. 1). More recently, Elizabeth Wing (1994, pers. comm.), Robert Chandler, and their associates at the University of Florida identified a bone as pertaining to the pearly-eye from an archaeological site on the Hope Estate, St. Martin. The bone has been dated to about 120 B.C. (2070 B.P.), a time when St. Martin was inhabited by ceramic-producing Amerindians represented by the Soladoid ceramic series.

The recent discoveries of the prehistoric presence of the pearly-eye on several islands from Anguilla to Montserrat notwithstanding, not all authors ascribe to the belief that the pearly-eye or even a proposed progenitor colonized the Caribbean islands from the west. Moreover, there is one integral piece of the puzzle missing. To date, no bones of *Margarops* spp. have been found anywhere in the Greater Antilles. To explain this enigma, Pregill and Olson (1981) postulated that *Margarops*' ancestors arrived in the Lesser Antilles prior to the Wisconsin glaciation, spreading to Puerto Rico and the Bahamas quite recently in geological time. Likewise, Lack (1976, fig. 21: 144–145), after considering the contemporary range of *M. fuscatus*, also deduced that the pearly-eye spread northward from the Lesser Antilles. However, taking an alternative, and apparently correct, point of view, Voous (1957) assumed *Margarops* to be an autochthonic (indigenous) genus originating in the Lesser Antilles. More than 40 years later, Voous' (1957) hypothesis was substantiated through genetic studies (Hunt et al. 2001).

In summary, a more complete history of the pearly-eye's colonization and radiation throughout the Caribbean islands, including further discoveries of fossilized bones and ensuing interpretations to augment, and compare with, the more recent genetic studies, is desirable. However, whether the genus *Margarops* originated in the Lesser Antilles, or instead its progenitor arrived in the region

early in geological time is not as important as the apparent fact that the genus first radiated throughout the southern islands and then spread northward into the Greater Antilles.

Range Contractions

Written accounts by early ornithologists, taxonomists, specimen collectors, and others suggest that the pearly-eye once had a more extensive range throughout the Greater Caribbean Basin. However, like most insular birds, thrashers undergo population and range fluctuations throughout the region (app. 3). Bond (1979b) wrote that “Formerly this thrasher was...more widespread in the Greater Antilles, for the type locality of the nominate race was given as Hispaniola and Puerto Rico (Vieillot 1807; corrected date 1808-Browning and Monroe, 1991), and a specimen was collected at Spanish Town, Jamaica, on July 22, 1865.” Similarly, Wetmore and Swales (1931) noted that Vieillot (1807/1808) wrote “La grive brune [brown thrush] se trouve dans les grandes îles Antilles et particulièrement a Porto-Ricco et a Saint-Domingue [Hispaniola].” Although Vieillot could have been referring to Beata Island specimens, it seems doubtful that he would have been so general in his locality description for a few records from a single location, especially a satellite island off the main coast of Hispaniola.

The pearly-eye experiences severe population oscillations in the southern extreme of its range. On Barbados, the most isolated of the Lesser Antillean islands, as early as 1750 at least two authors cited the presence of two species of “brown thrushes” (app. 3). They were most likely referring to both *Margarops* species. A specimen of *M. fuscatus* was collected on Barbados by C.J. Manning in 1889 (see chapter 5 and app. 3), suggesting that it may have been resident prior to the 20th century. However, after failing to encounter “thrushes” of any species (and aware of Manning’s specimen), Feilden (1889) concluded that *M. fuscatus* was no more than a straggler to the island. Both species of *Margarops* are now very rare (Evans 1990) or extirpated (if once resident) on Barbados as none was observed by the present author in 1984 or by D. W. Buden in 1991 (Buden 1992a, pers. comm.).

There is little information documenting the history of the pearly-eyed thrasher on St. Vincent. However, a few published accounts suggest that the species may once have been resident but is now extirpated. Unfortunately, the few published records that do exist are often ambiguous or even contradictory as to the thrasher’s historical status on St. Vincent. In his early *Check-lists of the Birds of the West Indies*, Bond (1945, 1950, 1956a) did not list the pearly-eyed thrasher as occurring on St. Vincent, either as a resident or vagrant. Later, though, Bond

(1957) reported a specimen from St. Vincent (April 23, 1890) examined in the British Museum by D.W. Smith. Ironically, Bond (1960, 1971a) then listed the thrasher as resident on St. Vincent in two early editions of his field guide to West Indian birds. Some years later, Bond (1977: 2) specifically stated that he considered *M. fuscatus* as a vagrant on St. Vincent. Unaccountably, however, in the same supplement (1977: 11) in a discussion of how thrasher numbers had been fluctuating among various islands for the past 50 years, he stated that the thrasher "...may be extirpated on St. Vincent..." thus connoting that it had been resident at one time. Later still, Bond (1979a) listed the pearly-eye as **resident** south to St. Vincent, and accidental (vagrant) on Barbados. Devas (1970), however, in his book of the birds of Grenada, St. Vincent, and the Grenadines, did not list the pearly-eye from any island in that group. Lack et al. (1973) did not observe the pearly-eyed thrasher in St. Vincent during their visits, which included transect censuses in March and July 1973, usually periods of peak pearly-eye activity. A decade later, Faaborg and Arendt (1985) did not observe a single pearly-eye during transect censuses in July 1983. Nor was a single individual captured during banding operations in March and April 1984, although some 300 birds were captured at two montane forest sites. Presently, the AOU's (1998) *Checklist of North American Birds* cites the pearly-eye's range as south to St. Lucia, with a disjunct population inhabiting islands north of Venezuela from Bonaire east to Los Hermanos Islands. It certainly is not obvious from published accounts whether or not the pearly-eyed thrasher has ever been resident on St. Vincent.

The pearly-eyed thrasher has been extirpated on La Horquilla Island in Los Hermanos Archipelago, Venezuela (Meyer de Schauensee and Phelps 1978, Paynter 1982, Phelps and Phelps 1963). It is noteworthy that there is some confusion regarding the identity of La Horquilla Island. It is sometimes spelled "Orquilla" and should not be confused with Orchila Island just east of Los Roques group about 117 km north of Cape Codera, Venezuela (Cory 1909).

Range Expansions

Bahamian Archipelago

The pearly-eyed thrasher has undergone population declines on some islands, resulting in notable geographical contractions in several areas of its traditional range. In the northern portion of its range, however, there have been increased sightings of dispersing individuals on the larger Bahamian islands (documented by several observers—see app. 3). This has led some authors, e.g., Brudenell-Bruce (1975), Buden (1987c; 1990; 1988, D.W. Buden 1988, in litt.), and Paulson (1966), to conclude that the pearly-eye is spreading its range northward. Undoubtedly, some

The pearly-eye is spreading its range northward and increasing in number in the south.

of the more recent sightings in the northern Bahamas may be due simply to an increase in the number of observers. However, two long-time residents and a third regional specialist have assured me that during the past couple of decades they have been observing thrashers more frequently in the northern islands. In addition, Christmas bird counts have been conducted in the Northern Bahamas for many decades without sightings of pearly-eyes in the early years.

Like other mimids, e.g., northern mockingbird *Mimus polyglottos* (see for example David et al. 1990), some populations of the pearly-eyed thrasher have increased in response to clearings in forest cover, expanding agriculture, and urban development. Pearly-eyes take advantage of the seeds, fruits, and associated insects of a wide variety of native, orchard, garden, and ornamental plants in secondary forests and a wide variety of altered (e.g., urban) habitats. Historical records show that in Puerto Rico, Montserrat, and Bonaire the pearly-eye has undergone significant intraisland population increases within the last 30 to 60 years (app. 3).

Puerto Rico

In Puerto Rico, for more than a century, pearly-eyes were scarce and only patchily distributed in the lowlands and hills. However, by the 1920s, resident biologists noted a steady increase in thrasher numbers throughout the island. Struthers (1923) reported the pearly-eye as “common” in montane forest at Maricao, and Wetmore (1927) listed the species as “quite plentiful” in montane forest in the upper Toro Negro area. By 1930, thrashers were reported up to 600 m in the Sierra de Luquillo (Danforth 1931). By the early 1950s, pearly-eyes became abundant in the Sierra de Luquillo, particularly within the confines of the Caribbean National Forest, also known as the Luquillo Experimental Forest (Snyder et al. 1987). It is noteworthy that the “explosion” (sensu Snyder et al. 1987) of pearly-eyes in the Sierra de Luquillo in the early 1950s closely followed Operation Bootstrap, a government-initiated program implemented to create more jobs on the outskirts of larger cities. This program culminated in the immigration of thousands of people to larger cities and subsequent urban sprawl. It is possible that urban development augmented thrasher populations by creating more food resources and nest sites. Dispersing young then could have easily emigrated to the nearby, species-poor Sierra de Luquillo, which might have acted as an ecological sink for dispersing individuals. Today, the pearly-eye is a common resident throughout the island (Raffaele 1983, Raffaele et al. 1998).

Montserrat

In Montserrat, pearly-eyes were considered common for the first three-quarters of the 20th century (Bond 1945, Danforth 1939b, Terborgh and Faaborg 1980). However, thrasher populations greatly increased in the late 1970s and early 1980s and have continued to increase ever since (*f.* Fred Payne, forest guard; and Franklin Margetson, Montserrat National Trust, 1984, pers. comm.). The pearly-eye's recent, marked increase in Montserrat led Steadman et al. (1984b) to consider it as the island's most common forest bird. This finding has been corroborated by subsequent researchers (e.g., Arendt 1990, Arendt et al. 1999, Faaborg and Arendt 1985), all of whom also considered the pearly-eye as one of Montserrat's most abundant passerines. With the possible exception of the bananaquit (*Coereba flaveola*), the pearly-eye may well be the island's most abundant landbird, even more so than the zenaida dove (*Zenaida aurita*) or common ground-dove (*Columbina passerina*), both of which are generally confined to lowland forest, agricultural lands, coastal, and residential areas. It is noteworthy that populations of the usually abundant and ubiquitous bananaquit are noticeably small in some habitats on Montserrat (pers. obs.), often resulting from pearly-eye nest predation (discussed further in chapter 8).

Bonaire

Historical accounts of the pearly-eyed thrasher on Bonaire suggest that populations, once quite restricted in number and range, have recently increased and spread throughout the island (app. 3). The first author to mention the thrasher's status on Bonaire was Hartert (1893a; specimen collected). He reported that the species was restricted to the Fontein Plantation. More than 50 years later, Phelps and Phelps (1948), although having collected specimens of other species throughout the island, found the pearly-eye still restricted to the Fontein Plantation (Voous 1983). However, a contemporary resident, (the late) Frater (Brother) Candidus van der Linden (1988, and C.V.D. Linden 1992, in litt.) reported the pearly-eye as "...not abundant, but rather evenly dispersed throughout the hilly, rocky parts of the island." (fig. 4.1). Although he concedes that the pearly-eye may nest in cavities and construct open-stick nests in Bonaire as it does on other islands, in his more than 20 years of observations, he has found them nesting only in "steep rock walls" at four locations (see fig. 4.1).

To update the pearly-eye's status on Bonaire, I visited the island for a week in July (25–31) 1997. The pearly-eye's status had not changed from that observed in the early 1990s. It was still common within the confines of the Fontein Plantation near water, but uncommon and evenly dispersed over most of the remainder of

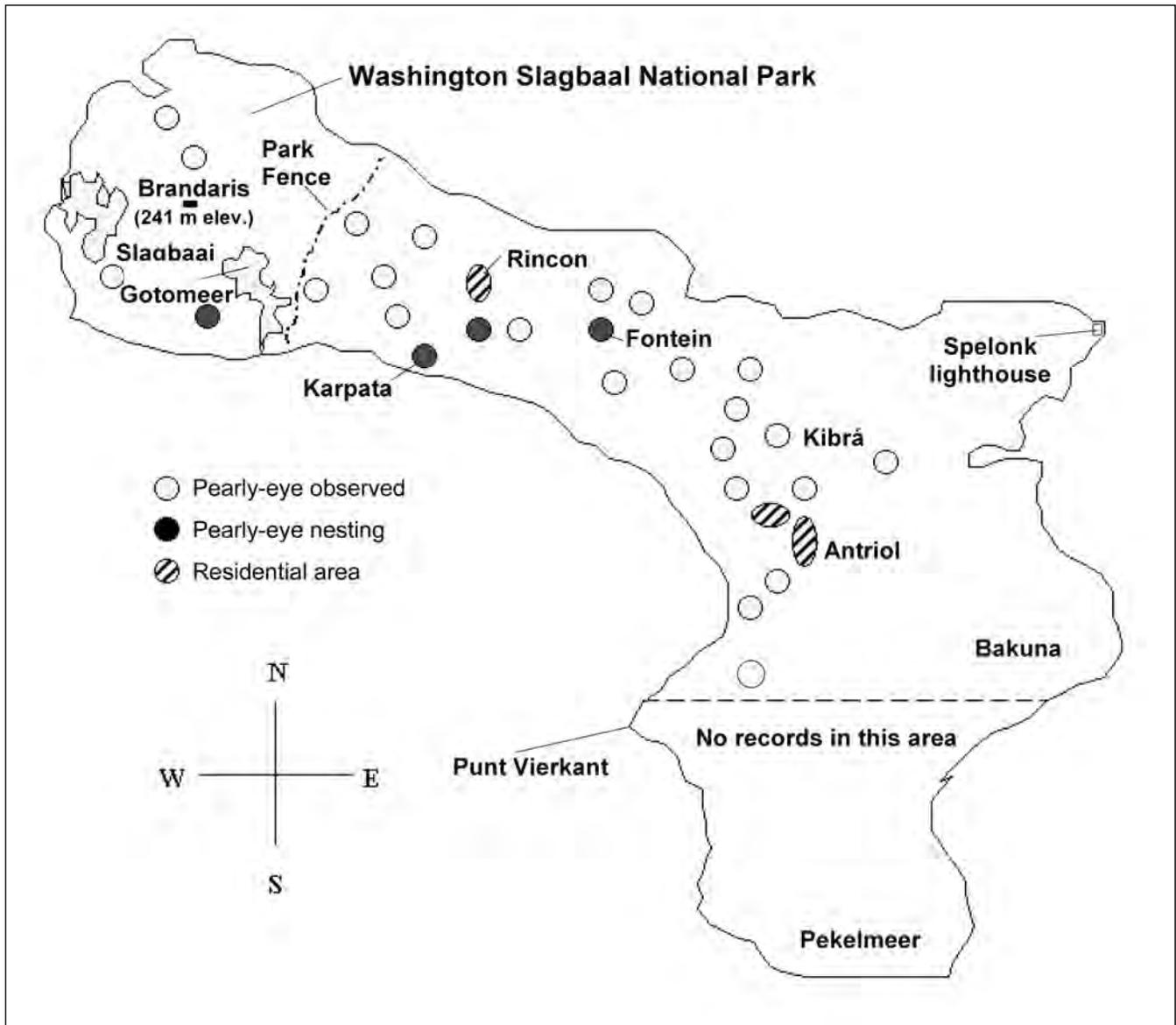


Figure 4.1—Contemporary distribution of the pearly-eyed thrasher on Bonaire, Netherlands Antilles, with documented records of nesting outside of the Fontein Plantation. Thrashers are especially common in and around human settlement, where they take advantage of additional food, water, and nesting sites. The original sketch and observations were supplied by (the late) Frater Candidus van der Linden, a long-time resident, author, and authority on Bonaire’s birds; he also had a broad knowledge of the island’s flora and other fauna.

the island, much of which is quite arid. Fontein was too small for an adequate point-count census, so a mist-net sample was taken. Pearly-eyes constituted 19 percent of the 68 captures of 15 species. Pearly-eyes, and many other species as well, are abundant in the Fontein Plantation because the owner maintains a year-round watering fountain for his livestock. That many birds of several species are attracted to the permanent water source is evident from the cumulative species curve presented in figure 4.2. After 100 net-hours, the number of new species continued to increase despite the fact that almost 70 individuals had been captured.

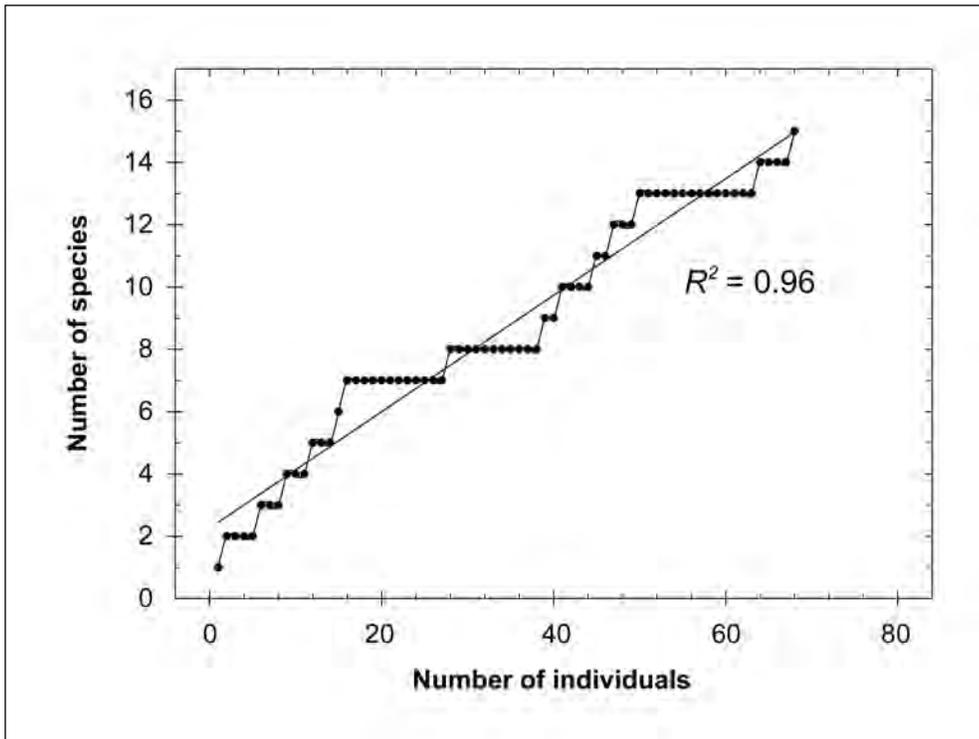


Figure 4.2—Cumulative species curve resulting from 100 net-hours of banding at a water trough on the Fontein Plantation, Bonaire, Netherlands Antilles. That an upper asymptote was not reached, even after the capture of almost 70 individuals, attests to the importance of the site for local birds.

Another attribute of the plantation was the tall stature of many of the trees in the immediate vicinity of the fountain. Of 10 trees sampled, the mean height was 14.9 m ($SE = \pm 2.6$; range: 8.4 to 21). Tree height was considerably greater at the fountain than in the Washington-Slagbaai National Park (see discussion below).

To compare the pearly-eye's abundance in a more natural setting, the author conducted a point-count census within the Washington-Slagbaai National Park (fig. 4.1). In total, 40 points were established throughout the park, and each was visited once. Tree height within a 25-m radius around each point was measured. Average tree height ($n = 160$; 4 trees/point) was 5.6 m ($SE = \pm 0.28$; range: 2.5 to 9). Thus, in general, tree height within the park was much lower than that within the Fontein Plantation as discussed above.

Of 295 detections involving 26 species of birds, 8 species comprising 215 (73 percent) of the detections were common enough to compare species' numbers. As suspected, the pearly-eye was not at all common in the park. Only six (3 percent) of the 215 individuals detected were pearly-eyes (fig. 4.3a). Whereas all but two species (smooth flycatcher, *Sublegatus*, gen. nov. *arenarum*, syn. *modestus*), and troupial, *Icterus icterus*) averaged almost 1 to 2 individuals per point, the mean number of pearly-eyes per point was only 0.13 (fig. 4.3b). Moreover, whereas half

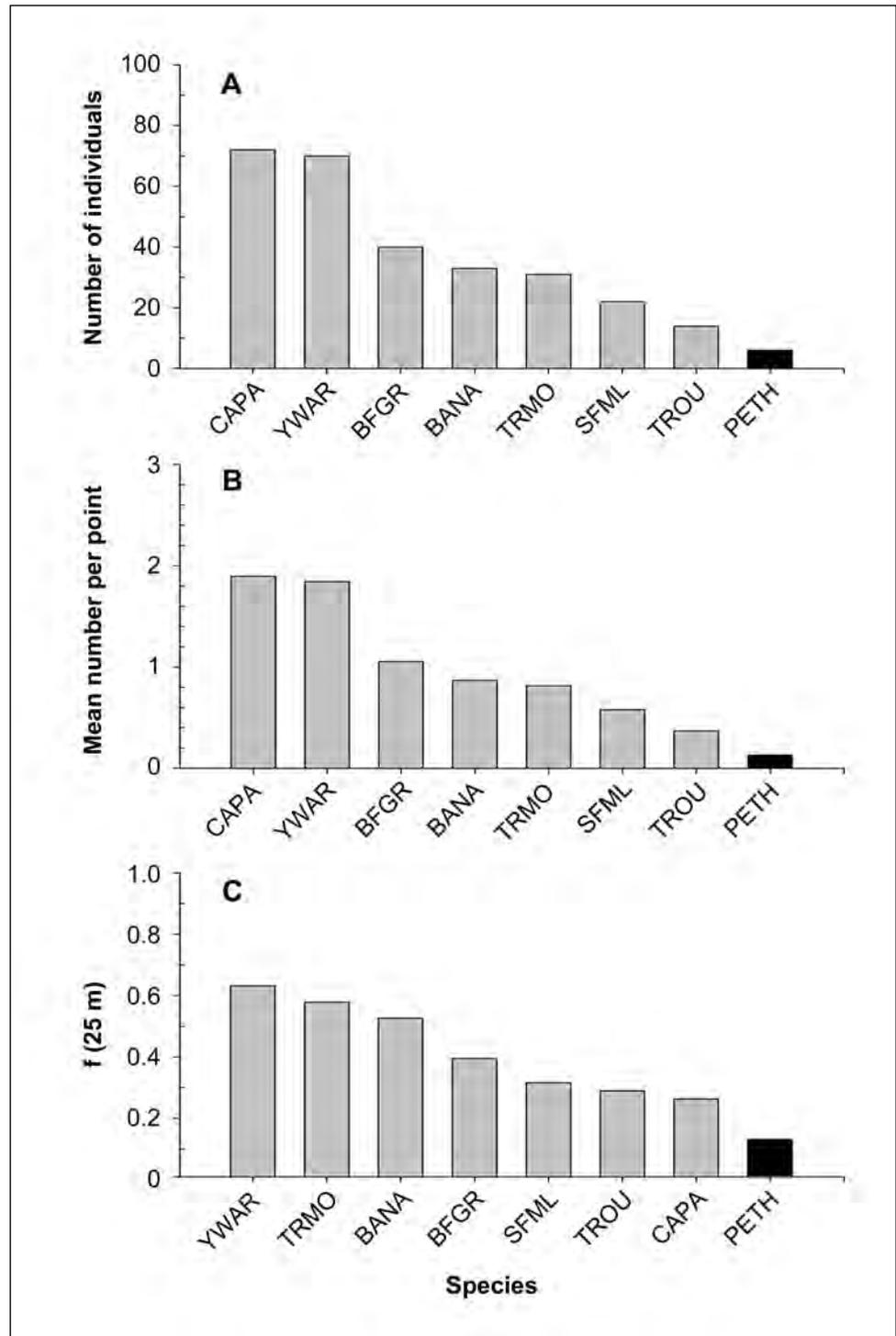


Figure 4.3—Comparative abundance of the pearly-eyed thrasher (PETH) and the seven most common species found within the Washington-Slagbaai National Park, Bonaire. Few thrashers were observed and had a limited, patchy distribution within the park. All pearly-eye sightings were at, or near, the park’s two permanent sweet-water wells (Pos Mangel and Put Bronswinkel). Because Bonaire is not part of the West Indian faunal region per se, the smooth (or northern scrub) flycatcher (*Sublegatus*, gen. nov. *arenarum*, synonym. *modestus*) (SMFL) and the Caribbean parakeet (CAPA) are not listed in appendix 1 as are the remaining species in this figure. The parakeet is classified as *Aratinga pertinax* and is also known as the brown-throated parakeet (AOU 1998). In graph 4.3C, “f (25 m)” is the frequency of occurrence at ≤25 m.

(4) of the other 7 species were detected at 40 percent or more of the 40 points, pearly-eyes were detected at only five (13 percent) of the 40 points (fig. 4.3c).

Information gathered through interviews with local residents living in urban areas suggests that pearly-eyes are attracted to the more settled areas, taking advantage of the increased human-supplied water and food sources. Those interviewed mentioned seeing thrashers drink from seasonal standing water on concrete surfaces or from other human-made structures such as open drains. Thrashers are often observed eating the fruits of citrus and ornamental trees, and they readily prey on the increased populations of vertebrates and invertebrates associated with such human-induced food sources. Frater van der Linden (1992, in litt.) also mentioned that pearly-eyes congregate in and around residential areas especially during the dry season (see discussion under “Pugnacity” in chapter 8). As on other Caribbean islands, it is highly probable that increased human settlement is a major cause for the pearly-eye’s population expansion on Bonaire.

Concluding from the examples outlined above, it appears that the pearly-eye is increasing and extending its numbers at both the northern and southern extremes of its current range.

History of Regional Abundance

Virgin Islands

The pearly-eyed thrasher inhabits numerous islands and cays, all varying in size and topography, along the full length of the Caribbean Islands Archipelago. Thrasher abundance differs significantly throughout the region. For many years, the status of thrasher populations on various islands has been summarized by using general terminology, e.g., rare, uncommon, common, or abundant. For example, in the U.S. Virgin Islands, thrashers are relatively abundant on all islands (University of the U.S. Virgin Islands 1988). Robertson (1962) reported the pearly-eye as “...probably the most abundant bird on St. John and certainly the most conspicuous land bird.” He found it from the coast to above 360 m on Bordeaux Mountain and at every locality visited except in the dense stands of cactus around Concordia Bay and Ram Head. Today, the pearly-eyed thrasher is the most abundant landbird in the U.S. Virgin Islands (Norton 1980). In the neighboring British Virgin Islands (BVI), pearly-eyes are most abundant on Tortola and Virgin Gorda. On Tortola, the pearly-eye is most abundant in coconut plantations and at mid elevations, where it is the most numerous landbird in the taller, denser vegetation (Mirecki et al. 1977). Its preference for taller vegetation may account for the thrasher’s scarcity or even absence on the smaller, flatter, windswept islands of the BVI group (Mirecki et al. 1977).

Thrasher abundance differs significantly throughout the region.

Sombrero Island and Anguilla

Status and abundance of the pearly-eye appear uncertain in the BVI's two most pelagic islands, Anegada and Sombrero. Nichols (1943) reported pearly-eyes from the BVIs including Anegada. LaBastille and Richmond (1973) reported a single individual near a freshwater pond in May 1970. However, the species' residency on Anegada is doubtful. More recently (7 to 8 October 1994), not a single individual was observed during a 2-day census (Arendt 1995, unpubl. rep.). It is possible that pearly-eye sightings on Anegada constitute dispersing individuals that apparently cannot establish a resident population.

There is but a single record of the pearly-eye from Sombrero Island. Lawrence (1867) reported that A. Julien collected a specimen from the island on 28 September 1863 (see also Ogden et al. 1985). On nearby Anguilla, by the late 1800s pearly-eyes were becoming rare, possibly owing to the island's low relief and conversion of much of the land to cattle grazing (Sclater 1892). Although the literature is scant regarding recent avian studies from Anguilla, Raffaele et al. (1998) considered the pearly-eye common there. More recently, as part of the Important Bird Areas initiative, Julian Hughes visited Anguilla during January and February 2000. On behalf of the Anguilla National Trust, Hughes produced the country's first checklist (for more details, see: <http://www.birdtours.co.uk/tripreports/caribbean/anguilla/index.htm>). Hughes reported the pearly-eyed thrasher as "Locally common throughout Anguilla, in scrub and trees around human settlements. The north and west of the island appears to contain the highest numbers." Thus, as on other islands, the pearly-eye has recovered by taking advantage of human-altered habitats and the increased food and nesting resources accompanying continued development.

Netherlands Antilles

Among the northern Netherlands Antilles (combined landmass of 993 km²), the pearly-eyed thrasher is more common in dense vegetation at higher elevations. On St. Martin, Danforth (1930b) reported thrashers locally common in the denser, brushy woods remaining on the higher peaks (max. elev. 424 m). Voous (1983) reported pearly-eyes common on this species-poor island, stating that the only common landbirds besides thrashers are bananaquits, gray kingbirds (*Tyrannus dominicensis*), black-faced grassquits (*Tiaris bicolor*), and common ground-doves. On Saba, Danforth (1938) reported the pearly-eye as the most common landbird, found from sea level to the highlands (max. elev. 870 m). It was found even in cloud forest at the highest elevations. On nearby St. Eustatius, Voous (1983) reported pearly-eyes as less common in the desert scrub, and more common at

higher elevations of the Little Mountains, especially in the remnant rain forest within the cone of the extinct Quill volcano (600 m elev. at its upper rim).

