Return to Part A

Chapter 6: Survival and Dispersal

The pearly-eyed thrasher has a wide geographical distribution, obtains regional and local abundance, and undergoes morphological plasticity on islands, especially at different elevations. It readily adapts to diverse habitats in noncompetitive situations. Its status as an avian supertramp becomes even more evident when one considers its proficiency in dispersing to and colonizing small, often sparsely inhabited islands and disturbed habitats.

The pearly-eye is a long-lived species, even for a tropical passerine.

Although rare in nature, an additional attribute of a supertramp would be a protracted lifetime once colonists become established. The pearly-eye possesses such an attribute. It is a long-lived species, even for a tropical passerine. This chapter treats adult thrasher survival, longevity, short- and long-range natal dispersal of the young, including the intrinsic and extrinsic characteristics of natal dispersers, and a comparison of the field techniques used in monitoring the spatiotemporal aspects of dispersal, e.g., observations, biotelemetry, and banding. Rounding out the chapter are some of the inherent and ecological factors influencing immature thrashers' survival and dispersal, e.g., preferred habitat, diet, season, ectoparasites, and the effects of two major hurricanes, which resulted in food shortages following both disturbances.

Annual Survival Rates (Rain-Forest Population)

In the early 1990s, the tenet that tropical birds survive much longer than their north temperate counterparts, many of which are migratory, came into question (Karr et al. 1990). Whether or not the dogma can survive, however, awaits further empirical evidence from additional studies. To compare annual survival rates of pearly-eyed thrashers with other tropical and north temperate birds, 12 years (1979–90) of mark-recapture (and resight) data from my sampled rain-forest population were analyzed by using program Jolly (Brownie et al. 1986, Jolly 1965, Pollock et al. 1990). Program Jolly provides parameter estimates by using four different capture-recapture models, and at the time of the analyses was considered the best for minimizing the usual biases associated with estimating avian survival. Karr's group and others (see also Faaborg and Arendt 1995, Johnston et al. 1997) used program Jolly in comparing survival rates of north temperate and tropical birds. The best fit of the thrasher data was generated by model A, the standard model for open populations assuming births, deaths, emigration, and immigration. Very small standard errors and coefficients of variation associated with the survival estimates phi (ϕ) substantiated that model A gave the best fit.

Recently, more sophisticated survival models have been developed to analyze indepth life-history information, for example, survival differences between not only the sexes but also between breeders and nonbreeders (see, for example, Sandercock et al. 2000). Unlike systematic mist-net generated survival rates (see following discussion of annual survival in a dry-forest thrasher population), my mark-recapture (and resight) study of a rain-forest thrasher population allowed me to look more closely at the concerns outlined in Sandercock et al. (2000) such as demography, transience, heterogeneous mortality rates between the sexes, reproductive performance, and breeding status (see also chapter 7).

Three survival analyses were performed (fig. 6.1a): sexes combined (n = 213), males only (n = 91), and females only (n = 122). For combined sexes, the mean annual rate of local survival was $\phi = 0.85$ ($SE = \pm 0.04$; range: 0.40 to 0.98) over a 12-year period. Except for 1990, the first posthurricane year in which survival dropped precipitously for both sexes (see below), the average annual survival for the resultant 11-year period jumped to $\phi = 0.90$ for the combined sexes, mainly owing to the high rate of survival in males. Even with the inclusion of 1990, almost 90 percent of all males survived to the next year (mean = 89 percent; $SE = \pm 0.05$; range: 31 to 100 percent). In contrast, however, on average only 82 percent of all females survived to the following year ($SE = \pm 0.04$; range: 40 to 98 percent). The mean annual survival rate of males was significantly higher (M-W R S: $T = 110$; $P = 0.02$) than that of females because breeding females suffer higher annual mortality, mostly owing to owl predation by the Puerto Rican screech-owl (*Megascops nudipes*) and dipteran ectoparasitism involving philornid botflies (see Arendt 2000, Loye and Carroll 1995).

Effects of a Major Habitat Disturbance on Adult Annual Survival

Changes in the environment and adaptive responses to such changes both influence population processes and tend to vary the density and age structure of a population (Ricklefs 2000a). There is a rapidly growing body of information on avian population responses to catastrophic, climatological events (e.g., Faaborg and Arendt 1992, Faaborg et al. 1984, Knopf and Sedgwick 1987, Pagney Bénito-Espinal and Bénito-Espinal 1991, Walker et al. 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993, Wingfield 1988, Wunderle 1995, Wunderle et al. 1992). Population responses to environmental perturbations differ widely and are highly species specific. "In birds, as in other vertebrates, endocrine secretions regulate morphological, physiological, and behavioral changes in anticipation of future events" (Jacobs and Wingfield 2000, Ricklefs and Wikelski 2002). Proximate responses involve physiological changes within individuals, namely a marked endocrine stress response. Wingfield (1988) showed that stressful events such as severe storms induce an increase in corticosterone that mobilizes energy reserves to combat reduced food intake. Moreover, corticosterone redirects an individual's behavior away from reproduction and defense of territory toward survival and increased foraging. In this process, LH (luteinizing hormone) and testosterone are not affected. Thus, the gonad remains functional (or near functional) so that renesting can begin immediately after adverse weather conditions ameliorate. Physiological responses notwithstanding, in general most populations of frugivores (e.g., pigeons and doves) and frugivorous passerines exhibit latent responses to such major habitat disturbances. Many populations of frugivorous birds remain low even 2 to 4 years following disturbance (Knopf and Sedgwick 1987; see also discussion in chapter 8 summarizing forest bird point-count results as part of this research).

Hurricane Hugo's short-term impact on the rain-forest thrasher population was severe.

During the course of this study, the thrasher population inhabiting the Sierra de Luquillo was subjected to two major environmental disturbances, namely Hurricane Georges (September 21, 1998) a strong class 3[1] hurricane (discussed in chapter 7), and Hurricane Hugo, a class 4 hurricane. Hurricane Hugo struck Puerto Rico on September 18, 1989. Its short-term impact on the rain-forest thrasher population was severe. Following the storm, adult annual survival rates plummeted from a 10-year, predisturbance mean for both sexes combined of 0.89 (*SE* = ± 0.02; range: 0.79 to 0.98) to 0.42 (sexes combined: 0.31 for males and 0.52 for females) during the first postdisturbance breeding season (fig. 6.1a). The 10-year mean annual survival rate (fig. 6.1b) for males prior to the storm was 0.94 (*SE* = ± 0.02; range: 0.82 to 1.00). For females it was 0.85 (*SE* = ± 0.03; range: 0.66 to 0.96), a significant difference of 9 percent per annum ($z = 3.55$; $P < 0.001$; *SE* of the difference = 0.02; power = 0.94). Similarly, there was a significant gender difference in survival as shown by a comparison of survival rates for the first 7 years following the hurricane ($z = 4.05$; $P = < 0.001$; *SE* of the difference = 0.03; power = 0.98). Moreover, a more recent (August 1998) 20-year comparison of annual survival rates for males (mean = 0.87) and females (mean = 0.77) revealed a significant difference between the sexes ($z = 4.26$; $P < 0.001$; *SE* of the difference = 0.02; power = 0.98). To quantify the effects of Hurricane Hugo and to further emphasize gender differences in survival potential, annual survival rates from 2 years before to 3 years following the storm were compared (table 6.1). Within each sex, pre- and postdisturbance rates of annual survival were similar. However, for both sexes, survival following the storm dropped significantly, more so in males.

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[1] In the Saffir/Simpson hurricane scale, there are five classes of hurricanes of progressive intensity (from 1 to 5) based on wind velocity and other physical parameters (e.g., extent of human evacuations, damage to trees, buildings, etc.) in the final designation; for example, Class 3 hurricanes (e.g., Georges, a strong 3.8) produce winds of 180 to 209 km per hour, topple large trees, and cause minor damage to structures. Class 4 hurricanes (e.g., Hugo) produce winds of 210 to 250 km per hour, with extensive damage to forests and human habitations.

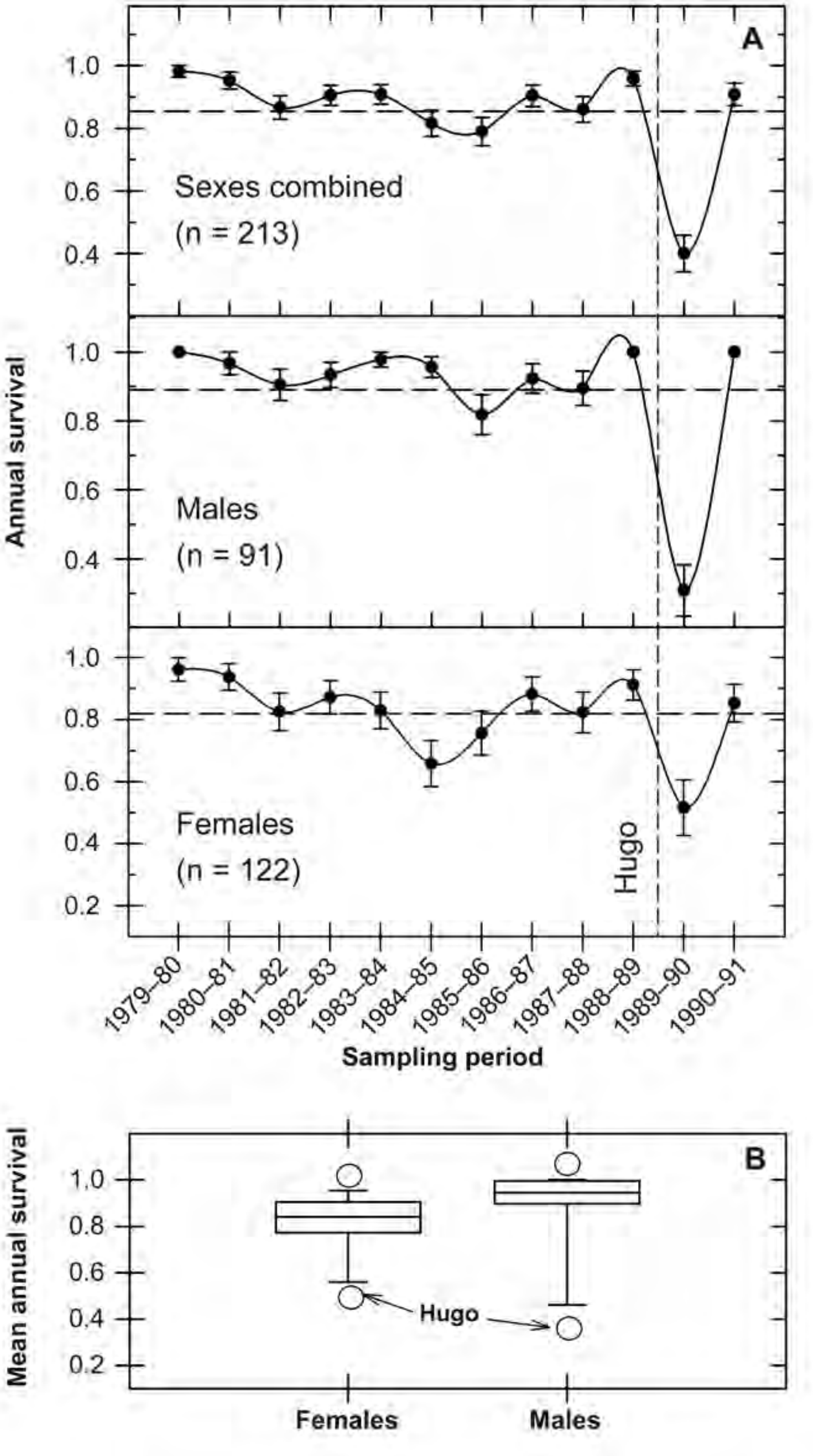

Figure 6.1—Annual survival of 213 adult pearly-eyes calculated by using mark-recapture Program Jolly's (Brownie et al. 1986) model A for open populations (A). Hurricane Hugo (1989) greatly affected annual survival rates. The 12-year mean annual survival rate (B) of males (89 percent) was significantly higher than that of females (82 percent). In contrast, annual survival of males dropped lower than that of females as a result of the storm (A). Box-plot parameters are defined in fig. 4.6.

Table 6.1—Annual survival rates of pearly-eyed thrashers 2 years before and 3 years following major habitat destruction caused by Hurricane Hugo, a class 4 hurricane[a]

	Males			Females			Combined		
Breeding seasons	**n**	**Percent[b]**	***P*[c]**	**n**	**Percent**	***P***	**n**	**Percent**	***P***
87/88 vs. 88/89	28/29	94	0.20	30/29	88	0.11	58/58	96	0.56
88/89 vs. 89/90	33/32	63	<.001	30/32	71	.01	63/64	69	<.001
89/90 vs. 90/91	33/32	64	<.001	37/32	72	.01	70/64	68	<.001
90/91 vs. 91/92	36/31	97	.49	36/38	85	.57	72/69	91	.28

[a] Class 4 hurricanes produce winds of 210 to 250 km/hr with extensive damage to forests and human habitations.

[b] Pooled proportion (X100) of individuals surviving to the following season for each of the paired breeding seasons.

[c] Probability resulting from a z-test comparing proportions; Yates' correction factor was applied.

That the highly frugivorous pearly-eye is truly a prime supertramp was confirmed by its ability to rebound to predisturbance survival levels by the second year following the storm's passage, although more males continued to survive each subsequent year than did females (table 6.1 and fig. 6.1a).

Effects of Dipteran Ectoparasitism on Adult Survival

Dipteran ectoparasitism has been reported throughout Puerto Rico, not only from forests, but even urban settings, and can be a major source of avian mortality (Pérez-Rivera and Collazo Algarín 1976a, Rivera Irizarry 1990, Snyder et al. 1987, R. Pérez-Rivera 1993, in litt.). Philornid botflies parasitize more than 20 avian species in diverse taxa including Falconiformes, Columbiformes, Psittaciformes, Cuculiformes, and many species of Passeriformes. In the Sierra de Luquillo, the pearly-eyed thrasher is a major host of the botfly (Arendt 1985a, 1985b, 2000; LaRue 1987). Nestlings generally experience a much higher prevalence and intensity of infesting larvae than do adults. In adults, ovipositing botflies seek areas in which the host is unable to preen, such as the head (fig. 6.2) and the ventral surface of the patagial membrane (fig. 6.3). However, as an example illustrating that parasitic flies can affect adult thrasher survival (and no doubt that of other species) the following account is given. For the first 13 years of this study (1979–92), no adult thrasher mortality was attributed to ectoparasitism. However, during the 1992 breeding season, an adult female thrasher was observed dying, apparently from a heavy infestation of botflies. Her wings were heavy laden with larvae. She was unable to lift them or keep her balance, and died floundering about on the forest floor (R. Díaz 1992, pers. comm.). Whether or not this female died as a direct result of the ectoparasitism, disease, malnutrition or, most likely, a combination of all of these, assuredly, the infesting larvae played a major role in her demise.

An adult female thrasher, wings heavy laden with larvae, died floundering about on the forest floor.

Figure 6.2—Adult pearly-eyed thrasher infested by a philornid larva implanted just under the right ophthalmic orbit. To avoid danger, either to themselves or their larvae, ovipositing female flies lay their eggs on adult thrashers in areas not readily accessible to the preening bird. Note how the developing larva is causing the closure of the right eye. Complete eye closures have been observed in adults harboring large, third-instars larvae. In nestling thrashers one and, occasionally, both eyes and auditory canals are permanently sealed closed by scar tissue resulting from infesting larvae in areas immediately surrounding the orbits and external ear orifices.

Figure 6.3—Adult pearly-eyed thrasher infested by philornid larvae implanted in the underside of the right patagial membrane. Note the posterior end of an infesting larva and its respiratory spiracles at the entrance of its furuncle (cavernous lesion with cornified epithelial walls and lined with the host’s connective tissues). As with the facial and nucal areas, patagial membranes are favorite implantation sites of ovipositing female flies trying to avoid contact with preening beaks.

Sustained high mortality in female thrashers owing to ectoparasitism and nest predation by owls, rats, and other thrashers undoubtedly impacts the age structure in this sampled population. Cichoń (1992) reported similar results in a population of the great tit (*Parus major*) inhabiting the Niepolomice Forest in Poland. He found that one-third of the females in the population (mostly incubating females) were killed by nest-box predators.

Annual Survival Rates (Dry-Forest Population)

To address the possibility of differential survival rates of thrashers found in different habitats, by using the same survival model as described above, annual survival in a population of pearly-eyes inhabiting the Guánica Biosphere Reserve of southwestern Puerto Rico was calculated and compared to that of the rain-forest thrasher population. Analyses using an 18-season (1973-90) mist-net study database (see Faaborg and Arendt 1990, Faaborg et al. 2000) showed the mean annual survival rate of 124 individual thrashers (sexes combined) captured 158 times (avg. = 1.5 captures per individual) was $\phi = 0.77$ (Faaborg and Arendt 1995: table 1). It is noteworthy that the annual survival estimate of $\phi = 0.77$ for thrashers inhabiting dry forest is significantly lower than the estimate of 0.85 for the rain-forest population ($z = 1.95$; $P < 0.05$; *SE* of the difference = 0.04). Why should thrashers inhabiting rain forest survive better than those living in dry forest? Biological causative factors no doubt play a major role. The Guánica Biosphere Reserve experiences periodic droughts (Faaborg 1982a, Faaborg and Arendt 1992, Faaborg et al. 1984). As a result, food and water shortages stress the resident flora and fauna, thus decreasing the probability of survival. In general, throughout their range, pearly-eyes abound in proximity to water sources (see discussion of thrashers inhabiting Bonaire, chapter 4) and are highly dependent upon fruits and insects produced directly, and indirectly, by plant growth when rainfall and ground water are in adequate supply. In other words, the rain-forest pearly-eye population may experience higher rates of survival by benefiting from their less seasonal, hygrophylous environment, with much higher rainfall (García-Martinó et al. 1996) and more available food year-round (Lugo and Frangi 1993). An additional ecological factor undoubtedly accounting for improved annual survival of the rain-forest thrashers is the low incidence of diffuse and interference competition they face by living in a species-poor avian community (Kepler and Kepler 1970).

From a more empirical perspective, however, a recent study of a Neotropical parrotlet inhabiting a highly seasonable environment in Venezuela has shown that annual survival in breeding adults can be fairly high ($\phi = 0.67$) even in a tropical species living under extreme climatic conditions (Beissinger and Gibbs 1993, Sandercock et al. 2000, Waltman and Beissinger 1992). Therefore, it is possible that if more life-history variables from the dry-forest population could have been included in the survival calculations, similar survival rates between the two Puerto Rican forest types may have resulted.

Annual Survival of North Temperate Vs. Tropical Birds

tTropical birds do live longer than north-temperate species, at least on islands.

Although the annual survival of pearly-eyes was shown to differ significantly between two habitat types (rain forest: $\phi = 0.85$, 12-year analysis; $\phi = 0.82$, 20-year analysis; and for dry forest: $\phi = 0.77$, 18-year analysis), all three survival estimates are much higher than those found by Karr et al. (1990) for either north temperate ($\phi = 0.54$) (see also Boano and Cucco 1991, Buckland and Baillie 1987, Spaepen 1988 for similar survival rates) or tropical continental bird populations ($\phi = 0.56$ reported by Sandercock et al. 2000). The average annual survival ($\phi = 0.81$) of pearly-eyes inhabiting two forest types in Puerto Rico (0.85 in rain forest and 0.77 in dry forest) equals that of the Florida scrub jay (*Aphelocoma coerulescens*), a semitropical and peninsular species. Over a period of about 15 years, 81 percent of both males and females survived each year (Fitzpatrick and Woolfenden 1988). Clearly the results from these and other island studies such as the Johnston et al. (1997) study of Trinidadian birds ($\phi = 0.65$) add credence to the traditional view that in general, tropical birds do live longer than north-temperate species, at least on islands.

Pearly-Eyed Thrasher Longevity

Rain-Forest Population

Model-based estimates of annual survival are preferable to observed maximum lifetimes for use in comparative life-history studies (Krementz et al. 1989b). However, to complement and compare the results from the previously discussed survival models, following is a discussion of observed longevity in the pearly-eye, with reference to differential survival between the sexes.

From 1979 to 2000, although more than a thousand rain-forest pearly-eyed thrashers were banded, 268 included both breeders in the sampled population ($n = 247$; 18 known- and 126 minimum-aged females, and 13 known- and 90 minimum-aged males) and 21 nonbreeding natal dispersers that were resighted at varying times after fledging. Of the 268 banded breeders and nonbreeders, 27 individuals survived for more than a decade. However, 20 of them (74 percent) were males, whereas only 7 (26 percent) were females, once again attesting to the fact that females suffer higher mortality than males from nest predators and ectoparasites because they spend much more time in the nest boxes (see Sandercock et al. 2000, who also report an increase in mortality for female parrotlets nesting in boxes).

Clearly, some individuals can survive several years, but many more pearly-eyes do not live more than 5 to 7 years. The average lifespan for 98 males was 6.43 years (range: 1 to 15; median = 6; mode = 11 years). The average female (n = 139) lived 4.86 years (range: 1 to 15; median = 4; mode = 3 years). On average, males live significantly longer than females (M-W R S: $T = 13\,554.5$; $P < 0.001$).

In light of the higher mortality rate for female pearly-eyes owing to predation, I forecasted an average further life expectancy by using a formula ($[2\text{-}m]/[2^*m]$ derived by Williams 1966 and used by Snow and Lill 1974 and Dowsett 1985). In the formula, "m" is annual mortality expressed as a decimal, and "2" represents two breeding seasons to include recaptures and to minimize the probability of mortality and emigration after only one season. By substituting for "m" the inverse (18 percent, range: 0 to 64.7 percent) of the adult female annual survival rate of 82 percent (range: 40 to 98 percent) obtained over an 18-year period and presented earlier in this chapter, the average further life expectancy is 5.1 years (range: 1.04 to 21.5 years). Therefore, based on the observed average longevity of 4.86 years for females, the average life expectancy for females is increased to 9.9 years. Given potentially higher rates of annual survival in the absence of predation, female pearly-eyes could in essence live a decade, or even more as attested to by those observed living as long as 15 years (minimum).

Dry-Forest Population

During a similar period (1973 to 2000), capture-recapture data for thrashers in the Guánica Biosphere Reserve were used to compare pearly-eye longevity between two different habitat types. In total, 170 pearly-eyed thrashers (data include only minimum-aged individuals, with sexes combined) were captured 269 times (avg. = 1.58 times per individual) in mist nets placed in the same location once or twice a year, generally in January or February, but once each in June 1973, July 1981, and November 1986. Of the 170 individuals captured, 127 individuals (75 percent) were captured only once. Twenty-four individuals were recaptured after a lapse of more than one season. Of the 24, only 2 individuals were captured more than a decade later (one after 12 years, and one after 17 years). However, half of the 24 individuals were captured 5 to 10 years after their original capture. Although the dry-forest population was sampled only once a year and sexes were combined, results were similar to those of the rain-forest population. The average dry-forest pearly-eye lived 5.5 years (median = 5; mode = 3 years; range: 1 to 17). Still, the fact that individuals of many Puerto Rican dry-forest species have been shown to live more than a decade (Faaborg and Arendt 1989, Woodworth et al. 1999) substantiates the possibility that thrashers inhabiting the Guánica reserve may also in fact survive longer than this limited analysis suggests.

In summary, although long-lived individuals of the pearly-eyed thrasher have been documented in both dry and rain-forest populations, the average individual lives from 5 to 7 years.

Pearly-Eyed Thrasher Longevity Compared to Other Landbirds

A 14-year study (1957–71), including 8 families and 15 species of Neotropical (Trinidadian) landbirds ranging in size from <10 to >100 g, resulted in longevity records of 10 to 14 years for more than half the species (Snow and Lill 1974). In a separate study, although working with captive birds, Collias (1984) clearly showed the longevity and reproductive potential of the village weaver (*Ploceus cucullatus*). The average age at death of captive birds was 11.2 years. To substantiate the reliability of the data obtained from the captive flock, Collias (1984) cited a record (Vernon 1975) of a free-flying, banded weaver alive after a minimum of 14 years (adult at banding). In Collias' study, a 19-year-old minimum-aged male was still virile, and an 18-year-old female was fertile. More recently, Fisk (1986) and Klimkiewicz and Futcher (1987) made a general survey of longevity records (max. ages reported) from millions of banding records (both within and outside of the same 10-minute latitude-longitude blocks) from the National Bird Banding Laboratory (hereafter BBL) at the U.S. Geological Survey's Patuxent Wildlife Research Center, Laurel, Maryland. Of 55 species of (sensu Fisk 1986) "woods and yard" birds reported (i.e., goatsuckers, doves, cuckoos, hummingbirds, woodpeckers, and passerines), the average species had a maximum lifespan of 10.3 years (min. = 4 years [whippoorwill, *Caprimulgus vociferous*]; max. = 21 years [common grackle, *Quiscalus quiscula*]; median = 10 years, mode = 11 years). These results, although representative, are not steadfast for a given species. For example, whippoorwills are probably not a short-lived species. Like so many other species of landbirds, they too may well live 10 years or more. It is more plausible that there are no records of longer lived individuals simply because this nocturnal forest bird is difficult to observe and study and thus fewer band recoveries have been reported to the BBL. Contrarily, and as the English vernacular so aptly describes, the common grackle is a generally diurnal and often abundant passerine that is easily observed and studied. It is gregarious and often abundant in human-induced environments. Its gregariousness and reproductive ecology (often nesting in colonies in which nests are easily accessed) render it conducive to study. As a result, thousands of grackles have been banded and thus many more band recoveries have culminated in extended longevity records for the species.

To further emphasize the species-specific disparities and unavoidable pitfalls in estimating the longevity of various species from band return records, I will briefly review the longevity records for North American mimids given to me by Danny Bystrak and Kathy Klimkiewicz of the BBL in Maryland. By 1996, bands from more than half a million (n = 660,326) banded individuals of 10 species of North American thrashers and mockingbirds had been reported. On average, 73,348 individuals of each species were banded (median = 11,668), 1,688 were recovered (median = 294), or 6.5 percent (median = 2.9 percent). From these data, the brown thrasher (*Toxostoma rufum*) and gray catbird (*Dumetella carolinensis*) are the two longest lived species. The average North American mimid has a maximum longevity of 7.8 years (range: 4 to 12; median = 7; mode = 11 years). Seven of the ten species are not known to live more than a decade. Yet, as predicted, there is a strong correlation (Spearman Rank Order test) between the number of birds banded and longevity (fig. 6.4). Thus, it is most likely that the seven species demonstrating maximum longevities of less than 10 years can, and probably do, live much longer, a fact that should be borne out as those species are further studied and more individuals are banded, thus augmenting the number of band recoveries.

Although a strong correlation was found between the number of mimids banded and longevity, unexpectedly there was no significant correlation between longevity and the percentage of individual recoveries ($r_s^2 = -0.17$; $P = 0.60$), or between the number of mimids banded and percentage of recoveries ($r_s^2 = -0.29$; $P = 0.38$). The negative correlation coefficients in both comparisons (-0.17 and -0.29, respectively) suggest an inverse effect. Undoubtedly, many unmeasured variables, e.g., inherent (genetic and metabolic), ecological (climate, habitat, diurnal and nocturnal periodicities), and human-related (persistence, intensity, and thoroughness of investigators and band reporters), enter into the longevity equation for individual species.

In the case of the pearly-eyed thrasher, if one were to rely solely on band returns to estimate its lifespan, one might conclude that *Margarops fuscatus* is a short-lived species (table 6.2). Fortunately, two long-term studies of well over a thousand individually identified thrashers in two disparate habitats (xerophytic and rain forest) have documented that this is not the case. Undoubtedly, as more band returns accumulate for other species of mimids, including the pearly-eye, most, if not all, species should show maximum lifespans similar to, or surpassing, those of the brown thrasher and gray catbird.

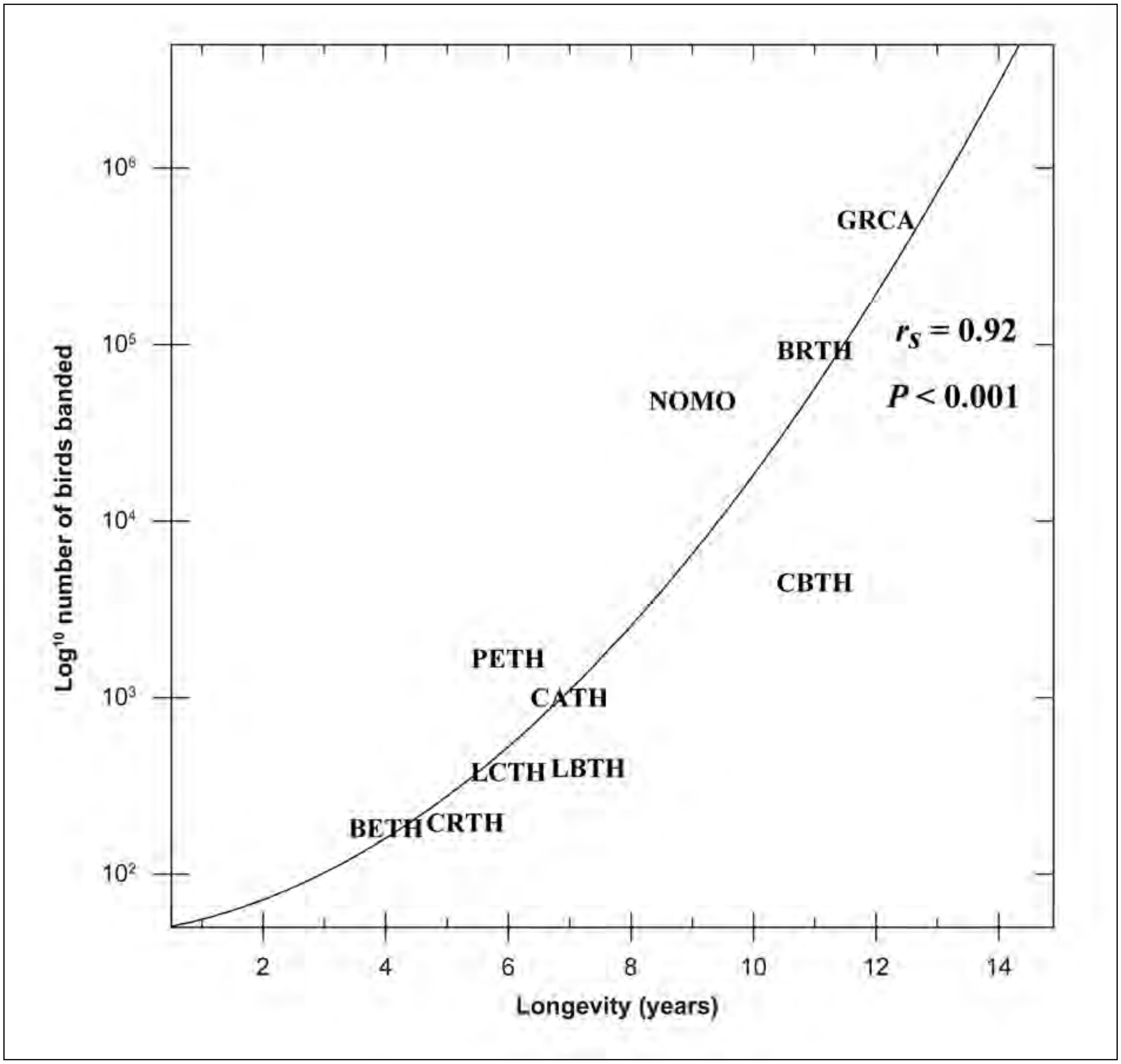

Figure 6.4—Regression analysis of mimid longevity vs. the number of birds banded. There is a significant correlation between the projected lifespan of individuals of a given species and the number of individuals banded. In contrast, however, there is no significant correlation between the percentage of recoveries and the number of birds banded, or longevity and the percentage of individual recoveries. Four-letter codes are as follows: BETH (Bendire's thrasher, *Toxostoma bendirei*), BRTH (brown thrasher *T. rufum*), CATH (California thrasher, *T. redivivum*), CBTH (curve-billed thrasher, *T. curvirostre*), CRTH (crissal thrasher, *T. crissale*), GRCA (gray catbird, *Dumetella carolinensis*), LBTH (long-billed thrasher, *T. longirostre*), LCTH (Le Conte's thrasher, *T. lecontei*), NOMO (northern mockingbird, *Mimus polyglottos*), and PETH (pearly-eyed thrasher, *Margarops fuscatus*).