St. Kitts and Nevis

Pearly-eyes have been reported as common on St. Kitts and Nevis, the two remaining high relief islands of the Leewards. On St. Kitts, Danforth (1936a) reported the pearly-eyed thrasher as “...abundant in the high forest on the Crater...” On Nevis, Danforth (1936a) reported the thrasher as the only common bird in montane forest. Lawrence (1879a) reported that pearly-eyed thrashers were becoming less common on Antigua by the end of the 1800s, being found only in the valleys among the southern hills where rivulets and trees remained.

Need for More Standardized Census Methods

As informative as the preceding historical and contemporary accounts are concerning the pearly-eye’s numbers on various islands, the terms used by the different authors such as “common” and “abundant” are relative and differ from person to person. Clearly, there is a need for a quantitative means of assessing thrasher populations. However, arriving at such a goal is not an easy matter (review methodologies and techniques in Ralph and Scott 1981). I have assessed thrasher populations quantitatively by using a combination of capture-recapture and standardized aural-visual census methods (see Arendt 1993 for methodology).

Comparisons of Regional Abundance

Mist Netting

Following standardized mist-netting procedures and regimes used as early as 1972 by John Terborgh and his students from Princeton University (Terborgh 1973, Terborgh et al. 1978), I began sampling Caribbean birds in 1979. For the present study, netting was used through 2000 to census the relative abundance (total number of captures relative to all captures) of resident forest birds, including pearly-eyes, in wet- and dry-forest habitat on 20 West Indian islands (for particulars, see app. 2, Faaborg 1985, Faaborg and Arendt 1985, Faaborg et al. 2000). Results of dry vs. wet-forest comparisons for 21 sites on 12 of the 20 sampled islands harboring resident thrasher populations are presented in figure 4.4. Numbers of pearly-eyes captured ranged from 1 individual (Antigua, Guadeloupe, and Marie Galante) to 174 individuals (Mona—discussed under “Density Compensation” below) per banding session in dry forest, and from 0 individuals (Dominica and Guadeloupe) to 82 individuals (Jubilee Heights, Montserrat) per site during each session in mesic and wet forest. Capture rates of all individuals of every species

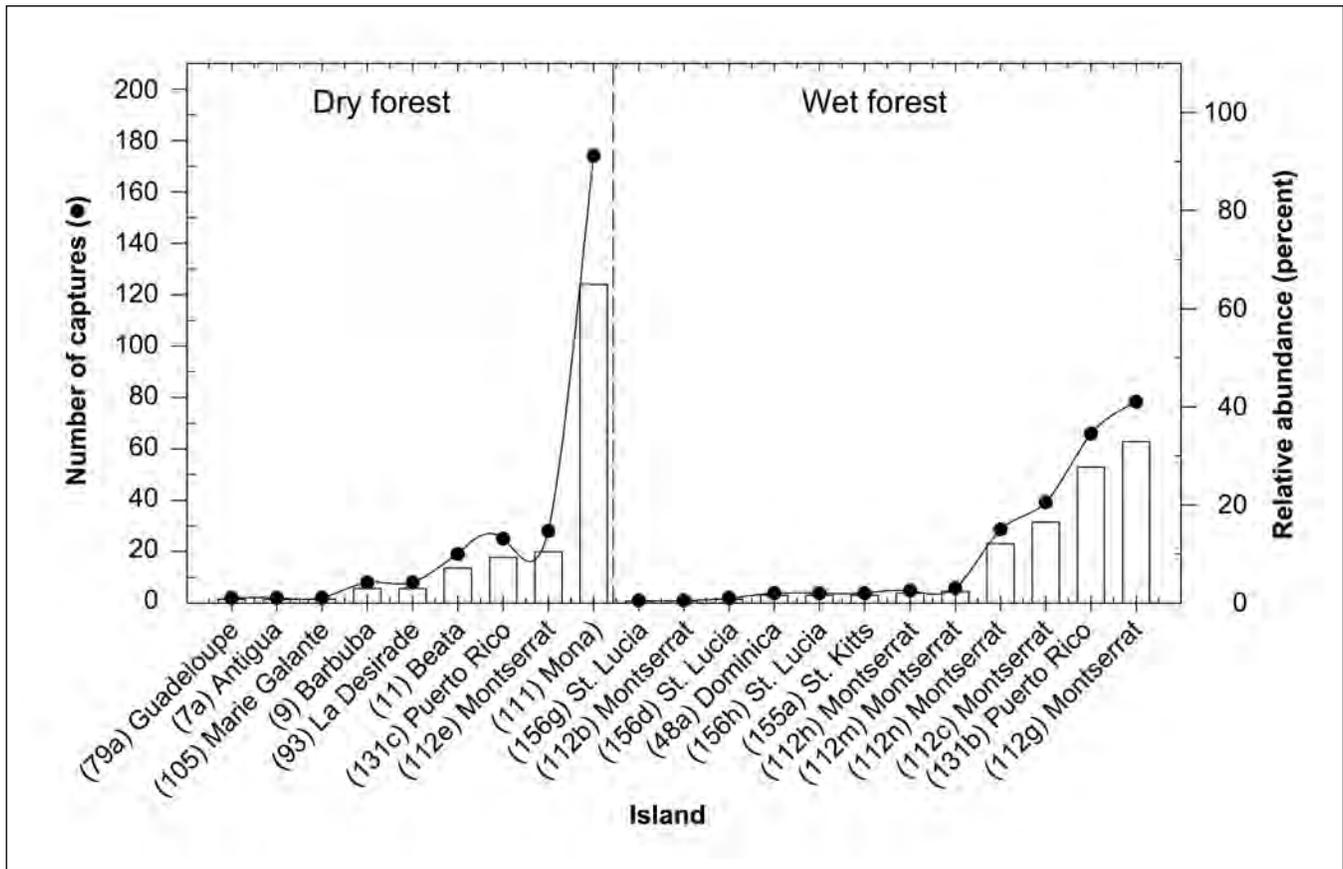


Figure 4.4—Capture rates (number of individuals) and relative abundance (percentage of total captures) of pearly-eyed thrashers at 21 sites on 12 West Indian islands in which the pearly-eye breeds. Results are based on a standardized mist-net sampling technique (see “Study Area and Methods” for details). In dry forests, pearly-eyes reached their highest relative abundance on islands in which, because of ecological release, it undergoes density compensation (e.g., Mona and Montserrat). In wet forests, pearly-eyes can constitute as much as 60 percent of the total captures. Respectively, island and forest type numeric and alpha codes follow appendix 2: 79a Basse Terre; 131b Caribbean National Forest; 112b Chances Peak; 112c Dannenberg Estate; 156d Forestière; 112e Garibaldi Hill; 93 Grand Anse; 131c Guánica; 112g Jubilee Heights; 112h Killiekrankie; 155a Lodge’s Estate; 48a Morne Plaisance; 11 NE near prison; 156g Pitón Flore; 111 Plateau; 105 Pointe des Basses; 156h Quillesse; 7a Shirley Heights; 9 Trail to Darby Cave; 112m Upper Pond; and 112n Wilkes’s Ghaut.

per 3-day netting session ranged from 66 (Cas-en-Bas, St. Lucia) to 474 individuals (trail to Darby Cave, Barbuda) per site in dry forest, and from 25 (Chances Peak, Montserrat) to 300 individuals (Quillesse, St. Lucia) per site in wet forest.

Excluding density-compensation islands such as Mona, in the absence of ecological stressors, e.g., prolonged droughts (see below), relative abundance of pearly-eyed thrashers ranges from <1 to 45 percent in dry forest and <1 to 59 percent in wet forest. To date, dry forest (Guana Island) is the habitat type in which I have found the highest relative abundance of thrashers (see “Point Counts” section). Nonetheless, on a regional scale, pearly-eyes tend to be consistently more abundant in wet-forest habitats.

The pearly-eye’s abundance in wet-forest habitat, especially at mid elevations, has been observed in the past, e.g., Kepler and Kepler (1970) in Puerto

Rico, Diamond (1973b) in St. Lucia, and Lack (1976: 366) in Dominica. This is not surprising because as a secondary cavity nester (Arendt 2004a), the thrasher prefers large trees which, generally, are most common in wet forests found at mid elevations.

The pearly-eye's high relative abundance in wet forest may be partially explained in terms of its supertramp status. It is well known that the wet forests of West Indian islands are generally more depauperate in bird species than dry forests (Terborgh and Faaborg 1980). As a supertramp, *Margarops* should survive better in species-poor communities as well as on species-poor islands. As an example, in Puerto Rico, there are about 20 species of resident forest birds in the Sierra de Luquillo, which harbors wet and hygrophylous forest types, whereas there are some 40 resident species in dry forest within the Guánica Commonwealth Forest and Biosphere Reserve (hereafter, Guánica Biosphere Reserve) (Hernández-Prieto 1993, Kepler and Kepler 1970, and Faaborg et al., ongoing monitoring).

On a regional scale, Terborgh and Faaborg (1980: fig. 1) used mist-net censuses to show that species richness is greater in dry than in wet-forest habitat. They postulated that a limit to the tolerance of competitors imposes a ceiling on diversity, offering many examples. Their discussion also included special note of the pearly-eye's distribution.

Based on mist-net captures on the 12 sampled islands in which the pearly-eye is resident, it reached its highest relative abundance in the wet forests of Puerto Rico and Montserrat (fig. 4.4). In Puerto Rico, within the Sierra de Luquillo, the pearly-eye is most abundant in the colorado (*Cyrilla racemiflora* L.) forest type at mid elevations, although it is found from forest edge to cloud forest (Snyder et al. 1987, Wiley and Bauer 1985, pers. obs.). As an example, in colorado forest at elevations between 500 and 800 m, the relative abundance of the pearly-eyed thrasher is about 30 percent (penultimate bar—no. 4 “El Yunque”—in “Wet forest” fig. 4.4). Although capture rates fluctuate greatly among seasons, it is possible to capture as many as 25 to 30 pearly-eyes (Arendt, unpubl. data) during a standard 3-day netting period. This is quite a substantial total capture in comparison with the numbers captured in other forest types within this forest. Contrarily, within the tabonuco (*Dacryodes excelsa* Vahl.) forest type near the forest's border at Sabana, located at an elevation of about 350 m, Faaborg and Terborgh (1980) failed to capture a single pearly-eye using the same 3-day netting regime.

On Montserrat, during banding operations in 1975, of 209 wet-forest birds sampled, 41 (20 percent) of the captures were pearly-eyes (Terborgh et al. 1978: table 4). Almost a decade later (1984), I sampled birds in dry and wet-forest

The pearly-eye's high relative abundance in wet forest is partially explained in terms of its supertramp status.

habitats over most of the island. In net samples taken at Fox's Bay and within each of Montserrat's three major hill regions (Centre, Soufrière, and South Soufrière Hills), pearly-eye numbers had increased to the point that they made up about 50 percent of the captures at three of the six banding sites. Moreover, of the 389 birds captured at all 6 sites, 152 individuals (39 percent) were pearly-eyes (Faaborg and Arendt 1985). In March 1990, 6 months following Hurricane Hugo (September 18, 1989), mist netting was virtually impossible because of the volume of felled trees and debris left by the storm. However, I conducted standard mist-net sampling at three of the original six banding sites: Upper Pond, South Soufrière Hills (cloud forest), Jubilee Heights, Centre Hills (wet forest), and Garibaldi Hill (dry forest). On average, pearly-eyed thrashers constituted 43 percent of the captures at the three sites: 44, 65, and 21 percent, respectively (note the significant decrease at the species-rich dry-forest site). The pearly-eye may have reached the carrying capacity of the remaining habitats on Montserrat.

Of the 12 wet-forest sites sampled on 5 islands, the relative abundance of the pearly-eyed thrasher was low at 6 sites on 4 islands (St. Lucia, Dominica, St. Kitts, and Montserrat cloud forest) (fig. 4.4). Species richness is relatively high in the wet forests of both St. Lucia and Dominica, which may partially account for the thrasher's scarcity in such habitats on those islands. The single site within Montserrat's wet-forest habitats with a low relative abundance was in cloud forest at the summit of Chances Peak, the island's highest peak (about 900 m prior to the 1990s volcanic eruptions). Thrashers are usually scarce at higher elevations in general, and in cloud forest in particular (see Beissinger et al. 2005 and Cook et al. 2003, 2004, 2005, for a plausible explanation). The pearly-eye's low numbers in the wet forests of St. Kitts is somewhat puzzling, especially as species richness is also low.

Variable-Width Line Transects

Rain-forest habitat—

Because of the inconspicuousness of many forest birds, aural-visual techniques often overlook the more secretive individuals. Thus, mist netting is often preferred when the main objective is to sample understory birds, especially the more reticent species. However, there are inherent problems associated with mist netting, especially in tall-statured forests and when time and personnel are extremely limited (see Waide and Hernández-Prieto 1981 for a comparative review of census methods and their tradeoffs, emphasizing Puerto Rican rain-forest vegetation). In these situations, mist netting should be used in conjunction with aural-visual census methods to obtain a reliable estimate of species richness and relative abundance of each species.

For years, many ornithologists interested in estimating densities per unit area favored a variable-width line-transect census technique designed by Emlen (1971) to census terrestrial bird populations. Working within the Luquillo Experimental Forest, Puerto Rico, Snyder et al. (1987) used a modified “Emlen method” in conducting 12 monthly censuses between 1970 and 1971. They found that, of 17 resident species, the pearly-eye was among the three most abundant in colorado forest (preferred habitat), and among the four most abundant in tabonuco forest (second most preferred habitat), but rather sparse in sierra palm (*Prestoea acuminata* var. *montana* [Graham] Nicholson) and cloud (dwarf) forest (Snyder et al. 1987: table 4.4). A decade later, Arendt conducted 45 monthly censuses (15 per year, 5 in each forest type) between March and July from 1980 to 1982 in the previous authors’ four study areas. However, only two censuses were carried out in cloud forest habitat (El Toro Trail) in May and June 1982. During the more than 10-year lapse between censuses, thrasher populations almost doubled in all four sampled areas (table 4.1) but, remained scarce in sierra palm and cloud forest. To make a 10-year comparison with the 1980, 1981, and 1982 results, and about a 20-year comparison overall, Emlen censuses were conducted in May and June of 1992. Results show that during the third decade, the thrasher population in the Sierra de Luquillo leveled off, and now, as a result of constant-effort monitoring, there are signs that it is on a slight decline (see text under “Study Area and Methods”).

Over the past three decades the thrasher population in the Sierra de Luquillo leveled off, and is now on a slight decline.

Table 4.1—Twenty-two-year comparison of pearly-eyed thrasher abundance^a in the Sierra de Luquillo, Puerto Rico

Years	Forest type				Reference
	Tabonuco	Colorado	Sierra palm	Cloud	
1970–71	8.0	8.9	1.5	0.9	Snyder et al. (1987)
1980–82	13.5 (9–26)	17.5 (5–17)	2.2 (1–7)	1.5 —	This study
1992	12.7 (3–15)	19.3 (9–28)	2.9 (1–11)	1.3 (0–3)	This study

— = no data.

^aTabular entries are mean number of thrashers seen and heard per kilometer by using the Emlen (1971) line transect census method. Numbers in parentheses are minimum and maximum numbers of individuals detected. All minimum numbers occurred before the main breeding season (e.g., November–March), whereas all maximum numbers occurred during the main breeding season (May–June).

Each year, the presence of 30 to 40 thrasher nest boxes, forming part of my long-term thrasher research within a few kilometers of the census areas, may account, at least in part, for the precipitous increase during the first decade following Snyder et al.’s censuses. Also, each year beginning in 1972, thrasher boxes have been available for occupancy in known and potential Puerto Rican parrot

(*Amazona vittata*) nesting areas (James Wiley 1992, pers. Comm.; Victor Cuevas 1992, pers. Comm.; and personal involvement). However, in light of the exceedingly high densities of thrashers recently found on other islands (see point-count results below), it is unlikely that a few artificial nest boxes have significantly increased the pearly-eyed thrasher population in the Sierra de Luquillo (see also discussion in the “Preface”).

Dry-forest habitat—

In dry forest within the Guánica Biosphere Reserve, when Kepler and Kepler (1970) assessed species richness and relative abundance of its forest birds, the relative abundance of the pearly-eye was <1 percent (10 thrashers observed out of 1,821 individual birds). Twenty-eight years of mist-net censuses reflect an average relative abundance of about 7 percent (134 thrashers out of about 2,000 total new captures). Thus, although aural-visual and mist-net census techniques are not comparable, both methods in the above examples show that the Guánica dry-forest thrasher abundance is low—much lower than in the wetter Sierra de Luquillo.

In conclusion, as evidenced by numerous investigators working in several different localities, pearly-eyes are more abundant in a species-poor, highland rain forest than in a more species-diverse, lowland dry forest in Puerto Rico, but thrasher populations fluctuate widely on a temporal basis. This is a common characteristic of r-selected, tramp species.

Point Counts

Hutto et al. (1986) designed a fixed-radius point-count method that can be used to generate data for either a density estimate or a relative index of bird abundance. Because of its convenience (cost effective in personnel and time spent in the field), it gained popularity over the years and was often preferred in comparative studies of bird populations for almost a decade before the advent of the more recent distant sampling method (Buckland et al. 1993). To compare data gathered by others on the abundance of the pearly-eye in Puerto Rico (tabonuco forest), St. John, and St. Thomas (dry and mesic forest), I conducted a series of fixed-width point counts in additional forest types (colorado and cloud forest) in Puerto Rico (1989 to 2000) and in dry- and wet-forest types in Montserrat (1990, 1997).

As shown previously by mist-net censuses, with the exception of Guana Island (see below), results from point-count censuses also show that the pearly-eye reaches its highest abundance in the dry and wet forests of Montserrat (table 4.2 and fig. 4.5). Note that in Puerto Rico’s tabonuco and cloud forest types, thrasher abundances are lower than all four dry-forest sites in Montserrat (table 4.2). To attach significance to the abundance results shown in table 4.2, a Kruskal-Wallis

Table 4.2—Descriptive statistics of thrasher abundance derived from fixed-radius point-count censuses in dry and wet forests on five West Indian islands between 1987 and 1994^a

Forest type and island	Number of points (n)	Number of individuals per point		
		Mean	±SE	Mode
Dry forest:				
80. ^b Guana Island (BVI ^c)	60	2.12	0.22	2
112. Montserrat (e)	30	1.24	.10	1
154. St. John ^d (a)	107	.81	.06	1
158. St. Thomas ^d (a)	18	.61	.16	0
Moist and wet forest:				
112. Montserrat (f, g, i, j, k, l, n)	50	1.89	0.19	2
131. Puerto Rico (b)	317	1.58	.07	1
154. St. John ^d (b)	181	1.4	.06	1
112. Montserrat (a, b, m)	40	1.08	.1	1
158. St. Thomas ^d (b)	37	.89	.12	1
131. Puerto Rico (a)	309	.24	.03	0
131. Puerto Rico ^e (c)	293	.2	.03	0

^aSee table 4.3 for a statistical comparison of thrasher numbers within and among forest types on four of the five islands.

^bRespectively, island and forest type numeric and alpha codes follow those in appendix 2.

^cBVI (British Virgin Islands).

^dData for St. John and St. Thomas, U.S. Virgin Islands (1987, 1990, 1992), courtesy of R.A. Askins, D.N. Ewert, and R.L. Norton.

^eData for (131c) tabonuco forest in Puerto Rico (1989-1991), courtesy of R.B. Waide.

One-way ANOVA on Ranks test (hereafter K-W ANOVA) was conducted by using the mean number of detections per count within a 25-m radius of each point ($H = 466.4$; $df = 9$; $P < 0.001$). A matrix of pair-wise comparison probabilities resulting from Tukey's HSD (post-hoc) Multiple Comparisons Test is presented (table 4.3). Results show that, in general, the pearly-eye is significantly more abundant in moist and wet forest than in dry forest. But, there are exceptions (see below). Thrashers are significantly more abundant in Montserrat wet forest than in wet forest on any other island that I have sampled. Likewise, the pearly-eye is significantly more abundant in Montserrat's dry forest than in either of the U.S. Virgin Island's dry forests.

In 1994, the pearly-eyes inhabiting tiny (299 ha) Guana Island (xeric vegetation with a max. elev. of 245 m) in the BVIs were sampled by using a fixed-radius point-count census method (Arendt 1995, unpubl. rep.). The mean number of individuals per 25-m-radius point count was 2.12, the highest number yet recorded for either dry or wet forest (compare with table 4.2 means). Thus, whereas thrasher abundance is generally higher in wet-forest habitat, there are notable exceptions. For example, although he used a somewhat modified point-count census method,

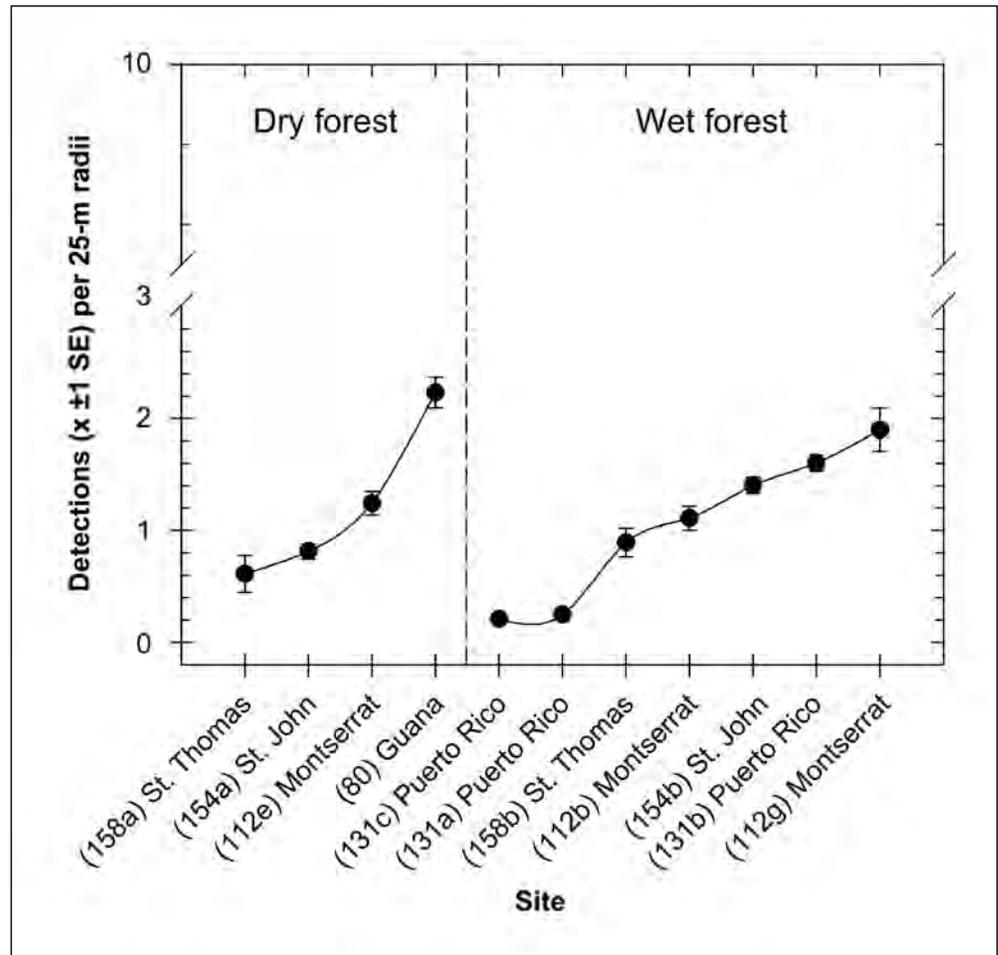


Figure 4.5—Relative abundance of pearly-eyed thrashers detected during fixed-radius ($\leq 25\text{ m}$) point-count censuses in dry and wet forests on five islands. With a few notable exceptions, in general, the pearly-eye is more abundant in moist- and wet-forest rather than in dry-forest habitats. Pearly-eyes are especially abundant in the dry and wet forests of Montserrat, an island on which the thrasher undergoes density compensation as a result of ecological release. Island and forest type numeric and alpha codes follow appendix 2: 158a fragments of dry forest; 154a extensive tracts in dry evergreen woodland; 112e Garibaldi Hill (trail to Fox’s Bay); 80 dry forest (Guana Island); 131c Guánica; 131a Cabezas de San Juan lighthouse, Fajardo; 158b fragments in moist forest; 112b Chances Peak, summit near fresh water pond (Soufrière Hills); 154b extensive tracts in moist forest; 131b Colorado forest (*Cyrilla racemiflora* L.) Icos Valley, Luquillo Experimental Forest; 112g Jubilee Heights (Centre Hills). Capped vertical bars (\perp , \top) are ± 1 standard errors. Data for St. John and St. Thomas, U.S. Virgin Islands, were supplied by R.A. Askins, D.N. Ewert, and R.L. Norton; for the two islands, 207 samples were taken, averaging 52 (min. = 35, max. = 75) samples per habitat. Data for Puerto Rico’s tabonuco forest type were supplied by R.B. Waide (n = 293 samples).

As species richness increases, the number of thrashers decreases and it undergoes density compensation on Mona Island.

by sampling four sites within the Guánica Biosphere Reserve (some very close to Faaborg and Arendt’s mist-netting sites), Hernández-Prieto (1993: appendices J through O) found large numbers of pearly-eyes at several well-forested sites. He also showed that as species richness increases, the number of thrashers decreases (Hernández-Prieto 1993: fig. 8b), thus lending additional support to the super-tramp concept.

Table 4.3—Comparison of pearly-eye relative abundance in dry and wet forest habitats on four West Indian islands.^a Presented is a matrix of pair-wise comparison probabilities ($\alpha = 0.05$) resulting from Tukey’s HSD post-hoc multiple comparisons test. Clearly, pearly-eyed thrasher abundance varies significantly among islands and forest types

	Forest type ^a									
	MTDRY	SJDRY	STDY	MTCDF	PRCDF	PRCF	PRTF	MTWET	SJWET	STWET
MTDRY	1.00									
SJDRY	.00	1.00								
STDY	.00	.08	1.00							
MTCDF	.97	.87	.23	1.00						
PRCDF	.00	.00	.00	.00	1.00					
PRCF	.00	.77	.98	.36	.48	1.00				
PRTF	.00	.00	.00	.00	.99	.17	1.00			
MTWET	.00	.00	.00	.02	.00	.00	.00	1.00		
SJWET	.57	.00	.00	.89	.00	.00	.00	.03	1.00	
STWET	.13	.99	.41	.99	.00	.71	.00	.00	.00	1.00

^aRespectively, island and forest type numeric and alpha codes follow those in appendix 2: 112(e) Montserrat dry forest (MTDRY); 112(a, b, m) Montserrat cloud forest (MTCDF); 112(f, g, j, k, l, n) Montserrat moist and wet forest (MTWET); 131(a) Puerto Rico cloud forest (PRCDF); 131(b) Puerto Rico colorado forest (*Cyrilla racemiflora* L.) (PRCF); 131(c) Puerto Rico tabonuco forest (*Dacryodes excelsa* Vahl.) (PRTF); 154(a) St. John dry forest (SJDRY); 154(b) St. John wet forest (SJWET); 158(a) St. Thomas dry forest (STDY), and 158(b) St. Thomas wet forest (STWET).

Density Compensation in Mona Island Birds

Of the nine dry-forest sites sampled, the relative abundance of the pearly-eye is low in all but two islands, Mona and Montserrat (fig. 4.4). Mona is a very small island that experiences extended droughts. Consequently, it has very few permanent resident landbirds. Only tramp species such as the thrasher, gray kingbird, and common ground-dove abound there. The results of a comparison of total captures and the relative abundance of pearly-eyed thrashers mist-netted in dry forest on Mona and the Guánica Biosphere Reserve on nearby Puerto Rico are presented in fig. 4.6. Although there are no significant differences in capture rates or relative abundances of other forest birds at either site, the capture rate and relative abundance of pearly-eyes on Mona are significantly higher than those in the Guánica reserve. Mist-net results clearly show that the pearly-eye undergoes density compensation on Mona. Encouragingly, the mist-net results under discussion (and those that follow) are in full agreement with results of a comprehensive avian community study using aural-visual census techniques conducted by Hernández-Prieto (1993). He compared avian species richness and abundance, among many other parameters, on a year-round basis and over several years (1986 to 1990) on Mona Island and within the Guánica reserve.

Like the pearly-eye, the common ground-dove (a D-tramp) is abundant on Mona Island, and it is also exemplary of density compensation in an avian tramp

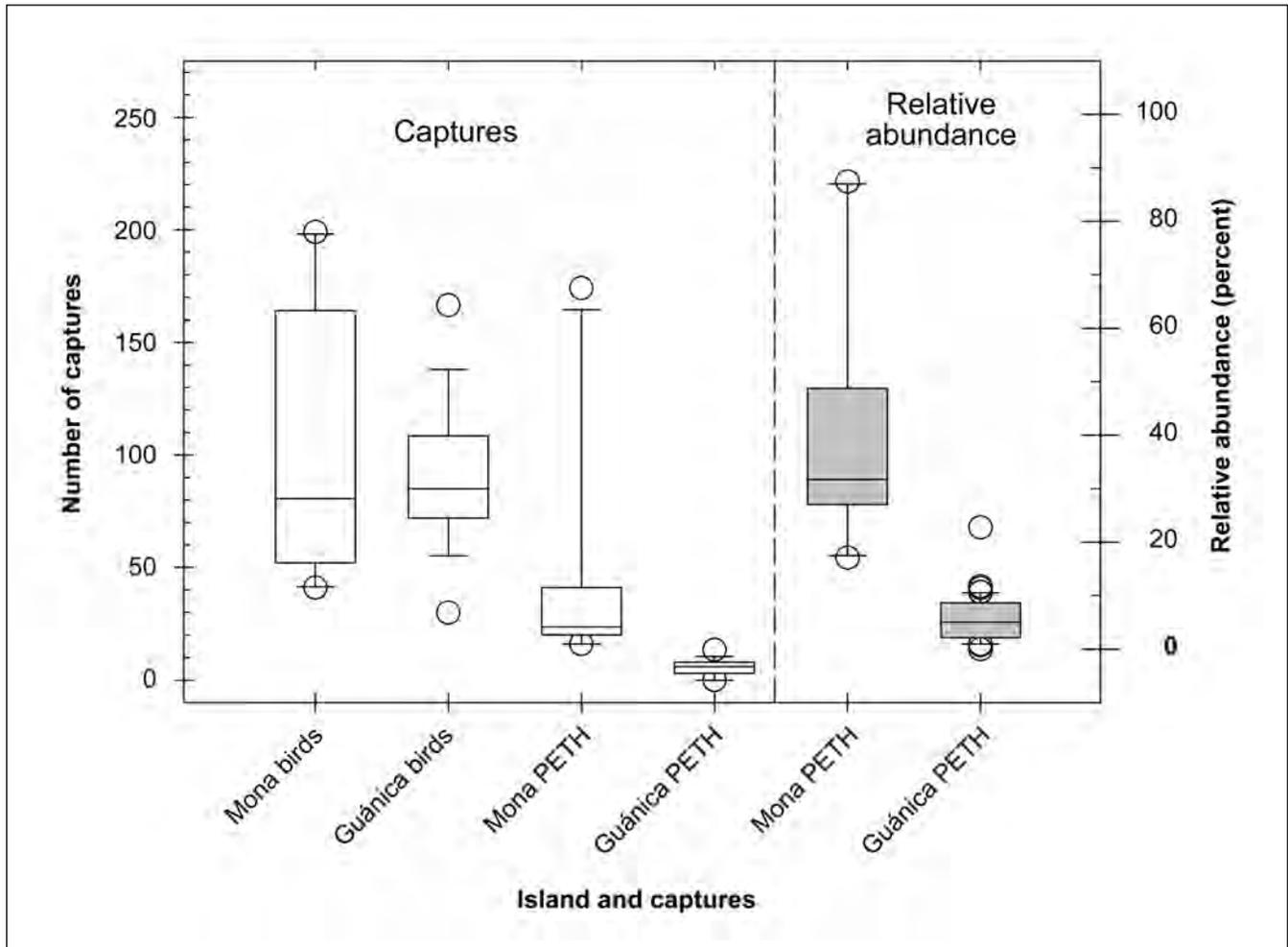


Figure 4.6—Capture rates and relative abundance of pearly-eyed thrashers (PETH) and other dry forest birds in mist-net samples from the Guánica Commonwealth Forest and Biosphere Reserve, Puerto Rico, and nearby Mona Island. Whereas captures of other birds are similar on both islands, thrasher numbers and relative abundance (shaded rectangles) on Mona are significantly greater than in the Guánica forest where species richness is much higher. Solid horizontal lines are medians, lower and upper hinges on the rectangles encompass the 25th and 75th percentiles, respectively; lower and upper caps (└, ┘) mark the 10th and 90th percentiles, respectively; open circles below and above the caps mark the 5th and 95th percentiles, respectively.

species. Ecological release and, consequentially, density compensation among Mona Island birds, have been observed by other authors (e.g., Faaborg 1980a, Terborgh and Faaborg 1973). However, the most quantitative information to date confirming previous observations has become available only recently (Hernández-Prieto 1993).

To illustrate the prevalence of, and density compensation in, Mona Island ground-doves, total numbers of individuals captured and relative abundance of the four most commonly netted species are compared (fig. 4.7). Whereas the relative abundance of the dove averages 41 percent ($SE = \pm 8.02$) per sample, with as many as 137 individual captures per sample, that of the remaining three species averages only 5 percent (avg. $SE = \pm 1.66$), with never more than 7 individual

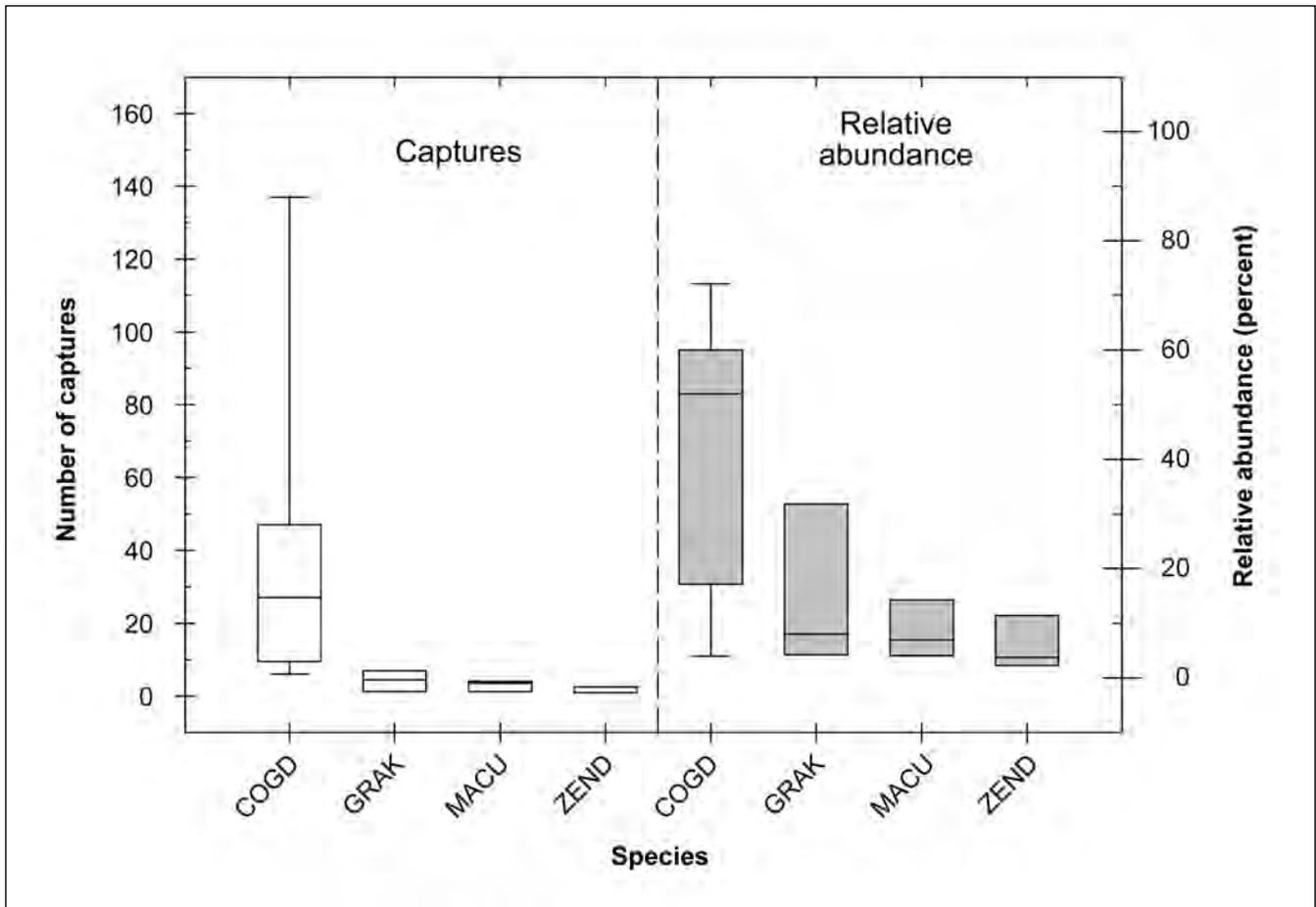


Figure 4.7—Capture rates and relative abundance (shaded rectangles) of Mona Island’s four most common species of resident landbirds. The common ground-dove was the only species clearly showing density compensation as revealed by mist netting. However, more recently, by using a point-count census technique, Hernández-Prieto (1993) showed that all four species undergo density compensation on Mona (see text for further discussion; see app. 1 for species’ four-letter alpha codes; box-plot parameters are explained in fig. 4.6).

captures per sample. It is noteworthy that like the common ground-dove, the remaining three species constituting Mona’s most common resident landbirds are also D-tramps, and are among the eight most widely distributed species in the West Indies (fig. 2.5a).

As a consequence of Hernández-Prieto’s research, all four species treated here (fig. 4.7) were shown to undergo density compensation on Mona, a fact not so apparent in the results obtained by the more brief and area-limited mist-net samples. His findings are not surprising. As D-tramps, all four species are expected to greatly increase in numbers and to broaden their ecological niches in the absence of interspecific competitors for water, food, and nesting resources. Thus, Hernández-Prieto’s data reassuringly confirm Diamond’s argument that tramps can, and often do, undergo density compensation on small, species-poor islands (see also Baker-Gabb 1986, Cox and Ricklefs 1977).

The pearly-eye's impressive abundance in Montserrat's dry forest may be explained in two ways. First, unlike the five low-relief islands on which thrashers are scarce, Montserrat, although also small, is a high-relief island with ample wet-forest habitat in which thrashers are abundant (source population) and undoubtedly continue to supply dry-forest (sink) populations. In addition, unlike in Puerto Rico, species richness in Montserrat's dry forest is low, thus making it easier for thrashers to compete.

The extreme variability in relative abundance of thrashers among islands, habitat types, and even the same, but geographically separated, habitat types is obvious and was anticipated. Not so obvious, however, is the fact that thrasher abundance differs, sometimes significantly, within the same habitat type at a single locale. In dry forest within the Guánica Biosphere Reserve, Puerto Rico, native and migratory forest birds have been monitored by using mist nets for more than 30 years (1972 to 2005) (for a review, see Faaborg and Arendt 1990; Faaborg et al. 2000). Nine sites have been sampled throughout the forest since 1989 to detect microhabitat differences among species richness and relative abundance of the various species. One site (fig. 4.8: Plateau 2) has been monitored for 30 of the 32 years (not sampled in 1977 or 1979). The eight remaining sites have been sampled from 1989 to present, with data analyses pertaining solely to the pearly-eyed thrasher covering a period of seven seasons (1989 to 1995). The relative abundance of pearly-eyed thrashers differs little among six of the nine sites (fig. 4.8), with an average relative abundance of 3 percent (range: 1 to 4 percent) among the six sites. However, the relative abundance of pearly-eyes is significantly higher at the remaining three sites, apparently owing to the more complex, closed-canopy vegetation and more humid microclimates at these sites. Results of vegetative analyses conducted by Hernández-Prieto (1993) along the Dinamita 2 trail show a closed canopy including a 10-m-high karst promontory, and complex vegetation. In an independent study of the vegetative characteristics along the remaining net lines included in figure 4.8, R.C. Kennedy and J.R. Faaborg (1993, in litt.) also found more stems per area at the Dinamita 2 banding site, once again attesting to the more complex and closed nature of the vegetation at this site. Although the relative abundance of pearly-eyes differs greatly among several banding sites within the same forest, as the tramp theory dictates, capture rates are inversely proportional to species richness (fig. 4.9a) (see also "Point Counts" below for discussion of fig. 4.9b).

Thrasher abundance differs, sometimes significantly, within the same habitat type at a single locale.

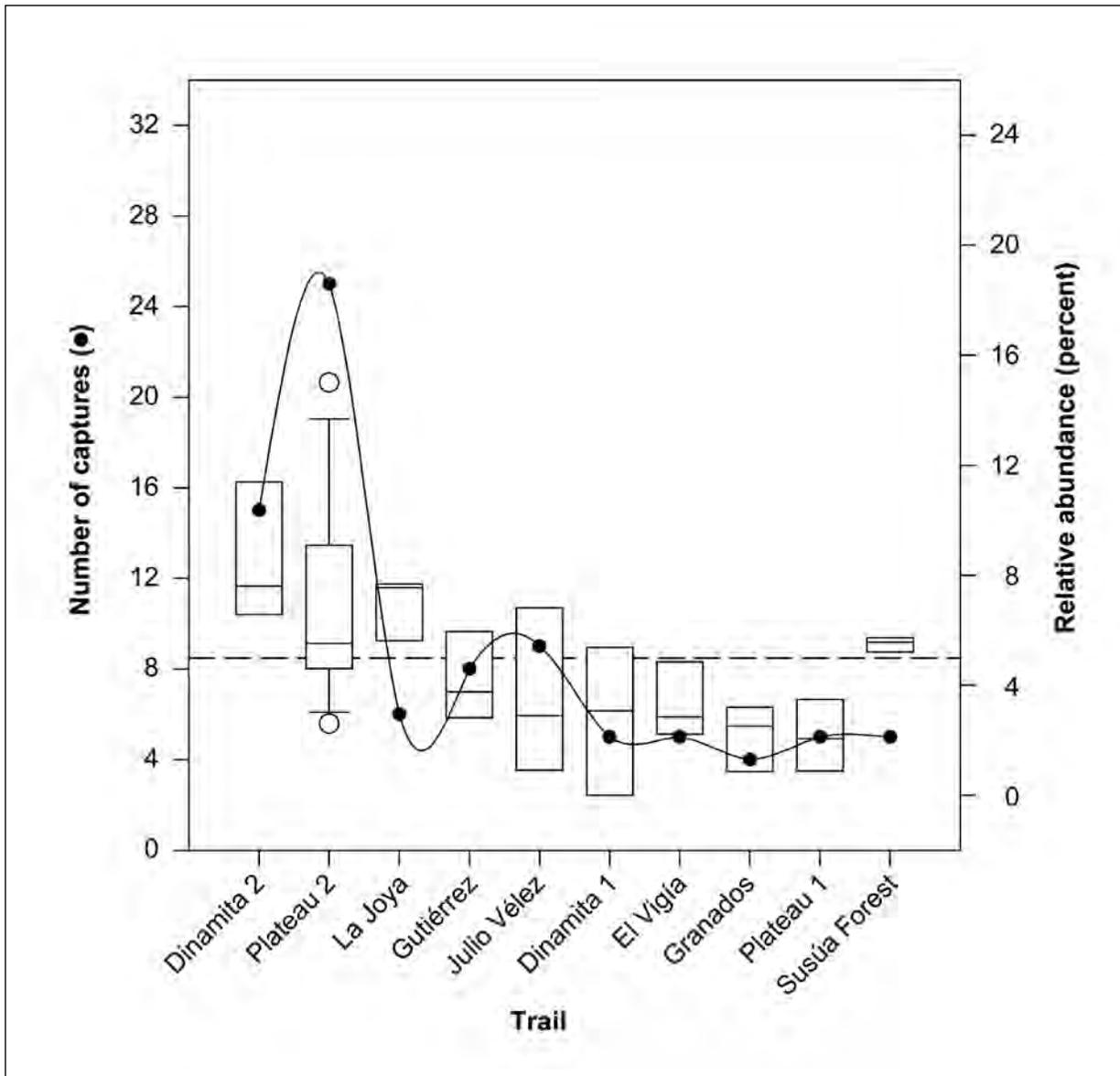


Figure 4.8—Capture rates (●) and relative abundance (box plots) of the pearly-eyed thrasher in mist-net samples at nine sites along trails within the Guánica Commonwealth Forest and Biosphere Reserve, Puerto Rico (spelling of trail names follows that of Silander et al. 1986 and Farnsworth 1991). Susúa Forest captures are included for comparison (see “chapter 4” within “Study Area and Methods”). Capture rates and relative abundance differ significantly among some of the sites. Pearly-eyes prefer moister sites with trees of taller stature, often forming a closed canopy. Plot-wide dotted line shows the overall relative abundance of thrashers among all sites. Box-plot parameters are explained in figure 4.6.

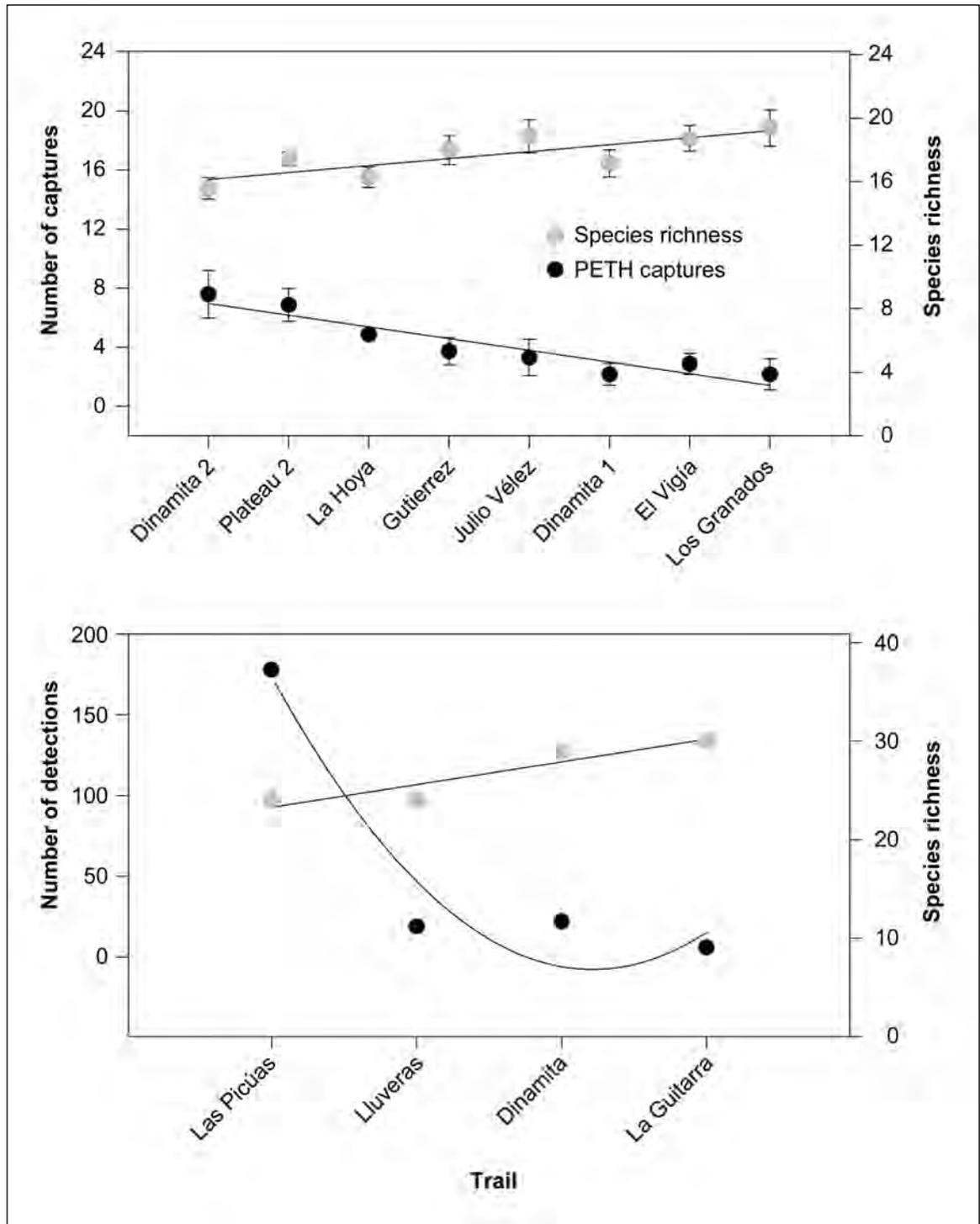


Figure 4.9—Inverse correlations between numbers of pearly-eyed thrashers (PETH) and species richness as a result of mist-net samples (A) and point-count censuses (B) conducted along trails in the Guánica Commonwealth Forest and Biosphere Reserve, Puerto Rico (spelling of trail names follows that of Silander et al. 1986 and Farnsworth 1991). In both sampling techniques, as the supertramp theory dictates, as species richness increases, thrasher numbers decrease. Mist-net data are from a long-term study by Faaborg and Arendt (Faaborg and Arendt 1990, Faaborg et al. 2000), whereas point-count data were taken from Hernández-Prieto (1993).

Extreme Temporal Fluctuations in Mona Island's Thrasher Population

Even on islands where the pearly-eye is common, its populations may undergo significant fluctuations over time. On Mona Island for example, beginning as early as 1903 most visiting ornithologists reported pearly-eyes as common or even abundant (app. 3). Beatty (cited by Bond 1964) found thrashers common along the coast and on the plateau. He estimated that 1,000 thrashers inhabited the island during the time of his visit. Thus, for centuries, the pearly-eye has been a very conspicuous component of the island's resident landbird community. However, some written accounts suggest periodic and, at times, extreme fluctuations in Mona's thrasher population. For example, Rollé (1961b), although listing the thrasher as "common on the plateau" after a visit from November through December 1960, later reported that he had seen "only a few individuals" [?] during his first visit (Rollé 1961a). He concluded that pearly-eyes had undergone "a large reduction in numbers" since the last (1944) avian survey was conducted by Barnés (1946).

Why should the abundant pearly-eye population on Mona undergo such extreme population fluctuations? Mona is a small island with xerophytic vegetation adapted to very dry conditions. Water is scarce at best and is sometimes contaminated; more often it is completely lacking owing to extended drought conditions. The harsh climatic and ecological conditions on Mona apparently impact even highly adaptable species such as the pearly-eyed thrasher.

Seasonal Fluctuations in Mona Island's Thrasher Population

Mist-net censuses of thrashers taken during three "wet-season" months (May to July) and three "dry-season" months (December to February) were used to determine potential seasonal population fluctuations. Banding results (fig. 4.10) are total captures and relative abundance (thrashers as a percentage of total captures) of birds caught during each 3-day banding session. Data were gathered over a 12-year period from two dry-forest sites by Faaborg and his colleagues from 1972 to 1976, and Faaborg, Arendt, and their associates in February 1984. Data were pooled after no significant difference in capture rates of thrashers (Mann-Whitney U -Statistic (hereafter M-W U) = 10.5; $X^2 = 0.15$; $df = 1$; $P = 0.69$) or total birds captured (M-W $U = 13.0$; $X^2 = 1.06$; $df = 1$; $P = 0.69$) was detected between the two banding sites on Mona's extensive plateau region. The relative abundance of pearly-eyes is significantly higher in the "wet-month" samples (range: 42 to 86;

Pearly-eye populations undergo significant fluctuations over time.

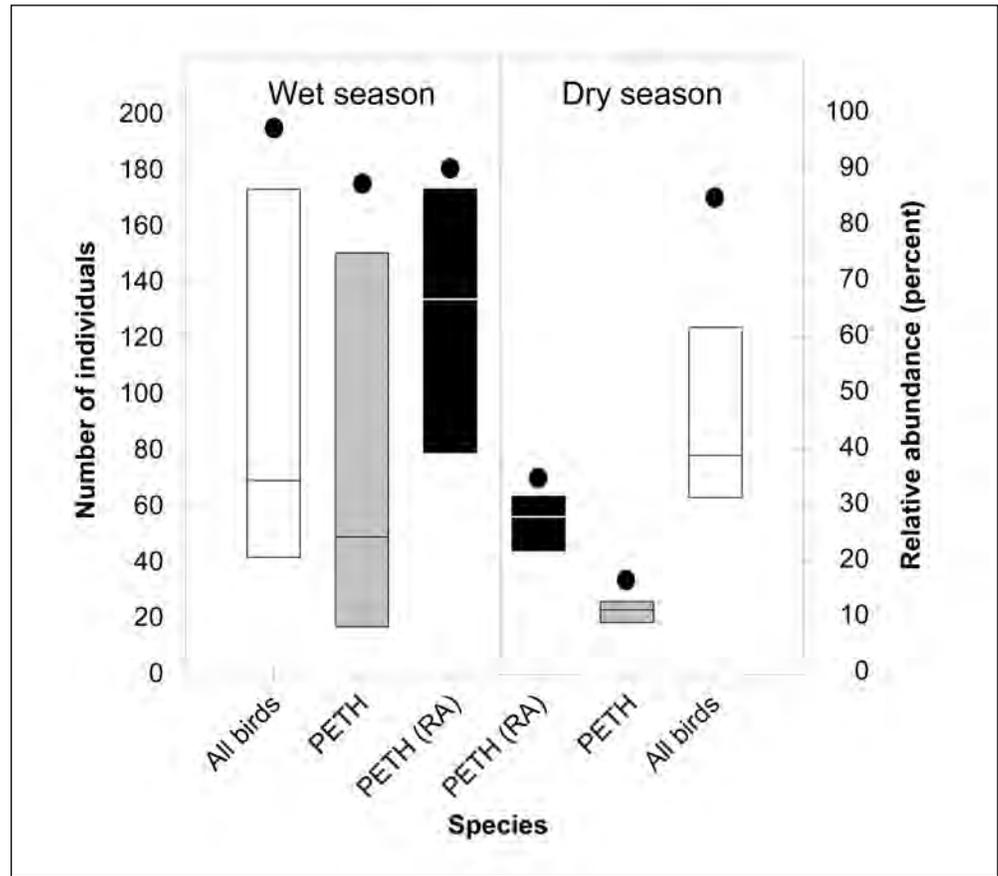


Figure 4.10—Comparison of the total number of individuals and relative abundance (percentage of all captures) of pearly-eyed thrashers (PETH) and all species captured in mist-nets on Mona Island during June and July (wet season) and December–February (dry season) 1972–1984. Whereas median capture rates of other forest birds (unshaded rectangles) are similar during both seasons, the capture rate (gray shaded rectangles) and relative abundance (RA, blackened rectangles) of the pearly-eye are significantly lower in the dry season. Box-plot parameters are explained in figure 4.6.

median = 65 percent) than in the “dry-month” samples (range: 24 to 28; median = 26 percent) (M-W U = 74.5; $X^2 = 9.83$; df = 1; $P < 0.001$). These banding results are illustrative of the highly dynamic seasonal nature of Mona’s thrasher population.

From December to February, some of Mona’s driest months outside of the main thrasher breeding season, populations are generally sedentary and capture rates are low. During June and July, both of which fall within the thrasher’s primary lowland breeding season, thrashers are more abundant and mobile, as adults are seeking food for their young. The low capture rates during January and February suggest that thrashers remain sedentary if there is an adequate supply of water. However, during severe and prolonged droughts, thrashers move long distances in search of food and water. For example, in figure 4.10, the maximum number of individuals (174) captured during a 3-day netting session in the

normally “wet” months of May to July coincides with severe drought conditions occurring on Mona and nearby Guánica reserve during the summers of 1973 and 1974 (J. Faaborg 1982a, and 1983, pers. comm.).

The pearly-eye’s contemporary and historical ranges have been reviewed, and three census techniques have been used to show striking differences in the pearly-eye’s abundance on different islands, among different habitat types, and even spatiotemporally within a single island and habitat. But, what are some of the factors governing the observed range and numbers of the pearly-eyed thrasher?

Environmental Factors Influencing Range and Abundance

Distribution and abundance of the pearly-eyed thrasher have been shown to be dynamic over space and time, and both geographic and demographic parameters continue to change even today. What are some of the principal factors influencing these spatiotemporal components of the thrasher’s range and abundance?

The contemporary range of the pearly-eye is no doubt the culmination of many geological, climatological, ecological, genetic, and human-induced influences acting together over many millennia (see discussions in Ricklefs 1989; Vuilleumier and Simberloff 1980; Wiens 1989a, 1989b).

From an autecological perspective, three of the most obvious environmental factors influencing the thrasher’s distribution and abundance are climate and two human-induced factors, namely habitat destruction and hunting.