Dispersal

There are three main types of avian dispersal: breeding, stochastic, and natal. Breeding dispersal occurs when adults change nest sites, often following reproductive failures (see chapter 7). Stochastic dispersal usually occurs when individuals are displaced from one geographical area to another, often by catastrophic climatic events such as hurricanes, as has been documented in the Caribbean

Table 6.2—Comparison of longevity records for North American mimids (mockingbirds and thrashers) and the pearly-eyed thrasher from encounters of banded birds[a]

English vernacular (scientific name)	Birds banded[b]	Birds recovered[b]	Recovery rate	Longevity
	- - - - - - - *Number*	*- - - - - - -*	*Percent*	*(Years – months)*
Brown thrasher (*Toxostoma rufum*)	93,000	4,650	5.0	12 – 10
Gray catbird (*Dumetella carolinensis*)	511,000	8,241	1.6	11 – 11
Curve-billed thrasher (*T. curvirostre*)	4,500	168	4	10 – 09
Northern mockingbird (*Mimus polyglottos*)	48,000	1,423	2.9	9 – 08
Long-billed thrasher (*T. longirostre*)	400	6	2	7 – 03
California thrasher (*T. redivivum*)	1,000	294	29	6 – 11
Le Conte's thrasher (*T. lecontei*)	380	4	1	5 – 08
Pearly-eyed thrasher (*Margarops fuscatus*)	1,668	2	0.1	5 – 08
Bendire's thrasher (*T. bendirei)*	182	25	14	4 – 02
Crissal thrasher (*T. dorsale*)	196	26	13	4 – 09

[a] There is a direct correlation between longevity and the number of birds banded (see text).

[b] Data released by the U.S. Geological Survey Biological Resources Division (former U.S. Fish and Wildlife Service) of the National Bird Banding Laboratory, Patuxent Wildlife Research Center, Laurel, Maryland.

Basin (chapter 4). As an example, even though there are no documented instances of stochastic dispersal in the pearly-eye, there is at least one report involving its congener, *M. fuscus*. Wells (1902) wrote that the scaly-breasted thrasher was unreported from Carriacou, a small island in the Grenadines (Lesser Antilles), prior to the passage of a major hurricane that devastated nearby St. Vincent on 11 September 1898. Following the storm, "numbers" of scaly-breasted thrashers were observed on Carriacou and apparently later successfully colonized. Yet, today, they are casual at best in the Grenadines (AOU 1998) or possibly already extirpated (Wiley and Wunderle 1993).

Natal dispersal is the net movement between the hatch site and the site of first breeding, and it determines the extent of gene flow, heterozygosity at allozyme loci, and population structure (Fleischer et al. 1984, Payne 1991; see also Wheelwright and Mauck, 1998, for a discussion on the complexity of the subject and the various geographic, ecogenetic, and neutral models necessary to adequately address the subject). There are two principal components of natal dispersal: spatial and temporal. Not only is it important to document the distances, directions, and routes taken by dispersing young, one must monitor the lapse of time between successive movements to determine the extent of postfledging parental care, or the period of "weaning" of the young from attendant adults.

From February 1979 and throughout the study, three monitoring methods have been used to study natal dispersal in fledgling pearly-eyed thrashers: (1) audiovisual contact with recently fledged young in the immediate vicinity of their nest boxes; (2) biotelemetry; and (3) banding, including band returns and sightings of uniquely marked individuals (see Arendt 1993 for methodology).

Each study method has its advantages and disadvantages (see North 1988 for a review). Nest-box observations are valuable because of the frequency of nest-box visits, usually daily, or on alternate days. However, audiovisual contact is limited to about a 50-m radius around the nest-box tree owing to a dense canopy and rugged terrain, thus biasing the observational data to short distances.

Biotelemetry data are advantageous because they are obtained from free-moving dispersers, often over long distances. However, the full benefits of biotelemetry could not be realized in this study for two reasons. First, because of the relatively large size of thrasher fledglings (about 104 g), monitoring was possible for only 2 to 3 months postfledging owing to size limitations of the transmitters and short life of the small batteries, especially during the early 1980s. Second, and most important, many thrasher nestlings in the study area suffered from heavy infestations of larvae from a parasitic botfly (see Arendt 1985a, 2000). First-year mortality of infested nestlings can reach 80 percent or higher (Arendt 1983, 1985a). Although young thrashers are often strong enough to leave their boxes, most heavily infested fledglings die within days no more than 20 to 30 m from their nests.

Banding data are invaluable because of the long life of metal leg bands and the positive identification of free-flying individuals with unique color combinations. Nevertheless, banding data suffer from potential erroneous identifications owing to fading colors, loss of, or misread, color bands. In addition, results from observational and banding data are contingent upon the observer's random location and chosen sampling areas, and the biases of limited study areas (for further discussion, see Baker et al. 1995, Moore and Dolbeer 1989, Payne 1990). With all the shortcomings and biases from each of these techniques in mind, I used a combination of all three to obtain the best results possible given the many limitations.

Short-Range Natal Dispersal Within the Sierra de Luquillo

At the onset of the study, results from the three study methods were to be combined to reveal the general pattern of pearly-eye natal dispersal. However, Student's *t*-Tests showed that fledgling dispersal data differed significantly among the three study methods, owing to the different spatiotemporal scales involved (table 6.3). Therefore, results must be presented separately.

Nest-box observations—

Once fledged, young were never observed to re-enter nest boxes, although they would come within less than a meter of the boxes while pursuing or begging food from the adults. Unparasitized young (usually a cohort of 2 to 3 siblings,

Table 6.3—Comparison of three study methods used in monitoring pearly-eye natal dispersal[a]

Sample data	Distance moved	Fledgling age
	Kilometers	*Months*
Observational (n = 648)[b]		
Mean	0.01[b]	0.53[b]
SE	.38	.15
Range	.01–0.3	.03–.97
Telemetry (n = 24)[c]		
Mean	.38[c]	.83[c]
SE	.17	.01
Range	.005–3	.03–2.43
Banding (n = 52)[d]		
Mean	1.17[d]	38.8[d]
SE	.17	3.61
Range	.1–6.5	6–120

[a] These dispersal analyses do not include the transmarine (Barbuda to Guadeloupe) or trans-island (rain forest to Mayagüez) dispersers.

Comparison	Distance moved	Fledgling age
[b] Observations vs. banding	(t = 5.61, P < 0.001)	(t = 8.61, P < 0.001)
[c] Observations vs. telemetry	(t = 2.55, P = 0.01)	(t = 3.65, P = 0.001)
[d] Banding vs. telemetry	(t = 2.91, P = 0.001)	(t = 9.85, P = 0.001

range: 1 to 4) often remained together from 1 to 4 days postfledging. At that time, the oldest (first-hatched) would often distance itself from the younger sibling(s) and venture farther from the nest tree on its own. Length of parental care differed among nest pairs and seasons, with parental feeding and tolerance of the fledglings within proximity of the nest box (a radius of about 30 m) being shortest between first and second broods, and longest after final nesting attempts. Both adults administered care, mainly food provisioning and protection from predators, while the fledglings remained in the natal area (defined as a radius of about 30 to 50 m around the nest-box tree). However, once the female renested, the male assumed most responsibility. Nevertheless, this was rare as most fledglings were forced out of their natal areas by their parents before subsequent nestings commenced. Fledglings dispersed from their natal areas on an average of 9 days before deposition of the first egg of a subsequent nesting (*SE* = ± 2.3; range: 32 days before to 4 days after). This general pattern of the fledglings remaining in their natal areas from 2 to 6 weeks postfledging has been observed in other forest birds such as pigeons, doves, flycatchers, thrushes, orioles, and cuckoos (pers. obs.). However, the length of time that fledglings remain in their natal areas before dispersing is highly variable among taxa and is mainly species-specific (Magrath et al. 2000; O'Connor 1984a, 1984b; Skutch 1960, 1969, 1976).

Fledglings dispersed from their natal areas on an average of 9 days before deposition of the first egg of a subsequent nesting.

Heavily parasitized fledglings (>30 infesting larvae) remained within 20 to 30 m of their nest boxes begging food from adults over a period lasting from a few days to a few weeks before succumbing to the effects of larval infestation. During the first (1990) breeding season following Hurricane Hugo, three **unparasitized** siblings remained for almost 2 months postfledging within 10 m of the nest box before dying of apparent malnutrition (see below). However, in general (combined data from parasitized and unparasitized fledglings before and after major habitat destruction), adults tolerated fledglings within 30 m of their hatch sites for about 2.5 weeks postfledging (table 6.3 and figs. 6.5a and 6.5b).

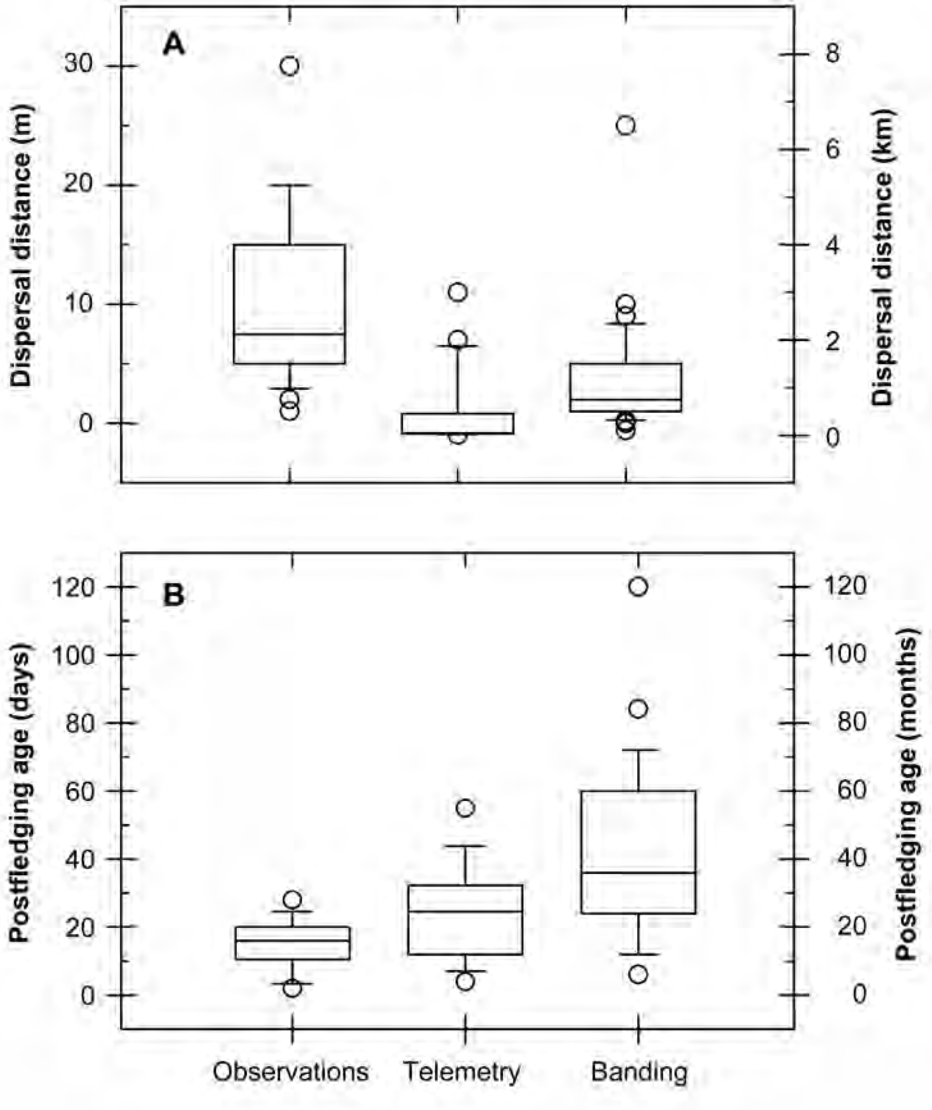

Figure 6.5—Spatiotemporal aspects of pearly-eye natal dispersal within the Luquillo Experimental Forest. Direct observations and biotelemetry sufficed for recently fledged and immature thrashers, but band returns resulted in the most information over much broader spatiotemporal scales; all distance measures are in meters and kilometers (A); ages for observational and telemetry results are in days, whereas ages for band-return results are in months (B). See text for trans-island and transmarine, long-distance dispersers.

Biotelemetry—

More than 3,000 locations of 24 radio-tagged fledglings were recorded. Telemetry data corroborated the observational (nest-box) data for fledglings within 50 m of the nest box. All radio-tagged fledglings remained within 3 km of their hatch sites during the first 2.5 months postfledging (table 6.3 and fig. 6.5a).

Banding—

Sightings of color-marked individuals and band returns have shed the most light on the spatial and temporal aspects of pearly-eye natal dispersal (table 6.3 and fig. 6.5). Nonetheless, only 52 banded fledglings (29 females and 23 males, or about 4 percent of the 1,363 banded nestlings) were later sighted and/or captured over a 21-year period (1979 to 2000). Although 4 percent is a very small proportion of the total number of birds banded, it falls within the normal 2- to 4-percent return rate for midsize, nongame, North American passerine forest birds (information supplied by the BBL at the U.S. Geological Survey's Patuxent Wildlife Research Center, Laurel, Maryland [Danny Bystrak 1992, pers. comm.]).

Data obtained from the 52 banded fledglings that were later sighted or captured as breeders were used to determine thrasher dispersal distances, survival, and recruitment into the sampled breeding population as well as possible between-gender dispersal differences (tables 6.3, 6.4, and fig. 6.6). There was no significant difference between the sexes in dispersal distances: M-W R S: $P = 0.76$; females (median = 0.6 km; 25 to 75 percentiles = 0.3 to 1.5 km, respectively); males (median = 0.8 km; 25 to 75 percentiles = 0.4 to 1.7 km, respectively). This result is contrary to the general rule in passerines, which is a predominantly daughter-biased natal dispersal. Females normally disperse over longer distances to reduce inbreeding (Gowaty 1993). There was, however, a significant gender difference in the number of years between fledging and first nesting (see below).

Table 6.4—Comparison of dispersal distances and lapse of time between fledgings and first nestings of pearly-eyed thrasher recruits within the Luquillo Experimental Forest

	Maximum distance			Lapse between fledgling and first nesting in sampled population		
Descriptive statistic	**Females**	**Males**	**Combined**	**Females**	**Males**	**Combined**
	- - - - - *Kilometers* - - - - -			- - - - - - - - *Years* - - - - - - -		
Mean	0.82	1.10	0.95	2.67	4.00	3.29
SE	.15	.32	.17	.62	.46	.41
99% CI	.45	.91	.46	1.85	1.42	1.13
Minimum	.15	.07	.07	1	2	1
Maximum	3	6.5	6.5	10	7	10

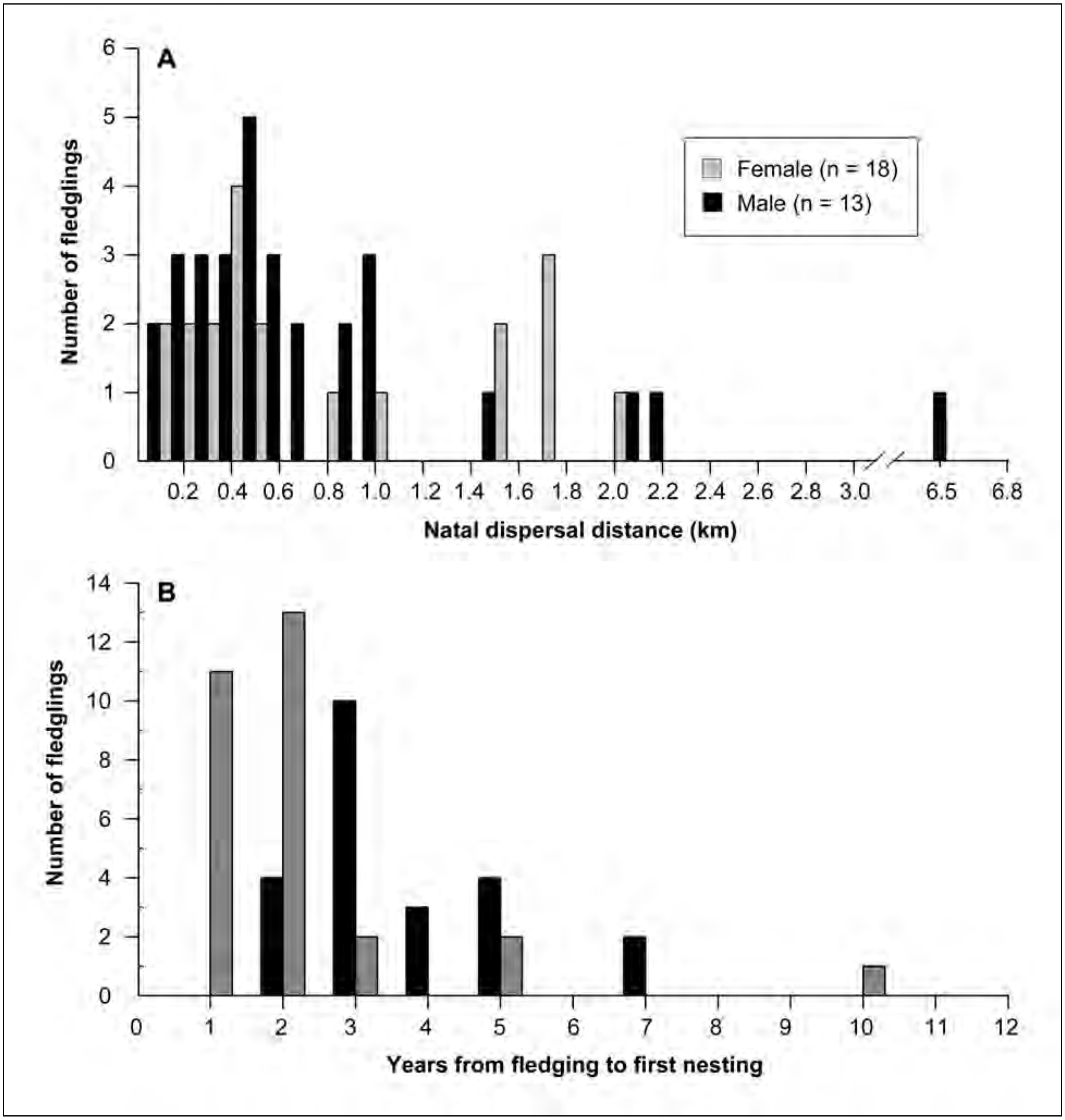

Figure 6.6—Frequency distributions by gender for maximum dispersal distances and years from fledging to first nestings for 31 pearly-eye recruits. Although, as shown in graph A, there is a tendency for males to disperse farther than females, it was not significant in this sample. However, female recruits (graph B) did enter the breeding population significantly earlier than males.

Banding data supported the observational and telemetry data obtained within the first couple of months postfledging. In addition, banding data gathered over a much longer period suggest that the dispersal data gathered within the first 2 to 3 months via observations and telemetry are representative of the extent of dispersal, i.e., most young thrashers remain within 3 km of their hatch sites. As an extreme example, a female nestling banded (USFWS 1143-29071) on April 21, 1982, was not encountered again until 4 years later, when it was captured in a mist net on March 26, 1986, only 0.5 km from its hatch site. It was not encountered again for another 6 years (May 1, 1992), when it nested in a thrasher box 0.2 km from the 1986 capture site (and closer to its natal box) after a lapse of 10 years and a distance of only 0.3 km from its hatch site.

Most thrasher dispersers remain within 3 km of their hatch sites.

Many life-history studies have shown that passerines remain within a few hundred meters of their natal areas and that postfledging dispersal is an exploratory movement within the bird's main habitat rather than longer flights in random directions (see Nielsen and Bensch 1995 for a discussion of different hypotheses that may explain postfledging dispersal). In a 25-year study of the great tit, Hudde (1995) showed that males and females of hundreds of natal dispersers remained within 500 m of their natal areas 15 weeks after fledging, and movements beyond 1 km were unusual (see also Báldi and Csörgő 1994, Harvey et al. 1979, Lemon et al. 1996). In a long-term study of the Florida scrub jay carried out since 1969, Woolfenden and Fitzpatrick (1986) found that female scrub jays disperse farther (see also Orell et al. 1999) and nest at an earlier age than males, as do female pearly-eye recruits.

One additional and compelling piece of evidence suggests that most pearly-eye natal dispersal (and reproductive dispersal—see chapter 7) is minimal. Banded and color-marked fledglings dispersing from my nest boxes have used six thrasher nest boxes placed around active and potential Puerto Rican parrot nest sites located within 2 km of my study area. Yet, during a quarter century of monitoring (through the 2004 breeding season), there has been only one report (F. Vilella 1993, pers. comm.) of a color-banded pearly-eye in a parrot nesting area about 3 km from its hatch site in the Icacos Valley. Moreover, there has never been a single report of nesting by a banded thrasher from my study area in or near the more distant (>3 km) active or potential parrot nesting areas (corroborated by T.H. White, Jr., USFWS, 9 Nov. 2004, pers. comm.), although thrasher nest boxes are placed near parrot nest cavities in these more remote areas. If long-range natal dispersal were common in the pearly-eye, surely at least a few more sightings and nestings of banded dispersers would have been documented in the more distant expanses of the forest, especially in and around the numerous and closely monitored thrasher nest boxes used in parrot research.

When resident thrashers of the sampled population disappear, banded individuals often replace them, suggesting that the wooden nest boxes used in this study are preferred over natural cavities. Most likely, thrashers hatched in nest boxes are imprinted on them and will form a "nest-box search image" when seeking nest sites. Many of the documented dispersing young remained in the vicinity of nest boxes (in some instances for many years) waiting for the opportunity to nest in them. This is exemplified by the female that waited 10 years within 0.3 km of her hatch site for an opportunity to nest in a wooden box.

Factors Affecting Natal Dispersers Within the Sierra de Luquillo

Hatch order (intrinsic factor)—

Hatch order (first to fourth) was not equally represented in the natal dispersers. Of the 52 fledglings later sighted or recruited into the breeding population, 16 of 522 (3 percent) were first-hatched, 24 of 551 (4 percent) were second-hatched, 11 of 442 (2 percent) were third-hatched, and only 1 of 78 (1 percent) was a fourth-hatched sibling. Although there were no significant differences in numbers of first-hatched vs. second-hatched young (z-test with Yates' correction: $z = 1.41$; $P = 0.15$) or first-hatched vs. third-hatched ($z = 0.89$; $P = 0.37$), there were significantly more second- than third-hatched sibling dispersers ($z = 2.49$; $P = 0.01$). Both distance (0.3 km) and postfledging age (2.5 years) were minimal in the sole fourth-hatched fledgling. It is noteworthy that botfly larvae did not infest this young thrasher as a nestling, which no doubt enhanced its chances of survival beyond the first year (see below).

Intrinsic as well as extrinsic factors affect pearly-eye natal dispersal.

Although not shown statistically that first-hatched fledglings disperse farther than their younger (second- and third-hatched) siblings (K-W ANOVA: $H = 3.8$; df = 2; $P = 0.14$), the sample size may be too small to be representative of the entire population. That oldest chicks may disperse farther was evidenced by the fact that the fledglings with the three longest dispersal distances were older siblings (two first-hatched, one second-hatched). In addition, as previously stated, nest-box observations have shown that often the oldest fledgling distances itself early (within 1 to 4 days postfledging) from younger siblings and begins a more long-range dispersal than its younger siblings.

There were no major differences among the first three hatch orders in reference to the number of intervening years between fledging and first nesting attempts in the nest boxes (K-W ANOVA: $H = 0.9$; df = 2; $P = 0.61$).

Brood number (intrinsic factor)—

Results were significantly skewed toward fledglings from first broods (usually two to four broods per season), which imply greater survival of first-brood fledglings. This was a direct consequence of less intense botfly larval infestations and lowered nestling mortality early on in each breeding season (see below). Of the 52 banded dispersers, 39 (75 percent) were among 808 fledglings from the 19 seasons' first nestings. Only 8 (15 percent of 52) were included in the 481 fledglings from second broods, 4 (8 percent of 52) accompanied the 248 fledglings from third broods, and just 1 disperser (<2 percent) of 56 fledglings was from a fourth brood. There were significant differences between the total number of first-brood dispersers and both second-brood (z-test with Yates' correction: $z = 5.95$; $P < 0.001$) and third-brood dispersers ($z = 6.73$; $P < 0.001$), but not between second- and third-brood dispersers ($z = 0.81$; $P = 0.41$). Greater fledging success in early broods is common in many species of birds, particularly passerines (e.g., Geering and French 1998).

Effects of ectoparasitism among broods (extrinsic factor)—
Of the 52 banded dispersers, 35 (67 percent) had received fewer than 30 botfly larvae as nestlings. In general, a larval intensity of 30 or fewer does not significantly affect growth, development, and subsequent survival (Arendt 1983, 1985a). Of the 35 dispersers that had received fewer than 30 larvae prior to fledging, about half of them had not received any botfly larvae as nestlings. The 35 dispersers that had suffered fewer than 30 larvae averaged 5.8 larvae per individual, with a maximum of 26 on one individual. Conversely, the remaining 17 heavily infested dispersers averaged 54.5 larvae per bird, with a minimum of 37 and a maximum of 85. Two of the three longest distance dispersers suffered no botfly larval infestations as nestlings, and the third experienced only three infesting larvae as a nestling. Of the 17 fledglings that had received more than 30 larvae as nestlings, only three were infested at less than a week old, the period of precipitous growth in nestling thrashers (Arendt 1985a). All three fledglings that had experienced larval infestations within their first week suffered heavy larval intensities (77, 78, and 85 larvae) throughout their 21-day nestling periods. The young thrasher that had received 85 larvae as a nestling harbored 20 larvae only 2 days after hatching (normally a lethal dose). Although it had dispersed only 0.75 km from its hatch site, it survived 3 years and successfully nested in a thrasher box. Unquestionably, at least a few heavily parasitized nestlings are surviving and being recruited into the breeding population.

Total numbers of botfly larvae per disperser were compared to brood number (first through fourth per season). More dispersers that received fewer than 30 larvae as nestlings fledged from earlier broods than those that received more than 30 larvae (80 vs. 64 percent for first broods; 11 vs. 23 percent for second broods; and 7 vs. 6 percent for third broods). However, the proportions (z-test with Yates' correction) were not significant at $\alpha = 0.05$ (first broods: $z = 0.85$; $P = 0.39$; second broods: $z = 0.72$; $P = 0.46$; third broods: $z = -0.21$; $P = 0.83$).

One of the main reasons brood number was skewed toward first broods is that nestling mortality in subsequent broods (generally attempted after April and May of each season) is often 100 percent owing to botfly ectoparasitism. As a result, there are very few surviving young to fledge and disperse during the latter months of the breeding season (Arendt 1983, 1985a). Many of the heavily infested nestlings that do survive long enough to fledge, leaving the safety of their nest boxes, fall to the ground and promptly become victims of mammalian predators such as mongooses and rats (observed on several occasions from study blinds). As do thrasher adults and nestlings (see below), fledgling pearly-eyes also fall prey to avian predators. On numerous occasions, radio-tagged thrasher fledglings in a weakened condition after suffering heavy larval infestations as nestlings fell prey to forest raptors, e.g., the red-tailed hawk (*Buteo jamaicensis*) (Arendt, unpubl. data). In a related study (Santana-Castellón and Temple 1984), E. Santana-C. (1983, pers. comm.) observed thrasher adults and unfeathered (<1-week-old) nestlings being brought as prey items to feed nestling red-tailed hawks.

Each season, nutritionally induced fault bars are frequently observed in the developing feathers of heavily infested thrasher nestlings. As an example, of 50 nestlings bearing fault bars in their flight feathers (remiges and rectrices) randomly chosen from broods studied between 1979 and 1987, all had been heavily parasitized (range: 74 to 196 larvae). Moreover, infesting larvae were clustered in and around the papillae of the developing feathers in every case (fig. 6.7). Heavily parasitized fledglings that consequentially suffer from malnutrition as nestlings fare more poorly than others. They are lethargic (fig. 6.8) and do not feed as actively as do unparasitized individuals (observed from study blinds with security glass panels mounted on the sides of nest boxes). Larvae infesting adult thrashers are occasionally implanted in easily preened locations such as the tibiotarsi, and yet often go unharmed. Even heavily parasitized nestlings often show no overt signs of discomfort or irritation. Thus, it is possible that infesting larvae may produce an anesthesia to deter their detection and removal, while ensuring physical protection from being inadvertently crushed by a suffering and overactive host irritated by their presence. However, to the author's knowledge, the existence of such a substance has not yet been substantiated. Fault bars also have been observed in the rectrices of thrasher fledglings brought as prey to the nests of red-tailed hawks (feathers provided by E. Santana-Castellón). For a more complete history of botfly ectoparasitism and its impact on thrashers and Puerto Rico's endemic and endangered parrot see Arendt (2000).

Prevalence and intensity of ectoparasitism in recruits (extrinsic factor)—
Of the 52 documented natal dispersers, 31 individuals (18 females and 13 males) were recruited into the sampled breeding population. The prevalence of botfly ectoparasitism among recruits was similar. Although only 61 percent (11 of 18) of the female recruits suffered from botfly larvae as nestlings, whereas 85 percent

Figure 6.7—A 2-week-old pearly-eyed thrasher nestling showing the propensity of ovipositing philornid females to strategically place their eggs within the papillae of developing flight feathers. The developing larvae take advantage of the rich blood supply to the fast-growing remiges (flight feathers). Furuncles are evident on the bird's left wing, demonstrating that the axillary infestation was even more severe than is depicted in this photo.

Figure 6.8—A 3-week-old, recently-fledged immature pearly-eyed thrasher demonstrating the observed lethargy that results from heavy philornid larval infestations. When it attempted to fledge, this individual fell to the forest floor. It was not only unable to fly; it could not lift its wings or even beg for food from the attendant adults. It subsequently died as a result of philornid ectoparasitism.

(11 or 13) of the males were infested, these proportions were not significantly different at $\alpha = 0.05$ (*z*-test: *z*-statistic = 1.24; $P = 0.21$). Likewise, the intensity of botfly ectoparasitism was similar between male and female recruits (M-W R S: $T = 220$; $P = 0.28$). Female recruits received 23.9 larvae on average (SD = 33.62; range: 0 to 95), and males received an average of 24.4 larvae (SD = 15.7; range: 0 to 44).

Gender differences among recruits (intrinsic factor)—
Young female pearly-eyes were recruited into the sampled breeding population at a significantly earlier age (M-W R S: $P = 0.01$) than males (female ages: median = 1.5 years; $SE = \pm 0.37$; range: 1 to 10 years; 25 to 75 percentiles = 1 to 2.75 years, respectively; male ages: median = 3.8 years; $SE = \pm 0.34$; range: 2 to 7 years; 25 to 75 percentiles = 3 to 5 years, respectively). Whereas 12 (67 percent) of the 18 females bred in thrasher boxes within their first 2 years (4 were less than a year old), only 3 males (23 percent) did so, and not one within its first year. More than half of the 13 males did not enter the sampled breeding population until their third year or later. Six males were at least 5 years old and two were 7 years old before they were able to replace resident males.

Higher mortality in female thrashers owing to owl predation and philornid ectoparasitism significantly decreases the time a female potential breeder must wait for an opportunity to breed, whereas male potential recruits must wait for longer periods, often more than 3 years (see “Survival” and “Longevity” above, and chapter 7). These results are similar to those from other studies involving passerines (Blondel et al. 1992; Clobert et al. 1988; Dowsett 1985; Eden 1987; Flux 1978; Greenwood et al. 1979; Matthysen and Schmidt 1987; Orell and Ojanen 1979; Pärt 1990; Payne and Payne 1990; Potti and Montalvo 1991; Robertson and Woodall 1987; Snow and Lill 1974; Winkel and Frantzen 1989; Woodworth et al. 1998, 1999). An exception to the rule, however, is the Florida scrub jay. As do pearly-eyes, scrub jays tend to mate for life and defend year-round territories. Unlike pearly-eyes, however, breeding-aged male and female jays experience equal survivorship. Yet, between the ages of 1 year old, when the sex ratio is equal, and their first attempt at breeding (usually 2+ years old), female jays experience higher annual mortality owing to “behavioral asymmetries between the sexes” (Fitzpatrick and Woolfenden 1988).

Results from adult survival analyses show that the pearly-eye is a long-lived species. This is no doubt a major limiting factor governing the observed small percentage of banded nestlings being recruited into the sampled breeding population. However, another important factor influencing the apparently poor recruitment record over the 21-year period is “natural” nest sites. Undoubtedly, an unknown percentage of dispersers nested in natural cavities and open nests elsewhere in the forest rather than in the monitored nest boxes. For example, minimum-aged thrashers banded as adults are observed from time to time nesting in natural situations, e.g., open-stick nests in bamboo, vine entanglements, and natural cavities.

Habitat and diet of natal dispersers (extrinsic factors)—
How and where did natal dispersers "fit into" the rain-forest thrasher population? Observational and telemetry results revealed that upon leaving their natal areas, many fledglings actively sought sierra palm brakes. As an example, the radio-tagged fledgling that was followed 73 days before the transmitter's battery failed was observed feeding and resting mainly in palm brakes (298 of 347, or 86 percent of the observations). However, it often roosted near a summer home in broadleaf trees with dense foliage, which may have afforded more protection from predators. Similar behavior was observed while radio-tracking fledgling Puerto Rican screech-owls. Although the family group (both parents or, more often, the female and 1 to 2 immatures) was often found in bamboo thickets during the day, at dawn the fledglings were usually found perched in the more dense foliage of broad-leaf trees. The fact that bamboo thickets themselves may also protect the young from diurnal predators such as red-tailed hawks suggests that the switch from bamboo to broadleaf may be in response to a different set of diurnal and nocturnal predators.

While tracking the above-mentioned pearly-eye fledgling, it was observed that the bird kept to a small area within the palm brake, on either side of which were singing (territorial) resident male thrashers. Resident males actively pursued the fledgling when it approached their territorial boundaries. The fledgling also did not move freely in the palm brake foraging area even when keeping away from territorial males. It was observed on several occasions being attacked by other foraging thrashers and additional resident males occupying territories adjacent to the palm brake. In general, within and away from their natal areas, dispersers actively fed on the fruits of the sierra palm, trumpet tree (*Cecropia* [*peltata* L.] *schreberiana* Miq.), and other preferred food trees and shrubs (fig. 6.9).

Postdisturbance food shortage (extrinsic factor)—
The confinement of three lightly parasitized fledglings (mean = 11 larvae per individual) within their natal area for more than a month following Hurricane Hugo was documented by nest-box observations and telemetry. This suggests a postdisturbance food shortage in the forest (discussed further in chapter 8; see also Wunderle 1999: fig. 2). Although effects of ectoparasitism cannot be ruled out, this possibility is slight. Monitoring of other lightly parasitized young

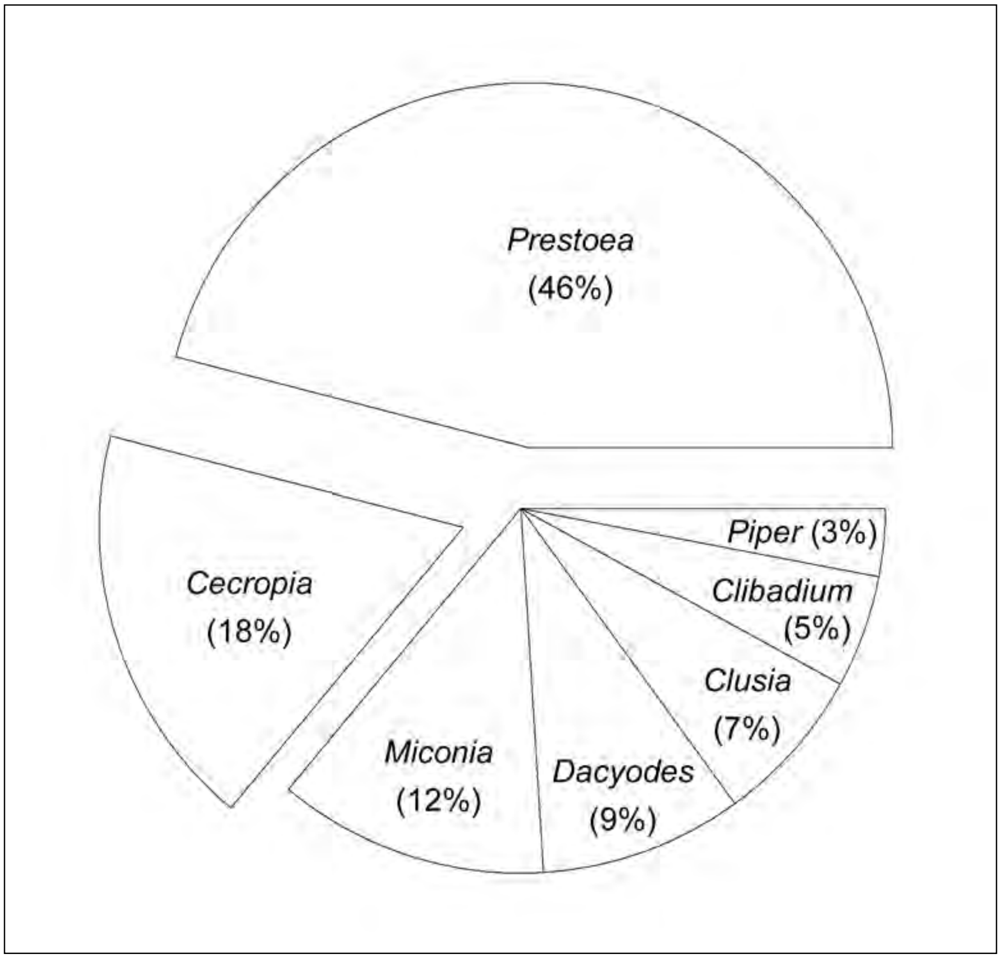

Figure 6.9—Food plants of dispersing, immature pearly-eyes. The size of each pie slice is the percentage of the total number of foraging observations (n = 472). Complete scientific names and percentage of observations for each food plant are as follows: *Prestoea acuminata* (Willd.) H.E. Moore var. *montana* (Graham) A. Henderson & G. Galeano; (46 percent), *Cecropia schreberiana* Miq. var. peltata L. (18 percent), *Miconia* spp. (12 percent), *Dacryodes excelsa* Vahl. (9 percent), *Clusia gundlachii* Stahl (7 percent), *Clibadium erosum* (Sw.) DC (5 percent), and *Piper aduncum* L. (3 percent). *Prestoea* and *Cecropia* fruit constituted more than half (64 percent) of the foraging observations, with *Prestoea* fruit most often eaten by dispersers. Some plant materials were identified by (the late) Roy O. Woodbury.

has shown that most are not deleteriously affected by so few infesting larvae. Furthermore, the fact that three unparasitized radio-tagged young that fledged in 1990 succumbed within 2 months after fledging strongly substantiates the food shortage assumption. Upon retrieval of the carcasses, all three fledglings showed signs of malnutrition. Each was underweight and underdeveloped, exhibiting shorter bones and feathers, and temporally retarded feather tract development.

Body masses and fledging dates of natal dispersers and survivors—
All of the above-mentioned intrinsic and extrinsic factors affect and confound the survival and natal dispersal of pearly-eye fledglings. I attempted several analyses comparing the body masses of superior survivors, dispersers, recruits,

and fledglings from early broods with those of the general population to evaluate the hypothesis that survivors, successful recruits, and fledglings from early broods are heavier at the time of fledging (e.g., Krementz et al. 1989a and references therein). Unfortunately, several factors, not the least of which were infesting botfly larvae and the effects of periodic cyclonic events, forced so many subsets of the data that the resultant sample sizes were too small for statistical comparisons. Having to equate the fledging date, age, hatch order, number of infesting larvae and year of fledging of each disperser-survivor-recruit with that of all fledglings from the population resulted in too few candidates for meaningful tests.

Short-Range Natal Dispersal Within Puerto Rico

Although most band recoveries or sightings were made within the confines of the forest, the potential for dispersal to other parts of the island was confirmed by two recoveries, one just outside the forest and one at the opposite end of the island. In spring 1983, I received a report of a recovery on May 16 about 7 km from the hatch site and beyond the forest boundary. Male 1383-17872 was 3 years old when it was shot (illegally) by a hunter. It had been banded on February 20, 1980. It was the oldest nestling from the female's first brood of the season and it remained unparasitized throughout the nestling stage. It had fledged from a thrasher box located along PR auxiliary 9938 ("Loop Road") near km 13 of Hwy. 191 (fig. 1.6).

Pearly-eye natal dispersers were recovered outside of the forest, from across the island, and from the Lesser Antilles.

The second recovery was an adult of undetermined gender that was found dead with no signs of external lacerations on a farm near Mayagüez, a large city located on Puerto Rico's western coast and a little less than 100 km from the disperser's hatch site. This band encounter was important, not only for the dispersal distance involved, but also from a longevity perspective. This individual was banded (USFWS 1163-17857) on June 17, 1981, at Km 13.4, PR 191, in the Icacos Valley located on the southern slope of the rain forest (fig. 1.6). This long-range, intra-island disperser was alive almost a decade after hatching.

Long-Range Natal Dispersal Among Islands

One additional and very important piece of information concerning pearly-eye natal dispersal was obtained during regional wildlife assessments (see Faaborg and Arendt 1985). On February 5, 1984, I banded (USFWS 1163-17772) a recently fledged, dark-eyed, pearly-eyed thrasher in a secondary dry forest along the trail to Darby Cave, Barbuda, a small island adjacent to, and politically affiliated with, Antigua in the Lesser Antilles. Later that year (December 23, 1984), the same thrasher was shot by a hunter (M. Georges Plonquitte) in a dry forest on the French West Indian island of Guadeloupe, some 175 km to the southeast.

The specific collection site was given as Pointe Noire (Mahaut) on the west coast of Basse-Terre, at an elevation of 230 m. The band was reported by a forest guard (M. Patrice Roch), and confirmation was made by the French ornithologist, Edouard Bénito-Espinal (1985, in. litt.). This single return confirms that pearly-eyes are capable of long-distance transmarine dispersal.

Numerous documented sightings of pearly-eyes on Caribbean islands in which the species does not breed strengthen the fact that pearly-eyes are quite capable of inter-island dispersal. Pearly-eyes do not regularly occur on any of the large, northern Bahamian islands. However, they have been sighted on six of them (Great Abaco, Harbour Island, Eleuthera, Cat Island, Great Exuma, and Long Island to see app. 3 for details). In addition, the published report by Bonhote (1903a, 1903b) of a pearly-eye striking a lighthouse on Bird Rock, Bahamas, at 2150 hours on November 14, 1901, strongly suggests night dispersal in the species. If this individual was taking advantage of the artificial light source by hawking insects attracted to the beacon, it most likely would have been a resident bird quite familiar with the tower and its immediate surroundings. That is, it is very unlikely that it would have collided with the structure. The late fall date suggests natal dispersal, i.e., the bird may have been a dispersing immature that had fledged earlier that same year from another island. Two additional accounts from the literature are suggestive of breeding dispersal. Maurice Collett, a former resident of Tarpum Bay, Eleuthera (Bahamas) observed pearly-eyed thrashers (total number not reported) near the village on April 10, 1956, observing them for a month. Similarly, Richard D. Wood of Philadelphia reported seeing a pearly-eye on Great Exuma in February 1964 (both cited in Bond 1964). Both dates suggest the pearly-eyes involved could have been dispersing in search of suitable breeding sites distant from competing conspecifics.

Most dispersal to the northern Bahamian islands was probably achieved by "island hopping" from nearby source islands or cays (D.W. Buden 1988, in. litt.). However, specimens taken on the more pelagic islands (greater distances to the main archipelago) such as Jamaica, Sombrero, Guadeloupe, and Barbados show that dispersing individuals do not have to "island hop" to reach their destinations, i.e., they are capable of more extended, over-water flight (see app. 3).

Homing Experiments on Adult Males

In support of the Bonhote (1903a, 1903b) observation, a few homing experiments involving resident thrashers from the present study also suggest the ability of night (or at least crepuscular) flights by pearly-eyed thrashers. At dusk on separate dates, I captured and released two resident males within the forest at varying distances from their nest boxes (e.g., one at Yokahú Tower and the other at the junction of PR Hwy 191 and PR auxiliary 9966—Jiménez Road). By 0600 the following day, both males were once again on territory and singing. A third male released outside of the forest on the island's north shore (Luquillo Beach) may have returned during daylight hours as it was not found singing from within its territory until dawn of the second day. A fourth male displaced to Puerto Rico's satellite island of Vieques was on territory within 9 days after removal. He may have returned even sooner but, owing to extraneous circumstances, his return was not monitored during the 9-day interval (table 6.5).

Table 6.5—Homing experiments involving breeding male pearly-eyed thrashers released at progressively greater distances from their nest boxes within and beyond the Luquillo Experimental Forest, Puerto Rico[a]

	Date		Hour			
Nest box	**Released**	**Returned**	**Released**	**Returned by**	**Release site**	**Displacement distance**
						Kilometers
26	10 May 82	11 May 82	1900	0600	Yokahú Tower	3
35	23 May 82	24 May 82	1845	0600	Intersection PR 191 and 9966	6
36	6 June 82	7 June 82	1900	0600	Nursery, CSC[a]	9
25	13 June 82	15 June 82	1830	0600	Luquillo Beach	12
25	9 July 99	≤9 days	—	—	Vieques Island[b]	30

— = hour unknown.

[a] CSC = The USDA Forest Service's Catalina Service Center located within the Caribbean National (= Luquillo Experimental) Forest at km 4 along Highway PR 191.

[b] Pearly-eye male was transported and released by Oscar Díaz of the U.S. Fish and Wildlife Service stationed on Vieques Island.

Though transported relatively short distances (3 to 30 km), the rapidity at which displaced pearly-eye males returned to their nesting territories is noteworthy considering the results of homing experiments with other passerines conducted by Able et al. (1984) and Dowsett and Dowsett-Lemaire (1986). Using biotelemetry, Able et al. (1984) showed that individuals of the wood thrush (*Hylocichla mustelina*), a nocturnal migrant, after being displaced over distances of 6.5 to 17.3 km, took several days to return to their breeding territories by moving in a series of short flights (mean = 2.1 km) performed primarily at dawn. In a separate homing experiment, Dowsett and Dowsett-Lemaire (1986) found that of 43 color-banded birds of 11 species displaced to other forest patches only 6 km apart, only 2 species (starred robin *Pogonocichla stellata*, and cape flycatcher, *Batis capensis*) showed homing ability and returned to their original sites. With the exception of one starred robin that returned to its original territory within 2 days, the remaining individuals took 1 to 3 months to return. Thus, pearly-eyes show a superior homing ability when compared to some other species of passerines, exemplifying yet another innate character in its arsenal of supertramp attributes.

Conclusions

Although the pearly-eye is unable to compete successfully on large, species-rich islands and in habitats with large, diverse avian communities, it can survive for several years, and even decades, on species-poor islands and habitats in which it can successfully establish itself. Although adults show a high mean annual survivorship throughout their lives, predation and natural disasters such as periodic storms can, and do, severely impact survival rates. However, the pearly-eye proves its resiliency to natural calamities by rebounding to preoccurrence survival rates within 2 years following major habitat disturbances.

In general, natal dispersal is governed by several intrinsic and extrinsic factors and is minimal, with many fledglings remaining in the forest, often within a 3-km radius of their hatch sites. However, more extensive dispersal does occur as confirmed by band returns and documented sightings from cooperators and as reported in the West Indian bird literature (app. 3). Fledglings from the sampled population were capable of dispersing to areas beyond forest boundaries. In addition, a single band return involving an immature thrasher whose natal and recovery islands were almost 200 km apart, as well as homing experiments and several documented sightings of stray individuals on islands with no breeding populations, confirm that the pearly-eye is capable of, and may even be inclined to, inter-island dispersal.

The pearly-eye's close relative, the European starling, has also been shown to be a champion disperser. Using banding data and genetic information based on allozyme allele frequencies from populations inhabiting Virginia, Vermont, Colorado, and California, Cabe (1999) found that the average distance moved by natal dispersers was 104 ± 307 km ($n = 131$). It is noteworthy, however, that more than half of the dispersers (69) were recaptured within their natal areas (see also Wheelwright and Mauck 1998). Therefore, starlings exhibit a dispersal pattern similar to that of the pearly-eye. Many starlings remain relatively close to their natal areas, whereas a substantial number disperse over long distances. Presumably, many more pearly-eyes also dispersed over much greater distances but simply were not detected. In comparison with the starling study, it was undoubtedly more difficult to confirm longer dispersal distances for the pearly-eye owing to its insular environment, more clustered human populations, and fewer observers in the region as compared to the North American continent.

Summary: Survival and Dispersal

The pearly-eye's high annual survival (90 percent in males and 82 percent in females), prolonged lifespan, regional dispersal capabilities, and strong homing instinct act in concert with its other supertramp attributes to facilitate successful colonization and maintenance of sustained populations on species-poor islands and habitats throughout the region.

In general, adults tolerated fledglings for about 2.5 weeks postfledging. Both adults administered care while the fledglings remained in the natal area. However, once females renested, males assumed most of the responsibility of their feeding and protection. Length of parental care differed among nest pairs and seasons, with parental feeding and acceptance of the fledglings within the proximity of the nest box (a radius of about 30 m) being shortest between first and second broods, and longest after the final nesting attempt. Older siblings, especially from first broods, tended to survive better and disperse farther than their younger brood mates. Fledglings dispersed from their natal areas on average about 9 days before deposition of the first egg of a subsequent nesting, although some heavily parasitized fledglings and those suffering from malnutrition following major hurricanes died within 20 to 30 m of their nest-box trees over a period lasting from a few days to several months. Even though fledglings are capable of long-distance dispersal, even over open water, radio-tagged immatures and numerous band recoveries confirmed that most dispersal is within 3 km of the hatch site. Of 52 documented natal dispersers, 31 individuals (18 females and 13 males) were recruited into the sampled breeding population. One banded female was recruited into the breeding population after a lapse of 10 years at a distance of only 0.3 km from her hatch site.

Chapter 7: Reproduction

The pearly-eye closely fits the supertramp mold in its ability to undergo long-range natal dispersal. It even has at least one characteristic of highly competitive (high-S) species, i.e., it is long lived. Nonetheless, one of the most essential characteristics of a true supertramp is its reproductive prowess. After reaching a new island or habitat, supertramps must undergo prolific breeding with extended breeding seasons and, most importantly, must recycle quickly after each nesting attempt by taking advantage of often patchy or ephemeral food sources to expedite recrudescence of reproductive organs. Reproductive success increases when breeders are long lived and maintain a high degree of site fidelity and strong pair bonds. The pearly-eye possesses all of these important attributes.

Pearly-eyes are prolific breeders with extended breeding seasons and rapid recycling.

Return Rates of Resident Breeders

Owing to an extended lifespan, breeding pearly-eyes should show high annual return rates, and thus enhance their reproductive success. I define “return rate” as the proportion of banded adults of each sex that returns each year to breed. At first, the following discussion of return rates of breeding thrashers appears to be a replication of annual survival discussed in chapter 6. The difference is that the annual survival rates in chapter 6 were based on local survival (ϕ) using mathematical modeling and included all thrashers banded in the forest over a 12-year period, whereas the following analyses treat only the proportion of returning nesters monitored over an 18-year period. Moreover, banded fledglings recruited into the breeding population and breeding for the first time are excluded. The use of these two methods, coupled with the difference in total number of inclusive years, explain the slight difference in the results.

Before presenting the results of pearly-eye return rates, I emphasize that, after having lived and worked daily in the study area throughout the breeding season during the first 10 years of my research, I am confident that (with very few exceptions) once a thrasher gained control of a nest box, it continued to breed in that box (or another, usually close by) throughout its reproductive life. Apparently, recruits that hatch in nest boxes are imprinted on them and, therefore, prefer them to natural cavities. Only under unusual circumstances, e.g., reproductive losses incurred owing to nest predation, ectoparasitism, or occasional human interference, have nest-box breeders (mostly females) given up a box and nested in nearby natural cavities (see discussion below). Pearly-eyed thrashers are so dense at the mid-level elevations of the forest within the palo colorado (*Cyrilla racemiflora* L.) forest type that, generally, breeders cannot simply move away from the study area to breed elsewhere, although this behavior has been observed on a few occasions over a limited area. To date (September 2005), all thrasher sightings in other areas within and beyond the forest boundary have been of natal dispersers, i.e., those banded as nestlings, rather than reproductive dispersers.

The annual return rate of almost 80 percent plummeted to about half following Hurricane Hugo.

The combined average annual return rate for 98 banded males and 137 banded females from 1979 to 1997 was 78 percent, with a higher rate of return for males (80 percent) than females (77 percent) (fig. 7.1a). Differences among the adult return rates were not significant at the 95-percent level of confidence for the 18-year period ($t = 1.56$; df = 34; $P = 0.12$). There was, however, a significant inverse correlation between return rates and ages of males and females as mortality increased each subsequent breeding season owing to not only aging, but also several environmental factors (see Arendt 2000) that intensified during the last 7-year period (fig. 7.1a).

Because the combined annual return rate plummeted to 41 percent (30 percent in males, 51 percent in females) by the onset of the first breeding season following Hurricane Hugo, a second analysis was conducted to evaluate return rates before the effects of the storm (fig. 7.1b). For a 10-year period (11 breeding seasons) prior to major habitat disturbance (1979 to 1989), there was a significant difference in return rates between the sexes ($t = -2.80$; df = 18; $P = 0.01$). Return rates were higher for males (92 percent) than for females (83 percent) owing to higher mortality in female nesters resulting from nest predation by owls. The larger correlation coefficient and greater probability value resulting from the latter analysis further exemplifies the higher annual rate of return by males. Owing to an increased frequency and intensity of hurricanes from 1995 to 1999 (thus adding an additional bias), no additional comparative return rate analyses were conducted after 1997. Indeed, it is the lowered return rates from 1995 to 1997 that caused the overall average return rate for both sexes to fall below 80 percent (fig. 7.1a).

Lastly, male and female return rates were compared to the number of banded adults during any given breeding season (fig. 7.1c). Not only do the annual return rates for both sexes fluctuate similarly, but so also do the number of breeders each season, which implies strong yearly effects on both first-time and returning nesters. This is not surprising as the availability of food, quality of nutrition, and even endogenous reserves of fat and protein in times of plenty are known to have profound influences on reproductive function (Follett 1984, Knobil and Neill 1994). For example, a lean year (such as one following hurricane damage) would result in decreased primary production and diminished food supplies, thus reducing the number of insects and small, introduced rodents, which in turn would result in elevated rates of owl nest predation and higher adult thrasher mortality. Moreover, an extremely wet year would elevate the number of philornid

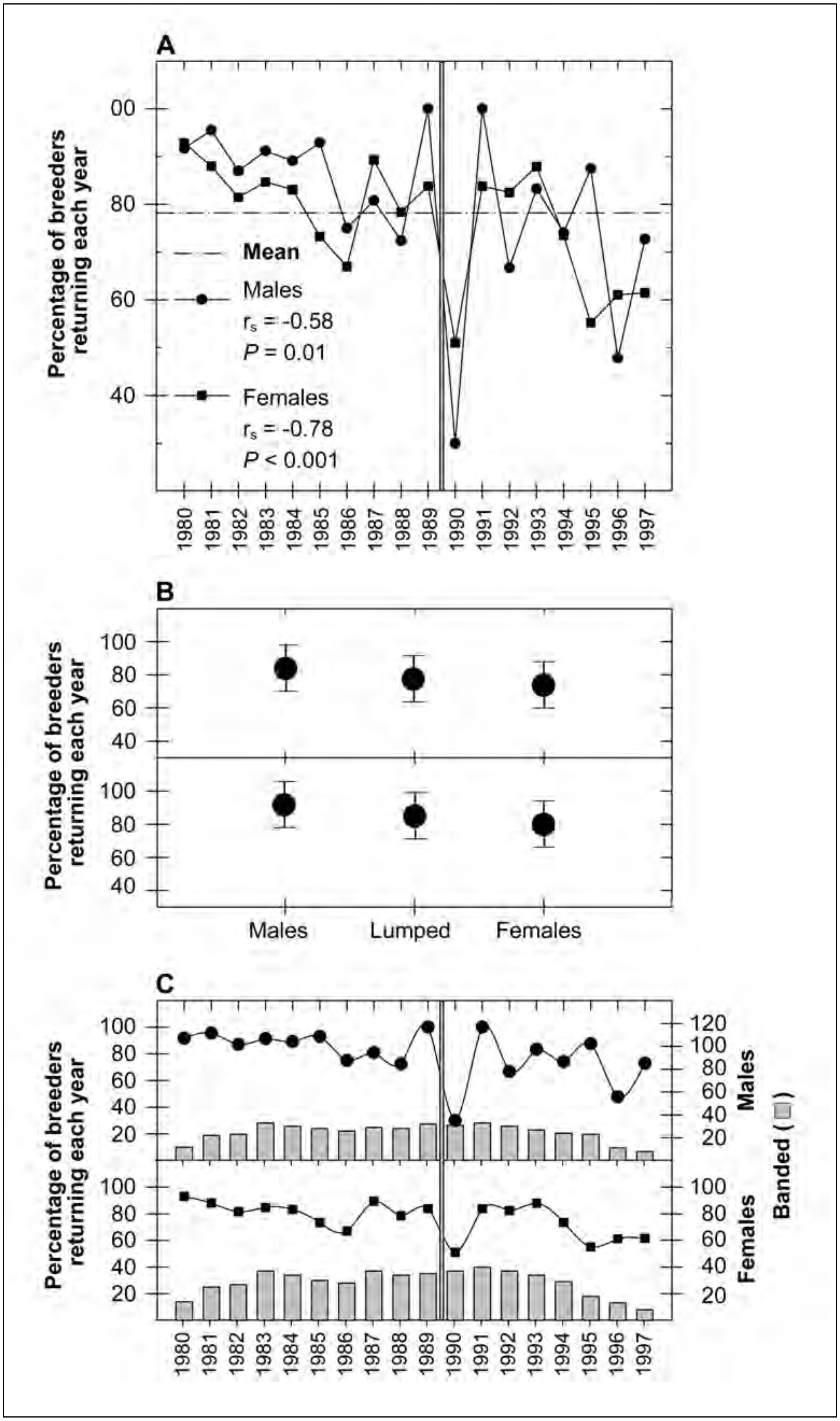

Figure 7.1—Annual return rates for 98 male and 137 female pearly-eyed thrashers breeding in nest boxes between 1979 and 1997. Graph A is a comparison of return rates between the sexes and shows the impact of Hurricane Hugo (shaded vertical bar) on each. Graph B compares the overall average return rates for each sex and sexes combined during all 18 breeding seasons and 11 prehurricane seasons, respectively. Graph C compares return rates of males (●) and females (■) to the number of banded adults (gray bars) breeding during any given year. Note the similarities between the sexes for both the annual return rates and the number of banded adults during a given year, which demonstrates the importance of yearly effects on both sexes.

botflies, which in turn would increase both nestling and adult thrasher mortality, thus resulting in fewer returning adult breeders and new recruits in the subsequent breeding seasons.

Nest-Site Persistence and Mate Fidelity

Below, rather than attempting a theoretical treatment of nest-site persistence and mate fidelity, study results are presented from an ecological perspective. Site and mate fidelity are just two more crucial elements in the pearly-eyes impressive arsenal of supertramp traits.

Pearly-eyes show high nest-site and mate fidelity.

Site persistence varies considerably among species and habitats. Kricher and Davis (1998) reported higher site persistence among 17 species of birds in both young (7 species) and mature forests (10 species) than in disturbed habitats (5 species). Site persistence and mate fidelity in this rain-forest population are more highly correlated with adult survival than with reproductive dispersal (see below). Many populations are found in several forest types, and both sexes are site persistent. However, from 1979 to 2000, site (nest-box) persistence was significantly higher (M-W R S: P <0.001) for 104 banded males (median = 5 years; 25 to 75 percentiles = 3 to 8 years, respectively) than for 143 banded females (median = 3 years; 25 to 75 percentiles = 1 to 4.5 years, respectively). The number of years that nest pairs nested in the same box is shown in figure 7.2a. Whereas the frequency distribution for females is skewed toward the left (1 to 3 years) and then gradually declines with each successive year, that of males is much flatter, rising to year four and then tapering off, with a much more elongated "tail" than that observed for females. Twice the percentage of females than males (16 percent vs. 8 percent, respectively), although not significantly higher (z = 1.41; P = 0.13), nested for only a single year (fig. 7.2a). The percentage of females and males nesting in the same box for 2 to 4 years was somewhat more balanced (67 percent and 53 percent, respectively). Likewise, a similar percentage of females and males (32 percent and 38 percent, respectively) nested in the same box for 5 to 10 years (fig. 7.2a). Whereas no female nested in the same box for more than 9 years, 10 percent of the males were site faithful for 11 to 15 years because males generally survived longer (mean = 5.3 years; SE = ± 0.34; min. = 1 clutch; max. = 15 years) than females (mean = 3.48 years; SE = ± 0.19; min. = 1 clutch; max. = 9 years). Hurricane Hugo apparently killed nine males that had bred in the same boxes from 1979 to 1989 but disappeared after the storm. Presumably at least some, if not most, of the nine would have nested longer had they survived the storm.