Climate

Climate, past and present, no doubt has greatly influenced the pearly-eye’s historical and contemporary ranges. Using the vertebrate fossil record and sea level changes, Pregill and Olson (1981) showed that environmental conditions in the West Indies during the last Pleistocene glaciation favored predominantly arid savanna, grassland, and xeric scrub forest. Subsequent environmental changes that led to more mesic habitats had a profound effect on the distribution of West Indian flora and fauna, including the pearly-eye (see also Olson and Hilgartner 1982). Although climate continues to influence the general distribution of West Indian birds, other, often more proximate, factors must also be considered when attempting to explain the pearly-eye’s contemporary range and population fluctuations throughout the region.

The pearly-eye’s contemporary range is the culmination of many geological, climatological, ecological, genetic, and human-induced influences.

Habitat Destruction

Natural stochastic events, such as droughts and hurricanes, have no doubt significantly impacted populations of West Indian birds throughout the region's long history (see review by Wiley and Wunderle 1993). The importance of disturbances in shaping forest-bird populations is clear; more than 8,000 tropical cyclones have been recorded within the region in the last 100 years (Evans 1990). Such frequent and violent habitat disturbances may even partially account for the observed present-day distributions of some species (Raffaele 1977, Wiley 1985a, Wunderle et al. 1992). However, with few exceptions, e.g., avian specialists and small populations of island endemics (Westermann 1953, Wiley 1985a), those species that persist in the region today are well adapted to such habitat disturbances and recover well (Ackerman et al. 1991, Wauer and Wunderle 1992).

Unfortunately, however, not many species have acquired the physiological, ecological, or behavioral traits necessary to withstand the types and extent of habitat alteration produced by humans (see Ricklefs and Wikelski 2002). Before the arrival of European settlers in the 16th and 17th centuries, forests dominated the West Indian landscape. Most forests were destroyed to accommodate agricultural crops such as sugar cane and bananas. Loss of forest habitat was often complete on low-relief islands such as Antigua and Barbados, and even on the small, higher relief islands such as Montserrat. This undoubtedly had profound effects on the distribution and viability of native plant and animal populations, greatly influencing the distributional patterns observed today. Encouragingly, with the return of secondary forests on many once-denuded islands, e.g., Montserrat (100-percent deforestation) and Puerto Rico (>95-percent deforested), forest-bird populations are recovering. In the case of the pearly-eyed thrasher, two islands, Barbados and Antigua, are exemplary of two reforestation extremes. On Barbados, virtually no reforestation has occurred, resulting in the extirpation of both *Margarops* species. However, on Antigua, a once-denuded island on which substantial tracts of secondary forests have been established, the pearly-eye has returned to some of its traditional forested areas.

The pearly-eye probably occurred throughout Antigua in limestone forests prior to deforestation in the 18th and 19th centuries, when forests gave way to sugar cane (Pregill et al. 1988). For many years following deforestation, pearly-eyes were confined to the forested hills in the volcanic southwestern part of the island (Holland and Williams 1978). Recently, however, pearly-eyes have begun to repopulate secondary dry limestone forest in the eastern and south-central portions of the island, including English Harbour. During wildlife assessments in 1983 and 1984 (Faaborg and Arendt 1985), numerous sightings were made in

these areas. Similarly, in January 1984 at a net line in the Shirley Heights area bordering English Harbour to the east, 1 of the 159 birds captured during a 3-day sampling period was a pearly-eyed thrasher (Faaborg and Arendt 1985). If intensive searches were made throughout the year, doubtless more pearly-eyes would be found at varying elevations in many additional locales in Antigua.

Hunting

Together with habitat degradation, hunting by aboriginals has been shown to be a contributing factor influencing the contemporary distributions of island birds in the Pacific (Steadman 1989, Steadman and Kirch 1990, Steadman et al. 1991) and the West Indies (Pregill et al. 1994, Steadman et al. 1984a). In the West Indies, humans did not arrive until well after the end of the Pleistocene, about 4500 to 7000 years B.P. in the Greater Antilles and 3700 years B.P. in the Lesser Antilles (Pregill et al. 1994, Steadman et al. 1984a). On Antigua, Lesser Antilles, the first Amerindians arrived at least 3600 years B.P. They were mainly hunters, gatherers, and fishermen and, although thought to have contributed to the demise of some species of native fauna, their influence may have been less than that of more recent arrivals. Europeans, with their arrival commencing some 500 years ago, began major habitat alterations that continue today throughout the region. Through overhunting and environmental degradation, Europeans and their introduced animals, e.g., rats (*Rattus* spp.), mongooses (*Herpestes auro-punctatus*), and browsing-grazing livestock, have caused the extinction of at least nine native vertebrate taxa, some within recorded history (Steadman et al. 1984a).

The remains of many bird taxa found in archaeological and paleontological sites on islands throughout the West Indies attest to the fact that birds were widely used as food by pre-Columbian peoples (Pregill et al. 1994, Watters et al. 1984, Wing 1989). The first record of the pearly-eye being used for human consumption comes from the Trant's archeological site, Montserrat, discussed above (Steadman et al. 1984b).

Numerous historical accounts (e.g., Bond 1945, 1950; Schwartz and Klinikowski 1965; Westermann 1953; Wiley 1985a) affirm that present-day populations of the pearly-eye on some West Indian islands are the results, at least in part, of colonial and even current hunting practices. For example, in his history of St. Lucia, Breen (1844) reported that "thrushes" (which no doubt included the pearly-eye) were favored gamebirds. Semper (1872) stated that, like the forest thrush, the pearly-eye was also a major gamebird on St. Lucia during the late 19th century. By the 1930s, Danforth (1935b) noted that the pearly-eye

had become uncommon and local on that island. He was unable to procure a specimen, as were most early 20th-century collectors. Diamond (1973b) found the pearly-eye to be “patchy,” inhabiting only the highland forests of St. Lucia, whereas the scaly-breast was equally abundant in highland and lowland forest habitats. Arendt, in 1981, and Faaborg and Arendt (1985) found the pearly-eye to be uncommon in mist-net samples in wet forest, and absent at dry-forest sites. Of almost 1,000 birds captured (1981 and 1985 totals combined), only 7 were pearly-eyes. Pearly-eyes were captured in wet forest only, and at but three of seven sites sampled in dry, mesic, and wet-forest habitats along an elevational gradient from coastal to montane forests ($n = 2, 2, \text{ and } 3$ individuals, respectively). Likewise, on Guadeloupe, Noble (1916) stated that by the early 1900s, pearly-eyes were very retiring, very arboreal, and found only in highland forests (see Pregill and Olson 1981, Terborgh et al. 1978). On Guadeloupe, the pearly-eyed thrasher is considered as valuable a gamebird as that island’s pigeons and doves. As recent as 1971, during a visit to a national park in Basse Terre, C.B. Kepler (cited in Snyder et al. 1987: app. 1) stated that “...hunters were bagging birds as small as thrashers.” Much more recently, however, and probably owing to the establishment and protection afforded by a national park in Basse-Terre, during a census of forest birds within the park, the two *Margarops* species (total individuals of both species combined) were among the most common species, with 8.9 individuals per hectare (Feldmann et al. 1998). Clearly, on islands without the establishment of national parks (or the enforcement of wildlife laws within them), thrasher numbers have been substantially reduced owing to overhunting, as have populations of the Antillean psittacines.

Ecological Correlates of Range and Abundance

Geological, climatological, and human-induced phenomena are not the only factors effecting the diversity, distribution, and abundance of West Indian avifauna. Many ecologists interpret distributional patterns from a more interactive, or synecological, perspective. They believe that contemporary avian communities are dynamic, continually influenced by an array of biological and ecological interactions taking place regionally and locally over space and time.

Evaluation of Ecological Correlates Via Categorical Modeling

There are a few obvious ecological factors that influence the present-day range of the pearly-eye and, at the same time, are amenable to statistical analyses. Categorical modeling (see Arendt 1993 for methodology) was used to analyze the contemporary distribution of the pearly-eyed thrasher as a function of

Contemporary avian communities are dynamic, continually influenced by an array of biological and ecological interactions.

(1) island size (SIZE); (2) the number of landbird species (potential competitors) per island in which the pearly-eye is either absent or present (NUMSPEC); and (3) the presence or absence of a potential competitor, the red-legged thrush (*Turdus plumbeus*). The red-legged thrush was selected over other mimids and other thrushes because other mimids, even the pearly-eye's congener, the scaly-breasted thrasher, and several species of thrush are sympatric with the pearly-eye. Consequently, most apparently are not strong interspecific competitors for shared resources. Conversely, in comparisons of the pearly-eye and red-legged thrush on a regional scale, there tends to be an inverse correlation, i.e., an absence of one species follows the presence of the other (app. 2). In general, where both species are sympatric and syntopic, if one species abounds, the other is scarce. Likewise, research results in Puerto Rico have revealed that many aspects of the thrush's ecology, such as diet and foraging niches, are similar to those of the thrasher's (A.I. Arendt, unpubl. data). Information gathered from that study, together with results from monthly point counts, show that these thrasher and thrush populations are interspecifically territorial.

Island Size

The pearly-eye inhabits islands and cays with landmasses ranging from 0.03 km² (Bird Rock, Bahamas) to 9000 km² (Puerto Rico) (table 4.4 and app. 2). However, it is virtually absent from islands with landmasses less than 0.1 km² (n = 25 islands), and does not occur on half of the islands with landmasses ranging between 0.1 km² and 1.0 km² (n = 46). In short, the pearly-eye generally does not colonize islands less than about 1 km², most likely because most small islands in the region are treeless, low-relief cays and islets that do not offer suitable habitat for this predominantly arboreal thrasher (app. 2). However, at the other extreme, the pearly-eye does not generally inhabit large islands with landmasses greater than about 1000 km². It is found in species-poor habitats on only four islands larger than 1000 km² (app. 2).

The effects of island size are nonsignificant but are masked because they are strongly correlated with number of species (tables 4.5, 4.6, and app. 2). Therefore, the variable "SIZE" was dropped from the model to allow for a clear evaluation of the effects that the number of species has on the thrasher (tables 4.7 and 4.8).

Number of Species

The pearly-eyed thrasher does not inhabit small islands with three or fewer resident landbird species (app. 2). However, it is resident on small islands with as few as four landbird species (Dutch Cap and Grass Cay, U.S. Virgin Islands) and on

The pearly-eye inhabits islands and cays with landmasses ranging from 0.03 km² to 9000 km².

Table 4.4—Landmasses and number of species of breeding landbirds for 177 islands on which the pearly-eyed thrasher is absent (n = 97) or resident (n = 80)

Statistic	Pearly-eyed thrasher		
	All islands	Absent	Resident
<i>Landmass in square kilometers</i>			
Mean	1,312.01	2,214.88	241.93
SD	10,150.46	13,718.34	1,026.47
Median	3.6	.9	12
Mode	.1	.1	.2
Minimum	.002	.002	.03
Maximum	114,524	114,524	9,000
<i>Number of breeding landbirds</i>			
Mean	14.42	12.78	16.37
SD	12.73	14.96	9.16
Median	12	7	15
Mode	1	1	14
Minimum	1	1	4
Maximum	73	73	55

Table 4.5—Maximum likelihood analysis of variance table resulting from an analysis of the geographical distribution (presence or absence) of the pearly-eyed thrasher as a function of island size (SIZE), number of landbird species per island (NUMSPEC), and the presence or absence of the red-legged thrush (RLTH)

Source	df	Chi-square	Probability
INTERCEPT	1	26.73	<0.001
SIZE	1	.41	.52
NUMSPEC	1	28.1	<.001
N ^{2a}	1	12.67	<.001
RLTH	1	15	<.001
LIKELIHOOD RATIO	149	174.86	.07

^aThis model includes a quadratic term (N²) for “number of species” to allow for the fact that the pearly-eye does not inhabit especially small or large avian communities (NUMSPEC). Note that both terms are significant. Note also that the likelihood ratio (residual variation) is not significant, implying that the model fits.

Table 4.6—Maximum likelihood estimates (MLE) obtained in the analysis of variance procedure from table 4.5

Effect	Estimate	Standard error	Chi-square	Probability
INTERCEPT	2.22	0.42	26.73	<0.001
SIZE	0		.41	.52
NUMSPEC	.25	.04	28.1	<.001
N ²	0	0	12.67	<.001
RLTH ^a	2.87	.74	15	<.001

^aIn this model, “RLTH” (red-legged thrush) was treated as a quantitative variable. Thus, the maximum likelihood estimate of 2.87 represents the gain in expected value of the logit when the red-legged thrush is present in the avian community.

Table 4.7—Maximum likelihood analysis of variance table resulting from an analysis of the geographical distribution (presence or absence) of the pearly-eyed thrasher as a function of the number of landbird species per island (NUMSPEC) and the presence or absence of the red-legged thrush (RLTH)^a

Source	df	Chi-square	Probability
INTERCEPT	1	26.89	<0.001
NUMSPEC	1	29.44	<.001
N ²	1	14.49	<.001
RLTH	1	15.16	<.001
LIKELIHOOD RATIO ^b	44	67.37	.01

^aThe variable “SIZE” has been dropped from the model.

^bNote that now the likelihood ratio (residual variation) is significant (0.01), but this is owing to a large decrease (105) in degrees of freedom.

Table 4.8—Maximum likelihood estimates obtained in the analysis of variance procedure from table 4.7

Effect	Estimate	Standard error	Chi-square	Probability
INTERCEPT	2.18	0.42	26.89	<.001
NUMSPEC	.24	.04	29.44	<.001
N ²	0	0	14.49	<.001
RLTH ^a	2.87	.73	15.16	<.001

^aRLTH = red-legged thrush.

large islands with as many as 60 or more landbird species (Puerto Rico) (table 4.4). The number of landbird species per island is highly correlated with the presence or absence of the pearly-eye (tables 4.4 through 4.8). As the supertramp theory predicts, the pearly-eyed thrasher inhabits species-poor islands. On average, the pearly-eye is present on islands with about 16 landbird species (table 4.4).

The overall number of breeding landbirds per island does not necessarily translate directly into the number of resident landbirds in particular forest communities on any given island. Mist netting at 25 locations at varying elevations and in two general (dry and wet) forest types on the Caribbean’s 10 most species-rich (≥ 20 species) islands in which the pearly-eye occurs, has shown that the actual size of forest bird communities is much smaller than the total reported for number of resident landbirds inhabiting any given island (Faaborg and Arendt 1985, Terborgh and Faaborg 1980, and table 4.9). Whereas the mean number of breeding landbirds per island reported for the 10 most species-rich islands in which the thrasher is resident was 35 ($SD = 12.29$; range: 21 to 61), the mean number of species per mist-net sample was 12 ($SD = 2.65$; range: 5 to 23). The difference is significant ($t = -4.45$; $P < 0.001$).

The number of landbird species per island is highly correlated with the presence or absence of the pearly-eye.

Table 4.9—Comparison of the number of resident landbird species reported for the 10 most species-rich islands (≥ 20 species) on which the pearly-eye occurs (app. 2), with the number of resident landbird species found in 25 mist-net samples (1 to 7 per island)

Island	Number of species		
	Species per island	Mean	Range
131. ^a Puerto Rico (a through h)	61	19.0	15—23
156. St. Lucia (a through h)	45	13.6	12—15
48. Dominica (a, b)	41	11.0	9—13
159. St. Vincent (a, b)	39	12.0	10—14
79. Guadeloupe ^b (a, b)	37	12.0	10—14
155. St. Kitts (a ^b , b)	23	11.0	9—13
112. Montserrat (b, c, e, g, h, m, n)	27	9.9	5—12
7. Antigua (a, b)	25	13.0	5—11
11. Beata ^b	30	11.0	—
105. Marie Galante ^b	21	10.0	—

— = single banding session.

^aRespectively, island and forest type numeric and alpha codes follow those in appendix 2.

^bMist-net data provided by John Faaborg.

The red-legged thrush is a competitor of the pearly-eye; in the Sierra de Luquillo they are parapatric (contiguous, but not overlapping).

Geographical Distribution of the Red-Legged Thrush

Field studies of the red-legged thrush in Puerto Rico suggest that it is a competitor of the pearly-eye, especially for food (A. I. Arendt, unpubl. data). In the Sierra de Luquillo, where there are dense populations of both species, they are parapatric (contiguous, but not overlapping) for the most part. In habitats in which the species are syntopic, e.g., the Guánica Biosphere Reserve, neither species is common. The thrush prefers clearings, edge, and open canopy with little understory. In the Sierra de Luquillo, it is found primarily at lower elevations in tabonuco forest and forest edge. However, seasonal migration occurs to upper elevations in colorado forest, where it follows gaps and corridors such as roads. The thrasher prefers mid-elevation colorado forest where its density is greatest, but is found at all elevations, even at the summit, in open and closed-canopy forest (Snyder et al. 1987: table 3.1).

There are a few historical accounts documenting that the thrasher and thrush have been geographically separated in the Greater Antilles for many decades, and possibly hundreds of years. On Hispaniola, Cory (1881) found the thrush abundant in the vicinity of Fort Jacques, Haiti, at an elevation of 762 m. In the Dominican Republic, Cherrie (1896) reported the thrush as “...not at all uncommon...” and “Found everywhere on the coast and high up in the interior.” Also reporting on the birds of the Dominican Republic, Christy (1897) likewise

found the thrush “pretty common” at La Vega (North-Central region), although shy and observed more often “...in the thicker parts of the forest.” On the Isle of Pines (Isla de la Juventud), Cuba, Read (1911) reported the thrush, but not the thrasher, on two consecutive Christmas bird counts. Red-legged thrushes, together with northern and Bahama mockingbirds, are resident on Cayo Coco (Garrido 1976), whereas the thrasher is absent. Likewise, Garrido and Schwartz (1969) reported the thrush resident on Cayo Cantiles, whereas the thrasher is absent. The thrush’s presence on the small islands off Cuba’s coasts may partially explain the thrasher’s paradoxical absence. On Cuba, the thrasher is absent, whereas the thrush is a well-established and widespread resident. Garrido and Schwartz (1968) reported the thrush uncommon but widespread in Cuba’s Guanahacabibes Peninsula in the southwestern extreme of the island. More recently (1991), in the Zapata Peninsula near the Zapata Swamp (also in the SW), Martin McNicholl found the thrush to be common (J. Faaborg 1992, in litt.). At 6 banding sites, of 560 birds captured (mean = 93.3; $SE = \pm 9.12$; range: 60 to 118 per site), 124 were red-legged thrushes (mean = 20.6; $SE = \pm 2.44$; range: 12 to 27 per site), resulting in a relative abundance (percentage of thrushes per total individual captures) of 22 percent (mean = 24; $SE = \pm 4.77$; range: 14 to 45 percent).

Likewise, the red-legged thrush may be a contributing factor behind the pearly-eye’s absence on the larger, northern Bahama Islands. Cory (1890a) stated that the thrush is “especially common” on New Providence and Abaco. Northrop (1891) found the thrush to be “common” on Andros, whereas the thrasher was absent. Similarly, Bangs (1900) reported the thrush as resident on New Providence, whereas the thrasher was not listed.

Following Diamond’s (1974) competitive classification scheme, the red-legged thrush is a C-tramp (app. 1). As a tramp, it should be a good disperser and colonizer. However, there are virtually no published accounts documenting the thrush expanding its range or even dispersing to other islands. However, Johnston (1969) reported a single, resident female red-legged thrush on Grand Cayman (first record for that island) from 1963 to 1966. He noted that it could have come from Cuba, the Isle of Pines, or Cayman Brac (the only island of that group inhabited by *Turdus plumbeus*). It is possible that the disappearance of the Grand Cayman thrush has allowed the commencement of a range expansion by the red-legged thrush onto all the Cayman Islands. The elevated species richness of Grand Cayman Island (25 resident species) may account for the absence of the pearly-eye on that island, but its absence on Little Cayman, with only 17 species of resident landbirds, is more puzzling.

Because of the distinct geographical and habitat separation of the two species, the distribution of the red-legged thrush was included as a variable in the categorical models to better quantify its apparent influence on the distribution of the pearly-eyed thrasher.

Island Size

Its disjunct distribution (Greater Antilles and Dominica) suggests that the thrush also may once have had a more extensive range. Nevertheless, presently, the red-legged thrush is found on only 19 of the 177 islands under consideration (app. 2). Unlike the pearly-eye, the red-legged thrush does not inhabit islands with landmasses smaller than about 20 km² but rather is found more often on large islands (table 4.10). Of the 19 islands inhabited by the thrush, 16 (84 percent) have landmasses larger than 100 km². Moreover, half of them have landmasses larger than 1000 km² (app. 2). That island size is not as important as the number of landbird species in governing the distribution of the red-legged thrush, is further illustrated by the fact that of the 177 islands under consideration, the thrush is absent on 52 islands with landmasses larger than 20 km² (app. 2).

Table 4.10—Descriptive statistics of landmasses and number of landbird species for 177 islands on which the red-legged thrush is absent (n = 158) or resident (n = 19)

Statistic	All islands	Red-legged thrush	
		Absent	Resident
<i>Landmass in square kilometers</i>			
Mean	1,312.01	132.25	11,122.62
SD	10,150.46	886.89	29,778.35
Median	3.6	1.45	660
Mode	.1	.1	None
Minimum	.002	.002	26.8
Maximum	114,524	10,989	114,524
<i>Number of breeding landbirds</i>			
Mean	14.42	11.85	35.78
SD	12.73	9.44	16.36
Median	12	10.5	31
Mode	1	1	20
Minimum	1	1	20
Maximum	73	67	73

Number of Species

As with the thrasher, the effects of island size in the categorical modeling analysis of the thrush’s geographical distribution was masked by the more important “number of species” variable. The number of landbird species per island is significantly correlated with the geographical distribution of the red-legged thrush (tables 4.11 and 4.12). *Turdus plumbeus* does not inhabit islands with fewer than 20 resident landbird species but rather is found more often on the most species-rich islands (app. 2). Of the 158 islands from which the thrush is absent, 132 islands (84 percent) have fewer than 20 landbird species, whereas only 26 islands (16 percent) have ≥ 20 species. Elevated species richness increases the probability that the thrush will be resident on an island.

Table 4.11—Maximum likelihood analysis of variance table resulting from an analysis of the geographical distribution (presence or absence) of the red-legged thrush as a function of island size (SIZE) and number of landbird species per island (NUMSPEC)

Source	df	Chi-square	Probability
INTERCEPT	1	45.96	<0.001
SIZE	1	.03	.86
NUMSPEC	1	21.37	<.001
LIKELIHOOD RATIO	151	82.01	1

Table 4.12—Maximum likelihood estimates resulting from the analysis of variance procedure from Table 4.13

Effect	Estimate	Standard error	Chi-square	Probability
INTERCEPT	4.59	0.67	45.96	<0.001
SIZE	8.94×10^{-6}	0	.03	.86
NUMSPEC	.12	.02	21.37	<.001

Thrasher-Thrush Distribution Analysis

To emphasize the inverse correlation between the presence or absence of the pearly-eye as a function of the presence or absence of the thrush and island size, a restricted analysis was done. It included only islands in the size range in which both the thrasher and the thrush occur (although they are not necessarily on the same island) (tables 4.9 and 4.10). The presence or absence of the thrush becomes the only significant factor in predicting the presence or absence of the thrasher (table 4.13). The coefficient was large and negative, indicating that the presence of the thrush implies an absence of the thrasher (table 4.14). However, that the thrasher and thrush are negatively associated over this range of the data, does

The presence or absence of the thrush becomes the only significant factor in predicting the presence or absence of the thrasher.

Table 4.13—Maximum likelihood analysis of variance table resulting from a restricted analysis^a of the geographical distribution of the pearly-eyed thrasher as a function of island size (SIZE) (where 20 ≤SIZE ≤11 000 km²) and number of landbird species per island (NUMSPEC) (where 20 ≤NUMSPEC ≤60) and the presence of the red-legged thrush (RLTH)

Source	df	Chi-square	Probability
INTERCEPT	1	0.45	0.5
SIZE	1	.6	.43
NUMSPEC	1	.2	.65
RLTH	1	9.48	<.001
LIKELIHOOD RATIO ^b	36	42.92	.19

^aThis analysis includes only the data space in which both the pearly-eyed thrasher and the red-legged thrush are present, but not often on the same island (see app. 2). By restricting island size, and thus number of species, these two variables become insignificant (see the following tables for the model with a full range of island sizes and number of species).

^bThe likelihood ratio is nonsignificant (0.19) for the range of the data in which both the pearly-eye and the red-legged thrush are present. Thus, the model fits, i.e., there is no significant unexplained variation.

Table 4.14—Maximum likelihood estimates resulting from the restricted analysis of variance procedure from table 4.13

Effect	Estimate	Standard error	Chi-square	Probability
INTERCEPT	1.02	1.53	0.45	0.5
SIZE	0	0	.6	.43
NUMSPEC	.02	.05	.2	.65
RLTH ^a	1.37	.44	9.48	<.001

^aIn this model, “RLTH” (red-legged thrush) was treated as a categorical (not quantitative) variable. Thus, the maximum likelihood estimate of 1.37 represents the effect of RLTH. Therefore, adding it to the intercept for cases where RLTH = 0 (absent), and subtracting it when RLTH = 1 (present) implies that:

$$P(\text{PETH}|\text{no RLTH}) = 1/(1+\exp*(1.0278+(-1.3728))) = 0.584$$

and

$$P(\text{PETH}|\text{RLTH}) = 1/(1+\exp*(1.0278-(-1.3728))) = 0.083$$

Thus, the thrasher is about seven times more likely to be found where the thrush is absent.

not imply a cause-and-effect relationship. As Wiens (1989a) pointed out, inferences drawn from correlative data are suggestive at best and remain equivocal in the absence of quantitative manipulation of a series of ecological variables and testing of alternative process hypotheses.

No doubt, besides the red-legged thrush, there are many other potential competitors of the pearly-eye that have gone undetected in these analyses, especially owing to diffuse competition. To further explore a cause-and-effect relationship of the thrasher’s contemporary range, what must be undertaken is extensive multi-variate analyses by using ordination and serial inclusions-exclusions of an array of physical and ecological variables. This would be, of course, a major study in itself.

In summary, categorical modeling has shown that, as Diamond's supertramp theory predicts, the pearly-eyed thrasher is virtually restricted to small, species-poor islands. Moreover, the pearly-eye's distribution is inversely correlated with a potential passerine competitor, the red-legged thrush, although additional research is needed to shed light on the cause-and-effect relationship of this observed pattern.

Competition Within West Indian Bird Communities

Inter- and intraspecific competition for resources such as food and nest sites may affect species richness, composition, population size, and even an individual's form and function within avian communities in some environments. This fact led to the early conceptualization and establishment of the competition paradigm in the study of community ecology. Interspecific competition occurs on at least three levels: individual, species, and community. As defined by Lincoln et al. (1983), competition at the individual and species levels (e.g., interference and resource competition, respectively) can be included in the competitive exclusion principle; i.e., two individuals or species having identical ecological requirements cannot coexist indefinitely (this is similar to the classic Gaussian hypothesis and Grinnell's axiom). Competition at the community level is indirect or "diffuse" (MacArthur et al. 1972); or more precisely, it is the "...simultaneous interspecific competition between numerous species each having a small degree of niche overlap with other species;" (Lincoln et al. 1983).

Supertramps face interspecific competition at all three levels with other members of the community. In this study, interspecific competition involving the pearly-eye has been inferred, but not confirmed, at the individual and species levels (presence or absence of the thrasher correlated to that of a potential competitor and predator, the red-legged thrush) and at the community level (absence of the thrasher in large avian communities) (see also chapter 8 for more compelling evidence). But, so far, little mention has been made of the ecological constraints influencing pearly-eye distribution and abundance.

In his comprehensive review, Wiens (1989b: chap. 3) outlined all of the major ecological factors influencing the structure of biological communities, including competition. He noted that support for intra- and interspecific competition is "convincing" in some instances (e.g., nectarivorous species in local assemblages), suggestive or circumstantial in others (e.g., comparative, correlative observations), or lacking in some (e.g., unstable, highly variable ecosystems such as grasslands).

**Supertramps
face interspecific
competition at
three levels with
other members of the
avian community.**

How important, then, might competition be in West Indian bird communities? Wiens stated that “Despite the weakness of a good deal of the observations (and some of the experimental) evidence, there are clear, strong indications that competition does occur as a proximate process among some groups of birds.” He further noted that “In some groups, such as the West Indies birds examined by Case et al. (1983)...the species that occur together do appear to differ morphologically more than would be expected by chance.”