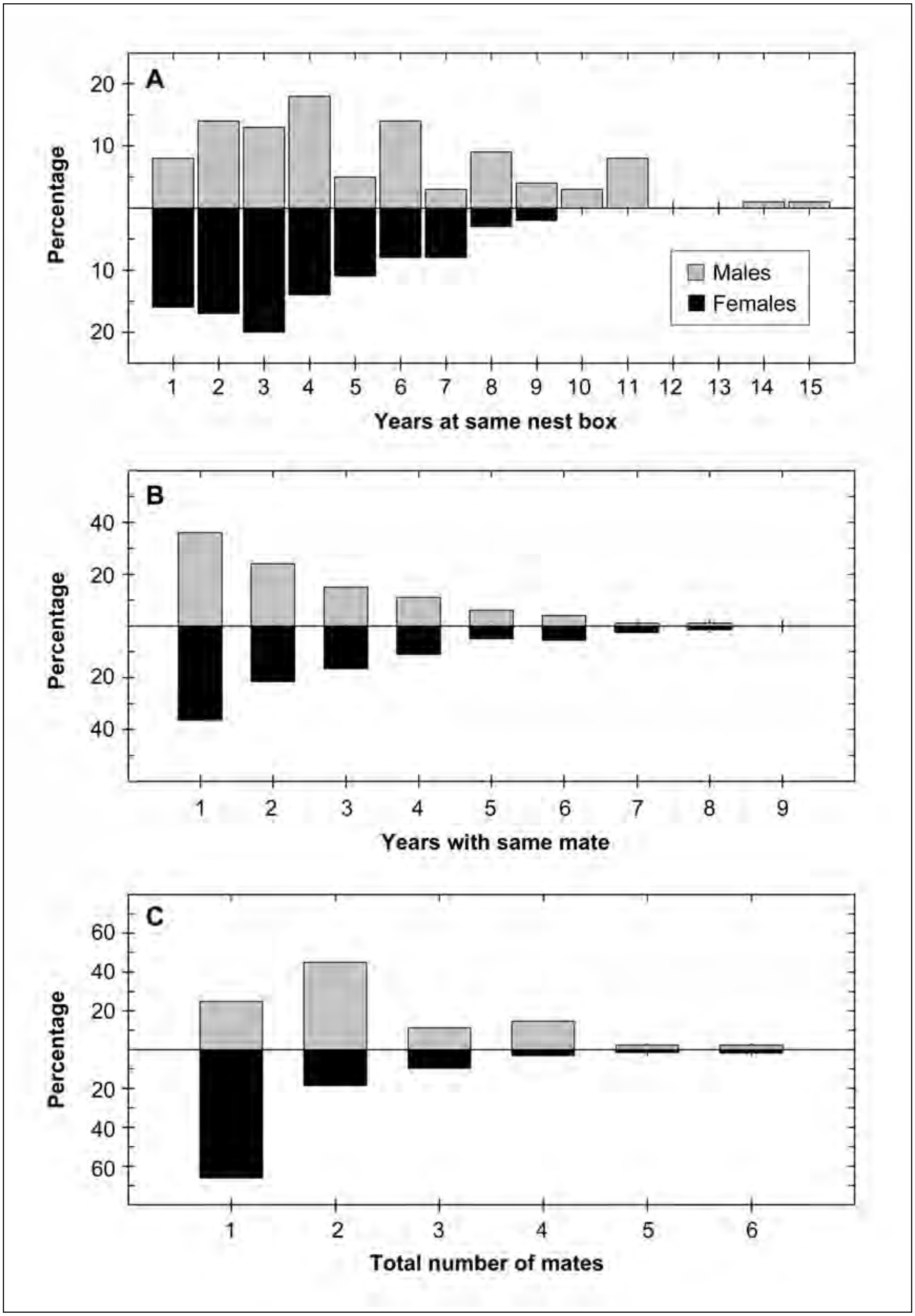

Figure 7.2—Site persistence (A) and mate fidelity (B, C) for 104 male and 143 female pearly-eyed thrashers that bred in nest boxes between 1979 and 2000. Results reflect disparate survival rates between the sexes (see also chapter 6) which, in turn, greatly influenced site tenacity and mate faithfulness.

Pair Bonding and Survival Rates

In birds, although highly dependent on intrinsic (e.g., female condition) and extrinsic factors such as nest predation (Bried and Jouventin 1999), there is a significant correlation between divorce rate and site fidelity. Species with little or no site fidelity are more likely to divorce (Cezilly et al. 2000). Therefore it is not surprising, as the pearly-eye is highly philopatric, that it also exhibits strong pair bonding. As with site persistence, pair bonding is also highly correlated with adult survival rates. Because most individuals of both sexes kept the same mates throughout their reproductive lives, the number of years an adult remained with the same consort coincides with its longevity. No nester bred with the same mate for more than 8 years (fig. 7.2b). Most nesters remained with their mates from about 1 to 4 years (females: mean = 2.4 years; *SE* = ± 0.13; min. = 1 clutch; max. = 8 years; males: mean = 2.3 years; *SE* = ± 0.12; min. = 1 clutch; max. = 8 years). These results are similar for both sexes (M-W R S: *P* <0.49; females: median = 2 years; 25 to 75 percentiles = 1.75 to 3.3 years, respectively; males: median = 2 years; 25 to 75 percentiles = 1 to 3 years, respectively). Of 208 female mates (not individuals, as some individuals were mated more than once), 75 (36 percent) of the males remained with the same female for a single year, 118 males (57 percent) retained the same female for 2 to 5 years, and 15 males (7 percent) remained paired with the same mate for 6 to 8 years. Similarly, of a total of 200 male mates, 73 (36 percent) of the females remained with the same male for a single season, whereas 108 (54 percent) of the females remained paired with the same males for 2 to 5 years, and 19 females (10 percent) remained mated to the same male for 6 to 8 years (fig. 7.2b). All the proportions tests comparing possible gender differences in the number of years conjugates remained paired were insignificant.

Number of Mates

Determining the number of mates over the reproductive lifetime of individual breeders is a more precise measure of pair bonding than is the number of years that pairs remained together. Not surprisingly, the number of mates shared by each sex also reflects adult survival. Because adult females generally have shorter lifetimes than males, intuitively they should have fewer mates. Of the 143 females, 94 (66 percent) had but one mate during their reproductive lives (fig. 7.2c), 27 (19 percent) paired serially with only 2 males, whereas only 22 females (15 percent) had 3 to 6 successive mates during their reproductive years (mean = 1.58; *SE* = ± 0.09; range: 1 to 6 mates). Conversely, of 104 males only 26 (25 percent) of the males had but 1 mate, a significantly smaller proportion than that observed in females (*z* = 5.73; *P* <0.001). An additional 47 males (45 percent) had 2 mates, and

31 males (30 percent) had 3 to 6 mates in succession throughout their reproductive lives (mean = 2.31; *SE* = ± 0.13; range: 1 to 6 mates). Combining all three mate classes for each sex, this gender difference in the total number of mates was significant at a 95-percent level of confidence (M-W R S: P <0.001; male breeders: mean = 2.31 female mates; *SE* = 0.12; median = 2 female mates; 25 to 75 percentiles = 2 to 3 female mates, respectively; and for female breeders: mean = 1.58 male mates; *SE* = 0.08; median = 1 male mate; 25 to 75 percentiles = 1 to 2 male mates, respectively).

Several other studies of birds have shown that in many species, especially passerines, males survive longer and, in many instances, maintain the same nest sites longer than females (Bryant 1989, Payne 1989, Simek 2001). Based on 109 data sets representing 70 species from 12 avian orders, Payevsky et al. (1997) showed that in most cases, not only do males survive longer, their higher survival rates occur significantly more frequently (73 percent) than those of females than would be expected by chance (80 cases out of 109 sets).

Courtship Behavior

Actual pairing was seldom observed. However, as an example, while monitoring a newly installed thrasher box at an active Puerto Rican parrot nest, I observed the following courtship behavior and eventual bonding of a thrasher pair. On March 1, 1981, at the traditional Palo Hueco blind, at 1105 hours, a male thrasher alighted at the entrance hole of a “sentry” (sensu Snyder et al. 1987) thrasher box that was placed about 20 m from the parrot cavity so that the resident thrasher pair would keep prospecting and predatory thrashers from entering the parrot nest cavity. The male thrasher carried a small oval-shaped, green leaf in its bill. The male began to turn inward and outward, inward and outward, poking its head inside the box and then withdrawing it, still grasping the leaf. (Similar behavior has been observed by the author at other thrasher boxes, and by other biologists studying a diverse array of avian taxa from gulls to grassquits.) The male thrasher then flew to a female (duller plumage, no prominent white-frosted tertiaries or secondaries, and white tips of rectricies much less pronounced) perched on a limb about 30 cm from the thrasher box entrance. The male dropped the leaf as it alighted about 10 cm below the female. He then thrust his bill upward to almost a 90-degree angle in a fashion similar to that of icterids when they are courting females or trying to intimidate rival males. The male then drooped its wings, cocked its tail, and puffed out its body feathers until it appeared much larger than its actual size. The female, however, remained indifferent. The male then mixed chattering (almost a rattle) with soft song. The female, however, continued to ignore the male. She flew up to the mid-story canopy and began feeding from a bromeliad. The male continued to sing at its previous site, but he deflated his body feathers and appeared more relaxed as he sang. Within a couple of minutes, the female returned to her original perch a few centimeters above the male. The male immediately puffed up his feathers, pointed his beak skyward, and began vocalizing. His body quivered slightly as he vocalized. He attempted to move very close to the female, but she withdrew and flew to the entrance hole of the nest box, peered inside, and appeared very anxious as if contemplating entering, but then flew off and resumed foraging. In the meantime, the male resumed normal posture and sang from the same perch until 1130 hours. At that time, both thrashers began foraging for insects in dead sierra palm fronds until 1210 hours. They then flew to the same site described above just in front of the thrasher box. The male then flew to the entrance hole, but immediately returned to the female, singing constantly. The female then flew to the box, alighted, and peered in, but immediately returned to within just a few centimeters of the male. This time, however, she perched below the male. For the third time, the male inflated its feathers, extended its bill upwards, and sang more strongly than during either of the two previous sessions. The female flew out of sight, but returned shortly with nest material (fine strands) in her beak, and began constructing her nest. Eventually, the pair successfully fledged two young. I do not know if every nest pair engages in this behavior before each nesting of every breeding season or if, instead, it is carried out only once, i.e., during the initial pair bonding. It is noteworthy that the male at this box previously had tossed in twigs over several days until a 30-cm deep “twig platform” was completed. Because the distance from the bottom of the box to the lower lip of the entrance hole is 47.1 cm, the pairs’ eventual nest was vertically recessed almost 20 cm down from the entrance hole. A predawn nest inspection earlier that same day confirmed that construction of the nest cup had not begun until the female entered with the first fine vegetal strands as described above.

Cuckoldry and Egg “Dumping”

In birds, cuckoldry (as opposed to mate switching—see below) usually involves unfaithful females. Although not actively pursued in this study, cuckoldry is suspected. In the case of the pearly-eyed thrasher, however, it may be the males who are the more frequent unfaithful partners in the pair bond. Throughout this study, whereas territorial females guarding their nest boxes did not allow intruders of either sex, on several occasions, especially late in the season, males were observed allowing what is assumed to be young, and probably first-time, female breeders not only to enter their breeding territories, but even approach and inspect their nest boxes. It is noteworthy that the last clutches of the season sometimes involved unbanded females in territories in which both resident breeders were banded for all the previous clutches of the season. This lends credence to the possibility that resident males not only permit prospecting females within their territories but probably also inseminate them and allow them to breed in their boxes. But, why do the resident females allow these intruders? Several observations suggest that resident females' gonadal hormone levels, and thus their territorial behavior, diminished before breeding seasons had ended, especially if they had laid several previous clutches. Over the years, and always near the close of the breeding seasons (late June and July onward) a few resident females were observed to simply cease maternal behavior often in the middle of incubation and even during brooding and feeding of the young. Although they would often remain in the area, females completely ignored their boxes until the following season. In some instances, otherwise healthy nestlings starved to death while the resident females remained close to, but would not enter, their nest boxes. In other passerines, including mimids, Wingfield (1988) and Logan and Wingfield (1995) have shown correlations between plasma steroids and breeding behavior. As food availability wanes, as it does toward the end of the pearly-eye's breeding season (Arendt and Wunderle 2004), the consequential diminished food intake often results in metabolic stress that, in turn, elevates plasma levels of corticosterone (which stimulate foraging and self maintenance) and depresses titers of gonadal hormones (which stimulate reproductive behavior, such as feeding and caring for the young). Thus, it is possible that, as food becomes scarcer, older, more experienced females complete their reproductive activities and revert to behaviors that promote self-preservation in light of increasing environmental stress before impending food shortages occur. At the same time, however, younger (and probably unbred) females are still in good body condition and have elevated hormone levels, thus allowing them to nest successfully late in the season.

Comparison of Survival, Nest-Site, and Mate Fidelity With Other Species

The survival, nest-site persistence, and mate fidelity results obtained in this study are comparable to other studies of tropical montane forest birds. For example, over a period of 10 years, Dowsett (1985) banded 2,030 individuals of 33 species of montane forest birds at elevations above 1800 m on the Nyika Plateau, Malawi/Zambia, in South-central Africa. He then monitored their survival and movements (1979 to 1982) and site fidelity (1972 to 1982), and found that 613 individuals remained within an average distance of 165 m (range: 0 to 3125 m) from the banding site. As in the pearly-eye, individuals that moved the greatest distances were often natal dispersers. However, postbreeding (reproductive) dispersal was observed and some natal dispersers nested within 400 to 600 m from their natal sites as do many pearly-eyes. Many African montane forest birds were also long lived. Four species had individuals that survived 9.7 to 10.8 years. Average annual survival ranged from 78 to 87 percent in well-monitored samples of the white-chested alethe (*Alethe fuelleborni*) and olive-flanked robin (*Cossypha anomala*). In a separate study of the starred robin, Oatley (1982) reported an average annual survival of 86 percent for males, but only 69 percent for females. Thus, as shown in the pearly-eye, males of other tropical montane species are known to survive better, and thus live longer, than their mates (for additional studies of survival and longevity in tropical landbirds, see Snow and Lill 1974 and Fry 1980, and more recent studies cited in chapter 6).

For several species of montane forest birds, the annual return to breeding territories was also high. As an example, annual return rates of 67 to 78 percent (n = 59) were documented for the starred robin. Moreover, most montane species maintain long-term pair bonds. However, as in the thrasher study, both males and females of several species show stronger site tenacity than mate faithfulness. Some adults (n = 1,127), especially males, held the same territories for as many as 10 years, with 39 percent of adult breeders (sexes combined) returning for at least two consecutive seasons and 19 percent defending the same territories for 3 years or more. In a shorter study of another mimid, the gray catbird, Darley et al. (1977) showed that return rates and site fidelity were strongly influenced by sex (males were more site persistent than females), slightly by reproductive success (successful breeders returned more often to previous sites), and not much at all by age (see references therein for several studies with similar results).

Reproductive Dispersal

In many avian species, breeding adults often change nest sites or even emigrate to different areas after suffering nesting failures or low rates of reproductive success resulting from a myriad of environmental and ecological stressors not the least of which include nest predation and parasitism (Haas 1998, Newton 2001, Powell and Frasch 2000, Stanback and Dervan 2001, Wunderle 1984). Such movements are termed reproductive dispersal (Jackson et al. 1989). With notable exceptions (e.g., Howlett and Stutchbury 1997), dispersers often do better at their postmove (auxiliary) sites, thus suggesting that breeders disperse in search of higher reproductive success (the nest-failure hypothesis, Jackson et al. 1989, Murphy 1996). Losses occurring late in the breeding cycle often increase the probability of reproductive dispersal (Jackson et al. 1989), whereas nesting success is frequently higher following dispersal early in the season, especially when dispersal distances are greater than the home range of nest predators (Powell and Frasch 2000). Moreover, prospecting for alternative nest sites is not only prompted by previous nest failures owing to such factors as nest predation but is often initiated by nesters seeking higher quality territories. As an example, in a 6-year study of the pied flycatcher (*Ficedula hypoleuca*) in a montane oak woodland in Spain, Montalvo and Potti (1992) found that nesters responded to variation in territory quality, choosing alternative boxes in higher quality territories for their second breeding attempts.

Often, however, there are heavy costs incurred as a consequence of breeding dispersal. As a result, return rates by dispersers are frequently lower than those for breeders that remain at their primary sites (Haas 1998). By dispersing, breeding females can more than double their risk of mortality resulting from an increased susceptibility to predation and a host of other environmental and ecological pressures (Daniels and Walters 2000). Many dispersers even fail to breed, which in itself is the ultimate form of nest failure (Danchin and Cam 2002).

In the pearly-eye, reproductive dispersal was minimal in both sexes from 1979 to 1989 (Arendt 1993). However, owing to an increase in nest predation and takeovers at thrasher nest boxes by competitors, e.g., owls (*Megascops nudipes*), rats (*Rattus rattus*), and honeybees (*Apis mellifera ligustica* and *A. m. scutellata*) after Hurricane Hugo (see Ackerman and Moya 1996, Arendt 2000), reproductive dispersal in female thrashers has greatly increased since 1990. The same trend, however, has not been observed in male thrashers, at least through the 2000 breeding season.

Many more females than males underwent reproductive dispersal.

Males Changing Nest Boxes

Only 5 of 104 banded males (5 percent) changed nest boxes on six separate occasions involving 10 different boxes between 1979 and 2000 (app. 5). Curiously, all but one of the nest-box changes by males occurred between 1979 and 1989; that is, prior to the major habitat destruction caused by Hurricane Hugo in 1989. Then, during the last decade of the study, it was not until the 2000 breeding season that the remaining male changed boxes. Moreover, the 2000 seasonal change was the only instance of an intraseasonal nest-box change, documenting for the first time in this study intraseasonal reproductive dispersal by male pearly-eyes.

To further explain appendix 5, a more indepth summary follows. An unknown-aged male (no. 9003) banded as an adult breeder at the onset of the study moved 300 m to a second box in its 7th breeding season. During the next five breeding seasons at his new box, male 9003 experienced a lower rate (42 percent) of productivity (fledging success) than he had at his original box (46 percent). Also in its 7th (1985) breeding season, a second unknown-aged male (no. 9030) left behind its second, 4-year-old (minimum-aged) mate and moved about 20 m away to a second box installed by another researcher conducting a separate study. Male 9030 returned to his original box and mate in 1986 when the independent research was completed and the postmove box was removed. It is interesting that male 9030 had left his second mate after four continuous seasons and a 36-percent fledging success overall to mate with a known-aged 3-year-old female banded as a nestling in 1982 and breeding for the first time in a newly erected thrasher box in 1985. The known-aged 3-year-old female nested in the box for only a single season, and her reproductive success was somewhat lower (33 percent) than that of the male's previous mate's. A third male (no. 7868) banded as an unknown-aged adult in 1980 nested for four seasons in the same box, but then prior to its 5th season moved to a second box about 100 m away. Male 7868 had three mates while nesting in his original box: one unknown-aged female during the 1980 breeding season, a 2-year-old (in 1981) female during the 1981 and 1982 seasons, and a third, unknown-aged female during the 1983 season. Male 7868 experienced a reproductive success rate of 39 percent overall in his original nest box. He remained in residence at his postmove box for the next six seasons before disappearing. In his postmove box, male 7868 had a single mate and experienced an overall average fledging success of 56 percent. This was the only instance of increased reproductive success for a male in a postmove box. In male 7868's original box, four of the six sources of lowered productivity involved possible female-related problems (congenital and behavioral), which might at least partially explain his nest box and mate change (app. 5). A fourth known-aged male (no. 7817) that had hatched in 1979 nested from 1982 to 1986. He had three mates in his original box: one during the 1982 and 1983 seasons, one during the 1984 season, and one during the 1985 and 1986 seasons. Male 7817 sired four clutches with his third mate, culminating in a 45-percent fledging success, and an overall fledging success of 41 percent with all three mates. Male 7817 changed boxes and mates before its 6th (1987) breeding season (although his third mate continued to breed there for the next two seasons) only to undergo a much lower reproductive success rate of 18 percent for the 12 clutches he sired in his postmove box before disappearing in 1992. The fifth and final instance involved a known-aged male (7497) hatched in 1993. He was not seen again until he nested 7 years later. Male 7497 sired but one clutch in December 1999 (initiating the 2000 breeding season) with an unknown-aged female and experienced a 33-percent fledging success. He then changed boxes and sired a second clutch in April 2000 with his new unknown-aged mate banded as an adult breeder in 1997. Male 7497 experienced a complete nesting failure in his postmove box. Curiously, his postmove box had a history of owl predation and usurpation for nesting. Moreover, all four nestlings disappeared and owl predation is suspected.

Interestingly, 80 percent of the males that changed boxes between seasons had suffered complete nest failures in their final nestings during previous seasons. Of 15 eggs laid during the last premove nestings in different seasons, only two fledglings were produced. Botfly ectoparasitism accounted for 53 percent (8 of 15) of the losses, whereas embryonic death, infertile eggs, human negligence in handling eggs, and missing eggs and chicks, each were responsible for single losses in the remaining five eggs.

To summarize, the overall (pre- and postmove) average reproductive success for the five males that changed nest boxes was 38 percent (app. 5). The males' average premove reproductive success was 40 percent; whereas the average postmove success rate was 30 percent. Only one of the five males (no. 7868) experienced an increase in productivity in its postmove box. The remaining four males suffered lower reproductive success as a consequence of changing boxes. The sampled population's overall fledging success between 1979 and 1997 was 35 percent. Therefore males that changed boxes actually had a higher fledging success (40 percent) than that of the general population before switching boxes. Their success rate in postmove boxes was below that of the populational average (30 percent vs. 35 percent, respectively).

Most males did *not* experience an increase in postmove productivity.

In conclusion, male breeders were highly nest-site persistent. The few males that underwent reproductive dispersal generally did not experience higher reproductive success. Consequently, although most moves followed previous nest failures, because males that changed boxes did not experience an elevated reproductive success, invoking the nest-failure hypothesis may be inappropriate because equal or lowered reproductive success in postmove boxes would be counter-selective. Although the sample size is small, these results may have relevance on a broader scale as shown by similar findings in other passerines. For example, in the United Kingdom, Harvey and Greenwood (1980) reported comparable results for a population of the great tit, a Palearctic migratory passerine under study for more than 30 years. Likewise, based on a 6-year study, Murphy (1996) reported similar findings for males of a Nearctic migratory passerine, the eastern kingbird (*Tyrannus tyrannus*).

Females Changing Nest Boxes

Prehurricane Disturbance Nest-Box Changes

For the first 10 years of the study leading up to Hurricane Hugo (1979 to 1989), only 7 percent (9 of 121) of the female breeders changed nest boxes on 12 separate occasions and occupied 16 different (pre- and postmove) boxes. In total, 126 nestings were involved, 27 in the original boxes and 99 in 9 postmove boxes (app. 5). The nine females that were forced to seek alternative boxes did so following usurpation of their nests by roosting owls (four individuals), climatic disturbance (3), interference competition (1), and botfly ectoparasitism (1). Four females (nos. 7809, 7721, 8986, and 9177) escaped predation by screech-owls but then were supplanted by them when the female owls usurped the boxes for roosting and nesting. Three females (nos. 0875, 9062, and 9086) were forced into alternative boxes after their original trees and boxes were destroyed by windstorms and heavy rains. The eighth resident female (no. 7816), a first-year breeder, was supplanted by a large, unbanded and very aggressive prospecting female. Numerous attacks and actual supplantings were observed. Before expulsion by the prospecting female, the first-time nester had laid two eggs and had successfully fledged both young in her original box. However, she failed to produce fledglings during the first season in her postmove box and averaged only 37 percent overall during the 4-year period she bred at her postmove box. Conversely, before disappearing, the very aggressive replacement female in the usurped box had an average fledging success of 58 percent over the next three seasons (67, 83, 0 percent, respectively). Finally, apparently in response to having suffered from the effects of heavy botfly ectoparasitism in her first box, the ninth female (no. 8930) moved to a second box and experienced a higher fledging success (from 0 to 32 percent). Her mate, however, remained at the pair's original box.

To summarize, prior to Hurricane Hugo, nine females that underwent reproductive dispersal had a fledging success rate of 41 percent before changing boxes, a much lower (27 percent) success rate in their postmove boxes, and a 33-percent success rate overall (average of pre- and postmove rates). Therefore, because the overall population fledging success rate was 40 percent prior to major habitat disturbance (January 1979 to August 1989), there is little compelling evidence to support the nest-failure hypothesis. Indeed, females experienced a fledging success 13 percent below the populational average in their postmove boxes.

Propensity for Posthurricane Nest-Box Changes

Many more females than males changed nest boxes over the course of the study, especially after Hurricane Hugo. Five females that survived 9 to 13 years changed boxes 1 to 6 times (avg. = 2.8), with the most numerous changes occurring after 1990, an opposite trend than that observed for males (app. 5). Because nest predation, competition for nest boxes, and botfly ectoparasitism increased following Hurricane Hugo, all the data from 1979 to 2000 were then analyzed to determine if these biological factors may influence the propensity of female thrashers to change nest boxes. However, because all but one of the 22 females that changed boxes between 1979 and 2000 did so during or before 1997, 8 predisturbance breeding seasons (1979 to 1988) were compared with 8 postdisturbance (1990 to 1997) seasons to achieve a better balance between the number of pre- and postdisturbance seasons (8 vs. 8, rather than 8 vs. 11, respectively). Overall, the sampled thrasher population attempted 650 nestings during 8 predisturbance breeding seasons between 1979 and 1988, and 693 nestings during the 8 postdisturbance seasons (1990 to 1997). In total, 27 of 42 available boxes (64 percent) were involved in reproductive dispersal between 1979 and 1997 (fig. 7.3). Of 137 banded females, 21 (15 percent) changed boxes on 36 separate occasions and attempted 265 nestings (109 in original boxes and 156 in postmove boxes). Comparing pre- and postdisturbance number of females changing boxes, there were more than twice as many (21 vs. 9) during the 8 breeding seasons following Hurricane Hugo than during the 8 predisturbance seasons. The number of different boxes used by females that changed boxes was 18 (pre- and postmove), and the number of postmove nest boxes involved was 15, not a marked increase (15 post- vs. 9 predisturbance). The number of postdisturbance changes tripled (36 vs. 12). The increase in the number of females that changed boxes and the number of boxes involved in the changes taking place after the disturbance were not significant at $\alpha = 0.05$ ($z = 1.77$; $P = 0.07$, and $z = 1.92$, $P = 0.06$, respectively). What was significant, however, was the increase in the **number** of changes (36 vs. 12) following the hurricane ($z = 2.24$, $P = 0.02$). One female (no. 7449) that bred for eight seasons following Hurricane Hugo (1990 to 1997) made five changes involving five boxes. Another female (no. 7541) nested in three different boxes within a single (1996) breeding season and changed boxes over three consecutive seasons. Although female 7541 nested in a single box during the 1997 breeding season, she nested in two different boxes in 1998 (not shown in app. 5) for a total of six different boxes in 3 years. Still, another female (7293) performed a "switchback" (original to auxiliary, and back to original box) within the same (1994) breeding season.

In the following discussion, the same female is often treated more than once because several of them laid multiple broods. Nest box changes by females often followed previous nesting failures. Female productivity between 1979 and 1997

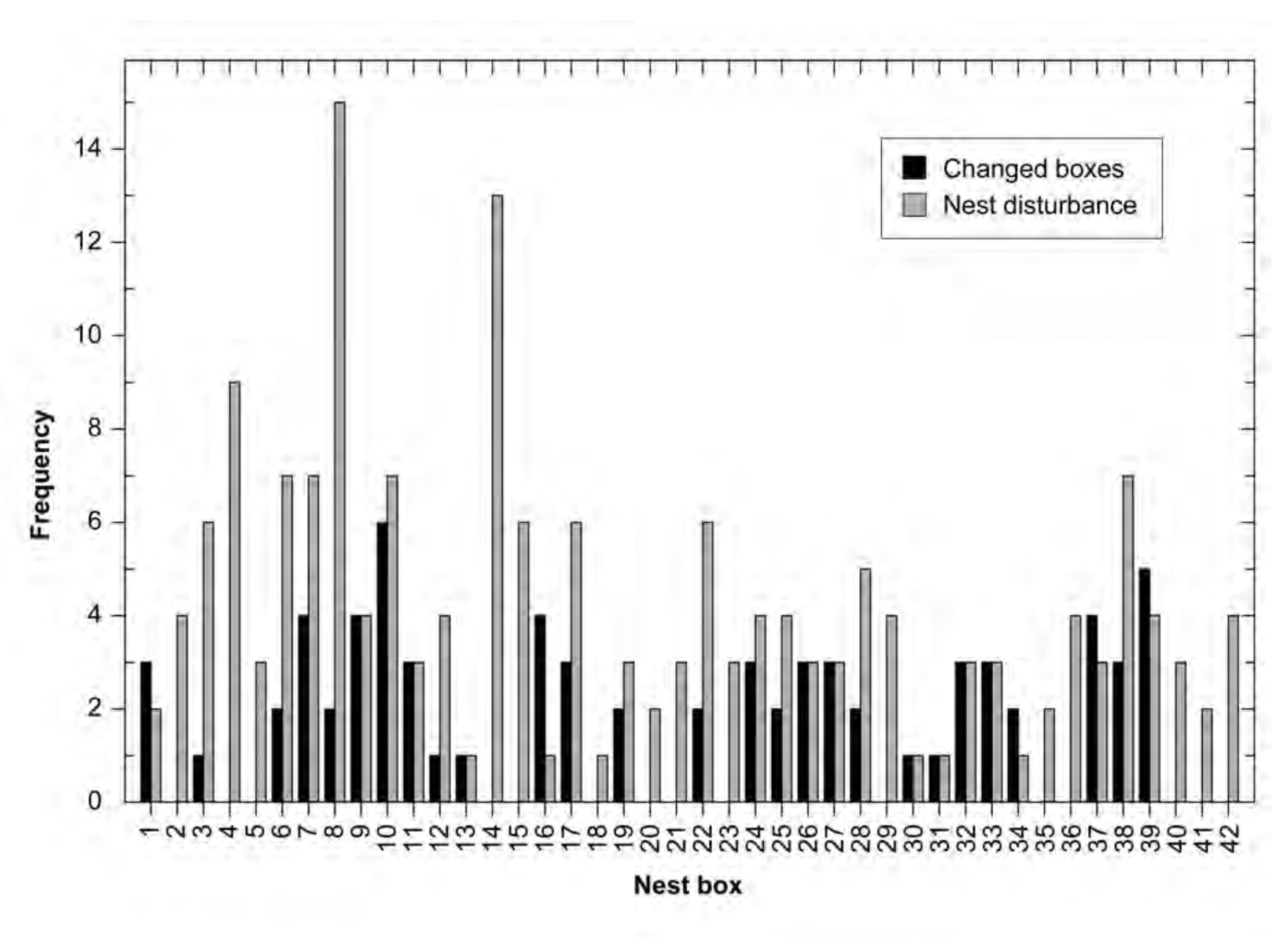

Figure 7.3—Number of nest boxes experiencing ecologically induced disturbances (mostly nest predation and ectoparasitism), and those involved in reproductive dispersal by nesting adults over an 18-year period (1979 to 1997). All 42 boxes experienced disturbances and 27 boxes (64 percent) were involved in reproductive dispersal. Many factors, in addition to nest predation, parasitism, and environmental disturbances, as well as the consequential reproductive losses they produce, influence interbox movements by nesters. Such factors include the physical state, aggressiveness, and even age of the individuals involved in defending or usurping boxes.

increased in 14 postmove nestings involving 10 separate females and 11 different boxes. However, 10 females that changed boxes experienced a lower reproductive rate during 14 postmove nesting attempts. Moreover, 6 of 14 (43 percent) of the diminished productivities were complete nest failures (no fledglings). Even though seven females that changed boxes nine times experienced the same rate of reproductive success (no change) in their postmove boxes, eight of the nine pre- and postmove nesting attempts culminated in complete nest failures (app. 5).

Some form of ecological stress was documented at every box before the female made the change (fig. 7.3). Yet, the relationship between ecological stresses and nest-box changes is not strong ($r_s^2 = 0.02$; $P = 0.85$, Spearman Rank Order Correlation). Although no nest-box changes occurred at boxes not having suffered from some form of ecological stress, only 27 boxes were involved in female changes, whereas all boxes have experienced some form of ecological stress over the course of the study. Of the 20 biological and ecological factors lowering reproductive success in females that changed boxes, one source, namely botfly ectoparasitism, accounted for almost 60 percent of the total (see also Arendt 2000).

Interseasonal Nest-Box Changes

Following, are brief discussions of inter- and intraseasonal reproductive dispersal involving female breeders. As with males, many more females were involved in inter- rather than intraseasonal reproductive dispersal. Of the 21 females that changed nest boxes within and among breeding seasons between 1979 and 1997, 17 (81 percent) underwent 25 box changes between breeding seasons, 19 premove and 21 postmove boxes were involved (15 were used as both pre- and postmove boxes) (app. 5). Combining early- and late-season premove nestings, of 25 nesting attempts, only 5 were successful (at least 1 fledgling per nest). Similarly, of 80 eggs laid during the final nestings in the premove boxes, only 16 (20 percent) produced fledglings.

Females experienced higher reproductive success after interseasonal dispersal, i.e., in first nestings in postmove boxes the following breeding season.

Early-Season Final Nestings in Original Boxes

Between 1979 and 1997, four final premove nestings occurred before the populational median egg-laying date for their respective years, which ranged from March 9, 1991 to May 26, 1990 (both of these extreme median dates were affected by Hurricane Hugo). Of the four early-season premove nestings, the earliest lay date was March 3, 1993, the latest was May 2, 1986, and the average was April 2. Unexpectedly, three of the four premove nestings were successful (all nine eggs produced fledglings). In fact, of 13 eggs laid in early-season nests, only 4 (31 percent) did not produce fledglings. Four nestlings died of botfly ectoparasitism in the fourth early-season final nesting. Thus, early-season premove nestings resulted in a 69-percent fledging success, well above the overall populational average.

Late-Season Final Nestings in Original Boxes

Of the 25 final nestings taking place in premove boxes, 21 (84 percent) occurred after the populational median egg-laying date. The earliest lay date for late-season nests was May 11, 1993, the latest was July 11, 1990, and the average late-season egg-laying date was June 7. Fifteen females attempted 21 late-season premove nestings in 16 different boxes. Only 2 (10 percent) of the late-season premove nestings were successful. Similarly, fledging success was also a meager 10 percent in all late-season premove nests. Of 67 eggs laid, only 7 (10 percent) produced fledglings.

In reference to nesting stage at the time of nest failure, whereas no late-season premove nests were lost during the egg-laying stage, there was a propensity for losses in nests containing older chicks. Frequencies for the various nesting stages at the time of loss are as follows: egg laying (0), incubation (2), young chicks ≤10 days old (2), older chicks >10 days old (10). Eight biological and ecological factors caused the 60 egg losses and chick mortalities. As usual, the most prevalent source was botfly ectoparasitism. Forty-three chicks (72 percent) succumbed to ectoparasitism. Frequencies of the 7 sources contributing to the remaining 17 egg and chick losses are as follows: owl predation on chicks (7), pearly-eye predation on eggs (3), habitat-disturbance malnutrition (3), and one each from missing and infertile eggs, young and developed embryo deaths. That most late-season premove losses involved the death of nestlings heavily infested with botfly larvae suggests that philornid ectoparasitism may be the major causative factor prompting late-season nest-box changes in this thrasher population.

Interseasonal Reproductive Success of First Nestings in Postmove Boxes

Reproductive success was high in first postmove nestings occurring early in subsequent breeding seasons. Of 71 eggs laid, 42 (59 percent) produced fledglings. Of the 25 interseasonal first nestings, 17 (68 percent) were successful. Although most (n = 23) first postmove nestings (range: March 24 to July 4; avg. = April 22) occurred before the populational average median date in their respective years, two first postmove nestings occurred afterwards (1 in late April, just after the median lay date, and one in July—preceded by an owl nesting in the box). Thirty chicks fledged within 10 of the 25 first nestings, with another 12 chicks fledging from an additional 7 nests in which partial contents were lost. Eleven biological and ecological factors were responsible for the remaining 29 egg and chick losses. Because most first postmove nestings occurred early in the season before the botfly population exploded, botfly ectoparasitism lowered reproductive success by only about a third (10 of 29 losses). Frequencies of the remaining sources contributing to egg loss and chick mortality are as follows: owls eating chicks (4), human negligence handling eggs (4), female abandoning eggs (3), chicks missing (2), rat predation on chicks (1), pearly-eye predation on eggs (1), infertile egg (1), egg missing (1), young embryo death (1), and developed embryo death (1). Nesting stage frequencies were as follows: egg laying (1), incubation (0), young chicks ≤10 days old (3), and older chicks >10 days old (2).

Intraseasonal Nest-Box Changes

Between 1979 and 1997, only 9 females changed boxes 11 times within a given breeding season. In total, 31 clutches were attempted in 12 different boxes, 8 premove, and 9 postmove (5 boxes were involved in pre- and postmove nestings). Six of the 11 changes occurred in February and March of different years. All six premove clutches were considered early nestings because all took place before the populational median egg-laying date (usually April of each year). Five nest-box changes occurred in May of various years and, thus, those clutches were considered late-season premove nestings. From these limited data, there was no convincing evidence that either early or late nesting failures trigger within-season nest-box changes in this pearly-eye population. Furthermore, among the final premove nestings, there was no strong bias for moves during a particular nest stage. Nesting stage frequencies were as follows: egg laying (1), incubation (4), young chicks ≤10 days old (2), and older chicks >10 days old (1). Contrarily, combining "early" and "late" premove nestings, 8 of the 11 intraseasonal nest-box changes (73 percent) followed complete reproductive failure (total loss of nest contents). Only about a quarter (8 of 31) of the eggs laid in premove boxes resulted in fledglings. Of the 6 sources of reproductive losses (owls, rats, unknown predation, botfly ectoparasitism, and box usurpation by a more aggressive female), 7 of 11 (64 percent) of the instances involved nest predators: rat predation on eggs (3), owl predation on chicks (2), and missing eggs (2). Only one female changed boxes within the same season after losing an entire brood of three to botfly ectoparasitism. Quite unexpectedly, two females changed nest boxes after 100-percent success (three chicks fledged from each nest). These results suggest that nest failure may be a main factor in motivating female pearly-eyes to seek alternative nest sites **within** the same breeding season.

Intraseasonal Reproductive Success of First Nestings in Postmove Boxes

Most (9 of 11) first postmove nestings (range: March 24 to July 4; avg. = May 17) within the same breeding seasons were after the populational median egg-laying date. Contrary to the high reproductive success (59 percent) documented for first postmove nestings in **subsequent** breeding seasons, of the 11 first nestings in postmove boxes **within** breeding seasons, not a single nesting was successful. Of 35 eggs laid, mortality was 100 percent and was attributed to five biological and ecological factors. As expected, 77 percent of the losses were a result of botfly ectoparasitism. The remaining four sources of loss were attributed to owl predation on chicks (3), pearly-eye predation on eggs (3), hatching abnormality (1), and "no hatch" (reason unknown) (1). At the time of reproductive losses, most nests (7 of 11) were in the young chick stage (≤10 days old). Two nests each were in the incubation or older chick (>10 days old) stages.

In summary, within and between breeding seasons, female pearly-eyes often changed nest boxes after suffering previous nest failures caused by nest predators, competitors for nest sites, botfly ectoparasitism, and a host of other biological and ecological pressures, thus supporting the nest-failure, or predator-avoidance hypothesis (Darley et al. 1977, Greenwood and Harvey 1982, Jackson et al. 1989, Murphy 1996). However, by comparing not only the last nestings in premove boxes, but also the first nestings in postmove boxes (both within and between seasons), it was found that it is more advantageous for the female to postpone a move until after the close of a current season and then take up residency in a different box before, or at the onset of, the following breeding season. It is probably safe to conclude that one of the main reasons why many more females initiated nest-box changes **between** seasons, rather than **within**, is that they experience a greater incidence of botfly ectoparasitism late in the breeding season. Botfly ectoparasitism in this pearly-eye population may be the driving force selecting for interseasonal nest-box changes by females that have suffered lowered reproductive success in previous broods. The preference shown by both sexes for interseasonal (vs. intraseasonal) reproductive dispersal is also observed in other species, suggesting a higher cost to intraseasonal reproductive dispersers (González-Solis et al. 1999).

Phenology of Reproduction

Length of Breeding Seasons

The pearly-eye's normal 7- to 8-month breeding seasons are cut in half following devastating hurricanes.

Breeding seasons are generally longer in the tropics than in temperate regions (Arendt 2004a, Baker 1939). Not surprisingly, the pearly-eye is engaged in breeding for more than half of each calendar year, and virtually throughout the year following major habitat disturbances (fig. 7.4). The average length of 19 breeding seasons between 1979 and 2000 was 203 days, or almost 7 months (*SE* = 13.7; range: 75 to 322 days) (fig. 7.5). Consequently, thrashers have about 5 months (mean = 161 days; *SE* = 13.6; range: 44 to 263 days) to recrudesce reproductive organs and replenish depleted fat reserves (fig. 7.5). Prior to Hurricane Georges (September 21, 1998), the shortest breeding season (3.8 months) recorded between 1979 and 1998 occurred during the first (1990) breeding season following Hurricane Hugo. However, the first (1999) breeding season following the habitat devastation caused by Hurricane Georges lasted only 2.5 months, or about a month shorter than even the 1990 postdisturbance season following Hurricane Hugo.

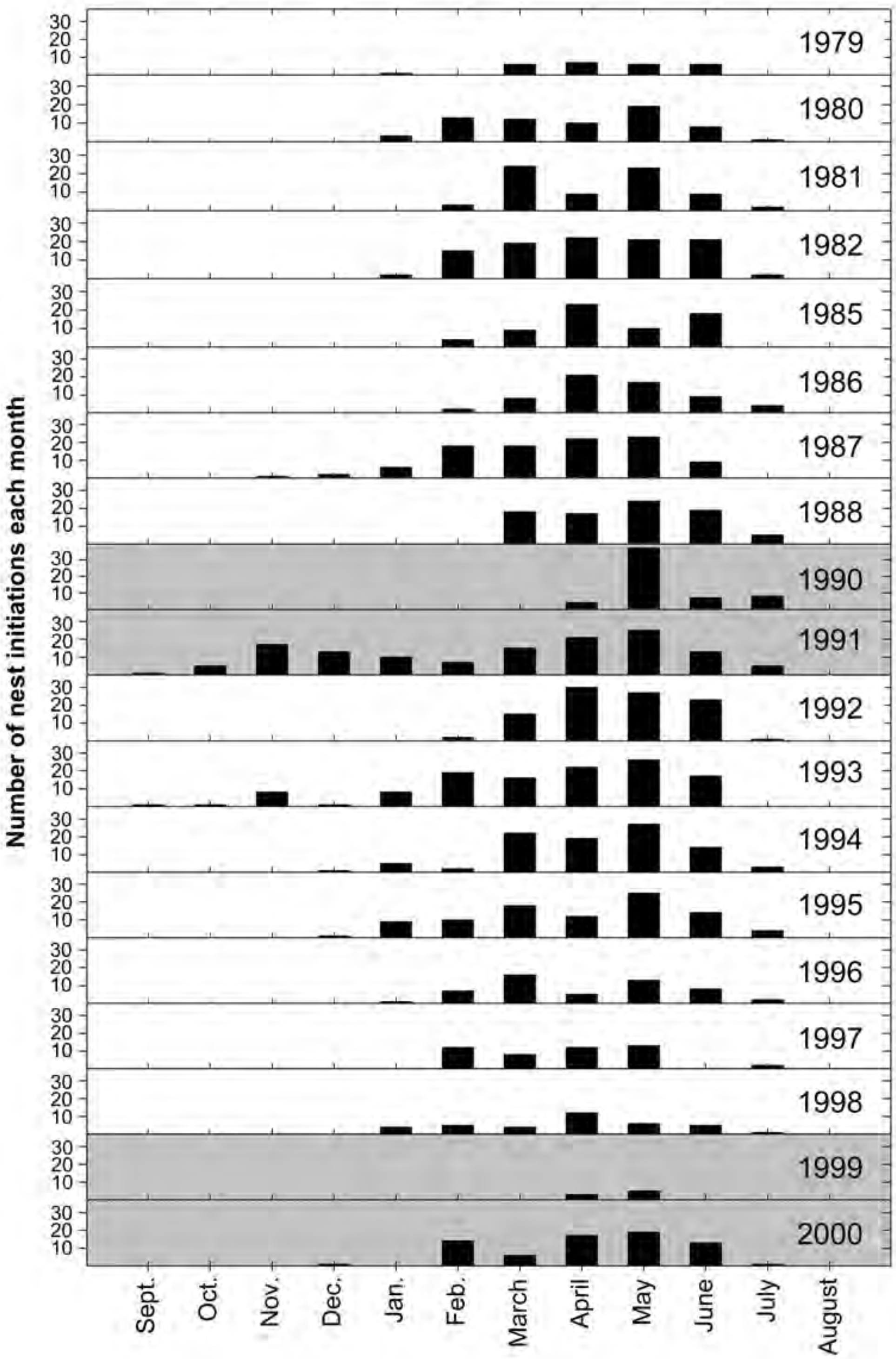

Figure 7.4—Distribution of the lay dates for first eggs of 592 initiatory clutches to show and compare monthly and yearly differences in the timing of each breeding season from 1979 to 2000. In most years, the bulk of the breeding occurred between March and June, with "attenuations" on either side as a consequence of habitat disturbances and age of each breeder. Hurricanes tend to suppress breeding during the first postdisturbance season and extend breeding during the second postdisturbance season (shaded areas). Older individuals tend to breed earlier in the season than first-time nesters, which often lay weeks and even months later.

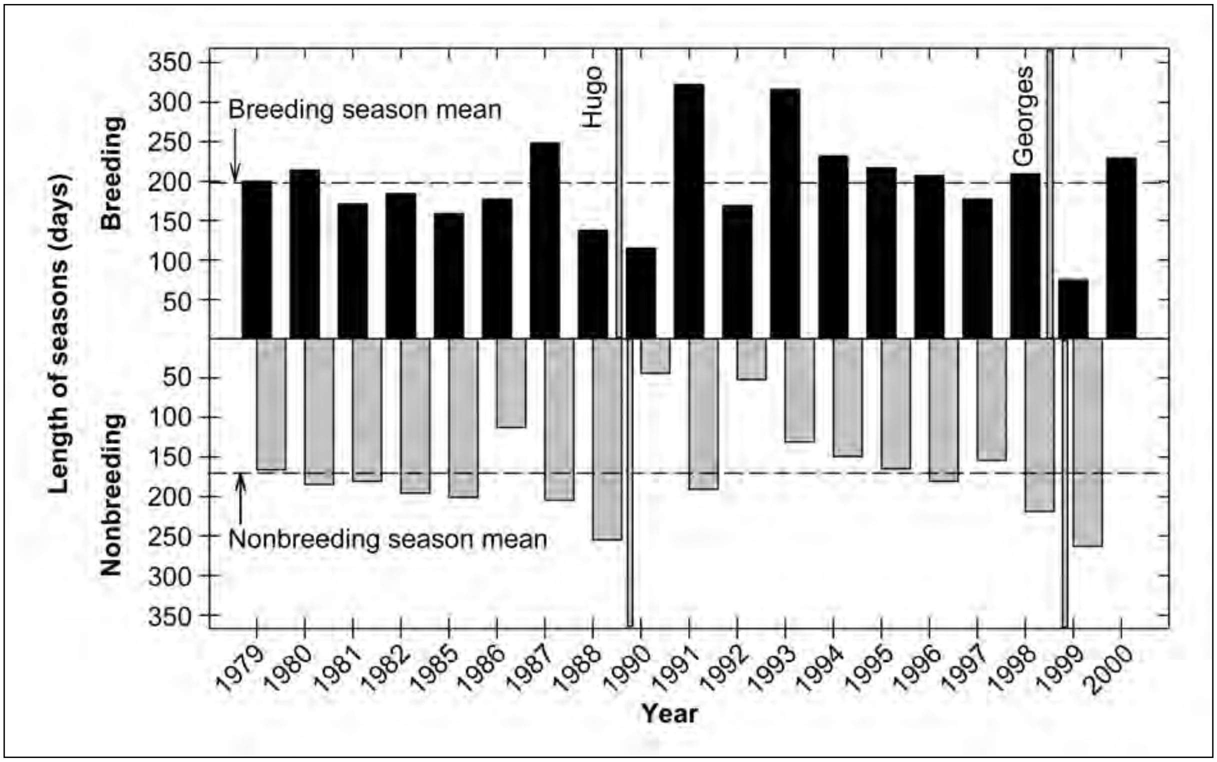

Figure 7.5—Comparison of the lengths (number of days) of 19 breeding seasons (black bars) and 18 nonbreeding seasons (gray bars) of a rain-forest population of the pearly-eyed thrasher from 1979 to 2000. Major habitat disturbances such as hurricanes significantly affected the general 7-month breeding and 5-month recovery cycles. Vertical shaded bars signify the passage of Hurricanes Hugo (1989) and Georges (1998).

However, unlike the second (1991) breeding season following Hurricane Hugo, which was the longest season on record (about 11 months), the second (2000) breeding season following Hurricane Georges was only the fifth longest on record, suggesting that the forest had not fully rebounded from the effects of Hurricane Hugo and several other less severe hurricanes passing through the region during the 9-year interim between 1990 and 1998. This suspicion is borne out by Thompson-Baranello (2000) who conducted a food resource and population modeling study of the Puerto Rican parrot within the Sierra de Luquillo following Hurricane Georges. Among other measures, Thompson-Baranello (2000) recorded the proportion of ripe palm infructescences produced from February 1999 to May 2000. He chose six study sites placed along an elevational gradient ranging from 350 m (El Verde) to 875 m (Mt. Britton). Two study sites were located in the Icacos Valley at 650 and 725 m, thus including the main thrasher study area. At all six sites, by June 1999 the proportion of ripe palm infructescences plummeted from between 0.4 and 0.6 percent to none with ripe fruit. No palm fruits were produced until December 1999 and, even then, production remained below the previous 0.4 to 0.6 percent levels until March 2000. Furthermore, his study documented that not only were the numbers of sierra palm fruits per infructescence reduced, so was fruit size, thus further limiting the pearly-eye's food intake and increasing the level of energy expenditure necessary to meet nutritional demands.

Length of Nonbreeding Seasons

The shortest nonbreeding season (1.5 months) occurred between the first (1990) and second (1991) breeding seasons following Hurricane Hugo. Conversely, and offering even more proof that the forest indeed has not recovered from the effects of the more frequent and intense hurricanes passing through or just off the coast of Puerto Rico in recent years, is the fact that instead of being the shortest, or even one of the shortest, nonbreeding seasons on record, the recrudescent period between the first (1999) and second (2000) breeding season following Hurricane Georges was in fact the longest thus far documented (263 days). It will be interesting to see what transpires should Puerto Rico suffer another "direct hit" by a major hurricane in the next few years.

Excluding from the analyses the breeding seasons most affected by Hurricane Hugo (1990 and 1991 seasons), the longest remaining breeding season (about 8 months) was shorter by almost 3 months. Similarly, the shortest remaining nonbreeding season (about 4 months) was increased by about 2.5 months. To appreciate the significance of the effects of Hurricane Hugo on the duration of the pearly-eye's breeding and nonbreeding seasons, compare the 1990 and 1991 results to all other years in figures 7.4 and 7.5.

In summary, the decimation of the sierra palm fruit crop following Hurricane Georges and the virtual absence of fruit for more than 6 months prior to the 2000 breeding season undoubtedly were prime factors influencing the pearly-eye's prolonged recrudescence period following Hurricane Georges. Likewise, the thrasher's poor reproductive performance during the second postdisturbance breeding season can also be attributed to the food shortage. Despite the synergistic effects of two major hurricanes occurring over a relatively brief period, the greatly extended second (1991) post-Hurricane Hugo breeding season lasting for almost a year clearly shows that the pearly-eye is a true avian supertramp and is able to respond immediately and prolifically to major habitat disturbances, thus validating the predictions of the supertramp theory.

Even the reproductively prolific pearly-eye cannot defy the synergistic effects on food resources caused by "back-to-back" major hurricanes.

Incubation Period in Relation to Adult Body Mass

As a general rule, a 10-fold increase in body mass is associated with a 46-percent increase in incubation time (Rahn et al. 1975). For the pearly-eye, I calculated the predicted incubation period $I = 9.105*B^{0.167}$, where B is body mass (Rahn et al. 1975). Substituting 112 g for B (the average body mass of rain-forest females), the predicted incubation period would be about 20 days. Because the pearly-eye's observed incubation period is about 14 days, or almost a week shorter than predicted, one could conclude that it has reduced the incubation period to increase reproductive output. However, it is noteworthy that rapid recycling (repeat breeding) as an adaptation to maximize reproductive yield hypothesized for the pearly-eye would be falsified if clutch size compensated for egg size (compare Smith and Fretwell 1974). In support of the notion that the pearly-eye has indeed adopted a short incubation period to increase its reproductive yield, with the exception of one-egg clutches appearing just after major habitat disturbances, its clutch size remained fairly static (modal clutch of three eggs) throughout each season for more than 20 years (see below). In fact, the intraseasonal static clutch size observed in the pearly-eye is contrary to birds in general as clutch size in most species declines with each subsequent nesting (Rowe et al. 1994). Therefore, the rapid recycling adaptation hypothesis remains a strong contender in selecting for short incubation periods in this species.

Number and Timing of Clutches and Egg Deposition Dates

Timing of the breeding seasons differed greatly among years.

The pearly-eye attempts one to six clutches per season. From the onset of the study in 1979 to the close of the 2000 breeding season, 1,386 successful clutches (592 initial and 794 subsequent clutches) were laid by 143 banded females (n = 1,041 clutches) and a minimum of 39 unbanded females (n = 345 clutches). The average number of clutches per female per season was 2.35 (median = 2.37; mode = 2; *SE* = 0.04; range: 1 to 6). Egg deposition dates were used to quantitatively compare the timing of each of the 19 breeding seasons. In the statistical analyses, only first eggs of initiatory clutches were used to evaluate seasonal patterns and yearly differences. The timing of the breeding seasons differed greatly among years (table 7.1 and fig. 7.6), and the effects of Hurricane Hugo had a significant impact on the temporal aspects of egg deposition (K-W ANOVA: $H = 195.6$; df = 17; $P < 0.001$). Egg deposition was significantly delayed in 1990 and advanced in 1991 (All pair-wise multiple comparison procedures, Dunn's Method: $P < 0.05$ in all but two of the 171 2-year comparisons). Even with the two hurricane-affected (1990 and 1991) breeding seasons eliminated from the analyses, all but 4 of the 136 comparisons were significant (K-W ANOVA: $H = 96.4$; df = 15; $P < 0.001$). In contrast to the grossly extended second (1991) breeding season following Hurricane Hugo that depicts a rapid recovery by the pearly-eye, the second (2000) breeding season following Hurricane Georges lasted only about a month longer than disturbance-free breeding seasons (fig. 7.6), which suggests

Table 7.1—Descriptive statistics for egg deposition dates based on first eggs of initiatory clutches (n = 592) between 1979 and 2000[a]

Year	N	Mid-season[b] lay date	Mean	Percentiles	
				25%	75%
1979	15	March 30	March 29	March 22	April 10
1980	25	February 19	February 26	February 7	March 7
1981	27	March 21	March 17	March 13	March 24
1982	38	March 9	March 12	February 22	March 29
1985	31	April 7	March 31	March 11	April 18
1986	33	April 5	April 4	March 25	April 8
1987	37	February 28	March 2	February 8	March 27
1988	34	April 1	April 19	March 26	April 12
1990[c]	39	May 16[c]	May 14[c]	May 10[c]	May 19c
1991[c]	41	November 7[c]	September 2[c]	April 27[c]	November 26[c]
1992	41	April 2	March 31	March 17	April 9
1993	36	March 20	May 6	February 15	June 21
1994	38	March 17	March 27	March 4	April 11
1995	35	February 21	March 7	January 31	March 12
1996	33	March 15	March 17	February 25	March 26
1997	27	March 15	March 24	February 20	April 11
1998	24	March 22	March 21	February 15	April 26
1999[c]	8	May 4[c]	May 4[c]	April 16[c]	May 18[c]
2000[c]	30	April 5[c]	March 26[c]	February 11[c]	April 30[c]

[a] Tabular entries in columns 3–6 are based on Julian calendar dates (365 days per year).

[b] Mid-season lay dates are the median dates.

[c] Nesting affected by hurricane.

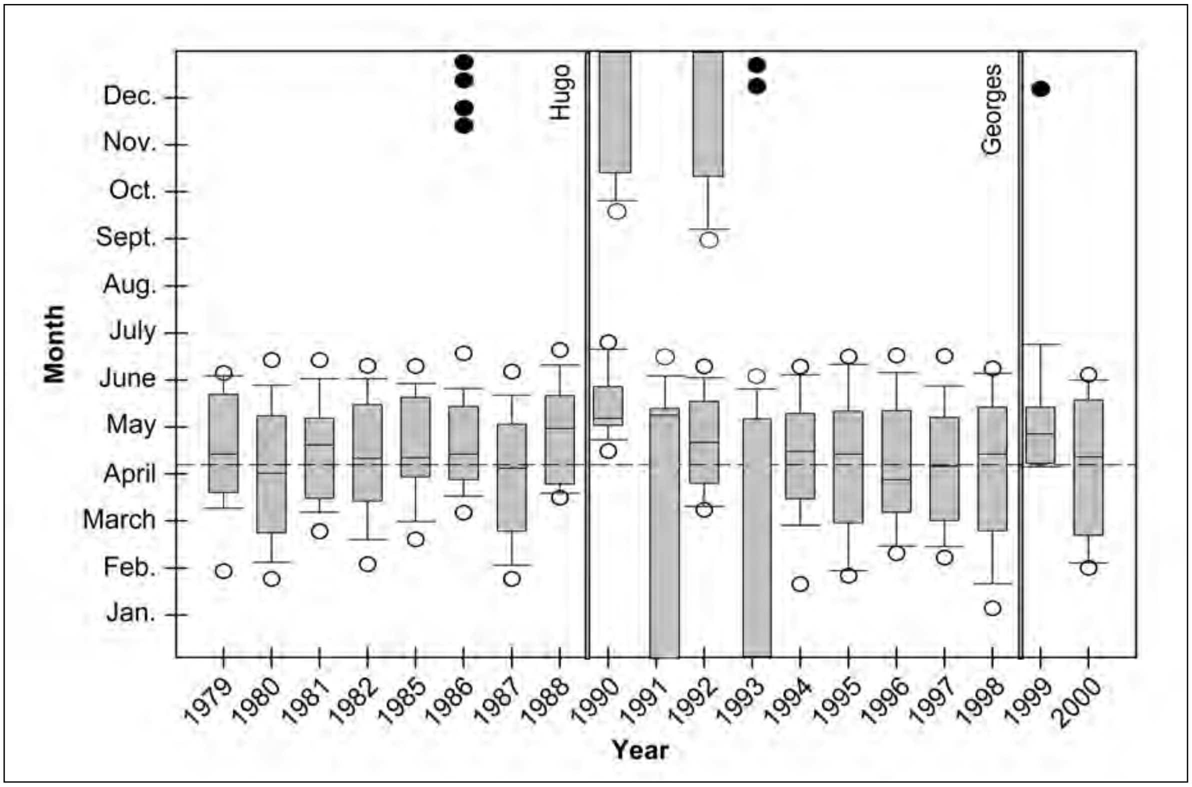

Figure 7.6—Distribution of 19 breeding seasons between 1979 and 2000. The passage of Hurricanes Hugo (1989) and Georges (1998) are represented by the vertical shaded bars. Black circles denote initiation of a single clutch. Box-plot parameters are defined in fig. 4.6.

that two major hurricanes within a 9-year period did not allow this rain-forest population of the pearly-eyed thrasher to recover as quickly as it might given longer interdisturbance intervals. The 1993 breeding season is the second most extensive on record owing to 11 older females that bred between September and December 1992, thus expanding it to almost a full year.

All clutches were then combined to examine the pearly-eye's overall egg-laying pattern. Eggs have been recorded in every month except August (fig. 7.7). However, there is a strong egg-laying "peak" that occurs from April to May, depending on the year. Whereas March is the modal egg-laying month, and no prehurricane Hugo (1989) or Georges (1998) median lay dates preceded or succeeded March by more than a month, the first postdisturbance breeding season median lay date was postponed 2 months after both hurricanes, and the second was advanced by 4 months after Hurricane Hugo.

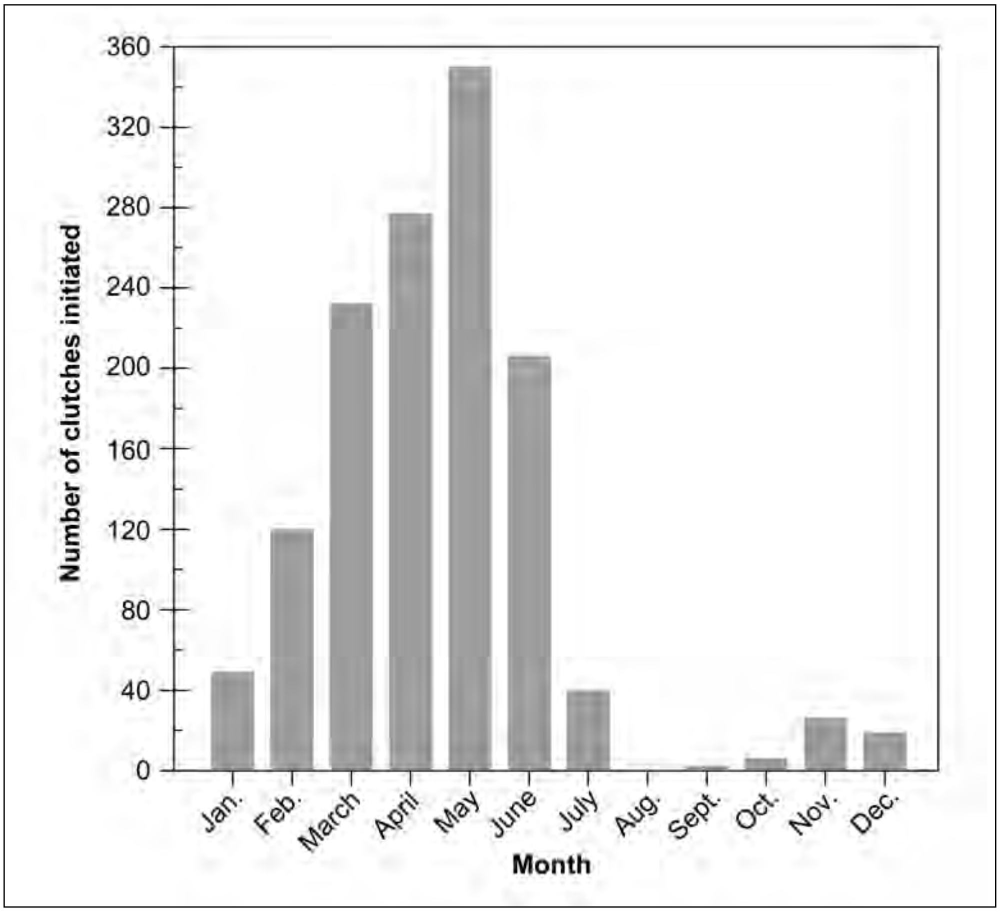

Figure 7.7—Monthly distribution of 1,386 clutches (order and type combined) initiated by 143 banded and at least 39 unbanded females over 19 breeding seasons between 1979 and 2000. The core of the pearly-eye's reproductive period encompasses March to June, with less breeding taking place outside of this 4-month period. Timing of breeding depends on several female-related factors in addition to rainfall, consequential fruiting, elevated arthropod and small vertebrate populations, and several other ecological and environmental factors.