Many of the data and ideas presented by Case et al. (1983) stemmed primarily from the investigations of Faaborg (1985; and more recently, 1988), who has been studying West Indian bird communities for more than 30 years. Although his data are of a correlative nature and thus open to alternative interpretations as to the cause-and-effect aspects of resulting patterns, Faaborg has shown that many complex ecological isolating mechanisms play a decisive role in influencing species richness and distributions of West Indian birds. By separating the region’s landbird fauna (excluding Falconiformes) into four basic foraging guilds (sets of species with similar diets and/or foraging habits), he found (1) a direct relationship between the total number of species and coexisting number of species in each guild and the size of the resident landbird community; (2) saturation curves for total number of species (about 30 in dry forest, 20 in wet) and guild membership within habitats on large islands; i.e., the number of species found in a habitat is constant on islands with more than about 30 species; and (3) size differences among coexisting guild members that closely adhered to the so-called “Hutchinsonian ratio” (Hutchinson 1959), i.e., in smaller guild members, one species is twice as large as the other, whereas in larger members, one species is 1.3 times larger than the other. Considering the last of these important and insightful observations, is it possible that the pearly-eye’s morphology also could be influenced by intra- and interspecific competition? This question will be addressed in the following chapter.

Summary: Distribution and Abundance

A review of the contemporary and historical distribution and abundance of the pearly-eyed thrasher shows that it fulfills all of the area and population-size prerequisites of a superior colonizer. It has a wide geographic and habitat range, exhibits local and regional abundance, and undergoes density compensation on small islands and in species-poor habitats. Today, the pearly-eye inhabits some 80 islands and cays throughout the Greater Caribbean basin, from Rum Cay and San Salvador in the Southern Bahamas south to Bonaire, Netherlands Antilles, over a north-south geographical range of almost 3000 km. With the exception of

Puerto Rico, on which it is common only in species-poor habitats, the pearly-eyed thrasher is noticeably absent from the larger islands, such as Cuba, Hispaniola, and Jamaica, inhabiting only their species-poor satellites. It generally does not colonize islands less than about 1 km² or with three or fewer resident landbird species. Nor does it inhabit large islands greater than 1000 km² unless they are species-poor and contain extensive, disturbed habitats. Although the pearly-eyed thrasher is resident on small islands with as few as four landbird species, it is found most often on islands and within habitats with about 16 resident species.

From an historical perspective, fossilized bones from an archaeological site near Trant's Bay, Montserrat, represent the first prehistoric record for both *Margarops* species anywhere in the Caribbean. Fossilized bones from Antigua suggest that the pearly-eye might have inhabited nearby Puerto Rico much earlier than has been reported. Written accounts show that the pearly-eye has experienced severe population fluctuations over time, resulting in a southern range contraction and northern expansion. It has undergone significant intra-island population increases within the past 30 to 60 years in Puerto Rico, Montserrat, and Bonaire. As a supertramp, excluding density-compensation islands, e.g., Mona (Puerto Rico), and samples taken during periods of ecological stress (e.g., droughts and hurricanes), the pearly-eye reaches its highest relative abundance in wet-forest habitats because wet forests are generally more depauperate in bird species than dry forests of the West Indian islands.

The pearly-eye reaches its highest relative abundance in wet-forest habitats because wet forests are generally more depauperate in bird species than dry forests.

Chapter 5: Morphology

Morphological characteristics of insular birds involving body dimensions and plumage have been interpreted as adaptive responses to the environmental conditions on islands (Grant 1965a, 1965b; Grant and Grant 1999). An important condition is the relative paucity of species. In the absence of close relatives, resident birds often extend their foraging activities, with concomitant modification of the feeding and locomotor apparatus and resulting in enhanced morphological variation (Grant 1965a). This phenomenon is known as ecological (or character) release. It is basically a broadening of the niche in the absence of a competitor or restrictive species. As both supertramp and competition theories predict, the pearly-eye shows substantial variation in body size among islands and habitats throughout its range. Does the pearly-eye undergo ecological release in the absence of close competitors? Conversely, could the evolution of ecological character displacement¹ have been a prerequisite to the observed syntopy (co-occurrence in a habitat) on some islands by the pearly-eyed thrasher and other interspecifics, e.g., the congeneric scaly-breasted thrasher, competing for the same resources via diffuse competition? (see discussions by Brown and Wilson 1956, Schluter and Smith 1986). Various analyses were performed to address this question. However, before investigating the potential effects of ecological release in the absence of competitors (or possible character displacement in their presence), one has to first consider potential intraspecific geographical, biological, and ecological sources of variation that might account for the pearly-eye's variable body size among sympatric and allopatric populations (for a general discussion of individual variation in birds, see Curio 1977). Before offering and discussing the results from numerous intra- and interspecific analyses that I conducted on museum specimens and live, free-flying thrashers, I will present and explain the statistical procedures used and the rationale behind their selection.

In the absence of close relatives, resident birds exhibit enhanced morphological variation.

Statistical Analyses

There are two main approaches to the most effective means of calculating overall body size in birds and other vertebrates. The more traditional approach advocates the use of uni- or bivariate analytical approaches using a variety of parametric and nonparametric statistical tests (see, for example, Johnson and Marten 1992). More recently, there has been a trend toward using multivariate procedures. The multivariate techniques most commonly used to determine and compare

¹Ecological character displacement may be defined as the effect of competition in causing two initially allopatric species to diverge from each other in some character upon attaining sympatry..." (Diamond et al. 1989).

vertebrate body size and shape are canonical variate analysis (Abbott and Abbott 1978, Albrecht 1980); principal components analysis or “PCA” (e.g., Freeman and Jackson 1990, Lande and Arnold 1983, Loughheed et al. 1991, Rising and Somers 1989); discriminant function analysis (DFA) (Sites and Willig 1994b, Storer 1989); and multivariate analysis of variance and covariance (MANOVA and MANCOVA) (Lande and Arnold 1983, Sites and Willig 1994a, Willig and Owen 1987, Willig et al. 1986). Some investigators use a combination of uni- and multivariate analyses (e.g., Abbott 1978).

For comparative purposes, confirmation of analytic results, and to appeal to a wider audience (namely, proponents of univariate methods and those advocating multivariate techniques), I chose both uni- and multivariate techniques to analyze the pearly-eye’s morphometric data. I used external morphological characters (and various ratios—see Amadon 1943) easily obtained in the field and from museum specimens, namely (1) body mass (mainly field) and various longitudinal measurements (appendicular lengths), (2) wing chord, (3) ninth primary, (4) culmen from the feathered base (exposed culmen), (5) culmen from the anterior portion of the nares (bill length from nares), (6) center rectrix, and (7) tarsus. For the multivariate analyses, I chose multivariate multiple regression, MANOVA, MANCOVA, and PCA (see “Study Area and Methods” for descriptions).

Before discussing several endogenous and exogenous factors affecting pearly-eye morphology, I will present the outcome of numerous statistical and comparative analyses to facilitate a more rapid and precise interpretation and assimilation of the information contained in this chapter (fig. 5.1). In summary, biological, e.g., genetic factors, followed by geographical and climatic factors, tend to have more effect on pearly-eye morphology than ecological factors, although the latter are significant contributors in many instances.

Biological factors, followed by geographical and climatic factors, have more effect on pearly-eye morphology than ecological factors.

Sources of Intraspecific Variation in Avian Body Size

Geographic Effects

Among allopatric populations of birds, body size is greatly influenced by a variety of site-specific and isolation factors, although such geographical isolation factors do not always precede other kinds of isolation (Thorpe 1945). In general, size variation is ordered clinally and is significantly related linearly to latitude, longitude, elevation (or isophane, a single function of the latter three), and landmass, or area (Abbott 1974b, Baker 1980, Diamond 1973b, Hamilton 1961, Murphy 1983, Power 1970, Rand 1936, Zink and Remsen 1986; but see Grant et al. 1985). Dispersal is also a factor, albeit indirect (Grant et al. 2001). Although there are exceptions (see Abbott 1974b), including the pearly-eye (see below),

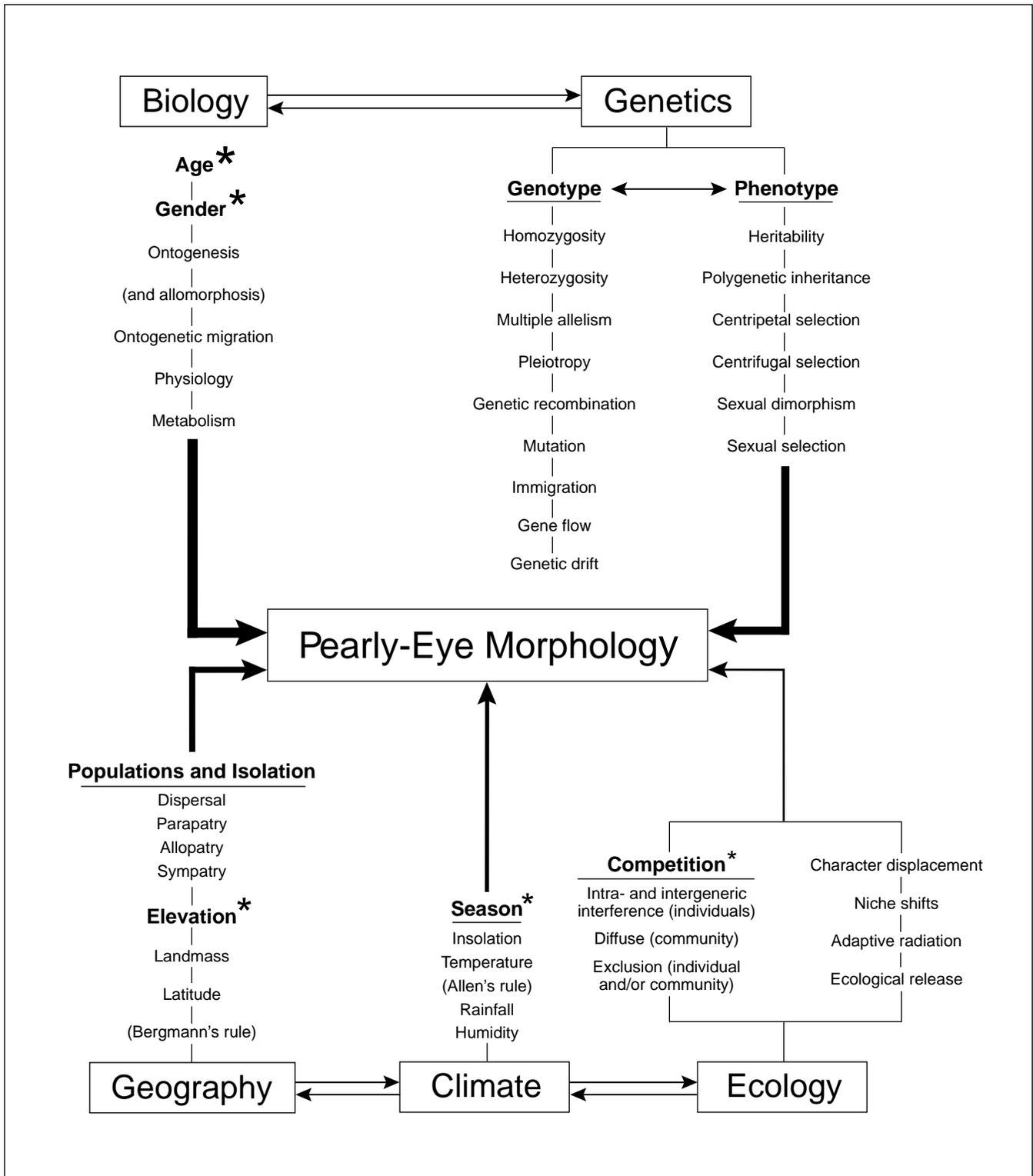


Figure 5.1—Biological, geographical, climatic, and ecological influences governing body size of the pearly-eyed thrasher throughout its range. The greater the influence, the more pronounced is its respective arrow (interior arrows only; exterior arrows not differentially sized). Asterisks signify the most influential biotic and abiotic factors (the larger the asterisk, the more important the factor). The most important factors are, in descending order, (1) age, (2) gender, (3) elevation, (4) season, and (5) competition.

birds as a taxon generally follow Bergmann's ecogeographic rule, i.e., body size in intraspecific and interspecific homeotherms tends to be positively correlated with landmass, latitude, and colder climates (see Graves 1991, James 1970, and references therein). Graves' (1991) and James' (1983, 2001) results support the hypothesis that climate, especially temperature, seasonality, and habitat type, are important environmental determinants of geographic size variation in homeotherms (see also Murphy 1985, Snow 1954). Likewise, a phenomenon similar to Bergmann's rule occurs in regard to elevation. In general, avian body size increases with elevation (see Diamond 1973a, Grant 1979, Graves 1991, and their respective references), which in turn is confounded with landmass as larger islands tend to be of greater topographical relief.

As a case in point, McLaughlin and Roughgarden (1989) noted a significant difference in the pearly-eyed thrasher's body size and diet among individuals from Anguilla and St. Eustatius. They attributed this apparent niche shift in the pearly-eye's body size to the abundance of its congener, the scaly-breasted thrasher. However, regardless of potential competitors or food resources, it is intuitive that Anguilla pearly-eyes would be smaller because the island's highest point is 65 m. Similarly, the pearly-eye is expected to be much larger on the island of St. Eustatius because all data were collected "...at various points along the rim of the Quill (highest elevation: 600 m)..." (McLaughlin and Roughgarden 1989). Although these authors' conclusions may be valid (and thus supportive of the competition and supertramp theories advocated in the present study), this may in fact simply be a good example of the widely observed thrasher body size shifts with elevation (see below).

To view the effects of latitude, landmass, and elevation on thrasher body size on a regional scale, these variables were included in the analyses of museum specimens from different island populations.

Latitudinal Effects (Museum Specimens)

To investigate the anticipated direct correlation between latitude and pearly-eye body size, I measured 584 specimens from five North American museums (see "Study Area and Methods" for details). Of the five characters measured, three were correlated with latitude. However, contrary to Bergmann's Rule, all three were negatively correlated with increasing latitude, i.e., external appendages were shorter at higher latitudes: tarsus ($R = -0.24$, $P < 0.001$, $n = 499$); wing chord ($R = -0.18$, $P < 0.001$, $n = 584$); and culmen from nares ($R = -0.14$, $P = 0.001$, $n = 492$). Length of the exposed culmen also tended to decrease with increasing latitude, but not significantly ($R = -0.03$, $P = 0.38$, $n = 549$). Only tail length tended to

increase with increasing latitude, but not significantly ($R = 0.07$, $P = 0.08$, $n = 485$). To reemphasize the importance of elevation in influencing the pearly-eye's morphology, most Lesser Antillean islands from which many specimens were collected are high-relief islands (e.g., Montserrat, Guadeloupe, Dominica, St. Lucia), whereas the northern islands such as those in the Bahamian Archipelago are all low-relief islands (max. elev. 67 m). Therefore, the inverse correlation between pearly-eye body size and increasing latitude may well be caused, or at least confounded, by the inclusion of large individuals from montane rain forests on several Lesser Antillean islands and small individuals from low-lying islands in the northern latitudes (app. 4.1). The narrow span of latitude (about 12 to 27°N) no doubt was also a contributing factor. It became evident from the onset that many more factors, besides latitude, affect the pearly-eye's body size.

Landmass and Elevational Effects (Field Measurements)

When the pearly-eye's external morphological characters were correlated with landmass, only tail length significantly increased as island size increased ($R = 0.15$, $P < 0.001$, $n = 485$). As with latitude, although none of the other four characters was strongly correlated with island size, there was a tendency for each to diminish in length with increasing landmass: tarsus ($R = -0.08$, $P = 0.06$, $n = 499$); wing chord ($R = -0.008$, $P = 0.84$, $n = 584$); culmen from nares ($R = -0.03$, $P = 0.41$, $n = 492$); and exposed culmen ($R = -0.02$, $P = 0.63$, $n = 549$). These simple correlation analyses notwithstanding, when included in more comprehensive multivariate analyses (see below), latitude and, to a lesser extent, landmass were shown to be significant factors in governing pearly-eye body size in four of five and two of five characters, respectively. After considering the effects of latitude and landmass, I then evaluated the more significant influences of elevation and climate on the pearly-eye's body size.

Elevational information is usually missing from museum tags, especially from older specimens. Therefore, to determine the effect of elevation on the pearly-eye's body size, I chose individuals from among populations within a single island. Three allopatric populations were sampled in Puerto Rico. Thrashers were captured and measured along an elevational gradient: (a) low (0 to 150 m, including coastal areas, the Guánica Biosphere Reserve, and other, mostly dry-forest habitats); (b) mid (250 to 400 m, mesic and wet forest, with several samples from the mid elevations of the Luquillo Experimental Forest and surrounding slopes); and (c) upper (650 to 800 m, the transition zone between colorado (*Cyrilla racemiflora* L.) and cloud forest, and the Icacos Valley on the southern slopes of the Luquillo Experimental Forest). For comparison with Puerto Rico's coastal and lowland

thrasher populations, the nearby, low-relief island of Mona (0 to 80 m) was included in the analyses. To reduce the influences of reproduction (potentially heavy females) and season (feather wear), samples were taken between November and February. During these months, plumage is “fresh” and few thrasher pairs are breeding. To investigate the potential role of seasonal effects, March through October samples were then compared to November through February samples (fig. 5.2).

In general, the pearly-eye’s body size, especially body mass, increases with elevation (see fig. 5.2; and discussion below). Coastal and lowland pearly-eyes average between 90 and 100 g, whereas highland individuals can average between 110 and 123 g. To date, the heaviest El Yunque (highland rain forest) pearly-eye measured was a nongravid female weighing 138 g, almost 50 g more than the lower average for coastal and lowland individuals. However, this is not the heaviest thrasher on record. In a montane rain forest on St. Lucia, J.L. Gullede (pers. comm.) collected a nongravid (small ovaries) female that weighed 153 g. To my knowledge, this is the heaviest individual reported thus far. The extreme size and striking plumage differences in St. Lucia’s pearly-eyes led Garrido and Remsen (1996) to propose a fourth subspecies (*M. f. klinikowskii*) for that island’s chromatically and morphologically distinct geographic race.

Climatic Effects

It is well known that the environment, especially climate (together with underlying genetic components), is an important factor influencing avian body size and appendicular characters (Boag 1984). Insular allomorphy, i.e., heterogeneity in allometric (differential) growth rates, has been shown to be a result of selection for heat exchange (Harrison et al. 1964). Still, it seems unlikely that the cornified surface of the tarsus and bill would be of much value in heat exchange (but see Power 1970). Instead, the larger dimensions of the bills and tarsi of insular birds are generally thought to be adaptations primarily to ecological conditions (but see Soulé and Rindge Stewart 1970, Willson 1969, Willson et al. 1975) concomitant with sexual dimorphism, ecological release, and niche shifts (Baker-Gabb 1986; Diamond 1975b; Diamond and Marshall 1977a, 1977b; Faaborg 1980a; Grant 1965a; Johnson 1966; Selander 1966; Terborgh and Faaborg 1973; Winkler and Leisler 1985). Island birds use a wider variety of perch types, tend to be more terrestrial, and are euryphagous (eat a wide variety of food items), resulting in a greater range of body sizes (Grant 1983b). For general discussions on ecomorphology and underlying hypotheses, see Lederer (1984) and James (2001).

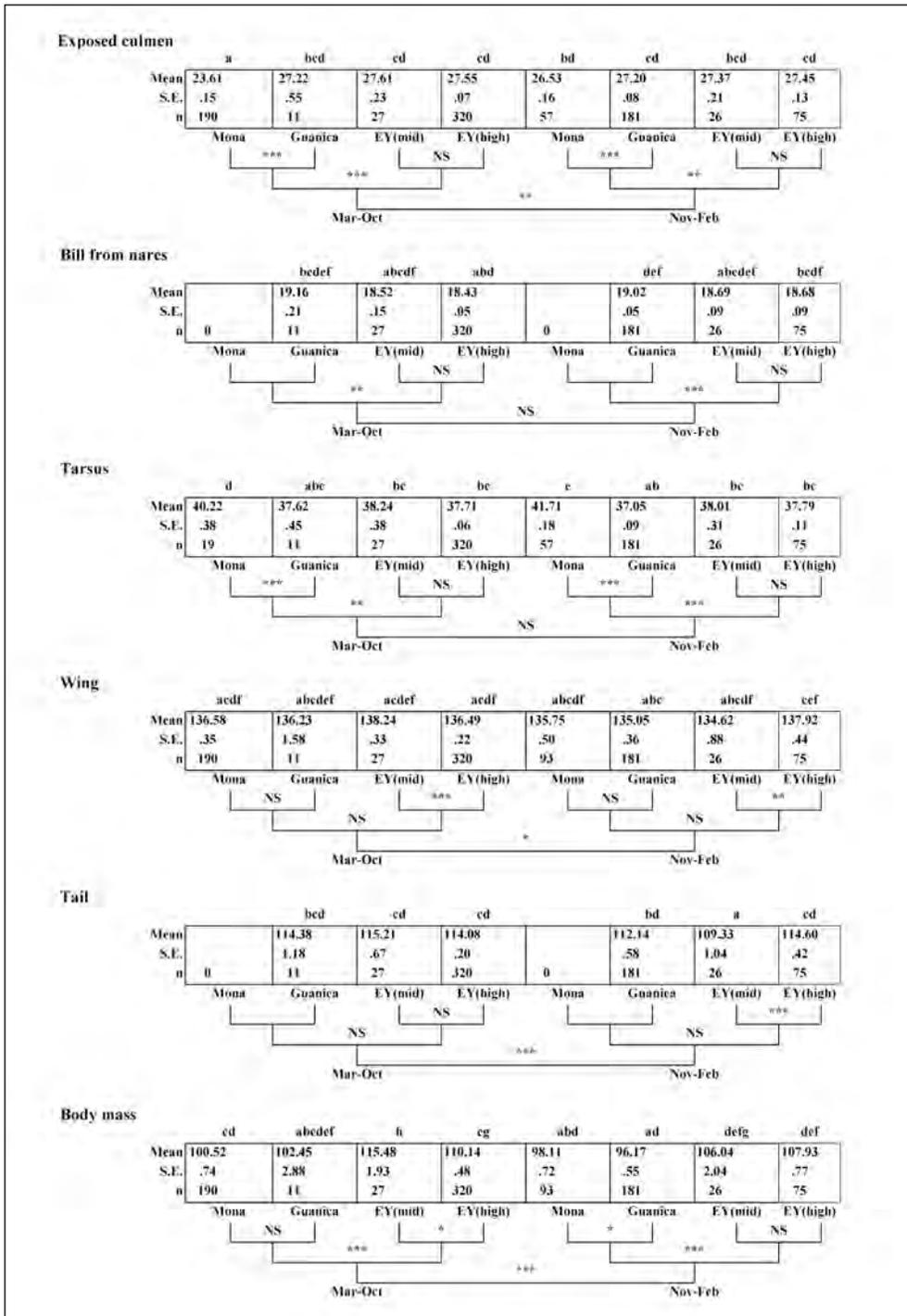


Figure 5.2—Descriptive statistics (mean, ± 1 standard error, [S.E.] and sample size [n]) of groups used in statistical analyses and defined by combinations of season (March–October vs. November–February) and elevation (Mona vs. Guánica vs. El Yunque [mid-elevation] vs. El Yunque [high elevation]) on each of six morphometric characters of the pearly-eyed thrasher. Treatment levels, e.g., combinations of season and island such as Mona in March–October, which share a common letter (a, b, c...h) are statistically indistinguishable at the specified alpha level of the test. Levels of significance are as follows: [*] $0.05 \geq P > 0.01$, [**] $0.01 \geq P > 0.001$, and [***] $0.001 \geq P > 0.0001$. Because few measurements of length of tail and bill length from the nares were available for specimens from Mona, seasonal data for that island could not be included in analyses for those characters, and those characters could not be included in multivariate analyses. All measurements are in millimeters.

Three of the six characters sampled from Mona Island thrashers were quite similar (exposed culmen and wing), or even larger (tarsus), in their linear dimensions when compared to those sampled from highland individuals (fig. 5.3). This was not surprising because it has been known for decades (e.g., Grant 1965a, 1980; Murphy 1938; Van Valen 1965) that island birds exhibit longer bills and tarsi than those of the mainland (or in this case a nearby high-relief island with a greater range of habitats and elevations as well as many more potential competitors). Is it possible that Allen's ecogeographic rule may explain the attenuated appendicular characters of Mona's pearly-eyes? This rule states that in polytypic species of endotherms, extensions of the body tend to be larger (and have a higher surface/volume ratio) in the warmer parts of the range and shorter (with a lower surface/volume ratio) in cooler parts (see also Baker 1980, Power 1970). Mona Island is desert-like in many respects, e.g., xerophytic vegetation, numerous species of cacti, and prolonged and severe droughts. Moreover, thrashers in general have long beaks, wings, tails, and tarsi, and most species are thought to have originated in xeric habitats (e.g., *Toxostoma* spp. and *Mimus* spp.).

Effects of Dispersal on Local Body Size

Because the pearly-eye is known to undergo inter-island dispersal, e.g., Barbuda to Guadeloupe (chapter 3), the possibility that Mona may be an ecological sink for dispersing thrashers from neighboring, high-relief islands, many with wide elevational gradients (see below), must be taken into consideration. As a case in point, I was informed (M. Frost 1999, in litt.) in June of that year, Dr. Phil Hansbro of Cambridge University, United Kingdom, examined a pearly-eye specimen now housed at Cambridge that was collected at Bagatelle, Barbados, on March 2, 1889, by C.J. Manning (see also app. 3). After considering all the external plumage and appendicular measures, Dr. Hansbro concluded that the specimen is of the newly designated (Garrido and Remsen 1996) St. Lucian subspecies (*M. f. klinikowskii*). Confirmation through genetic testing is desirable. Still, this may be yet another example of inter-island dispersal by a large-bodied pearly-eyed thrasher from a high-relief island that, when collected, was assumed to be a permanent resident on a low-relief island.

Effects of Investigator Bias, Genes, Age, Gender, and Season

Investigators themselves influence avian morphometric results by making simple, individually biased measurement errors. However, if care and standard measurements are taken, accuracy (repeatability) is usually over 95 percent, and measurement error among investigators is minimal and will not significantly affect the

Transmarine dispersal affects local body size.

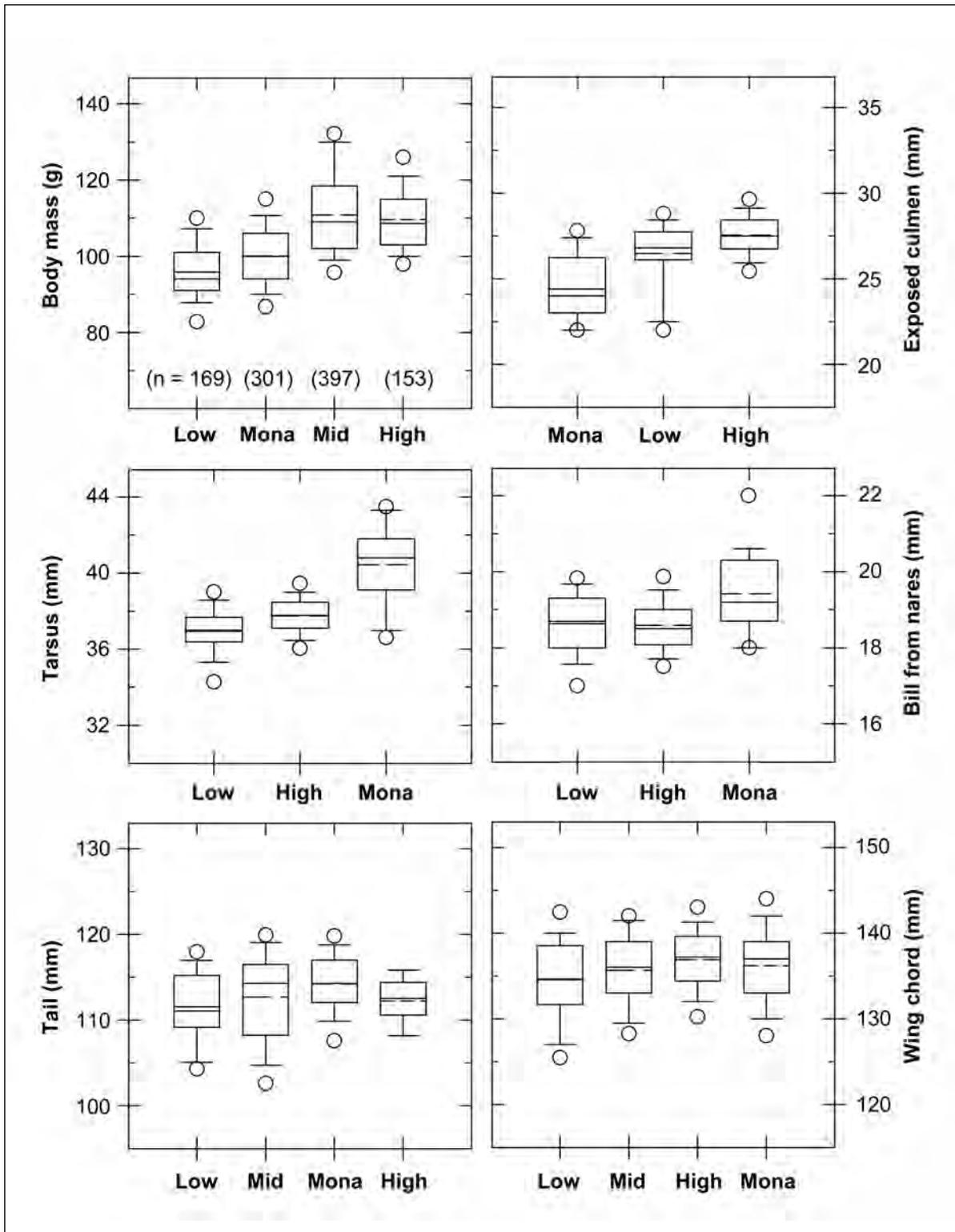


Figure 5.3—Variation in the pearly-eye’s body size with increasing elevation. Individuals were captured and measured at low (0–150 m), mid (250–400 m), and upper elevations (650–800 m) in Puerto Rico. To investigate the possibility of small-island effects, a sample from nearby Mona Island was included for comparison. Although overall body size increases with ascending elevation, there were some unexpected exceptions, e.g., significantly longer bills and tarsi in the Mona Island population. Body mass is in grams and longitudinal measures are in millimeters.

results (Arendt and Faaborg 1989, Boag 1984, Gannon et al. 1992, Price and Grant 1984). More important are the biological and ecological effects of age, gender, and season on the body size of individuals within a population (Arendt and Faaborg 1989, Rising and Somers 1989).