To exemplify yearly differences in the timing of egg deposition and thus breeding season variation, sequential clutches were separated and compared among years. The average timing of all clutches combined is mid-April, and that of first clutches is mid-March, whereas most second clutches are laid in May, followed by third and fourth clutches in June, and finally fifth and sixth clutches from June into July. Hurricane Hugo had the greatest impact on egg deposition and therefore seasonal variation (fig. 7.8). Following the storm, most egg laying was suppressed until May, with a lesser peak again in November of the same year. All but four clutches laid between September and December over the entirety of the study pertain to the 1991 breeding season. Egg laying and the timing of breeding returned to predisturbance levels by the third postdisturbance breeding season. Nevertheless, postdisturbance variance about the yearly means tended to be greater than that experienced in predisturbance years. This pattern is similar to one found in a related fruit phenology study within the forest (Wunderle 1999). Whereas predisturbance fruit production followed a fairly consistent cyclic pattern with major monthly oscillations, the pattern disappeared following Hurricane Hugo when annual fruiting shifted out of phase, was suppressed (or both), and individual trees began producing fruit more erratically throughout the year (Wunderle 1999: fig. 1). Thrashers, and other frugivorous birds such as the parrot (see Meyers et al. 1993, Vilella and Arnizaut 1994), took advantage of this extended production period, thus laying multiple clutches over a wider monthly span (figs. 7.8 and 7.9). This response to fruit abundance is common among frugivores, granivores, and even insectivores, and adds credence to the belief that reserve proteins in breeders is often the proximate factor controlling the timing of breeding, brood spacing, and successive brood sizes, as well as immature and adult survivorship (Jones and Ward 1976, Lemon 1993, Murphy et al. 2000). In dry and mesic habitats, some passerines are able to produce as many as six (MacKay 1970, Woodworth 1995) and even seven (Gibbs et al. 1984) broods in a single season, especially during unusually wet years when more food is available. One must not forget, however, to consider endogenous circannual mechanisms, which are paramount in governing the reproductive timing of tropical organisms (Gwinner and Dittami 1990).

Over the breadth of this study, eggs were laid from September to July (fig. 7.4a). Most initiatory clutches (n = 592) were laid between February and April (fig. 7.9b). However, initiatory clutches have been recorded from November to June over a span of eight breeding seasons prior to Hurricanes Hugo (1989) and Georges (1998), and from September to July over a period of 9 seasons following Hurricane Hugo. There have been as many as 7 months between initiatory clutches within any given season, and 9 months over the 19 seasons (table 7.2). Second clutches (n = 458),

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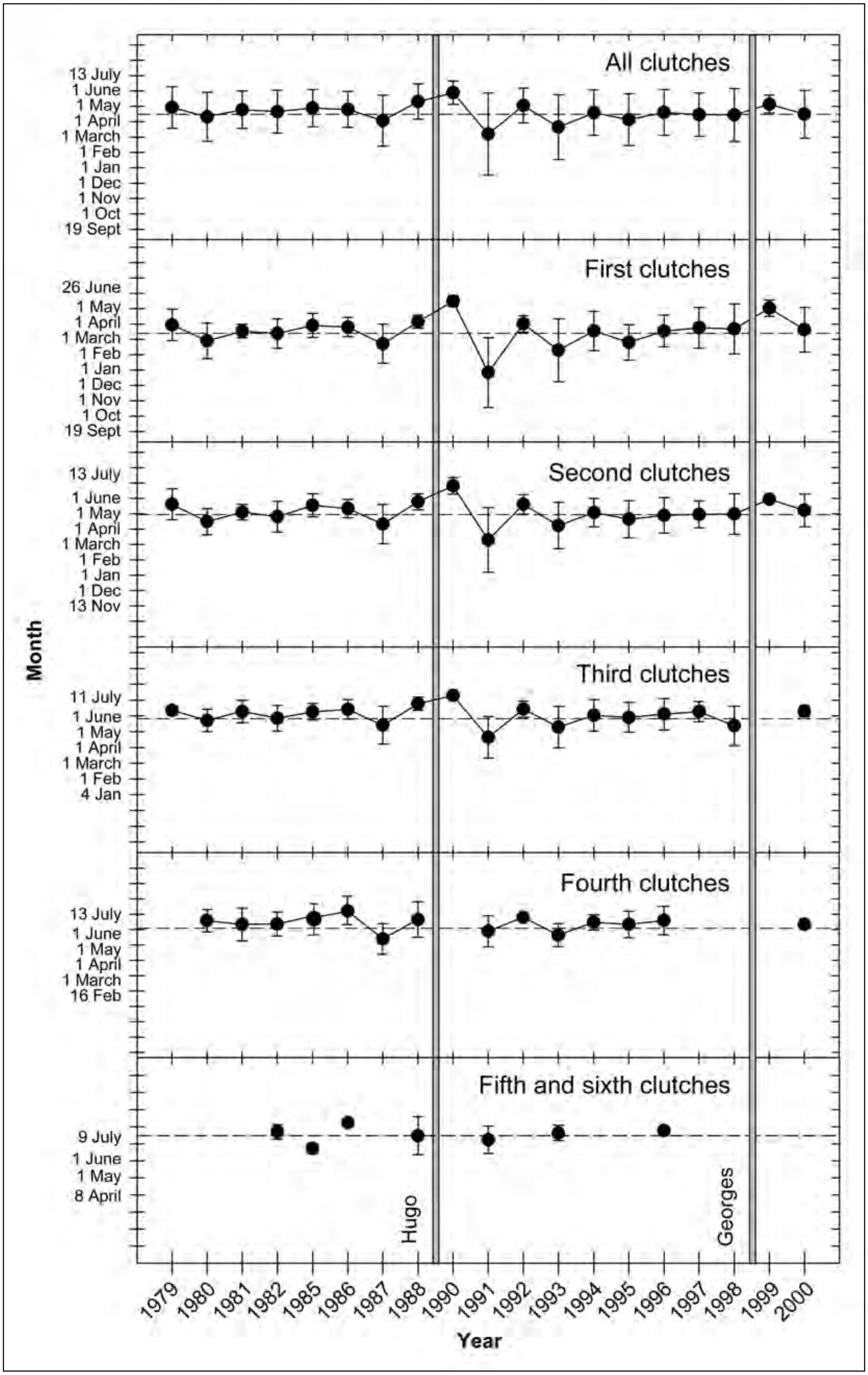

Figure 7.8—Range and average dates of egg deposition of 1,327 clutches for 19 breeding seasons between 1979 and 2000. Hurricanes Hugo and Georges (represented by the two shaded vertical bars) had the greatest impact on the timing and production of clutches. Following Hurricane Hugo, note the extreme departure from the overall average for the study (plot-wide, horizontal dashed line) in the first two postdisturbance (1990 and 1991) breeding seasons. Although similar, this pattern was less dramatic following Hurricane Georges, after which very few thrashers nested during the first two (1999 and 2000) postdisturbance seasons.

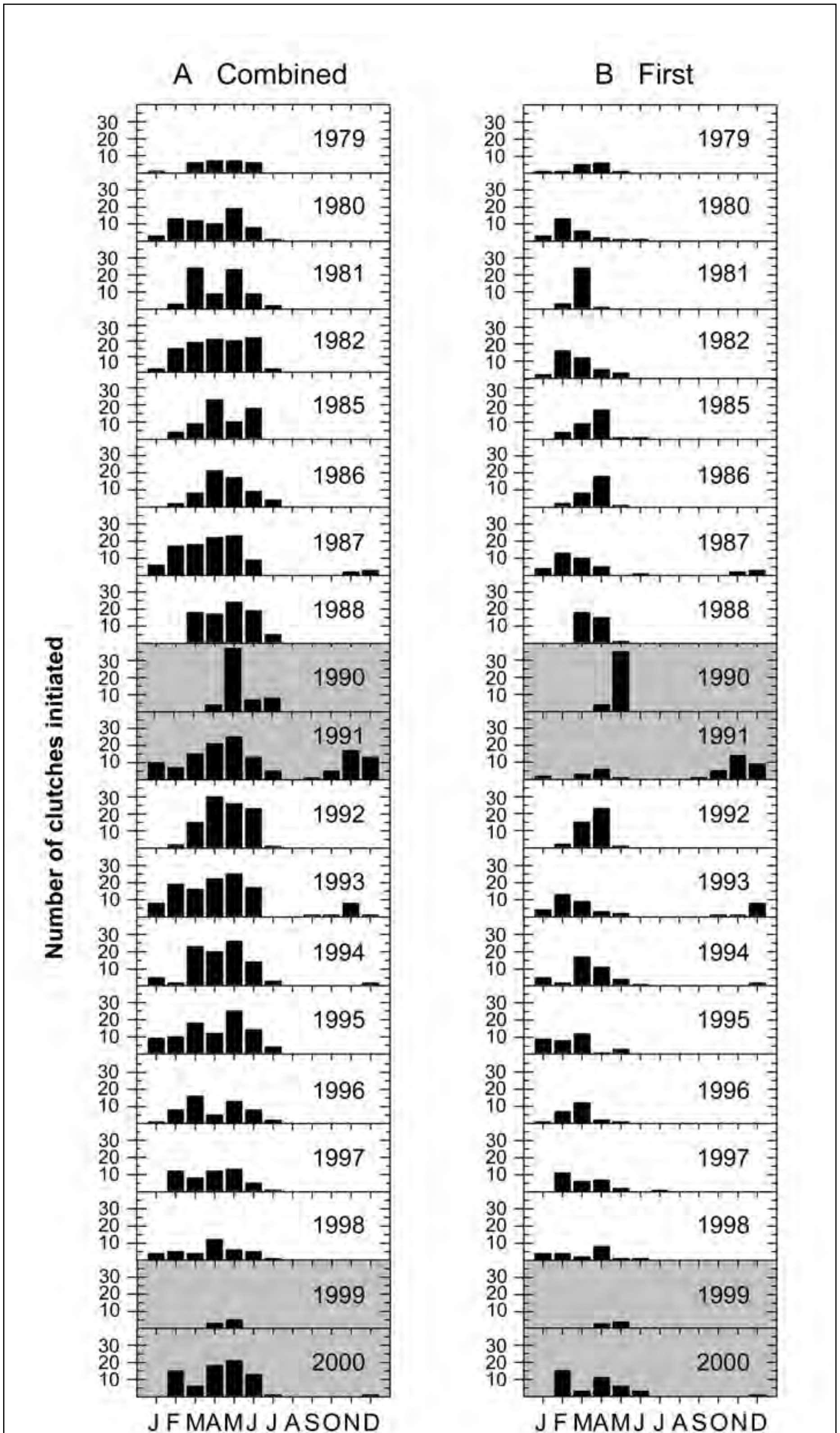

Figure 7.9—Monthly distributions of 1,327 multiple clutches (A–F), including replacements (unshaded bars), laid by banded female thrashers during 19 breeding seasons from 1979 to 2000. Fifth and sixth clutches (F) are combined because so few were laid. The crosshatched bars (May 1991 and June of 1993, 1995) designate the three sixth-replacement clutches (F) recorded from 1979 through the 2000 breeding season. Excluding the four shaded hurricane-impacted (1990–1991 and 1999–2000) breeding seasons, in general, combined clutches and first through fourth clutches show an expected normal distribution throughout the years and within each season. However, the curves are flatter and the "tails" more attenuated following Hurricanes Hugo and Georges as a result of more erratic fruit production in the forest following the disturbance.

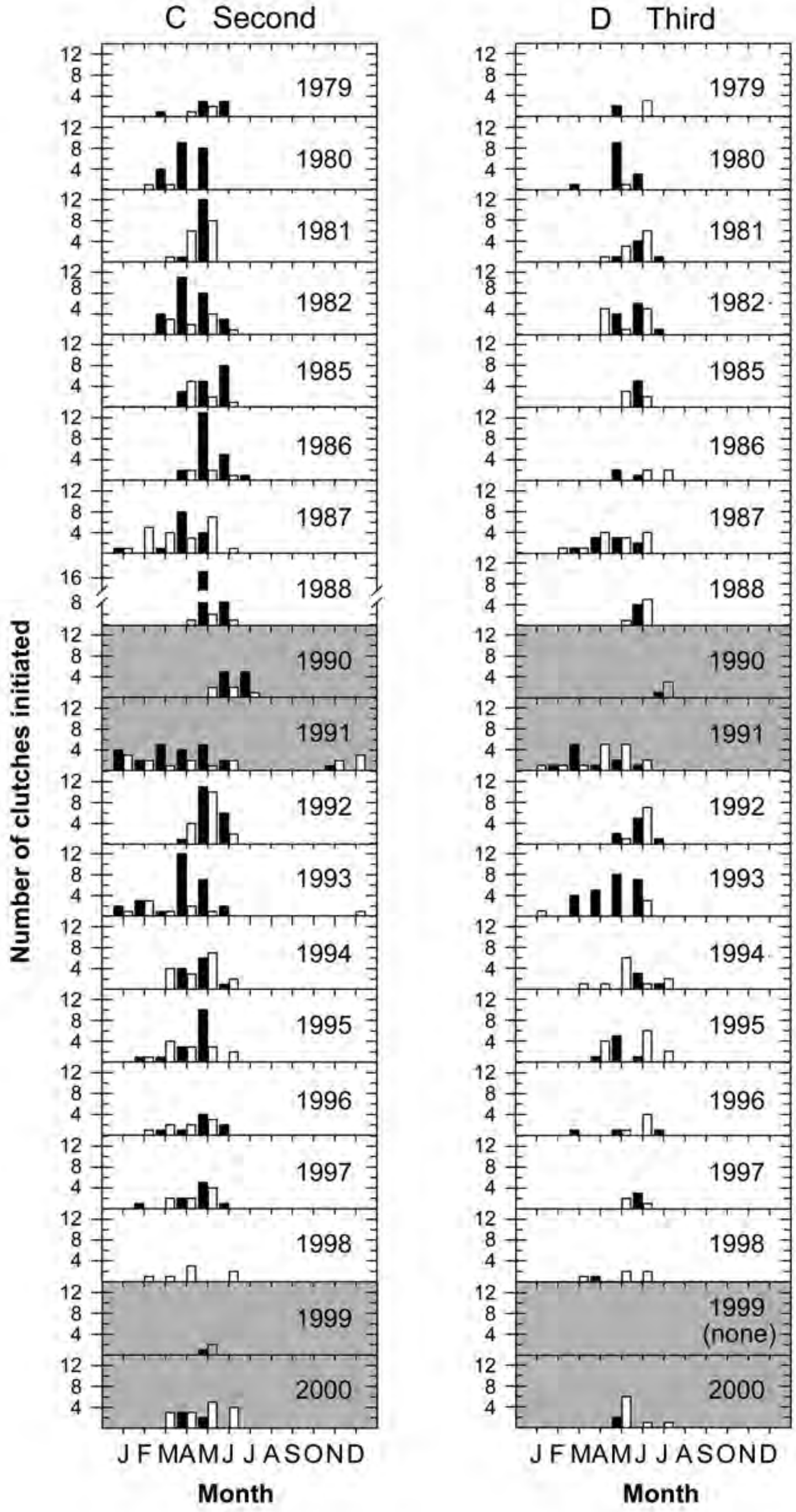

Figure 7.9—Continued.

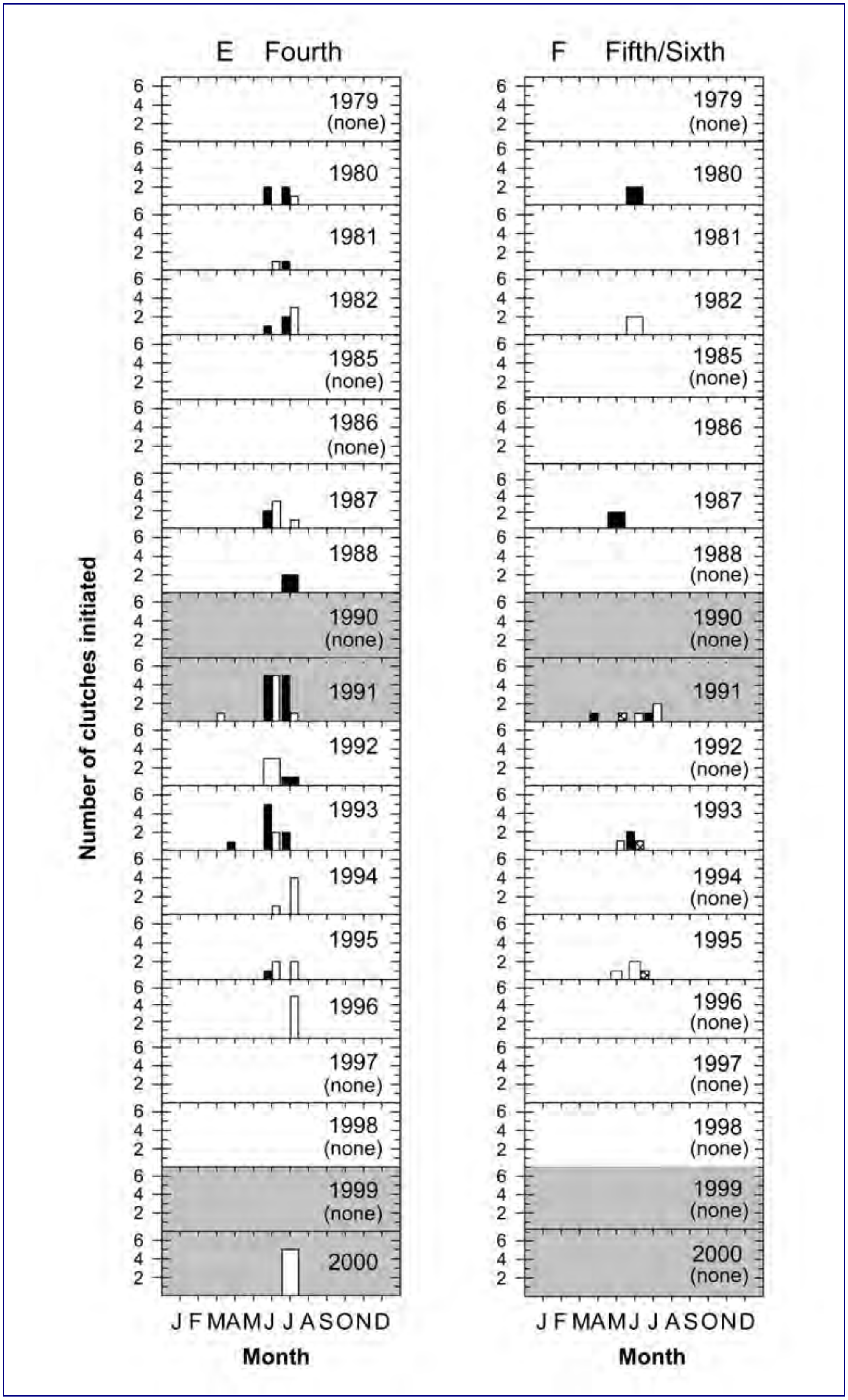

Figure 7.9—Continued.

including 258 that followed successful initiatory clutches and 200 replacement clutches (following complete failure of the first clutch, i.e., not a single fledging), have been recorded from January to July prior to Hurricane Hugo, and from November to July thereafter (fig. 7.9b). Third clutches (n = 242), including 102 following successful second clutches and 140 replacements, have been recorded from February to July before Hurricane Hugo, and from December to July subsequently. However, most third clutches are laid in May and June (fig. 7.9c). It is also noteworthy that but a single third clutch was initiated in the first (1990) breeding season following Hurricane Hugo. Naturally occurring fourth clutches were not common. Of the 74 fourth clutches recorded between 1979 and 2000, only 29 (39 percent) followed successful third nestings, whereas 45 (61 percent) of the fourth clutches were replacement clutches (table 7.2 and fig. 7.9d). Prior to Hurricane Hugo, most fourth clutches, including replacements, were laid in June (range from May to July). Only two clutches (both replacements), one each in March and April of 1987, were laid prior to the normal May to July range. Following the storm, only two fourth clutches (both were replacements, one each in February and March) were laid prior to the normal period from May to July. Only 17 fifth clutches (11 of which occurred following Hurricane Hugo) have been documented, ranging from May to June before the storm, and April to July thereafter (fig. 7.9e). Whereas 60 percent of the prehurricane fifth clutches followed successful fourth clutches, only 18 percent of the eight postdisturbance fifth clutches followed successful fourth clutches. The average age of the 17 females that laid fifth clutches was 4 years (median = 3; mode = 2; *SD* = ±2.62; range: 1 to 9). Only three sixth clutches—one in May (May 21, 1991) and two in June (June 6, 1993, and June 30, 1995)—have been documented, all three of which were laid 2 to 6 years following Hurricane Hugo and were replacement clutches for previous nesting attempts that

Table 7.2—Descriptive statistics of egg-laying dates for 1,386 clutches laid by banded and unbanded females between 1979 and 2000

	Egg-laying dates for respective clutch numbers						
Statistic	Combined (1,386)[a]	First (592)	Second (458)	Third (242)	Fourth (74)	Fifth (17)	Sixth (3)
Mean	April 16	March 14	April 27	May 23	June 2	June 13	June 9
Median	April 23	March 22	May 4	May 31	June 1	June 20	June 6
25th percentile	March 20	Feb. 19	April 9	May 5	May 16	May 30	May 25
75th percentile	May 24	April 12	May 23	June 17	June 23	July 2	June 24
Earliest	Sept. 19	Sept. 19	Nov. 13	Dec. 20	Feb. 16	April 8	May 21
Latest	July 18	July 5	July 14	July 18	July 13	July 9	June 30

[a] Numbers in parentheses under clutch numbers are sample sizes.

had failed in the egg stage (fig. 7.9f). Two of the three sixth clutches were laid by the same female (min. of 7 years old in 1991 and 9 years old in 1993). The third 6th clutch was laid by a (min.) 2-year-old female.

Age of Female Breeders and the Onset of Egg Laying

A general trend among birds is that of older females initiating the breeding season and yearling females laying their initiatory clutches often several weeks, or even months, later (Askenmo and Unger 1986, Cichoń 1992, Clutton-Brock 1988, Newton 1989). In the Caribbean, this trend has been documented in a D-Tramp, the bananaquit (chapter 2 and app. 1, and Wunderle 1982). In the present study, there was also an inverse correlation between female age and commencement of egg laying, with older nesters laying as early as October (even in September, two seasons following Hurricane Hugo) and first-time breeders not laying until late May to June when they were at least 9 months old. The correlation between age and lay date was not significant for known-aged females, possibly owing to the small sample size (n = 29 first clutches, $r_s{}^2 = -0.19$; $P = 0.35$). It was significant, however, among the more numerous (n = 126) minimum-aged females (n = 592 first clutches: $r_s{}^2 = -0.48$; $P = 0.04$). Although the current sample size is too small to speculate for the entire population, very old females (>10 years old) in this study reverted to nesting later in the season (March to April) and laid fewer (1 to 2 vs. 3 to 4) clutches in the last years that they were observed nesting (see also Dhondt 1985; and Bureš and Král 1995, for similar results in two other passerines, respectively, the great tit and collared flycatcher, *Ficedula albicollis*). Nonetheless, major habitat disturbances can cause females of all ages to synchronize the timing of egg deposition. As an example, during the second (1991) post-Hurricane Hugo season, 29 females (constituting 66 percent of the nesters and several age groups) laid before January. Conversely, there were only four documented instances of pre-January egg laying during eight seasons prior to Hurricane Hugo. In 1986, 3 years prior to the storm, four older females (only 10 percent of the nesters) laid in November and December.

Older pearly-eye females bred (often months earlier) than first-time breeders, except following major habitat disturbances, after which breeding was synchronized across all age groups.

Most birds exhibit age-dependent survival and reproductive traits. Even experimental manipulations of food, predation pressure, and breeding experience do not usually remove age effects (Martin 1995). It is noteworthy that the pearly-eyed thrasher is an obvious exception to the tenet that age at reproductive maturity increases dramatically with increasing adult survival rate (Ricklefs 2000a). Although females nest at less than a year old, the pearly-eye has a prolonged lifespan. This is yet another preadaptation of the pearly-eyed thrasher to the supertramp reproductive strategy.

Reproductive Recycling

Just as might be expected of a supertramp, the pearly-eye has been shown to be a prolific breeder, laying as many as six clutches within a single breeding season, with most seasons lasting more than half a calendar year. As an extreme, one breeding season following a major habitat disturbance lasted 11 months. And yet from a population perspective, and more germane still to the supertramp life-history strategy, is the pearly-eye's ability to recycle rapidly, especially when losses have occurred during previous breeding attempts.

Comparison of Clutch Types

A species capable of laying six clutches within a single season has 16 possible clutch types, i.e., the initial nesting potentially followed by five nestings succeeding previously successful clutches (at least one nestling had to have fledged in a previous nesting attempt); and a second potential for 10 replacement clutch types, two (1 replacement each for previous nestings that failed in either the egg or chick stage) for each of the 5 subsequent clutches following initial nestings. In the graphs corresponding to the discussion that follows, initiatory clutches ("**F**irst nestings") are labeled **F**1; each of the four potential clutch types following "**S**uccessful clutches" are labeled **S**2 through **S**5. No sixth clutch (**S**6) following a **successful** fifth clutch has been recorded. Only three replacement sixth clutches have been recorded. "**R**eplacement clutches" that follow nesting attempts that failed in the "**E**gg stage" are labeled **R**E2 through **R**E6, whereas those that represent replacements for nestings that failed in the "**C**hick stage" are labeled **R**C2 through **R**C5 (no **R**C6 clutch type has yet been documented).

Of 1,386 clutches laid between 1979 and 2000, 14 of the possible 16 clutch types attributed to 143 banded females and a minimum of 39 unbanded females have been documented (fig. 7.10). Overall, 592 first clutches (F1) were laid. Only 17 banded females nested but once during the study. Moreover, only 79 single, within-season nesting attempts involving 68 females were recorded (a few females laid single clutches in two or more seasons). Of the 79 within-season single nesting attempts recorded, 28 (35 percent) occurred in the first (1990) post-Hurricane Hugo breeding season. The number of single, within-season nesting attempts dropped to 51 when the hurricane-affected (1990) breeding season was removed from the analyses. The average number of single nesting attempts (excluding "problem" nests, such as those depredated) per breeding season (n = 19 seasons) was 7.3 when the effects of Hurricane Hugo were included, and 5.2 excluding the storm's impact. Of 143 banded females, 132 (92 percent) were involved in 794 renesting attempts (second and subsequent clutches, including replacements). The

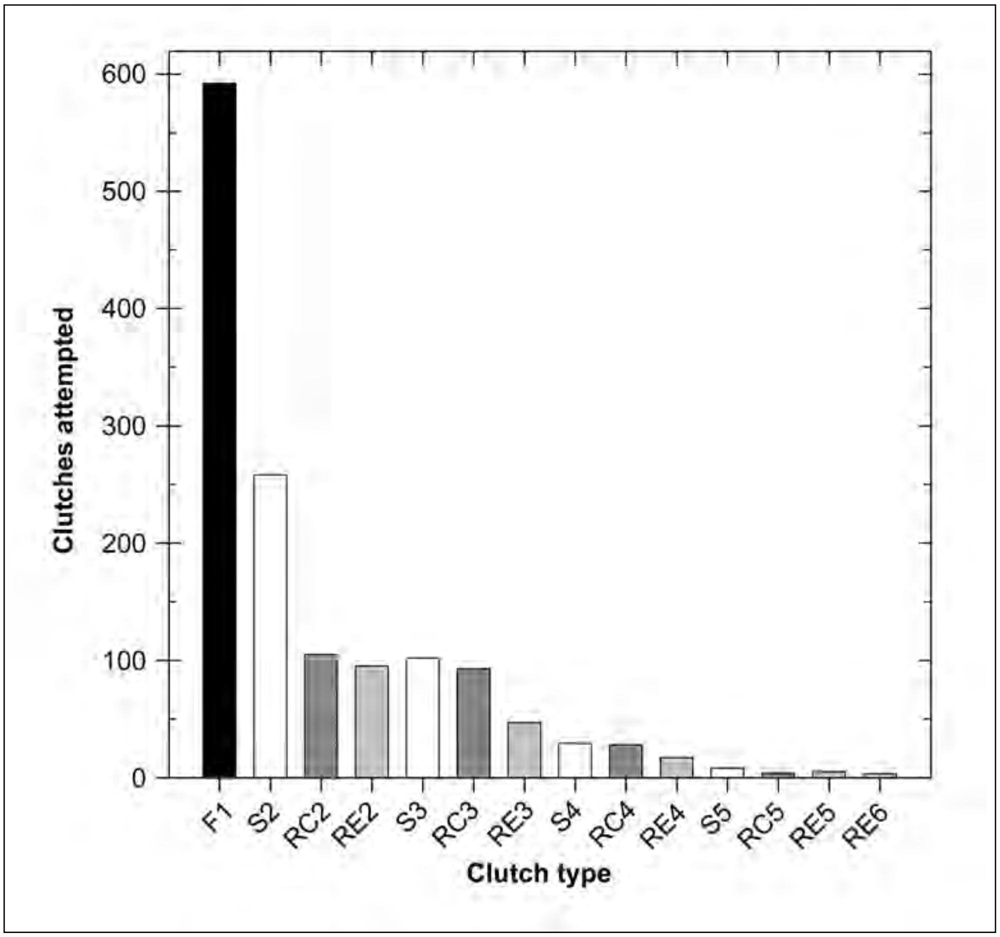

Figure 7.10—Frequency distribution of the various clutch types constituting 1,386 nestings attempted by a minimum of 179 female pearly-eyes (143 banded and at least 39 unbanded females) during 19 breeding seasons between 1979 and 2000. F1 represents first clutches (black bar); S2–S5 (white) are second through fifth clutches laid after the successful completion (at least one chick fledged) of previous first–fourth clutches. RC2–5 (dark gray) are, respectively, subsequent clutches following second through fourth clutches that failed (no fledglings) during the chick stage. RE2–6 (light gray) are, respectively, subsequent clutches following second through fifth clutches that failed during the egg stage.

average number of lifetime renesting attempts per female was 4.68 (range: 1 to 39).