Among birds, real size differences in internal characters (e.g., skull and dimensions of long bones) as well as external characters, e.g., body mass and the lengths of such characters as culmen, tail, wing, and tarsus, result from the influence of many biological and ecological factors. Three relatively easily measured and highly germane biological and ecological factors are age, gender, and season. Several ecological factors will be discussed below. But first, from a genetic perspective, it is noteworthy that phenotypic variation reflects underlying genetic (heritability) and ontogenetic (dynamic allometry) variation (Grant 1984, Smith and Dhondt 1980, Smith and Zach 1979). Heritability often accounts for 80 to 90 percent or more of the observed variation in passerine morphological characters (Boag 1983, Grant 1983a, Grant et al. 2001). Furthermore, morphological character variation increases with allozymic (multiform enzymes) homozygosity (identical alleles at a given locus) and decreases with heterozygosity (two alleles at a given locus) (Eanes 1978, Fleischer et al. 1983, Lande 1980, Loughheed and Handford 1993) (but see Handford 1980 as an exception). In general, island populations have less allozyme variation than mainland populations, and insular endemic populations show reduced genetic variation (Frankham 1997). Genetic studies have shown that the basic features of complex morphologies result from polygenic (multifactorial) inheritance with multiple allelism (multiple forms on the same locus), pleiotropy (more than one phenotypic effect), and genetic recombination, mutation, and immigration. Genetic models show population variation is in a state of balance between the two opposing forces of mutation and immigration, which tend to elevate variation, whereas selection (including sexual selection) and genetic drift, tend to decrease it (Grant and Grant 1983, Grant and Price 1981, Huxley 1955, Price et al. 1984a). A similar phenomenon occurs at the level of the phenotype (Gerhart et al. 1997, Rothstein 1973). Elimination of extreme individuals, i.e., selection for an optimum phenotype (directional, or centripetal selection) results in a directional shift in gene frequencies of the character concerned and leads to a state of adaptation (see Grant 1972b, 1985; Schluter and Smith 1986) in a progressively changing environment (Lincoln et al. 1983). Conversely, selection for phenotypic extremes (disruptive, or centrifugal selection) in a polymorphic population preserves and accentuates discontinuity (Lincoln et al. 1983). Moreover, environmental heterogeneity is correlated with large continuous, morphological variation (see, for example, Grant and Grant 1979, Grant et al. 1976).

Phenotypic variation reflects underlying genetic and ontogenetic variation.

Ontogenesis (growth and development), which often continues after fledging, is also responsible for the morphological variation observed in avian external characters (Smith et al. 1986). For example, wing chord and tail length vary with age. Wing length and body mass often increase from the first to second year in passerines (Freeman and Jackson 1990, Stewart 1963). This ontogenetic effect is treated separately below from that of seasonal influences (climatic effect) of feather wear (Arendt and Faaborg 1989, Boag 1984, Grant 1971, Rising and Somers 1989).

Internal organs (see Davis 1961), body mass, and especially bill length, vary through time (e.g., seasonally). Variation in bill length is a result of rhamphothecal growth, frictional wear, and change in diet commensurate with seasonal variation in food types and quantities (Clancey 1948, Davis 1954, Freeman and Jackson 1990, Grant 1983b, Marshall 1948, Miller 1941, Packard 1967, Price et al. 1984b, Rising 1972, Rothstein 1973, Schluter 1982, Schluter and Grant 1984). Even with these factors taken into account, however, a pronounced size difference exists between the sexes in adult pearly-eyes. Therefore, the influences of age, gender (sexual dimorphism), and season will be addressed.

Age and gender of live pearly-eyed thrashers are difficult to ascertain (more so in free-flying individuals, and only slightly better in the hand) because the species is basically monochromatic and obtains its definitive “adult” plumage within its first year. Even with years of practice at detecting subtle differences in plumage coloration (including hue, contrast, and brightness, especially in the scaling effect of the breast feathers) in combination with morphological measures and “skull-ing” (the use of cranial bone ossification to determine age), it is difficult to determine age and sex of pearly-eyes with complete accuracy. Even trying to attribute the masculine gender to a singing pearly-eye is risky because, as in many other species, estrogen production in older females diminishes, causing them to exhibit “male” characteristics such as “male” plumage and song (Baptista et al. 1993; see also Baumgartner 1986 for an example in a 4-year-old northern cardinal *Cardinalis cardinalis*; and Arendt 1987 for an example and explanation of sex reversal in a 7-year-old minimum-aged American redstart, *Setophaga ruticilla*, that had made at least 15 flights between North America and Puerto Rico). During the course of the present study, three female thrashers older than 4 years of age (5, 7, 13) often were observed singing from within 2 m of their nest boxes. One female habitually sang from a song perch several meters high in a bamboo stand about 4 m from her nest box. Female song in mimids was reported as early as 1899 (Cohen 1899). Cohen shot a female California thrasher (*Toxostoma redivivum*) that “...was singing, perched on top of a bush.” Interestingly, Cohen added that it “was covered

with vermin, especially the neck and breast.” Although not specified, the vermin might very well have been a species of the common chewing lice (*Mallophaga*), an ectoparasite that has been found in much higher intensities in very old female pearly-eyes (see discussion under lifetime reproductive success in chapter 7). This heavy infestation of ectoparasites, especially in the head and upper breast regions, suggests that Cohen’s singing female most likely was a very old individual that had acquired male characteristics as she aged.

Female song in general, although once thought to be rare in birds, especially in female oscines in north temperate latitudes (Kling and Stevenson-Hinde 1977, Nice 1943, Ringleben 1982), is now known to occur more frequently in nature than originally thought. Moreover, besides aging, female song has been attributed to several other physiological, biological, and ecological functions such as fluctuating estrogen levels in females of all ages throughout the year, and guarding of nest sites, territories, food supplies, and even male breeders (Arcese et al. 1988, Baptista et al. 1993, Kern and King 1972, Thorpe 1961). As more and more long-term studies are undertaken, undoubtedly not only several more examples but, more importantly, many more functions of female song within much broader contexts will be discovered.

Owing to the difficulty in determining age and sex of free-flying thrashers, the following analyses are based on banded adults of known gender, including known- and minimum-aged individuals, that breed in thrasher boxes as part of my ongoing life-history study within the Luquillo Experimental Forest. For purposes of comparisons on a regional scale, additional analyses are then conducted based on museum specimens of pearly-eyes of known sex (age data were scant, and thus excluded). Males often prevail in museum collections simply because singing males are more readily detected and, thus, are more frequently collected than are females.

Early in this study, age was shown to be a better predictor of pearly-eye body size than was season (Arendt 1993: app. 4.2), although seasonal feather wear is appreciable in the pearly-eye, and thus can significantly affect wing and tail measurements (Arendt and Faaborg 1989). Tail length in recently fledged pearly-eyes falls far short of its asymptotic (definitive) length and thus increases with age. Therefore, it is not surprising that age was the best predictor of tail length, followed by gender. A regression of the three effects (age, gender, and season) on tarsus length showed that any one (or combination) of them does not significantly affect it. Furthermore, tarsus length reaches more than 90 percent of its asymptotic length before nestlings fledge (Arendt 1985a). Thus, the tarsus is a good predictor of the pearly-eye’s body size.

Age is a better predictor of pearly-eye body size than is season: pearly-eyes are sexually dimorphic; each sex is smaller in some characters, but larger in others.

In another study of avian body size by using a combination of statistical methods (bivariate correlations, stepwise regression, and principal-components analysis), Freeman and Jackson (1990) also found tarsus (and mass) to be the best predictor of overall body size. In an earlier study using a multivariate approach, Miles and Ricklefs (1984) determined that only tarsus and mid-toe lengths contributed strongly to foraging behavioral correlations. For most field biologists who rely solely on measurements of live birds, tarsus may be **the** best single predictor of a bird's overall size and foraging behavior. Although intuitively body mass would seem to be a good indicator of body size, it is well known that body mass varies in response to many geographical, genetic, physiological, and environmental factors. Body mass, although a good candidate for comparing body size, is too variable owing to these many and diverse influences. That is, unless linear (appendicular) measurements are compared as ratios to the cube root of body mass (Amadon 1943, Winkler and Leisler 1985). Comparisons using body mass alone would be misleading in the case of the pearly-eye because body mass increases throughout the day and with the ingestion of fruits with large seeds. Conversely, body mass generally decreases in both sexes as the reproductive season progresses, except in fecund females during the egg-laying months, at which time it significantly increases (Arendt 1993, Arendt and Faaborg 1989).

Also in the infancy of this study, to test for sexual dimorphism in the pearly-eye, both uni- and multivariate statistics were performed on the El Yunque nest-box adults (Arendt 1993: app. 4.4). Results revealed that each sex is smaller in some characters, but larger in others. For example, whereas the wing chord, ninth primary, and tail are longer in males, females measure as large (tarsus) or larger (e.g., bill) in other external longitudinal characters (fig. 5.4). As early as the late 1800s, Newton and Newton (1859: 142), referring to pearly-eyes collected in St. Croix, Virgin Islands, stated that "The sexes do not differ materially," [but] "...the bills of individuals vary greatly in size." Furthermore, as in the pearly-eye, females of the closely related tremblers also have longer bills than do males (Storer 1989), which may be an example of character displacement to allow both sexes to exploit different-size plant and animal foods within the same territory.

A multivariate multiple regression model showed that gender, and interaction terms including it, had the most influence on six of the seven measured characters, tarsus being the only exception (Arendt 1993: app. 4.1). Storer (1989) also found tarsus to be the least variable between sexes of the closely related tremblers.

Additional univariate and multivariate analyses were conducted to further evaluate the spatiotemporal effects of elevation and season on the pearly-eye's morphology. Descriptive statistics (mean, standard error, and sample size) for

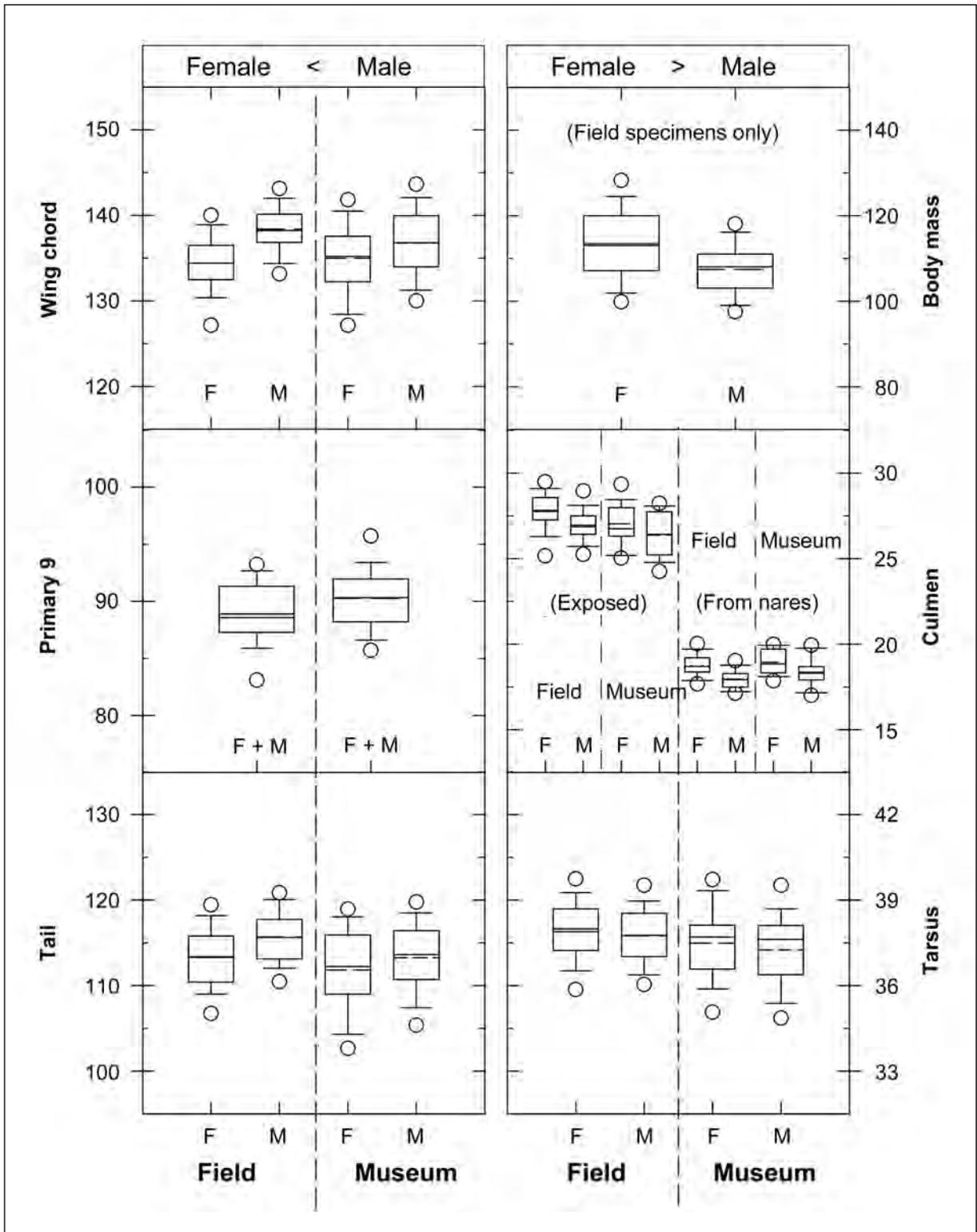


Figure 5.4—Sexual dimorphism in the pearly-eyed thrasher. Typical of most mimids, males (M) tend to have longer wings and tails than females (F). Pearly-eye females are generally heavier, with longer bills. Data were taken between 1979 and 1992 from 95 female and 88 male thrashers inhabiting the Sierra de Luquillo Mountains, Puerto Rico. To demonstrate the extent of sexual dimorphism on a regional scale, 546 museum specimens collected from 40 different islands are included for comparison (box plots). “Primary 9” is the ninth primary flight feather. Body mass is in grams, all other measurements are in millimeters.

treatment groups are summarized in figure 5.2, along with results of a priori and a posteriori analyses. Loadings of characters on size and shape, respectively, are base, -0.103, 0.949; mass, -0.990, -0.095; wing, -0.097, -0.080; and tarsus, -0.014, -0.289.

Both multivariate and univariate approaches suggest that elevational differences in morphology depend on season (table 5.1). There was a highly significant two-way interaction in the MANOVA, and significant two-way interaction for five of the six characters separately. Moreover, all six characters contributed to this response. Alternatively, this may be conceptualized as if

Table 5.1—Results of statistical analyses assessing the effects of season (March–October vs. November–February) and elevation^a (Mona vs. Guánica vs. El Yunque [midelevation] vs. El Yunque [high elevation]) on each of six morphometric characters (two-way ANOVA^b), as well as based on all characters together (two-way MANOVA^c)

Character	P-values			
	Explained df = 7	Elevation ^d df = 3	Season df = 1	Elevation × season df = 3
Exposed culmen	<0.001*	<0.001	<0.001	<0.001
Bill from nares ^d	<.001*	<.001	.035	.369
Tarsus	<.001*	<.001	.154	<.001
Wing	<.001*	.015	.637	<.001
Tail ^d	<.001*	.039	.147	<.001
Body mass	<.001*	<.001	<.001	.021
MANOVA		<.001	.04	<.001

* Denotes significance after Bonferroni’s sequential adjustment.

^a Analyses are based on the ELEVCOMP data set (see “Study Area and Methods”).

^b ANOVA results for each should be interpreted with df = 5, 2, 1, 2 for each of the sources of variation in columns 2 through 5, respectively.

^c Bonferroni’s sequential adjustment corroborates the overall significance of the MANOVA and suggests that all six characters contribute to the differences in multivariable space.

^d “Bill length from nares” and “Tail” have few data for elevation = 1 (Mona Island); therefore, they were not included in the MANOVA.

seasonal differences in morphology are contingent on elevation. Furthermore, for each elevation category (fig. 5.5), seasonal differences are related to size (PC-1) rather than shape (PC-2). At various elevations, diverse climatic and ecological factors such as insolation, temperature, humidity, rainfall, and consequential edaphic effects all govern the life cycles of the residing flora and fauna, and thus the availability and abundance of the pearly-eye’s food resources. This in turn influences the timing of molt in individuals of all ages and, in immatures, the rate and pattern of growth (increase in body mass, long bones, and rhamphotheca). Note that in figure 5.5 the variation ($\pm 1 SE$) in size and shape is greatest in the March through October samples, the period of heaviest breeding, peaks in

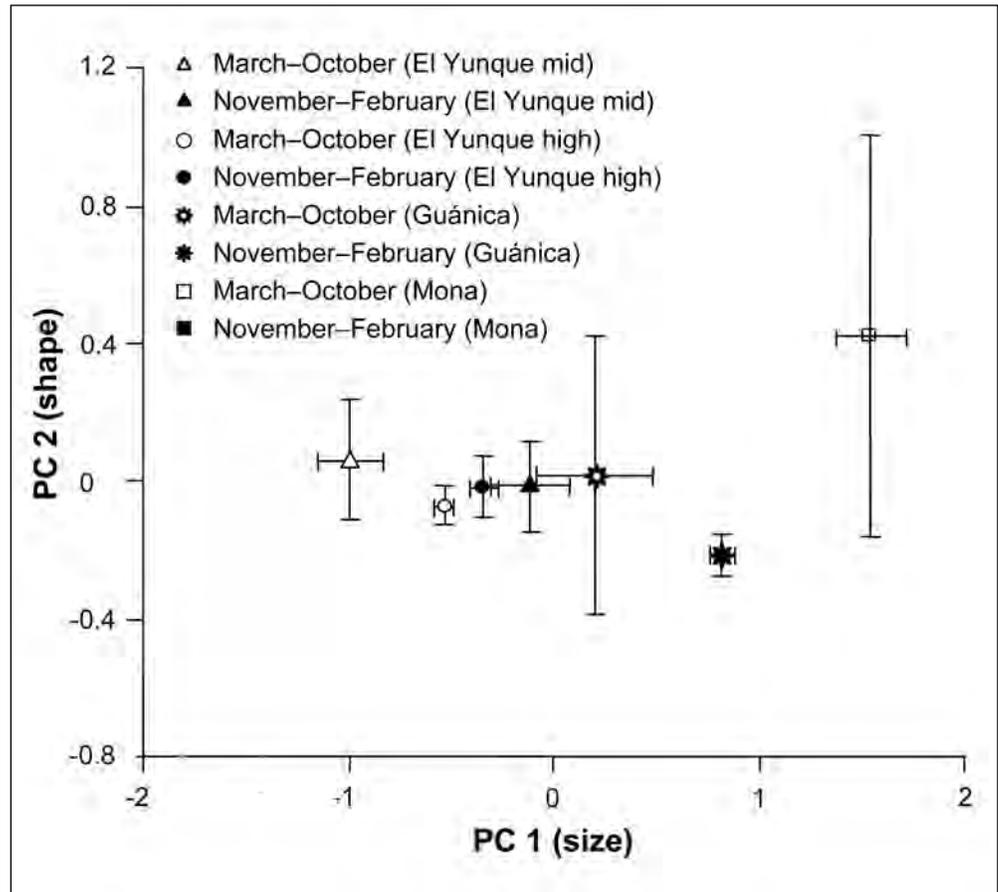


Figure 5.5—Graphical portrayal of results from a principle components analysis (PCA) of log-transformed morphometric characters (table 5.1) of the pearly-eyed thrasher. Groups were defined by combinations of season and elevation as in table 5.1. Vertical and horizontal lines that intersect centroids represent one standard error for PC-2 (shape) and PC-1 (size), respectively. Analyses are based on the ELEVCOMP data set.

flowering and fruiting food trees, and inclusion of most postfledged young in the net samples. In addition, variation is greatest in the coastal lowland thrasher populations (Mona and Guánica), the geographic locations and habitats most likely to first receive dispersing immatures from other islands or more saturated and highly competitive upland forest habitats (explained further in Ricklefs and Cox 1972, 1978, in their discussions of the taxon cycle). Conversely, the November through February samples at all elevations show less variation among sampled individuals (fig. 5.5). This is the period of less primary and secondary production in the forest, and the time by which the early-fledged (March through August) immatures have attained asymptotic proportions in most external morphological characters and are preparing to breed for the first time.

Controlling for temporal effects, elevational trends within seasons (fig. 5.5) mostly involved size, although shape is important in distinguishing groups in November through February. More specifically, the elevational sequence “Mona

Island–Guánica–high-elevation El Yunque–mid elevation El Yunque” forms a gradient of size from small to large in March through October samples. Intuitively, one would predict the correct sequence to be “Mona Island–<Guánica–<El Yunque mid–<El Yunque high” and thus might consider these test results erroneous, possibly owing to other unknown physical or ecological influences. However, subsequent analyses of thrasher populations on other high-relief islands (e.g., Montserrat) showed the same trend; that is, an increase in body size from the coast to montane forest, but then a decrease in body size from samples on the highest peaks, especially near summits in cloud forest. Plants and their fruits are known to decrease in size on the higher slopes owing to physical, climatic, and edaphic conditions. I offer two possible explanations that are by no means the only ones, nor are they mutually exclusive. Highland thrasher populations feeding near mountain summits may have adapted to the reduction in food size, resulting in smaller phenotypes. Or, it is possible that more of the individuals foraging at the highest elevations are dispersers or “floaters” (mostly young, and thus smaller individuals) searching for food in less competitive habitats (avian species richness decreases at higher elevations in the Sierra de Luquillo as well as on other islands). Although as many as 30 nest boxes have been available for nesting in cloud forest on the higher peaks for the past 10 years, nesting has occurred only at the lowest extremes in the transition zone from colorado to cloud forest (see Beissinger et al. 2005 and Cook et al. 2003, 2004, 2005 for plausible explanation).

Based on size (PC-1) in the November through February categories (fig. 5.5), as anticipated, groups from Mona Island and Guánica are indistinguishable, and elevational groups from El Yunque are larger than those from Mona Island or Guánica. Elevational groups from El Yunque are sometimes indistinguishable from each other probably because the elevational range is minimal.

In the November to February samples, large shape differences characterize the contrast between Mona and Guánica samples. A plausible explanation would be that climatic and environmentally induced microhabitat differences, e.g., differences in rainfall and vegetation (especially plant species richness and composition), may be causing the divergence in shape among the sampled external characters. The fact that Mona Island pearly-eyes have longer tarsi corroborates the assumption that, owing to the island’s drought-resistant vegetation with its more diminutive stature, thrashers there are more terrestrial than are those on the main island. Coastal and dry-forest populations on the main island often inhabit forests of greater stature with a wider variety of plant and animal food resources (but see discussion below on adaptation to terrestrial living).

Region-wide comparison of pearly-eye sexual dimorphism supports the ecological release concept.

Extent of Regional Sexual Dimorphism

From a regional perspective, and to obtain a more composite picture of the effects of gender and season on pearly-eye morphology, more comprehensive univariate and multivariate tests were performed. Descriptive statistics (mean, standard error, and sample size) for all morphometric characters differed considerably with season and gender (table 5.2). After controlling for the effects of age as a covariate, season and gender each had a consistent effect on morphometric variation based on MANOVA and Bonferroni's sequential adjustment of univariate results (table 5.3). In general, males are distinguished clearly from females based on size and shape, and this is consistent in all seasons (fig. 5.6). Loadings of characters on size and shape, respectively, are wing, 0.004, 0.133; mass, -0.883, 0.385; base, -0.297, -0.612; nares, -0.306, -0.639; primary 9, -0.168, 0.114; tarsus, -0.101, 0.164; and tail, -0.020, 0.112. Results from these more indepth analyses uphold those previously obtained from simpler univariate tests and multiple regression models.

To further investigate the extent of sexual dimorphism within sympatric populations and among subspecies throughout the region, following techniques used by Storer (1989), I compared the variation in external morphological characters by calculating a dimorphism index. Age was excluded in this analysis because it is often unattainable from museum specimens. Within a single population (El Yunque), as shown earlier (Arendt 1993: app. 4.4), sexual dimorphism was most prevalent in body mass and bill measurements (table 5.4). A comparison of the El Yunque population to an average of several region-wide populations (table 5.5) supports the ecological release concept. Recall, with the exception of the red-legged thrush in some "edge" habitats, there are virtually no keen competitors of the pearly-eye in the Sierra de Luquillo. Thus, as predicted, both sexes in this single population show greater divergence in bill size because they are exploiting a greater variety and size of food items than if they had to compete with several other species. On the other hand, wing and tail lengths (indicators of overall body size) differ much less than in multiple populations in the absence of keen competitors and several other island and geographic effects.

In contrast to the El Yunque thrasher population considered separately, on a regional scale, i.e., including sympatric and allopatric populations of pearly-eyes, sexual dimorphism was most prevalent in wing and tail lengths, with males measuring longer in both (table 5.6). Conversely, females generally had the longest bills. Once again, tarsus length was least variable between the sexes. As anticipated, sexual dimorphic trends among the four subspecies were less definite, most probably owing to several confounding effects, especially elevation. The most isolated subspecies, *M. f. bonariensis*, presented prominent sexual dimorphism

(text continues on page 129)

Table 5.2—Descriptive statistics (mean, standard error [SE], and sample size [n]) of groups used in statistical analyses^a (table 5.3) and defined by combinations of season and gender for each of seven morphometric characteristics of the pearly-eyed thrasher

Character (mm)	Season = 1 (March–June)						Season = 2 (July–October)						Season = 3 (November–February)					
	Males			Females			Males			Females			Males			Females		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
	<i>Millimeters</i>																	
Exposed culmen	27.32	0.097	152	27.72	0.106	176	27.16	0.343	15	28.82	0.262	23	26.90	0.194	32	27.77	0.212	27
Bill from nares	18.09	.069	152	18.70	.064	176	18.12	.161	15	19.10	.141	23	18.00	.129	32	18.92	.137	27
Tarsus	37.82	.088	152	37.59	.076	176	37.73	.228	15	36.99	.399	23	38.04	.159	32	37.95	.179	27
Wing	138.46	.261	152	135.01	.276	176	137.37	1.370	15	134.49	.886	23	139.44	.463	32	137.21	.708	27
Tail	115.13	.261	152	113.18	.273	176	115.58	.834	15	113.20	.800	23	116.91	.494	32	114.02	.722	27
Body mass	106.70	.197	152	112.17	.183	176	103.41	.628	15	112.23	.507	23	106.36	.430	32	109.98	.468	27
Primary 9	90.79	.342	152	89.18	.281	176	89.84	.630	15	89.17	.558	23	89.56	.466	32	89.55	.720	27

^a Analyses are based on the ELYUNQUE data set (see “Study Area and Methods”).