As in many other reproductive parameters, the frequency distribution of clutch types reflects the major impact of philornid ectoparasitism on this pearly-eye population (fig. 7.10). The number of second clutches (S2; n = 258) following successful first clutches is more than double the number of third clutches (S3; n = 102) following successful second clutches because on average second clutches are laid by late April, and as early as mid-November (table 7.2), just prior to the period in which often 100 percent of the pearly-eye's nestlings begin succumbing to the effects of philornid ectoparasitism. In the same vein, whereas the number of second clutches laid after initiatory clutches were lost in the egg stage (RE2; n = 95) was about the same as second clutches following losses in the chick stage

(RC2; = 105), the number of RC3 clutches (n = 93) was almost double that of RE3 clutches (n = 47), once again owing to increased nestling mortality by late April and early May as a consequence of more intense botfly ectoparasitism. Because two is the average, median, and modal number of clutches laid by a female each breeding season, the number of clutches, and thus clutch type, drops precipitously following third clutches. However, clutch types are about equally represented during each subsequent nesting attempt (fig. 7.10).

Temporal Aspects of Recycling (Clutch to Clutch)

Pearly-eye females are able to recycle faster after each successive clutch.

The pearly-eye has the ability to recycle more rapidly with each subsequent clutch (fig. 7.11). This ability is imperative to increasing the thrasher's reproductive yield as each successful nesting takes on average a little more than a month: usually about 31 to 35 days: a 14-day incubation period (defined by Skutch 1945 as the interval between the laying of the last egg and the hatching of the last nestling); and a 17- to 21-day nestling period (interval between the hatching of the first egg and the fledging of the last nestling). The best way to quantify and evaluate the pearly-eye's proficiency in recycling is to compare and subject to several analyses the number of days between the various clutch types, both collectively and especially among individual females. In the following analyses, "clutch-to-clutch" data were used (namely, number of days between the date of oviposition of the first egg in a previous clutch to the laying of the first egg in a subsequent clutch). Because of Hurricane Hugo's significant impact on the timing of nesting and recycling, the results of separate analyses are presented in which hurricane effects are included and excluded.

Intuitively, the longer a previous nesting attempt lasts, greater is the number of days between nestings because the breeding pair will have expended more energy in previous nestings of longer duration and, thus, will need more time to recuperate physiological and nutritional losses (see Robinson et al. 2000). Therefore, there should be more days between second clutches that follow successful first clutches than between those that follow first clutches that failed in the nestling stage, which in turn should take longer than second clutches that follow first nestings that failed in the egg stage, and so on with each subsequent clutch (compare **intraclutch** types, e.g., S2 vs. RC2 vs. RE2, in table 7.3 and fig. 7.11). What is not so intuitive, however, and what may not be commonplace among other mimids or passerines in general, is the pearly-eye's ability to recycle more rapidly as the breeding season progresses (compare **interclutch** types, e.g., S2, S3, S4, and S5, among subsequent clutch numbers in table 7.3 and fig. 7.11). Regression analyses revealed that within each clutch type, the number of days between

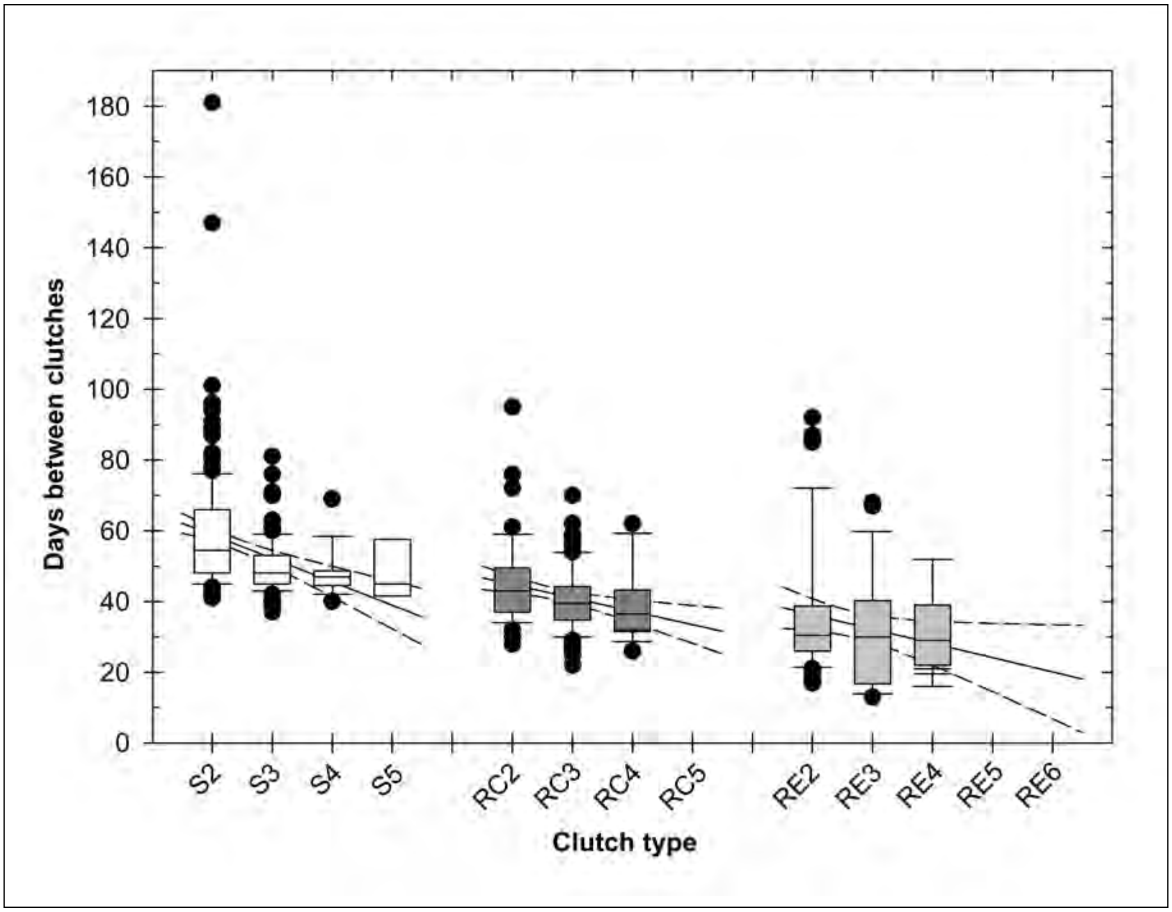

Figure 7.11—Days between successive clutches among the various clutch types (clutch types are defined in the text). Four breeding seasons (1990, 1991, 1999, and 2000) have been omitted to eliminate the effects of Hurricanes Hugo and Georges, which significantly affected the analyses. Within each clutch type, the number of days females needed to replace depleted energy reserves in order to recycle diminished significantly with each successive clutch. Box fills are: S2–S5 white, RC2–RC5 dark gray, and RE2–RE6 light gray. Box-plot parameters are defined in fig. 4.6.

subsequent clutches was significantly reduced ($P < 0.001$ in all three analyses; S2 to S5: $R^2_{adj.} = 0.99$; RC2 to RC5: $R^2_{adj.} = 0.96$; and RE2 to RE6: $R^2_{adj.} = 0.89$). By combining clutch types and then comparing clutch numbers, it was also revealed that the number of days between clutches significantly diminished with each subsequent clutch (K-W ANOVA: $H = 74.3$; df = 3; $P < 0.001$). In four of the six interclutch comparisons, the number of days between each subsequent clutch was significantly shorter ($P < 0.05$ in the all pair-wise comparison procedures, Dunn's Method). Only third vs. fourth, and fourth vs. fifth and sixth (combined), clutch comparisons were not significantly different. The median number of days between **first** and **second** clutches was **50** (43 to 62 days for the 25 to 75 percentiles; mean = 53; $SE = \pm\ 0.96$; between **second** and **third** clutches was **44** days (37 to 49 d for 25 to 75 percentiles; mean = 43 d; $SE = \pm 0.89$), between **third** and **fourth** clutches was **43** days (32 to 47 d for 25 to 75 percentiles; mean = 40 d; *SE*

Table 7.3—Descriptive statistics for the number of days between clutch types and subsequent clutches (n = 794 second through sixth clutches, including successful and replacement clutches)

				Percentiles	
Clutch type[a]	N	Mean	Median	25%	75%
		- - - - - - - - - - - - - *Days* - - - - - - - - - - - - -			
S2	258	58.8	54	48	66
S3	102	49.8	48	45	53
S4	29	47.9	47	45	48.5
S5	8	48	45	42	54
RC2	105	45.1	43	37	49.3
RC3	93	40.5	39.5	35	44
RC4	28	38.5	36.5	32	43
RC5	4	32.5	32.5	31	34
RE2	95	36.4	30.5	26	38.5
RE3	47	31.1	30	17	40
RE4	17	30.9	32	25.2	44.5
RE5	5	22	24	15	28
RE6	3	20.7	23	15.5	24.7

[a] S2 to S5 are second through fifth clutches laid following successful preceding clutches; RC2 to RC5 are second through fifth clutches laid following preceding clutch failures in the chick stage. RE2 to RE6 are second through sixth clutches laid following preceding clutch failures in the egg stage.

= ±1.67), and between **fourth** and **fifth/sixth** clutches was **33** days (28.5 to 42.5 d for 25 to 75 percentiles; mean = 31 d; *SE* = ±2.30).

Temporal Aspects of Recycling (Interclutch Recovery Period)

Female thrashers clearly show the ability to maximize their reproductive yield by taking less time to produce eggs with each subsequent clutch (fig. 7.11). The previous "clutch-to-clutch" analyses revealed the general inverse correlation between the progression of the breeding season and the time required to recycle. Natural selection, however, acts directly upon individuals within a population. Therefore, it is more evocative from both biological and ecological standpoints to take a closer look at the sampled population in general and individual females in particular. In the following analyses, interclutch data were used (namely, number of days between the last date that a previous clutch was **active**, to the laying of the first egg in a subsequent clutch; or in short, the interim between clutches).

The frequency distribution of interclutch recovery periods (clutch number and types combined) for 143 banded females from 1979 to 2000 is presented in figure 7.12. The overall mean number of days between the cessation of a previous clutch and the initiation of a subsequent clutch is 24 (± 0.73 *SE*). The median number of days is 17 (mode = 12; range: 3 to 181 days). Excluding the effects of Hurricane Hugo (by eliminating the 1990 and 1991 seasons and 120 clutches), the number of interclutch days diminished as follows: mean = 21 (± 0.64 *SE*); median = 15; mode remained 12; range: 3 to 136 days). The significance of Hurricane Hugo's impact on the thrasher's reproductive recycling was further revealed by comparing pre- and postdisturbance number of interclutch days. When the 1990 and 1991 seasons were included in the analyses, the number of postdisturbance interclutch days (pre- and postdisturbance medians of 15 and 18 days, respectively) increased significantly (M-W R S: $T = 106\ 647$; $P < 0.001$). Conversely, after excluding the 1990 and 1991 seasons, there was no significant difference between the number of pre- and postdisturbance interclutch days ($T = 95.46$; $P = 0.33$; pre- and post disturbance medians were 15 and 16 days, respectively).

To emphasize how the number of days needed to recycle diminishes with each successive clutch, the frequency distributions of interclutch recovery periods for each clutch type were then summarized (fig. 7.13). For most of the sampled population, there are sufficient data for the first four clutches to show a general

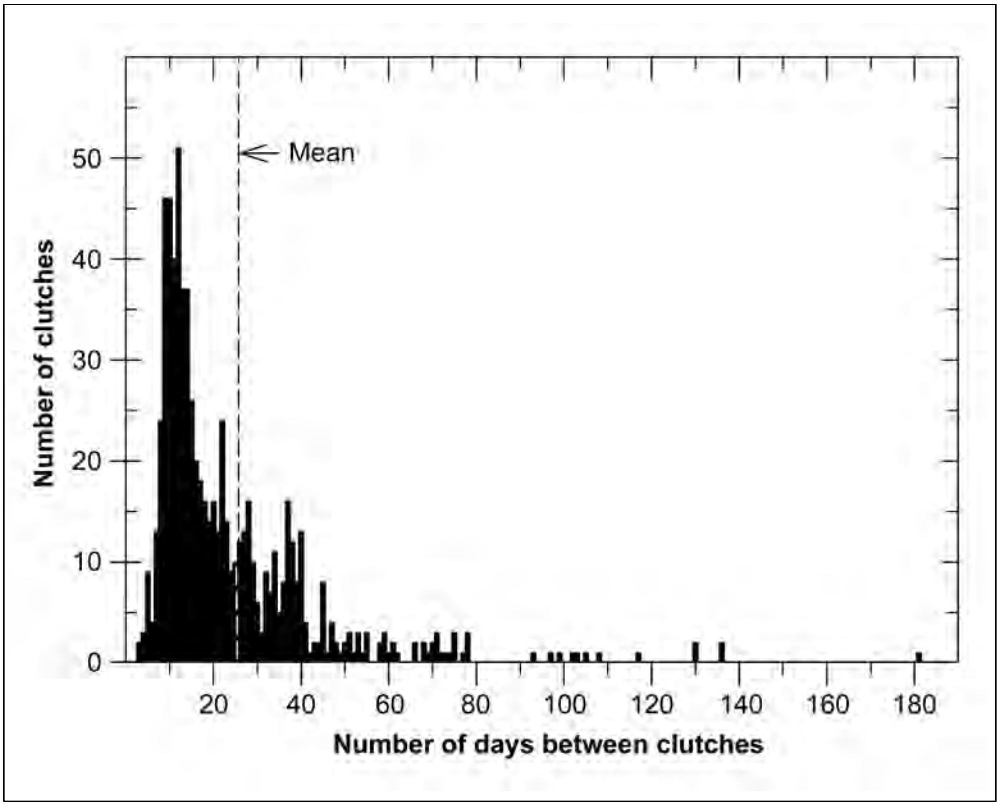

Figure 7.12—Frequency distribution of clutch-interim recovery periods (clutch number and types combined) for 143 banded females breeding from 1979 to 2000. Most females were able to recycle in fewer than 20 days. Many physiological, ecological, and environmental factors influenced females needing more than 40 days to recycle.

normal distribution for interclutch recovery periods. The elongated "tails" common among most clutch types represent longer periods involving "unique" (very young, or extremely old) nesters and extenuating circumstances (e.g., nest predation and usurpation, as well as hurricane-affected seasons). For example, most of the outlying bars (going to the right) in figure 7.13 pertain to the second (1991) breeding season after Hurricane Hugo.

Although illustrative in showing the overall pattern of interclutch recovery periods for the sampled population in general, to visualize and better understand the temporal aspects of recycling, the data were then analyzed by clutch type and year (fig. 7.14). The time needed by females to restore depleted energy reserves between successive clutches varied significantly (K-W ANOVA: $H = 116.4$; df = 16; $P < 0.001$) among years (table 7.4). There were only 80 instances of females taking longer than 40 days to recycle. Sixty-eight (85 percent) of the renestings taking more than 40 days to commence occurred in post-Hurricane Hugo seasons. Thirty-five (more than half of the post-Hurricane Hugo renestings of ≥ 40 days) took place in 1991, just two seasons after major habitat disturbance throughout the forest. After making the necessary adjustments to reduce the possibility of committing a type 1 (false positive) error inherent in multiple comparisons, 20 of the 136 Interyear comparisons were found to be significant (all pair-wise multiple comparison procedures, Dunn's Method). Twelve of the 16 yearly comparisons involving the second (1991) post-Hurricane Hugo breeding season were significant. Other significantly different interclutch periods involved the years 1980, 1982, 1988, 1992, and 1995.

Why were interclutch recovery periods so long and variable in 1991 (65 vs. about 20 days in other years)? One of the most plausible explanations is that by 1991, forest trees had initially rebounded from the effects of Hurricane Hugo, a fact that has been documented in several studies (Walker et al. 1991, special hurricane volume; see also Thompson-Baranello 2000, and Wunderle 1999). Within 2 years after the disturbance, the total number of species of fruiting trees, species with ripe fruit, and number of plants with ripe fruit remained elevated virtually throughout the entire year (Wunderle 1999: fig. 1). The pearly-eye and other frugivores such as the parrot took advantage of this and greatly extended their breeding seasons, which allowed them to attempt more nestings, while at the same time lengthening the recovery period between nestings to increase the probability of success in subsequent broods (see also Meyers et al. 1993, Vilella and Arnizaut 1994). One might argue, however, that because food was more abundant over a longer period, and since the pearly-eye is preadapted to recycling more rapidly after each nesting, it should have attempted even more nestings

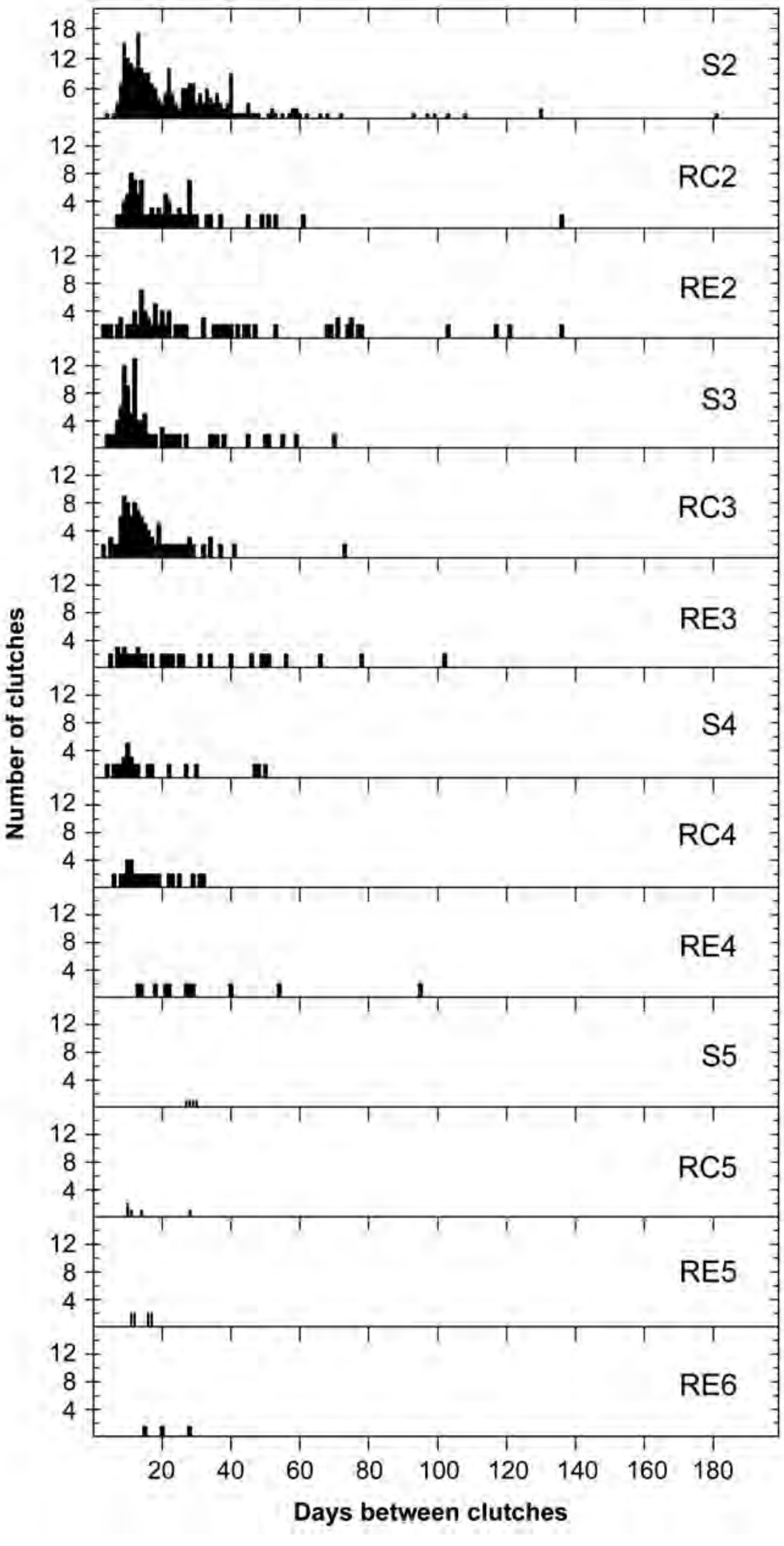

Figure 7.13—Frequency distribution of clutch-interim recovery periods by clutch type for 143 banded females breeding from 1979 to 2000. Most of the outlying bars (>80 days between clutches) pertain to the second (1991) post-Hurricane Hugo-affected breeding season. S2–S5 are second through fifth clutches laid after the successful completion (at least one chick fledged) of previous first–fourth clutches; RC2–5 are, respectively, subsequent clutches following second through fourth clutches that failed (no fledglings) during the chick stage; RE2–6 are, respectively, subsequent clutches following second through fifth clutches that failed during the egg stage.

Table 7.4—Descriptive statistics comparing yearly differences[a] in the number of days between the last date a previous clutch was active and the lay date of the first egg in a subsequent clutch (n = 794 second through sixth clutches, all types)

				Percentiles		
Year	N	Mean	Median	25%	75%	Range
		Days				
1979	14	24.1	19.5	14	36	7–52
1980	41	28.6	37	15	38	8–45
1981	43	17.2	14	12	21	5–40
1982	65	15.7	12	10	22	3–45
1985	34	20.5	16	12	25	7–75
1986	33	17.8	14	12	21	8–55
1987	65	21.4	19	11	32	4–61
1988	50	15.8	11.5	9	19	5–69
1990[b]	17	15.3	14	12	18	9–25[b]
1991	90	42.5	34	18	55	8–181
1992	56	14.6	12	10	18	8–40
1993	78	25.8	16	12	29	9–136
1994	53	22.6	16	12	29	7–78
1995	60	25.2	21	13	34	3–75
1996	31	20.9	14	12	24	9–75
1997	24	23.5	16.5	12	30	10–71
1998	17	28.8	18.5	14	30	4–136
1999[b]	5	15.4	15	12	18	4–28[b]
2000	18	25.2	19.5	13	31	3–118

[a] Several yearly comparisons were significant for the median number of days between clutches.
[b] Note the rapidity of renestings (last column) during two hurricane-affected breeding seasons.

with shorter interims than usual between broods in response to the abnormally abundant food and consequentially longer breeding season. One must remember, however, that because the energetic cost of each reproductive bout is so high, as a consequence of rapid recycling, fitness of older siblings is often increased at the expense of the younger ones. This is one reason why brood reduction is so common in the pearly-eye. Although it has adapted a rapid recycling strategy allowing it to produce several broods a season, the pearly-eye pays a heavy price as so few nestlings survive to breed (discussed below). At the other extreme, during times of abundance of food resources, as was observed within 2 years after both hurricanes, natural selection should favor longer recovery periods to maximize fitness and, thus, survival of **all** the siblings in every brood, which will greatly increase the number of recruits entering the breeding population, which, in turn, will promote the rapid recovery of disturbance-depleted populations.

One other noteworthy factor accounting for the observed increase in number and success of the 1991 broods is the observed patchiness of tree damage. Studies have shown that the impact of Hurricane Hugo was not uniform throughout the forest (Francis and Gillespie 1993, Frangi and Lugo 1991). Thus, the wide-ranging pearly-eye undoubtedly took advantage of remnant food sources among the numerous vegetational refugia observed in less impacted areas (pers. obs.), allowing it to increase its reproductive success in these areas (e.g., Icacos Valley and western slopes) to compensate for less (or no) breeding in hard-hit areas in the eastern and northeastern sections of the forest.

By separating the interclutch recovery periods by clutch type and year, a general pattern of increased variance around the yearly means for each clutch type was also revealed during the nine postdisturbance breeding seasons between 1990 and 1998 (fig. 7.14). This is the same pattern shown in figure 7.6 for the timing of egg deposition in the first eggs of initiatory clutches that exemplified the extreme variability in the onset of the post-Hurricane Hugo breeding seasons. Once again, the increased variability is most likely owing to the disruption of the cyclic pattern of fruit production following the storm, and the almost year-round availability of fruit during the first 2 to 3 postdisturbance years.

Extremities in Interclutch Recovery Periods

The record for the least number of days between the loss of a previous brood to the laying of the first egg in a replacement clutch is 3, and it is shared by two females. The first instance occurred in the 1982 season and involved a 4-year-old (minimum-aged) female banded as a breeding adult in 1979. She laid a replacement third clutch (RC3) on March 26, 1982, just 3 days after the last (oldest) of three nestlings from the second clutch died at 11 days old as a consequence of heavy botfly ectoparasitism. Subsequent to the 1982 breeding season, this female nested for another three seasons before disappearing and was presumed dead because most older females that are supplanted by younger, stronger females are at least occasionally observed in the area of their usurped boxes for weeks or even months after eviction. The second record for recycling within 3 days did not occur again for more than a decade. In 1995, a 3-year-old (minimum-aged) female laid a replacement second clutch (RE2) on April 23, 3 days after her first clutch failed in the egg stage (rat predation) and just 7 days after the laying of the first egg of the initial clutch. This female also nested for another three seasons before disappearing.

Although a few females can recycle in as few as 3 days, and many within 1 week, *most* do so within 2 weeks.

The record maximum number of days between replacement clutches was 181, occurring during the second (1991) breeding season after major habitat disturbance. The individual involved was a 12-year-old (min.) female banded as a breeding adult in 1979. She was recaptured and processed on December 11, 1990. Her

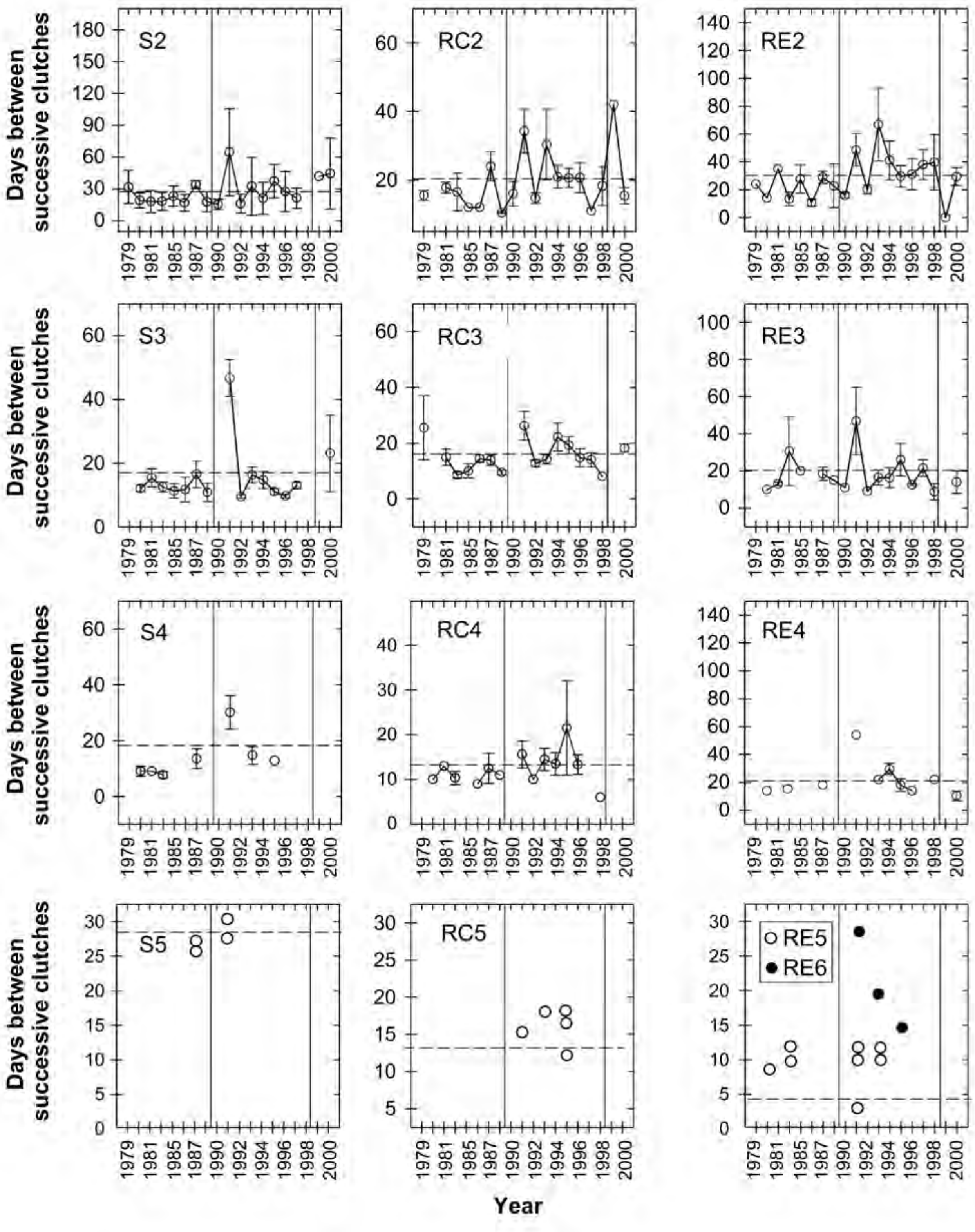

Figure 7.14—Yearly variation of clutch-interim recovery periods for each clutch type. Note the extreme delay in recycling two seasons following Hurricane Hugo (left-most black vertical bar within each graph) and a few, e.g., S2 and S3, in 2000 two seasons following Hurricane Georges (right-most black vertical bar within each graph). Also note the postdisturbance general trend of increased variation (capped vertical bars [⊥, ⊤] are ±1 standard errors) around the annual means (open circles). S2–S5 are second through fifth clutches laid after the successful completion (at least one chick fledged) of previous first–fourth clutches; RC2–5 are, respectively, subsequent clutches following second through fourth clutches that failed (no fledglings) during the chick stage; RE2–6 are, respectively, subsequent clutches following second through fifth clutches that failed during the egg stage.

left tibiotarsus was severely bowed, suggesting advanced arthritis. She laid her first (two-egg) clutch on November 8, 1990. Within the first egg laid, the embryo died young. The chick from the second egg fledged on December 13, 1990. Following rectrix molt, a further physiological stress, the female was tailless by February 27, 1991. As a likely consequence of a weakened body condition, although she was observed guarding her box from February through May, she did not lay her second (3-egg) clutch until June 12, 1991. She bred for three additional seasons before disappearing. In her last (1994) breeding season, she also laid two clutches, a 3-egg clutch on April 14 (all three nestlings died as a consequence of botfly ectoparasitism), and another 3-egg clutch on June 12, 1994. This very old female abandoned the eggs of her second clutch about midway through the incubation stage and was never seen again. Thus, she may have died during what might have been her final nesting attempt. It is noteworthy that on May 5, this female was recaptured and processed between clutches. The presumed arthritis in her left tibiotarsus had worsened. She also exhibited a heavy infestation of feather-chewing lice (Mallophaga), and was virtually devoid of auricular and orbital feathers.