Table 5.3—Results of statistical analyses^a assessing the effects of season, gender, and age on each of seven morphometric characters after log-transformation (two-way ANOVA), as well as based on all characters together (two-way MANOVA^b)

Character	P-values				
	Explained df = 6	Gender df = 1	Season df = 2	Gender × season df = 2	Age df = 1
log (exposed culmen)	<0.001*	<0.001	0.017	0.015	0.218
log (bill from nares)	<.001*	<.001	.191	.290	.743
log (tarsus)	.004*	.025	.011	.305	.133
log (wing)	<.001*	<.001	.002	.511	<.001
log (tail)	<.001*	<.001	.022	.581	.006
log (body mass)	<.001*	<.001	.514	.218	.057
log (primary 9)	.001*	.002	.705	.331	.001
MANCOVA		<.001	.002	.069	.003

* Denotes significance after Bonferroni’s Sequential Adjustment.

^a Analyses are based on the ELYUNQUE data set (see “Study Area and Methods”).

^b Bonferroni’s Sequential Adjustment corroborates the overall significance of the MANOVA and suggests that all seven characters contribute to the differences in multivariate space.

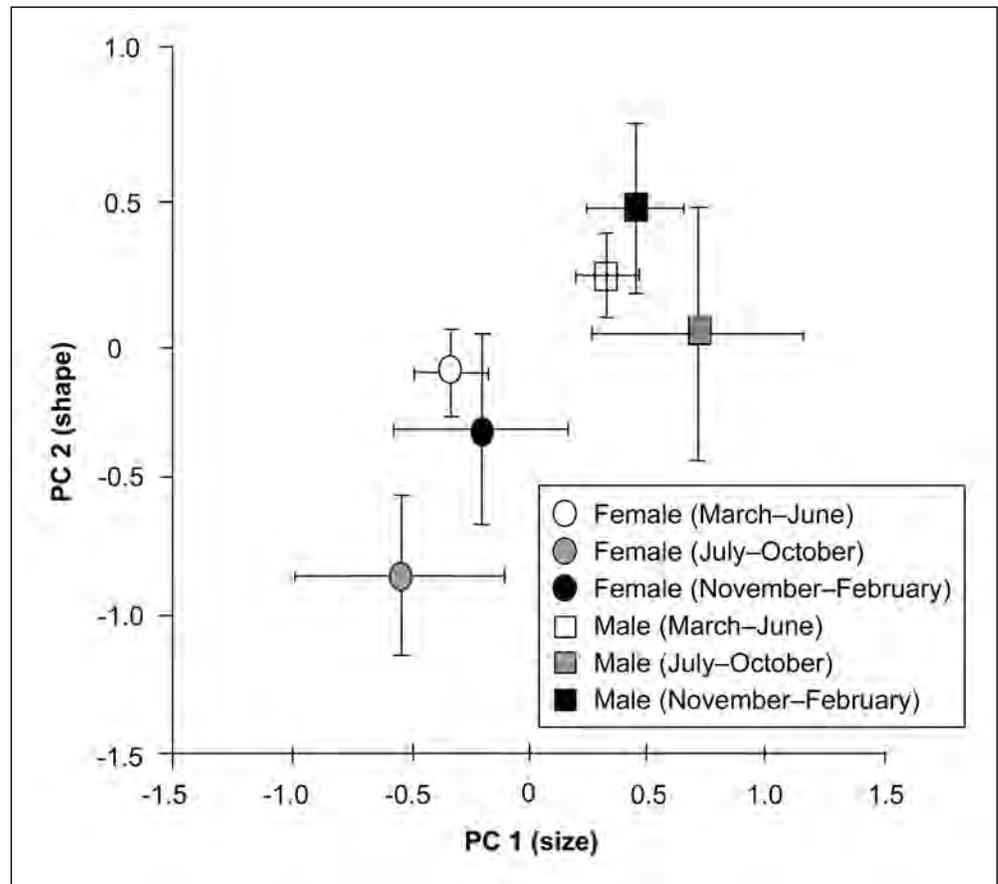


Figure 5.6—Graphical portrayal of results from a Principle Components Analysis (PCA) of log-transformed morphometric characters (tables 5.2 and 5.3) of the pearly-eyed thrasher. Groups were defined by combinations of season and sex as in tables 5.2 and 5.3. Vertical and horizontal lines that intersect centroids represent one standard error for PC-2 (shape) and PC-1 (size), respectively. Males exhibit consistently smaller size (PC-1) than females and differ in shape (PC-2) as well, with no overlap between the sexes in any season. Analyses are based on the ELYUNQUE data set.

Table 5.4—Extent of sexual dimorphism in a pearly-eyed thrasher population at 600 m elevation in the Luquillo Experimental Forest, Puerto Rico^a

Morphological character	Male				Female				No. of mimid and thrush competitors	Dimorphism index ^b
	N	Min.–Max.	Mean	SD	N	Min.–Max.	Mean	SD		
	----- <i>Millimeters</i> -----				----- <i>Millimeters</i> -----					
Wing	159	127.8–148	138.52	3.44	211	116.9–145.1	135.21	3.96	0	2.41
Body mass	164	92.3–128	106.39	6.5	212	86–138	112.18	8.91	0	-5.3
Exposed culmen	149	22.71–30.59	27.22	1.19	192	20.4–32.74	27.82	1.39	0	-2.19
Bill from the nares	158	12.9–19.95	18.03	.82	209	12.63–20.69	18.79	.85	0	-4.15
Culmen depth	146	5.64–9.55	8.11	.49	189	5.34–9.71	8.47	.44	0	-4.34
Culmen width	147	5.35–8.17	6.58	.7	188	5.44–8.72	6.81	.71	0	-3.5
Primary 9	152	82.7–141.2	90.96	5.85	205	77.8–105	89.3	3.67	0	1.83
Tarsus	159	33.98–40.6	37.89	1.04	213	27.72–40.14	37.57	1.18	0	.84
Tail	153	106.5–126	115.61	3.16	204	103.7–123	113.59	3.61	0	1.76

^aThere are no other mimid or thrush competitors except for the red-legged thrush, which is usually parapatric in this forest. However, immediately following two major hurricanes (Hugo in 1989 and Georges in 1998), thrashers and thrushes (together with other species) formed loose, meandering flocks in search of food.

^bDimorphism index obtained by dividing the difference between the means for the sexes (male minus female) by the overall mean and multiplying by 100; negative values denote females are larger in the particular character.

Table 5.5—Comparison of dimorphism indices to evaluate the extent of sexual dimorphism in a single (“EL Yunque”) pearly-eye population within the Luquillo Experimental Forest (LEF), Puerto Rico, compared to several allopatric populations throughout the Caribbean

Morphometric character (mm)	Sexual dimorphism index ^a		Extent of sexual dimorphism LEF vs. many populations
	LEF	Many populations	
Bill from nares	-4.15 ^b	-1.13 ^b	Almost quadruple
Exposed culmen	-2.19 ^b	-1.77 ^b	Pronounced
Tarsus	.84	-.11 ^b	Greater
Wing chord	2.41	3.45	Less than
Tail	1.76	3.39	About half

^aDimorphism index was derived by dividing the difference between the means for the sexes (male minus female) by the overall mean and multiplying by 100.

^bNegative values denote females are larger in a particular character.

Table 5.6—Use of a dimorphism index^a to compare body size differences between the sexes among subspecies of the pearly-eyed thrasher

Subspecies	Male				Female				Dimorphism index
	N	Min.–Max.	Mean	SD	N	Min.–Max.	Mean	SD	
	----- Millimeters -----				----- Millimeters -----				
Wing length									
<i>M. f. fuscatus</i>	214	134.1–142.4	138.07	3.00	169	130.4–139.6	135.48	3.47	1.86
<i>M. f. densirostris</i>	51	130.4–142.1	137.74	3.88	46	128.6–138.3	133.14	3.62	3.39
<i>M. f. klinikowskii</i>	10	141.1–148.2	145.02	2.26	11	124.0–144.9	139.73	5.94	3.72
<i>M. f. bonariensis</i>	18	125.2–137.2	132.68	3.47	14	120.4–133.5	126.41	4.18	4.84
Tail length									
<i>M. f. fuscatus</i>	208	109.6–118.9	114.12	3.43	176	107.0–116.6	111.82	3.75	2.15
<i>M. f. densirostris</i>	52	106.6–116.8	111.96	3.55	44	101.1–112.1	106.25	4.05	5.25
<i>M. f. klinikowskii</i>	10	112.2–122.6	116.52	2.96	11	105.5–120.1	115.12	4.48	1.21
<i>M. f. bonariensis</i>	18	100.1–119.0	110.95	4.49	14	100.4–114.8	105.61	4.24	4.93
Tarsus length									
<i>M. f. fuscatus</i>	215	36.3–38.8	37.46	0.95	167	36.0–38.9	37.71	1.09	-0.41
<i>M. f. densirostris</i>	54	35.2–38.9	37.1	1.34	44	35.4–38.0	36.86	0.94	0.62
<i>M. f. klinikowskii</i>	10	38.5–40.6	39.61	0.67	11	38.1–41.7	40.03	1.09	-1.07
<i>M. f. bonariensis</i>	18	33.9–38.3	37.05	1.1	14	34.8–39.5	36.89	1.12	0.43
Exposed culmen length									
<i>M. f. fuscatus</i>	214	25.0–28.3	26.67	1.23	172	25.6–28.7	27.09	1.2	-1.4
<i>M. f. densirostris</i>	51	24.5–27.5	26.05	1.04	43	24.7–27.5	26.3	0.93	-0.92
<i>M. f. klinikowskii</i>	10	25.5–28.3	26.85	0.98	11	25.4–29.5	27.14	1.14	-1.08
<i>M. f. bonariensis</i>	18	26.4–29.6	27.57	0.93	14	26.4–30.5	28.6	1.22	-3.67
Bill length from nares									
<i>M. f. fuscatus</i>	233	17.5–19.4	18.38	0.69	169	18.0–19.7	18.87	0.65	-2.11
<i>M. f. densirostris</i>	47	17.1–19.0	18.11	0.64	31	17.1–18.8	18.18	0.59	-0.33
<i>M. f. klinikowskii</i>	10	18.1–20.2	19.06	0.64	11	18.1–19.8	19.1	0.61	-0.23
<i>M. f. bonariensis</i>	18	17.9–20.5	19.26	0.82	14	18.0–21.2	19.62	0.83	-1.85

^a Dimorphism Index was derived by dividing the difference between the means for the sexes (male minus female) by the overall mean and multiplying by 100; negative values denote females are larger in the particular character.

in four of the five characters (table 5.6 and fig. 5.7). In contrast to the El Yunque population that has few competitors, the thrashers on species-rich (30+) Bonaire show a much greater divergence in overall body size, not just bill size. Bonaire is a dry, low-relief island on which water is scarce and patchy. As a result, both interference and diffuse competition are keen (see discussion in chapter 4 and below). As in the tremblers (Storer 1989), character displacement in the pearly-eye may be an adaptation conducive to its continued survival on Bonaire.

Character displacement in the pearly-eye may be an adaptation conducive to its continued survival on Bonaire.

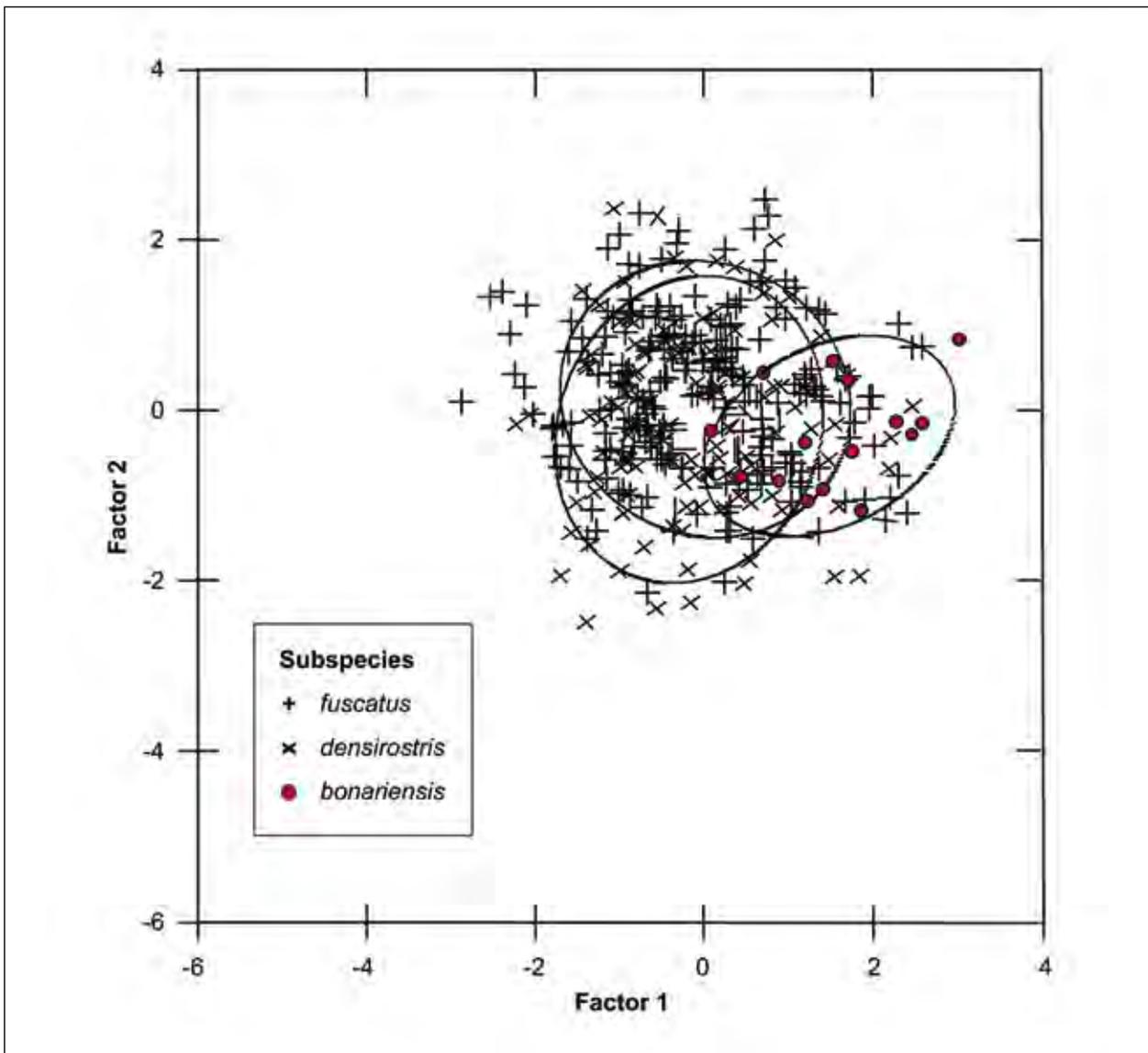


Figure 5.7—Discriminant Function Analysis results from using five morphological characters (lengths of exposed culmen, bill from the nares, tarsus, wing chord, and tail) to compare body size among three subspecies of the pearly-eyed thrasher (*Margarops fuscatus fuscatus*, *M. f. densirostris*, and *M. f. bonariensis*). The most predictive variables showing *bonariensis*' dissimilarity to the other two subspecies were, in descending order of importance, bill length from the nares, tarsus, and wing chord (similar to tail in importance). To illustrate gene flow among the *M. f. fuscatus* and *M. f. densirostris* populations, the classification matrix, as well as a jackknifed classification matrix, showed that 80 percent of the *M. f. bonariensis* characters was correctly classified, whereas only 50 percent of each of the other two was.

Tremblers are now thought to be one of the closest relatives of the pearly-eye (Hunt et al. (2001). Thus, it is not surprising that the trends and extent of sexual dimorphism are strikingly similar among at least three external morphological characters (wing, tail, and tarsus) amid subspecies of tremblers and pearly-eyes (table 5.7 and Storer 1989: table 1). Even culmen and bill lengths follow the same trend (longer in females), but the extent of the sexual dimorphism is greatly exaggerated in the tremblers (Storer 1989: table 1). With the exception of the tarsus, the same sex of each species measures longer or shorter in the remaining characters. Although sexual dimorphism in the trembler does not increase with an increase in competitors, it tends to in some characters of the pearly-eye.

As anticipated, the more ubiquitous subspecies *M. f. fuscatus* (Bahamas to Antigua—and thus presumed greater gene flow and increased homozygosity) showed the least dimorphism in wing and tarsus lengths. Both of the more allopatric subspecies *M. f. densirostris* and *M. f. klinikowskii* presented the least variation among one or more of the remaining three characters (table 5.6). Little sexual dimorphism in bill measurements for the subspecies *M. f. densirostris* and *M. f. klinikowskii* was unexpected because of their more limited and isolated ranges and smaller populations. Furthermore, samples were taken from high-relief islands in the Lesser Antilles, which should increase variation owing to elevational effects (app. 4.1). Finally, the small sample size for the subspecies *M. f. klinikowskii* must be considered as a potential factor contributing to the observed results.

It is likely that the thrasher propagules colonizing la Désirade were of the subspecies *M. f. fuscatus*, originating from islands much farther north.

The pearly-eye population inhabiting la Désirade, a small satellite island off of Guadeloupe in the Lesser Antilles, is currently assigned to the subspecies *M. f. densirostris*. Yet, with the exception of the tarsus, it shows the least sexual dimorphism among all the populations of the five islands on which the race occurs (app. 4.1). In fact, its dimorphism indices results are most similar to those of the much more northern populations of *M. f. fuscatus*. Why should this be? Recall that DNA testing (chapter 3) showed very little mitochondrial differentiation between pearly-eye populations on Puerto Rico, Barbuda, Montserrat, Guadeloupe, and Dominica. And, inter-island natal dispersal (Barbuda to Guadeloupe) was documented (chapter 4). It is likely that the thrasher propagules colonizing la Désirade were of the subspecies *M. f. fuscatus*, originating from islands much farther north. A statement by Garrido and Remsen (1996) corroborates this view. These authors noted plumage differences in La Désirade specimens from those collected on nearby islands. This led them to “...agree with Hellmayr’s (1934) assignment of specimens from La Désirade to more distant nominate *M. f. fuscatus* rather than to *M. densirostris* of nearby Guadeloupe and Montserrat.”

Table 5.7—Comparison of sexual dimorphism indices between pearly-eyes (PETH) and their close relatives, the tremblers (TREM)

N (TREM)	TREM subspecies	TREM competitors x̄ (min.–max.)	Dimorphism index ^a		PETH competitors x̄ (min.–max.)	PETH subspecies	N (PETH)
			TREM	PETH			
	<i>Cinlocerthia</i>				<i>Margarops</i>		
Wing length							
35	<i>C. r. pavidata</i>	2.3 (2–3)	2.40	1.89	1.2 (0–3)	<i>M. f. fuscatus</i>	383
35	<i>C. r. tremula</i>	4	3.57	3.39	4.2 (2–6)	<i>M. f. densirostris</i>	97
88	<i>C. g. ruficauda</i>	6	3.39	3.72	7.0	<i>M. f. klinikowskii</i>	21
12	<i>C. g. gutturalis</i>	5	3.50	4.84	10.0	<i>M. f. bonariensis</i>	32
47	<i>C. g. macrorhyncha</i>	8	3.42				
41	<i>C. r. tenebrosa</i>	4	4.75				
	Average		3.50	3.46			
Tail length							
28	<i>C. r. pavidata</i>	2.3 (2–3)	3.22	2.15	1.2 (0–3)	<i>M. f. fuscatus</i>	384
27	<i>C. r. tremula</i>	4	2.06	5.25	4.2 (2–6)	<i>M. f. densirostris</i>	96
61	<i>C. g. ruficauda</i>	6	3.01	1.21	7.0	<i>M. f. klinikowskii</i>	21
9	<i>C. g. gutturalis</i>	5	—	4.93	10.0	<i>M. f. bonariensis</i>	32
30	<i>C. g. macrorhyncha</i>	8	2.93				
27	<i>C. r. tenebrosa</i>	4	5.02				
	Average		3.25	3.39			
Tarsus length							
43	<i>C. r. pavidata</i>	2.3 (2–3)	1.48	-.41	1.2 (0–3)	<i>M. f. fuscatus</i>	382
41	<i>C. r. tremula</i>	4	.38	.62	4.2 (2–6)	<i>M. f. densirostris</i>	98
89	<i>C. g. ruficauda</i>	6	.65	-1.07	7.0	<i>M. f. klinikowskii</i>	21
10	<i>C. g. gutturalis</i>	5	—	.43	10.0	<i>M. f. bonariensis</i>	32
49	<i>C. g. macrorhyncha</i>	8	-.13				
40	<i>C. r. tenebrosa</i>	4	3.30				
	Average		1.14	-.11			
Exposed culmen length							
25	<i>C. r. pavidata</i>	2.3 (2–3)	-14.27	-1.40	1.2 (0–3)	<i>M. f. fuscatus</i>	386
17	<i>C. r. tremula</i>	4	-21.85	.92	4.2 (2–6)	<i>M. f. densirostris</i>	94
46	<i>C. g. ruficauda</i>	6	-17.11	-1.08	7.0	<i>M. f. klinikowskii</i>	21
4	<i>C. g. gutturalis</i>	5	—	-3.67	10.0	<i>M. f. bonariensis</i>	32
21	<i>C. g. macrorhyncha</i>	8	-10.21				
18	<i>C. r. tenebrosa</i>	4	-12.69				
	Average		-15.23	-1.77			
Bill from nares							
43	<i>C. r. pavidata</i>	2.3 (2–3)	-18.75	-2.11	1.2 (0–3)	<i>M. f. fuscatus</i>	402
35	<i>C. r. tremula</i>	4	-19.61	-.33	4.2 (2–6)	<i>M. f. densirostris</i>	78
88	<i>C. g. ruficauda</i>	6	-19.55	-.23	7.0	<i>M. f. klinikowskii</i>	21
12	<i>C. g. gutturalis</i>	5	-16.56	-1.85	10.0	<i>M. f. bonariensis</i>	32
45	<i>C. g. macrorhyncha</i>	8	-12.75				
37	<i>C. r. tenebrosa</i>	4	-16.21				
	Average		-16.93	-.80			

— = no data.

^aDimorphism index was derived by dividing the difference between the means for the sexes (males minus females) by the overall mean and multiplying by 100; negative values denote females are larger in the particular character.

To visually portray and compare sexual dimorphism within and among island populations, morphometric data taken from the free-flying thrashers and museum specimens included in previous analyses are presented in figure 5.4. Note that mean lengths of the five morphological characters included in both analyses are remarkably similar, although as would be expected, the ranges (data extremes) in the museum specimens are generally much wider because they represent samples from numerous islands and include geographic and island effects.

Terrestrial Vs. Arboreal Adaptations (Museum Specimens)

Before moving on to interspecific determinants of avian body size, I must treat one final intraspecific factor influencing the observed pronounced variation in the pearly-eye's morphology, i.e., the potential for a predisposition to a more terrestrial existence on dry, heat-stressed low-relief islands and cays. The wing-to-tarsus ratio in birds has been used in the past (e.g., Grant 1966, Storer 1989) to evaluate the adaptation to a more terrestrial life (smaller ratio) than the more common arboreal habit (larger ratio). Recall that on Mona Island (exemplary of the above-mentioned physical and climatic conditions), pearly-eyes unexpectedly rivaled, or even surpassed, highland individuals in wing and tarsus lengths. To evaluate the possibility of a transition to a more terrestrial mode, I compared wing-to-tarsus ratios not only from Mona Island pearly-eyes with those of Puerto Rico's highlands, but also among thrasher populations from several islands and habitats. An analysis of the available museum specimens did not reveal a consistently smaller wing-to-tarsus ratio in coastal and lowland individuals, often found in vegetation associations of short and diminutive stature, or vice versa (larger ratios in upland thrashers from tall-stature forests). Tarsus and wing length among the 546 specimens of pearly-eyes from some 40 islands (with elevations from sea level to more than a thousand meters) ranged from, respectively, 35.70 to 40.11 and 129.9 to 142.1). Although lowland pearly-eyes were somewhat longer legged than upland individuals (wing-to-tarsus ratio 3.5 vs. 3.6), the overall wing-to-tarsus ratio revealed very little variation (range: 3.36 to 4.03; avg. = 3.65) among islands (table 5.8). Furthermore, there was no significant correlation between the wing-to-tarsus ratio and landmass. As an example, the wing-to-tarsus ratio of Mona Island pearly-eyes was 3.62, whereas that of St. Lucian thrashers (most of which were collected in montane rain forest) was 3.52, or just the opposite of what was expected. In any case, the mean wing-to-tarsus ratios were not significantly different between the two groups (Mann-Whitney Rank Sum Test (hereafter M-W R S): $T = 91$; $P = 0.86$). In support of these results, Hernández-Prieto (1993), after conducting intensive comparative foraging studies on Mona and in adjacent

Is the pearly-eye predisposed to a more terrestrial life on dry, heat-stressed islands?

Table 5.8—Wing-to-tarsus ratios derived from museum specimens of the pearly-eyed thrasher from several low- and high-relief islands as a measure of potential adaptation to a terrestrial existence

Island	No. of study skins	Elevation (m)	L (low relief ^a) H (high relief)	Average wing tarsus ratio
Barbuda	12	44.5	L	3.71
Caicos	27	<48	L	3.68
Beata	7	50	L	3.56
Sombrero	1	<65	L	3.68
Anguilla	2	65	L	3.58
Crooked Island	2	<67	L	3.76
San Salvador	80	<67	L	3.75
Great Inagua	32	<67	L	3.7
Mayagüana	1	<67	L	3.6
Rum Cay	12	<67	L	3.57
Desecheo	10	79.1	L	3.72
Mona	17	80	L	3.62
Culebra	13	198.1	L	3.65
Isla Piñeros	3	<200	L	3.77
Luis Peña	1	<200	L	3.72
Culebrita	4	<200	L	3.72
Caja de Muertos	8	<200	L	3.66
Bonaire	32	239	L	3.51
La Désirade	18	270	L	3.64
Vieques	17	300	L	3.59
Jost Van Dyke	1	335.3	L	3.36
St. Croix	9	355	L	3.63
St. John	4	392	L	3.65
Antigua	18	402	L	3.58
Tortola	5	<450	L	3.67
Virgin Gorda	2	<450	L	3.47
St. Thomas	26	477	L	3.66
St. Martin	4	<880	H	3.62
St. Eustatius	14	<880	H	3.6
Saba	7	887	H	3.68
Montserrat	13	900	H	3.67
St. Lucia	26	950	H	3.54
Nevis	4	985.1	H	3.56
St. Kitts	12	1156	H	3.56
Puerto Rico	41	1338	H	3.66
Martinique	4	1397	H	3.62
Dominica	34	1441	H	3.75
Guadeloupe	22	1484	H	3.68
Jamaica	1	2256	H	4.03
Total or (count):	546	—		(39)
Minimum	1	44.5		3.35
Maximum	80	2256		4.03
Mean	14.3	512.5		3.64
SD	15.4	535		0.11

— = incalculable.

^aLow relief = <600 m; high relief = >600 m, or about midway up the moisture and vegetational gradient on most Caribbean islands; ratios should be minimal for small, low-relief islands, but no clear trend is evident.

coastal dry forest within the Guánica Biosphere Reserve, Puerto Rico, showed that Mona's pearly-eyes were not more terrestrial than Guánica's, but rather both populations are mainly arboreal. It is obvious that factors other than perch substrates and an adaptation to terrestrial life are having a greater impact on the longitude of appendicular characters in the pearly-eyed thrasher.

What else might be behind the evolution of disparate body size and sexual dimorphism in the pearly-eye? From an ecological perspective, morphological disparity between the sexes may be the result of interference competition and consequential character displacement (see Schluter and Smith 1986, Schoener 1965). Both sexes compete for the same food resources, often in highly disturbed or "edge" habitats in which food may be limited. From a reproductive perspective, whereas females tend to guard the nest and a small area around it (reflected in their more pugnacious behavior and larger beaks), males guard a much greater area from intra- and interspecifics, especially around the perimeter of the territory. Over time, this behavior could result in an increase in wing and tail length to enhance the male's aerial maneuverability. Not only is wing chord longer in males than in females, so is the ninth primary, a very important feather in forward propulsion, speed, and agility: M-W R S: $P < 0.001$, including 209 females (median = 88.8; 25 to 75 percentiles = 87.4 to 91.4, respectively) and 155 males: (median = 90.3; 25 to 75 percentiles = 88.2 to 91.9, respectively) from the El Yunque sampled population.

Some of the intraspecific factors governing pearly-eye body size have been reviewed. Next, interspecific effects will be treated, namely the possibility of competition from closely related species, such as the scaly-breasted thrasher, among others.

Sources of Interspecific Variation in Avian Body Size

Effects of Competition on Body Size

In habitats where avian communities are not often subjected to resource limitation, e.g., grassland and shrubsteppe, intra- and interspecific competition play at best a minor role in influencing community structure or phenotypic variation (Wiens 1977, Wiens and Rotenberry 1981). In general, however, although occasionally disputed (Connor and Simberloff 1978, Simberloff 1978, Simberloff and Boecklen 1981, Strong and Simberloff 1981, Strong et al. 1979), competition and its consequences (e.g., ecological release, character displacement, and adaptive radiation) have been well documented (Alatalo 1982; Amadon 1966; Boag and

Competition plays a role in avian body size.

Grant 1981; Brown and Wilson 1956; Case and Sidell 1983; Case et al. 1983; Cox and Ricklefs 1977; Diamond 1978; Faaborg 1982b, 1985; Grant 1968; Grant and Abbott 1980; Grant and Grant 1982; Graves and Gotelli 1993; Hendrickson 1981; Hernández-Prieto 1993; Lundberg et al. 1981; Schluter and Grant 1984; Schoener 1965). Therefore, competition was included as a variable in several statistical analyses.

Potential for Intrageneric Competition

Competition theory predicts that the pearly-eye's keenest competitor for resources should be a similar species, i.e., the most closely related phylogenetically, and with the most similar ecology (e.g., feeding, nesting, and behavioral). The pearly-eye and its current congener (pending possible replacement in the genus *Allenia*), the scaly-breasted thrasher, will be treated first because both species are (1) similar in plumage, (2) mostly arboreal, (3) mainly frugivorous, and (4) habitat generalists. These similarities led early taxonomists to conclude that the scaly-breast must be the pearly-eye's closest living relative. Indeed, even ecologists have used the two *Margarops* species as evidence for character displacement in sympatric congeneric species (see McLaughlin and Roughgarden 1989). As a further example, Schoener (1965: table 1.34) reported that *Margarops* spp. show the most pronounced "ratio of large to small culmen" (1.56) among 14 species of mimids (min. = 1.02, avg. = 1.2).

Recently, however, with the aid of DNA testing, Ricklefs and Bermingham (1997) and Hunt et al. (2001) have shown that the two species of tremblers (*Cinclocerthia gutturalis* and *C. ruficauda*) are the pearly-eye's closest relatives. To many field ornithologists, the apparent close affinity of the pearly-eye and scaly-breast was always questioned because of several striking dissimilarities, including morphology (body size), behavior, aspects of the diet (preferences, shifts, seasonal trends), and foraging techniques. The scaly-breast's morphology, behavior, and disposition are more similar to that of the sage thrasher (*Oreoscoptes montanus*) of North America, which, incidentally, is more closely related to mockingbirds (*Mimus*) than to other continental (*Toxostoma* spp.) thrashers (Sibley and Ahlquist 1990: fig. 379; Zink et al. 1999). Nonetheless, because of the similarities between the two species' geographic and habitat ranges, and especially their nesting ecologies and frugivory, the scaly-breast is still considered a good candidate species to explore the possibility of a shift in the pearly-eye's body size in the absence (or presence) of a potentially keen competitor.

Combination of Uni- and Multivariate Analyses (Museum Specimens)

To identify and evaluate potential competitive factors responsible for observed differences in the pearly-eye's body size, analysis of variance and covariance, both univariate (ANOVA and ANCOVA) and multivariate (MANOVA and MANCOVA) tests, were performed on museum specimens (tables 5.9 and 5.10, respectively). Dependent variables included the same set of five external morphological characters used in the preliminary univariate analyses. These more comprehensive and inclusive analyses also were chosen to compare results with those from the preliminary analyses and to summarize simultaneously all of the main treatment (and covariate) effects of gender, season, and the presence or absence of the scaly-breast, on the pearly-eye's body size. It is noteworthy that regardless of either a univariate or multivariate approach, three-way or two-way interactions generally were not significant before (table 5.9) or after (table 5.10) controlling for the effect of covariates. Thus, the effects of the main treatment factors are consistent when significant. Season, gender, and presence or absence of the scaly-breasted thrasher (SBTH) each had a significant effect in the MANOVA (table 5.9), although only season and gender had a significant effect after controlling for the influence of the covariates in the MANCOVA (table 5.10).

The disparity in significance (before versus after controlling for covariates) for the effect of the scaly-breast on morphometric variation in the pearly-eye has at least two possible explanations. First, the scaly-breast has an effect on the pearly-eye, but the covariates: SSPNET (species present per netting session), SPPISLA (landbird species per island), elevation, latitude, and area, represent environmental variables that determine the distribution of the scaly-breast, so that once the effects of those variables are removed in ANCOVAs or MANCOVA, the effect of the scaly-breast is removed as well. Alternatively, the covariates may have a direct effect on morphometric variation in the pearly-eye, and the scaly-breast only appears to have an effect in ANOVAs and MANOVA because the distribution of the scaly-breast is highly correlated with the underlying environmental variables to which the morphology of the pearly-eye responds. These two interpretations are not mutually exclusive, and are equally plausible. The covariates, coupled with the other two main treatment effects (gender and season), no doubt greatly influence the distribution of both the pearly-eye and the scaly-breast and, at the same time, are influencing both the pearly-eye's and the scaly-breast's morphologies. Consequently, although interspecific competition may be present, and thus influencing body size of both species, a multiplicity of environmental and ecological factors acting in concert may play a more major role in governing both species'

Table 5.9—Results of statistical analyses^a assessing the effects of season (March–June vs. July–October vs. November–February), gender (male vs. female), and presence or absence of the scaly-breasted thrasher (SBTH) on each of a set of five morphometric characters (three-way ANOVA), as well as on all characters together (three-way MANOVA^b), of the pearly-eyed thrasher

SOV	ANOVA						MANOVA
	df	Exposed culmen	Culmen from nares	Tarsus	Wing	Tail	
Explained	11	<0.001*	<0.001*	<0.001*	<0.001*	0.008*	
SBTH	1	.014	.105	.005	<.001	.721	<0.001
Gender	1	<.001	<.001	.759	<.001	.001	<.001
Season	2	<.001	.635	<.001	.537	.218	<.001
SBTH × gender	1	.645	.786	.585	.046	.041	.406
SBTH × season	2	.465	.708	.067	.514	.198	.430
Gender × season	2	.745	.687	.929	.492	.61	.902
SBTH × gender × season	2	.110	.758	.7	.732	.213	.337

*Denotes significance after Bonferroni’s Sequential Adjustment.

^aAnalyses are based on the MUSEUMPET data set (see “Study Area and Methods”) and do not control for the effects of a set of geographical and ecological covariates (SOV), i.e., elevation, latitude, area, species per net, and species per island, on morphometric variation in the pearly-eyed thrasher.

^bBonferroni’s Sequential Adjustment corroborates the overall significance of the MANOVA and suggests that all five characters contribute to the differences in multivariate space.

Table 5.10—Results of statistical analyses^a controlling for the set of geographical and ecological covariates (SOV), i.e., elevation, latitude, area, species per net (SPPNET), and species per island (SPPISLA), and assessing the effects of season (March–June vs. July–October vs. November–February), gender (male vs. female), and presence or absence of the scaly-breasted thrasher (SBTH) on each of a set of five morphometric characters (three-way ANCOVA), as well as on all characters together (three-way MANCOVA^b), of the pearly-eyed thrasher

SOV	ANOVA						MANOVA
	df	Exposed culmen	Culmen from nares	Tarsus	Wing	Tail	
Explained	16	<0.001*	<0.001*	<0.001*	<0.001*	0.008*	
Season	2	<.001	.047	<.001	.511	0.32	<0.001
Gender	1	<.001	<.001	.751	<.001	<.001	<.001
SBTH	1	.189	.067	.671	.147	.927	.234
Gender × season	2	.733	.415	.827	.653	.639	.954
SBTH × season	2	.554	.329	.017	.237	.133	.148
SBTH × gender	1	.613	.855	.603	.062	.065	.586
SBTH × gender × season	2	.128	.692	.749	.71	.221	.389
All covariates	5	<.001	<.001	<.001	<.001	.263	<.001
SPPNET	1	.36	<.001	.37	.033	.32	.239
SPPISLA	1	.005	.001	.063	.86	.518	.811
Elevation	1	.001	.028	.198	.159	.78	.084
Latitude	1	<.001	<.001	<.001	<.001	.714	<.001
Area	1	.069	.622	.773	.151	.03	.326

*Denotes significance after Bonferroni’s Sequential Adjustment.

^aAnalyses are based on the MUSEUMPET data set (see “Study Area and Methods”).

^bBonferroni’s Sequential Adjustment corroborates the overall significance of the MANCOVA and suggests that all five characters contribute to the differences in multivariate space.

body sizes (review fig. 5.1). For extreme examples of how, through natural selection, the environment and a species' foraging ecology can direct the size and shape of the resultant phenotypes, see Boag and Grant (1981) and Price et al. (1984b).

Besides the ANOVA tests, a PCA was conducted, not only to help identify and prioritize predictor variables but also to visually depict their effects on thrasher morphology. Based on the PCA, a detailed exposition of group differences among museum specimens before controlling for covariates is presented in fig. 5.8. Loadings of characters on size and shape, respectively, are base, -0.710, -0.145; nares, -0.658, 0.055; tarsus, -0.247, 0.331; wing, -0.025, 0.503; and tail, 0.035, 0.783.

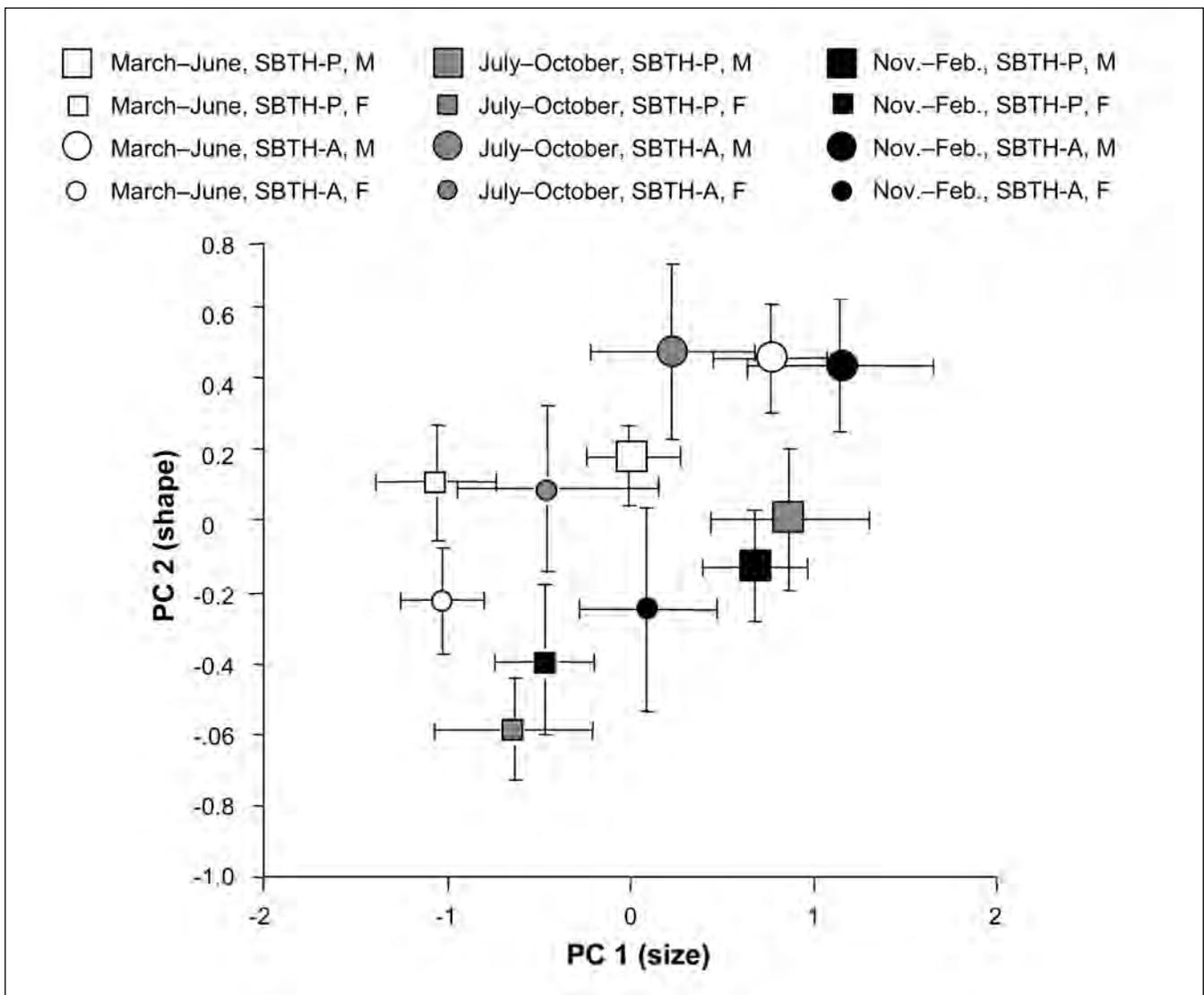


Figure 5.8—Graphical portrayal of results from a Principle Components Analysis (PCA) of log-transformed morphometric characters (tables 5.9 and 5.10) of the pearly-eyed thrasher. Groups were defined by combinations of season, presence (SBTH-P) and absence (SBTH-A) of the scaly-breasted thrasher (SBTH) and sex as in tables 5.9 and 5.10. Vertical and horizontal lines that intersect centroids represent one standard error for PC-2 (shape) and PC-1 (size), respectively. Within each season, groups defined by combinations of sex and the scaly-breasted thrasher do not overlap, with males smaller than females and the presence of SBTH affecting size and shape. Analyses are based on the MUSEUMPET data set.

As competition theory predicts, body size of both male and female pearly-eyes is more variable within and among the three seasons when the scaly-breast is absent (fig. 5.8). Neither male nor female pearly-eye body size is highly variable in either the postbreeding period (July to October) or early in the breeding season (November to February) in habitats in which the scaly-breast is present. The presence of more juveniles in the samples may contribute to the greater variation in body size during the main breeding season (March to June). Also, as would be anticipated if competition were influencing morphology, shape of the pearly-eye’s external characters is highly variable during the breeding season when the scaly-breast is present (fig. 5.8).

Seasons and competitors affect pearly-eye body size.

Combination of Uni- and Multivariate Analyses (Field Measurements)

To corroborate the results obtained from museum specimens, i.e., that season and the presence or absence of the scaly-breast affect pearly-eye morphology, both univariate and multivariate approaches were undertaken on data collected from free-flying pearly-eyes and scaly-breasts captured during mist-net sessions on several Caribbean islands. Descriptive statistics for morphometric characters (mean, standard error, and sample size) are summarized in table 5.11. Loadings of characters on size and shape, respectively, are base, -0.627, 0.093; nares, -0.766, -0.211; tarsus, -0.117, 0.356; wing, -0.010, 0.510; tail, -0.076, 0.748. External appendicular characters vary considerably with the influences of season and the presence or absence of the scaly-breast. In general, the effect of the scaly-breast on the morphology of the pearly-eye depends on season (significance of two-way interactions) based on univariate and multivariate approaches (table 5.12). As

Table 5.11—Descriptive statistics (mean, standard error [SE], and sample size [n]) of groups used in statistical analyses^a and defined by combinations of season and presence vs. absence of the scaly-breasted thrasher (SBTH) for each of five morphometric characters of the pearly-eyed thrasher

Character	SBTH present						SBTH absent					
	March–October			November–February			March–October			November–February		
	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N
	<i>Millimeters</i>											
Exposed culmen	26.06	0.109	501	26.89	0.103	197	27.45	0.09	167	23.2	0.279	60
Culmen from nares	18.42	.053	335	18.69	.078	136	18.64	.06	167	18.45	.229	13
Tarsus	37.77	.065	358	38.54	.179	199	37.7	.094	166	38.05	1.152	11
Wing	136.41	.181	571	135.53	.29	290	135.83	.322	166	137.13	.464	91
Tail	113.99	.206	348	112.85	.386	146	110.3	.384	163	112.57	1.052	11

^aAnalyses are based on the FIELDPET data set (see “Study Area and Methods”).

Table 5.12—Results of statistical analyses^a assessing the effects of season (March–October vs. November–February) and presence or absence of the scaly-breasted thrasher (SBTH) (see table 5.11) on each of five morphometric characters (two-way ANOVA), as well as based on all characters together (two-way MANOVA^b)

Character	<i>P-values</i>			
	Explained df = 3	SBTH df = 1	Season df = 1	SBTH × season df = 1
Exposed culmen	<0.001*	0.881	0.011	<0.001
Bill from nares	.008*	.033	.011	.094
Tarsus	<.001*	.489	<.001	.461
Wing	.005*	.563	.194	.001
Tail	<.001*	<.001	.042	.016
MANOVA		<.001	.010	.037

*Denotes significance after Bonferroni's sequential adjustment.

^aAnalyses are based on the FIELDPET data set (see "Study Area and Methods").

^bBonferroni's sequential adjustment corroborates the overall significance of the MANOVA and suggests that all five characters contribute to the differences in multivariable space.

expected, from March to October, the presence of scaly-breast has no effect on the pearly-eye's body size but does have a significant effect on its shape (fig. 5.9). Corroborative of the season and scaly-breast effects obtained from museum specimens (fig. 5.8), and supportive of competition theory, results from the same set of statistical tests conducted on free-flying thrashers once again reveal that season is a major factor governing pearly-eye body size. Still, pearly-eyes definitely show much more morphological variation in the absence of the scaly-breast (fig. 5.9, November to February), which suggests that competition does in fact influence its morphology.

Intergeneric Competition

On most islands, because the pearly-eye is a habitat generalist, it competes with several species of thrushes and other mimids besides the scaly-breasted thrasher (see, for example, Zusi 1969), all of which are fairly similar in size, diet, and reproductive ecologies. Therefore, I performed a simple correlation analysis of five of the pearly-eye's external morphological characters taking into account the total number of potential competitors on each island. That is, those species most likely to compete with the pearly-eye through diffuse, interference, and exclusion competition.

Twelve mimid and thrush species are potential competitors of the pearly-eye (app. 4). Despite the pearly-eye's wide geographic distribution, it is absent from most large islands. As a result, it generally inhabits islands with an average of three competitors, ranging from zero to eight (app. 4). As shown earlier for the

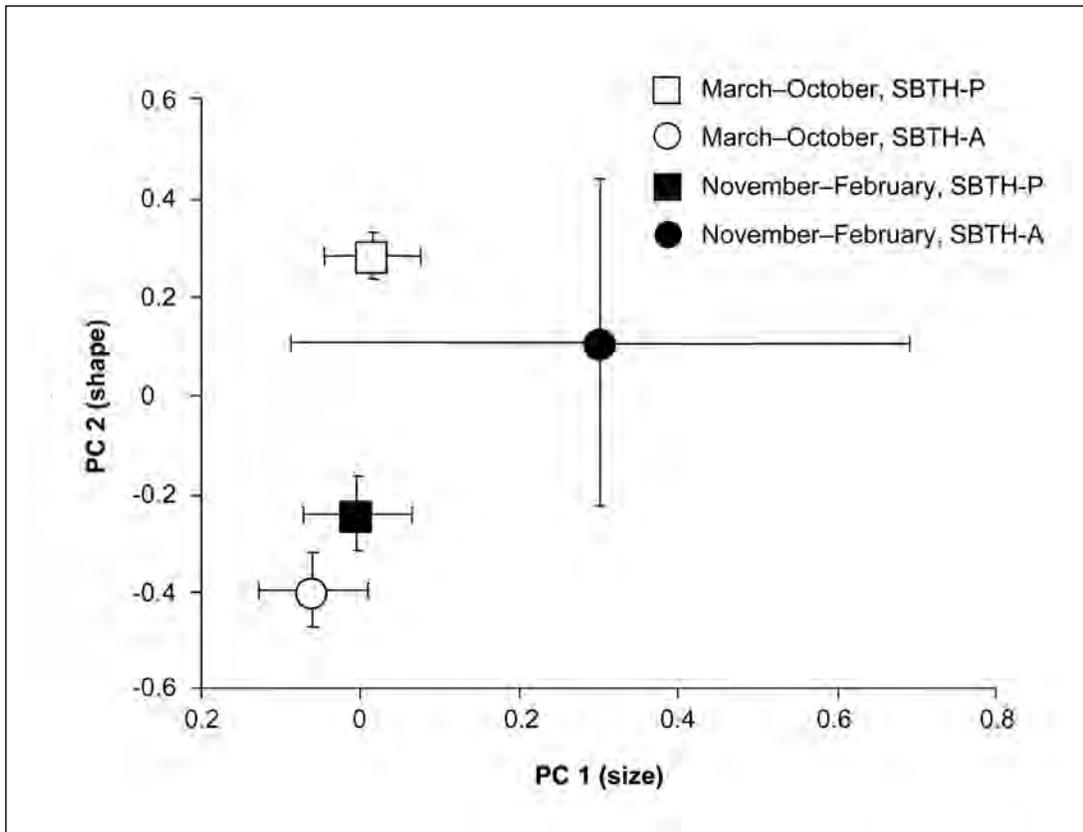


Figure 5.9—Graphical portrayal of results from a Principle Components Analysis (PCA) of log-transformed morphometric characters (tables 5.11 and 5.12) of the pearly-eyed thrasher. Groups were defined by combinations of season and presence (SBTH-P) and absence (SBTH-A) of the scaly-breasted thrasher (SBTH). Vertical and horizontal lines that intersect centroids represent one standard error for PC-2 (shape) and PC-1 (size), respectively. The effect of the scaly-breast on morphology depends on season. From March to October, the effect of the scaly-breast is reflected mostly in shape differences. From November to February there is substantial variation in morphology in the absence of the scaly-breast (black circles). Analyses are based on the FIELDPET data set.

El Yunque thrasher population, and as competition theory predicts, in the absence of keen competitors all vying for limited resources (e.g., food), body size in the pearly-eye (particularly bill dimensions) will increase, whereas sexual dimorphism will decrease as its niche widens, especially the foraging niche. Conversely, under keen competition for food and other resources and, as a consequence of the aforementioned individual and community-based competition, body size and appendicular characters should diminish and sexual dimorphism should increase as the foraging niche narrows. To test this hypothesis, I compared pearly-eye sexual dimorphism indices (SDI) to the number of mimid and thrush competitors either absent or present on respective islands. I did this assuming there would be a direct correlation between the SDI of the five sampled external morphological characters with an increase in the number of interspecific competitors. Among the results, there were two significant correlations, wing chord

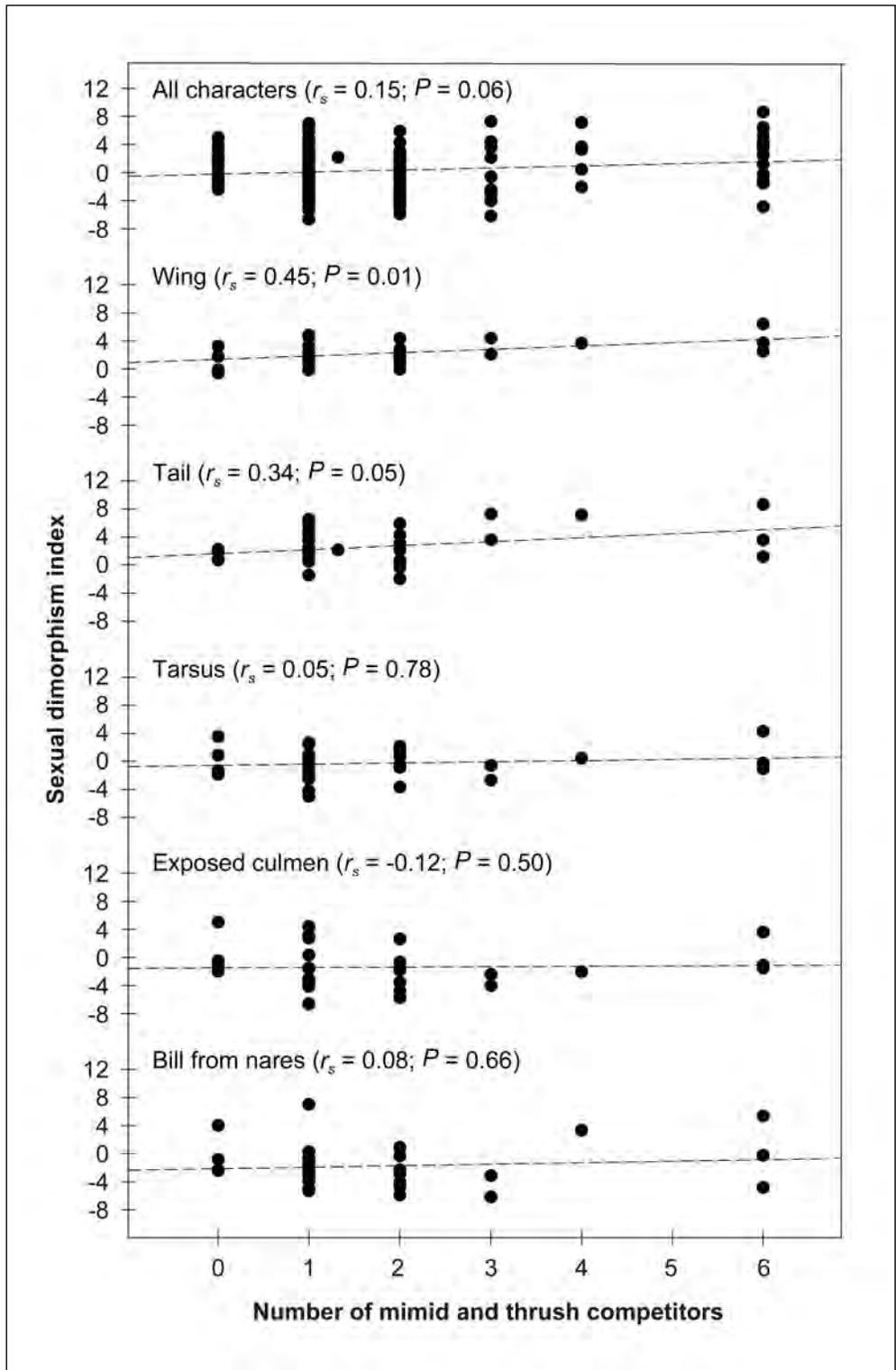


Figure 5.10—Correlation between the extent of sexual dimorphism and the number of potential mimid and thrush competitors. Only wing and tail lengths showed a significant direct correlation with an increase in the number of competitors.

and tail length, indicating an overall shift in body size (fig. 5.10). There was no correlation between tarsus and, in terms of food acquisition and handling, the more important bill dimensions (fig. 5.10). These results suggest that interference competition (one on one with individual competitors, and thus selection for larger body size) plays a more important role than that of diffuse competition, namely selection for smaller phenotypes with greater disparity in bill measurements between the sexes resulting from the influence of the “competitor community” as a whole (see chapter 8 for further discussion).

Conclusion

As depicted in figure 5.1, there are many geographic, climatic, biological, and ecological factors affecting the pearly-eye’s body size and morphology throughout its extensive geographical and elevational range. Although all of these factors (and surely many more) are intertwined and thus cannot be treated separately, both uni- and multivariate statistical analyses showed that biological factors, coupled with geography (especially elevation) and climate (season), play a more major role in governing the pearly-eye’s overall size and shape than do ecological and environmental factors, although the latter are often important contributors. Thus, a hierarchy of the key factors influencing pearly-eye morphology would be Age > Gender > Elevation > Season > Competition.

**Hierarchy of
the key factors
influencing pearly-eye
morphology: age >
gender > elevation >
season > competition.**

Summary: Morphology

Character displacement resulting from ecological release has been observed in various vertebrate taxa, including island birds. Univariate and multivariate statistical procedures were used in assessing and interpreting shifts in body size within and among thrasher populations in species-poor (and rich) communities and in the absence or presence of potential, interspecific competitors. More than 1,200 museum specimens and live, free-flying individuals of the pearly-eyed thrasher were measured on a local and regional scale. Various external morphological characters were then compared to quantify and explain several observed and anticipated patterns in the often-pronounced morphological disparity found within sympatric, and among allopatric, populations.

Five main effects (in descending order of importance): age, gender, elevation, season, and the presence or absence of potential competitors, greatly influenced the analytic results. For example, the pearly-eye’s body size (especially mass) generally increases with elevation. Morphological variation in allopatric populations at similar elevations is, as predicted by the supertramp and competition theories, characterized by shape, but not size, differences. The effects of interspecific

competition were diminished when several environmental and ecological variables were controlled because competition itself is a product of all these factors, as well as many others. Furthermore, climatic effects, although previously shown to be an important factor, play an even more integral role in influencing the pearly-eye's body size than was first recognized. From these results, it is evident that there is no single, major causative mechanism dictating the observed variation in the pearly-eye's body size within and among populations throughout the Caribbean, but rather a profusion of intrinsic and extrinsic determinants that influence its morphology throughout each year, and throughout its life. One must use caution when attempting to attribute avian body size differences to various environmental or ecological factors. Prudence is especially paramount when attempting to evoke competition as a major causative factor.