Females Recycling in Fewer Than Two Weeks

By recycling more rapidly with each subsequent clutch, females are able to maximize the number of fledglings produced each season, thereby increasing annual productivity and, ultimately, lifetime reproductive success. It is more important for females to minimize the recovery period between each nesting attempt, regardless of clutch number or season. To evaluate the pearly-eye's efficiency in minimizing the recovery time between all successive clutches, a subset of females able to renest within 2 weeks was chosen for analyses. Of the 143 banded females that attempted 794 renestings (second-to-sixth clutches, including replacements), females attempted 413 renestings in 2 weeks or less (mean = 2.64 renestings per female, median = 2, mode = 2, 95 percent *CI* = 0.63; range: 1 to 9). From a seasonal perspective, over the entire 19 breeding seasons, 105 females (73 percent) attempted an average of 22 renestings in 2 weeks or less each season (median = 23, mode = 13; 95 percent *CI* = 5.11, range: 0 to 39 per season). There does not appear to be a strong trend in the number of renestings (fig. 7.15a). However, there is an apparent cyclic pattern to the data (fig. 7.15a). More seasons are needed to better discern how the cycle will fluctuate in the absence or presence of additional major habitat disturbances. A comparison of the median number of pre- and post-Hurricane Hugo renestings (1979–88 vs. 1990–98—1 month prior to Hurricane Georges) did not result in a significant difference (M-W R S: *T* = 98; *P* = 0.41). Percentages

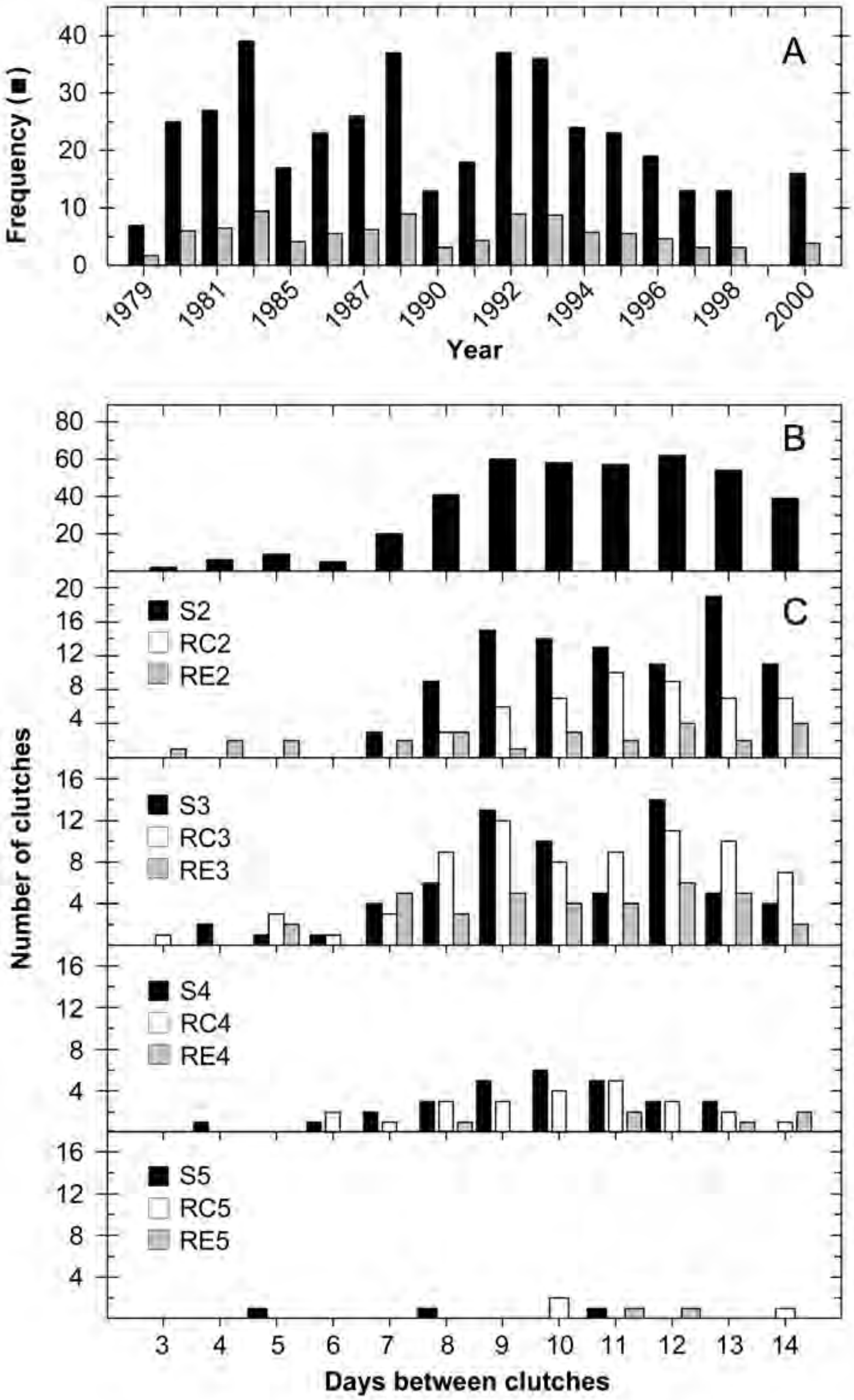

Figure 7.15—Frequency distribution by year (A) and clutch type, first combined (B) and then separated (C), for number of days between multiple clutches laid within 2 weeks or less. More than half of the sampled pearly-eye females recycled within 2 weeks or less regardless of the clutch number or type. S2–S5 are second through fifth clutches laid after the successful completion (at least one chick fledged) of previous first–fourth clutches; RC2–5 are, respectively, subsequent clutches following second through fourth clutches that failed (no fledglings) during the chick stage; RE2–6 are, respectively, subsequent clutches following second through fifth clutches that failed during the egg stage.

of renestings among all 19 seasons were as follows: mean = 5 percent, median = 6 percent, mode = 3 percent, 95 percent *CI* = 1.23, range: 0 to 9 percent. Combining years to assess the frequency distribution of renestings over the 2-week period (fig. 7.15b) revealed that, although females can, and do, recycle in as few as 3 days, most needed at least 8 to 12 days to do so. Separating the data by clutch order and type revealed a generally uniform distribution among clutch types (fig. 7.15c). The two most important findings to emerge from these analyses, however, are that more than half of the renestings (413 of 794) took place within 2 weeks or less and almost three-quarters of the breeding females (105 of 143) were involved.

Females Recycling in Less Than a Week

As prolific a breeder as it is, even the pearly-eye is not generally able to renest within less than a week. Of 794 renestings, only 42 (about 5 percent) were initiated by 28 different females in 7 days or fewer, with most renestings requiring almost the full 7 days: mean = 6, median = 6, mode = 7, range: 3 to 7 days. There was no propensity for recovery periods less than a week occurring noticeably more often in certain years: mean = 3, median = 2, mode = 2, range: 1 to 6 (6 occurred in 1988). Nor, did certain females account for most of the renestings taking place within 7 days or less (mean = 1, median = 1, mode = 1, range: 1 to 3).

Annual Reproductive Success and Influential Factors

As a prime example of an avian supertramp, the pearly-eye has been shown to breed for extended periods and to recycle within as few as 3 days after a loss. Yet, the goal of any species or individual must be to maximize its reproductive success on a yearly and, ultimately, a lifetime basis. To evaluate how proficient the pearly-eye is in its reproductive efforts, in the following sections I will first present the reproductive yield on an annual basis and then evaluate and compare the various reproductive parameters commonly associated with overall reproductive success in birds, e.g., number of clutches per female per season, clutch size, total number of eggs laid (number and percentage hatched, plus mortality factors), nestlings fledged per eggs laid and hatched (including mortality factors), young recruits (subsequent breeders) and, finally, individual adult lifetime reproductive success (LRS) (see Clutton-Brock 1988, and Newton 1989 for comprehensive syntheses of LRS, and Pierotti 1991 for a provocative review of these books; see also Murray 2000 for an insightful discussion of the various methods and problems encountered when evaluating reproductive success).

Reproductive Yield

Following hurricanes, by compressing the length of their breeding seasons, clutch sizes, and the number of eggs laid, females maintain or even surpass predisturbance productivity.

The results presented in the following sections are based on 1,386 nesting attempts by 182 females (n = 143 banded females and 1,327 nestings, plus a maximum of 39 unbanded females and 59 nestings). When female identity was required, only the 1,327 nestings of the banded females were used in the analyses. On average, from 1979 to 2000, 37 banded females (range: 7 to 47) attempted a total of almost 80 nestings (range: 8 to 132) each breeding season (fig. 7.16). The substantial fluctuations in the annual number of nestings are the results of a complex set of environmental and ecological factors, prime examples being rainfall (including humidity) and habitat disturbance, and all their direct and indirect influences on natural processes such as annual fruit production (discussed previously).

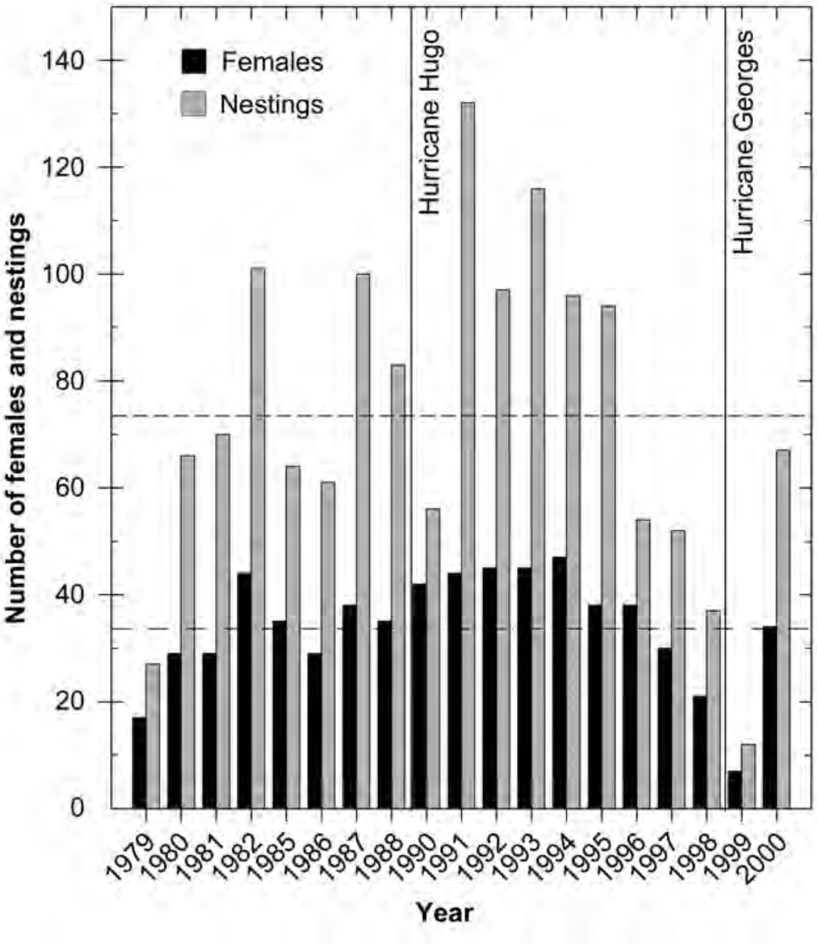

Figure 7.16—Numbers of breeding females and nestings recorded between 1979 and 2000. Horizontal plot-wide lines are mean number of nestings (upper dashed line) and number of females (lower dash-dot-dot-dash line) recorded over the entirety of the study. On average, some 34 females attempted about 73 nestings each year. The number of females and nestings varied markedly, often significantly, after hurricane disturbance.

Except for the initial (1979) breeding season when fewer boxes were available and, consequently, fewer females were present, the annual average number of nestings per female for the first post-Hurricane Hugo breeding season (1990) was significantly smaller (fig. 7.16) than the average number of nestings occurring during the 7-year predisturbance period. Conversely, there were significantly more nestings per female during the second post-Hurrican Hugo breeding season (fig. 7.16) than during any season prior to disturbance. However, by the third year after habitat destruction, the annual number of nestings attempted by individual females had returned to within the normal range of predisturbance annual averages, but began to plummet after the 1995 breeding season because of aging females and an increase in cyclonic disturbances during the mid-1990s.

The reproductive yield for the sampled thrasher population is summarized in figure 7.17. Of the 3867 eggs laid during 19 breeding seasons, 84 eggs were broken during handling, by females startled during nest visits, or used in experimentation, and were therefore subtracted from the original total. Of

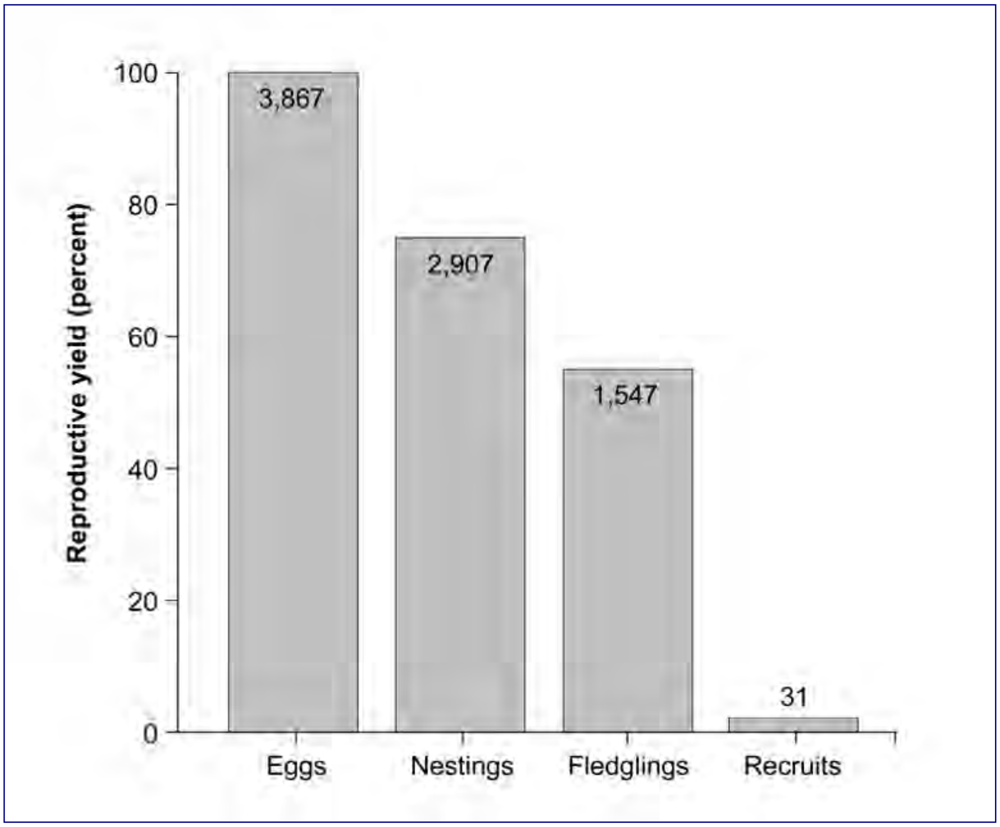

Figure 7.17—Reproductive yield for 104 banded males and 143 banded females attempting 1,327 nestings between 1979 and 2000. Numbers within each column are sample sizes. On average, each breeding female and male produced, respectively, 16 and 28 nestlings, 9 and 15 fledglings, and 0.2 and 0.3 recruits during this 27-year study. The poor recruitment (about 2 percent) into the breeding population reflects the prolonged lifetimes of the breeders, nest-site persistence, and the resultant keen competition for nest boxes.

the remaining 3,783 eggs, 2,907 (about 77 percent) hatched. Of these, 46 nestlings were excluded from analyses because they were used in experiments or died during handling. Of the remaining 2,861 nestlings, 1,547 (54 percent) fledged. Of these, 2 percent (18 females, 13 males) were recruited into the sampled breeding population.

Many stochastic environmental and ecological factors influence the annual reproductive performance and success of individuals in natural populations. For example, variation in season length, clutch size, and the number and success of each nesting bout are all important components influencing the total number of young produced each breeding season. The length of each nesting bout is positively correlated with both clutch size and nest success and shows a strong correlation with the annual number of young fledged (Ricklefs and Bloom 1977). In addition, as it has been shown in this study, natural habitat disturbances such as tropical storms can significantly influence annual return rates of breeders, breeding season length, timing of egg deposition, and the temporal aspects of recycling, thereby further increasing the extent and variation in annual reproductive success. As a further example, during the first post-Hurricane Hugo breeding season (1990), the mean annual clutch size per female was **not** significantly smaller than that of an 8-year predisturbance mean (tables 7.5, 7.6, and fig. 7.18). However, the second year (1991) postdisturbance mean clutch size **was** significantly smaller, resulting from the laying of 1-egg clutches for the first time during the study. Although the laying of 1-egg clutches continued into the third postdisturbance breeding season, mean clutch size had once again increased (and slightly surpassed) that of the 8-year predisturbance period. Pre- and post-Hurricane Georges analyses comparing clutch size and number were not performed because so few females (n = 7) nested in 1999.

Table 7.5—Pre- and post-Hurricane Hugo comparisons of annual mean clutch size and number of nestings per female

	Predisturbance seasons	Postdisturbance seasons		
Parameter	**1979–1988**	**1990**	**1991**	**1992**
Clutch size:				
N	572	56	132	97
Mean	2.98	2.98	2.79	3.02
SE	.01	.05	.05	.05
Range	2–4	2–4	1–4	1–4
Nestings:				
N	572	56	132	97
Mean	1.9	1.32	1.65	1.78
SE	.03	.06	.06	.07
Range	1–5	1–3	1–6	1–4

Table 7.6—Tukey's multiple comparisons matrix of pairwise probabilities for annual differences among clutch sizes and number of nestings per female (n = 857 for both clutch size and number of nestings)

	Season										
n	1979 (27)	1980 (66)	1981 (70)	1982 (101)	1985 (64)	1986 (61)	1987 (100)	1988 (83)	1990 (56)	1991 (132)	1992 (97)
Clutch size:											
1979	1.00										
1980	.192	1.00									
1981	.832	.972	1.00								
1982	.936	.980	.964	1.00							
1985	.948	.181	.771	.892	1.00						
1986	.998	.894	.996	.990	.992	1.00					
1987	.562	.997	.982	.994	.522	.998	1.00				
1988	.980	.861	.997	.999	.954	.995	.998	1.00			
1990	.956	.962	.993	.925	.919	.997	.992	.996	1.00		
1991	.046*	.023*	.035*	.039*	.042*	.045*	.042*	.047*	.013*	1.00	
1992	.186	.791	.683	.972	.794	.745	.952	.874	.962	.039*	1.00
Nestings:											
1979	1.00										
1980	.638	1.00									
1981	.995	.999	1.00								
1982	.603	.98	.999	1.00							
1985	.968	.523	.994	.484	1.00						
1986	.999	.446	.986	.411	.999	1.00					
1987	.178	.999	.977	.999	.997	.979	1.00				
1988	.999	.918	.999	.999	.998	.993	.998	1.00			
1990	.042*	.001*	.014*	.001*	.022*	.041*	.001*	.013*	1.00		
1991	.001*	.046*	.043*	.048*	.001*	.001*	.045*	.002*	.001*	1.00	
1992	.792	.964	.989	.999	.689	.692	.998	.957	.579	.042*	1.00

* Significant difference at α = 0.05.

The number of clutches per season for each female showed more prominent yearly vacillations than did clutch size, owing to correlative factors such as rainfall, fluctuating seasonal fruit production, and especially major habitat disturbances (hurricanes), which greatly influenced the timing and, consequently, the total number of possible nestings. Following Hurricane Hugo, the annual average number of clutches per female for the first postdisturbance breeding season (1990) was significantly smaller (table 7.6 and fig. 7.18) than the 8-year predisturbance period. Conversely, there were significantly more clutches per female during the second postdisturbance breeding season. However, by the third year after habitat destruction, the annual number of clutches attempted by individual females had returned to within the normal range of predisturbance annual averages, but began to plummet after the 1995 breeding season. Because the previous results and conclusions derived from statistical tests comparing very large samples (e.g., n = 572 for eight separate seasons) to much smaller samples (e.g., n = 56 for a single season) may be equivocal, comparisons of annual clutch

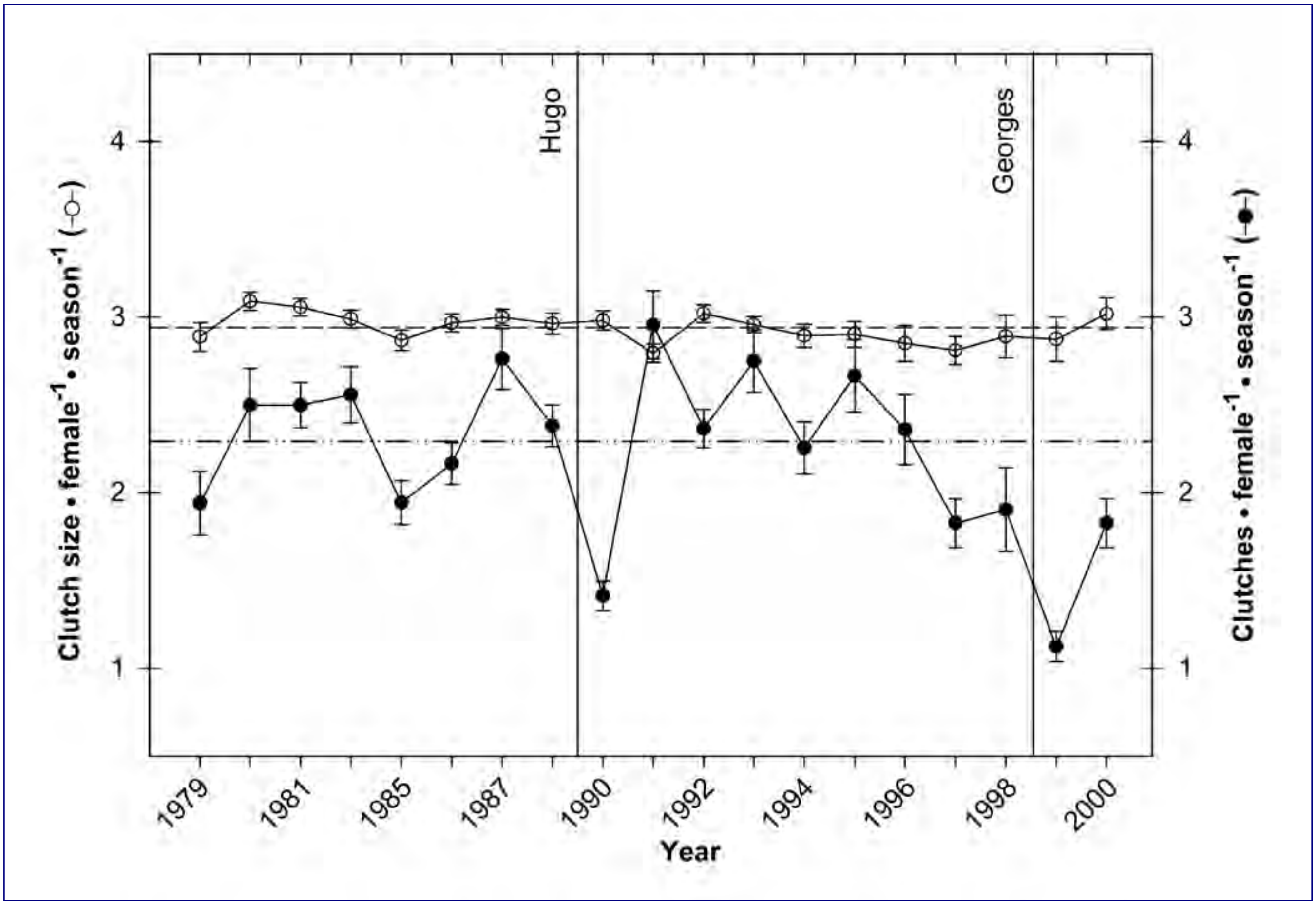

Figure 7.18—Size and number of clutches (n = 1,327) per banded female pearly-eye (n = 143) for 19 seasons between 1979 and 2000. Capped vertical bars (⊥, ⊤) on symbols are ±1 standard errors. Plot-wide upper horizontal dashed line (clutch size) and dash-dot-dot line (number of clutches) are overall means for the sampled population throughout the entire study.

sizes and number of nestings were made. The results were the same, i.e., clutch size was significantly smaller only in the second postdisturbance breeding season, whereas the number of clutches was significantly fewer during the first two postdisturbance seasons, returning to previous averages by the third postdisturbance breeding season (fig. 7.18).

Besides primary factors such as climate and a variety of ecological constraints, biologists are not exempt from causing reproductive losses in their study organisms (see Rotella et al. 2000 for a statistical method to simultaneously estimate daily nest survival and observer effect). It is virtually impossible to monitor any wild population without inadvertently influencing study results. Therefore, two analyses were conducted to evaluate the pearly-eye's reproductive performance during the egg and nestling stages between 1979 and 1998. However, in the following presentation, egg and chick mortality caused by human-induced factors have been eliminated from the analyses.

Egg Mortality

Of 3,783 eggs laid, 23 percent (n = 876) failed to hatch. Infertility and predation by thrashers, rats, owls, and unknown causes were by far the major causes of egg mortality (17 percent combined). Nesting females accounted for about 3 percent ("female abandons" and "broken female"). Other factors combined accounted for about another 3 percent. (fig. 7.19).

Infertility and nest predation were responsible for most egg mortality.

Most infertile eggs are from the earliest and latest nests of the season (about 80 percent in each of the four lay-order categories) suggesting that males are not always successful in inseminating females before they begin egg-laying at

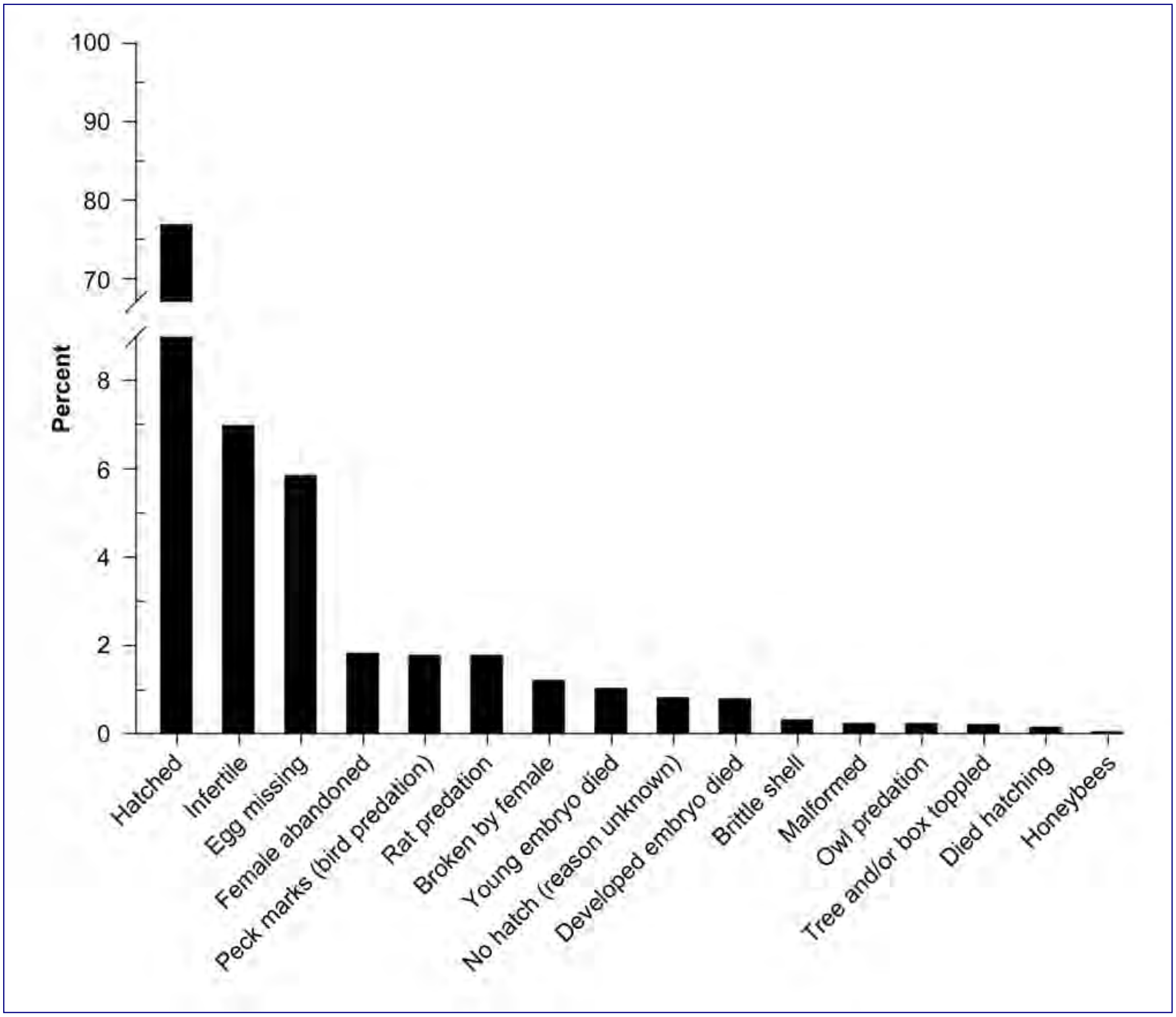

Figure 7.19—Frequency distribution of egg fates. Infertility and predation were by far the main causes of hatching failure. Cumulative effects of endogenous (female-related), ecological (predation, disease, and parasites), and environmental impacts (cyclonic disturbances) lowered hatching success.

the season's onset. Late in the breeding season, diminishing gonadal hormones in both members of the pair may explain why some females lay infertile clutches at that time. Most infertile eggs were the first laid in a clutch, also suggesting that the male did not have the opportunity to inseminate the female prior to the onset of ovulation. This propensity for initial eggs being infertile is not uncommon among passerines (e.g., Cordero et al. 1999).

Comparing eggs by lay order (fig. 7.20), first-laid eggs showed the lowest hatching success (72 percent), attributed mostly to infertility (7 percent). Similarly, last-laid eggs (third- and fourth-laid eggs sharing equal percentages) showed the second lowest hatching success (79 percent) and second highest infertility rates (82 percent). Therefore, regarding second-laid eggs from a hatchability standpoint, there are some biological advantages to being a chick from the second-laid egg in a clutch. Potti and Merino (1996) reported similar results for a population of the pied flycatcher in central Spain. During a 4-year study, they noted that hatching failure as a whole, and egg infertility in particular, followed a convex trajectory across the laying sequence, thus indicating an optimum for egg hatchability in intermediate positions of the clutch (see also Birkhead and Goodburn 1989).

The subsequent disappearance of eggs previously found in a nest ("egg missing" label in figs. 7.19 and 7.20) was attributed to nest predation. The remains of partially eaten eggshells confirmed predation by birds (peck marks) or rats (gnawed shells). The white-necked crow (*Corvus leucognaphalus*), a corvid belonging to a large avian family of well-known "nest robbers," may once have played a major role in the depredation of pearly-eyed thrasher nests, but the crow is now believed to be extirpated from the island. Other large birds such as the Puerto Rican lizard-cuckoo (*Coccyzus vieilloti*) are also potential predators. However, the cuckoo is not common in the study area and is most likely not a major nest predator at pearly-eye nest boxes. The design of thrasher nest boxes makes predation by the Puerto Rican boa (*Epicrates inornatus*) very difficult. The snake probably accounts for very few, if any, egg losses. The major avian culprit is presumably the pearly-eye itself. Thrashers are constantly observed entering other pairs' territories and nest boxes, especially when the owners are away from their boxes. Interlopers steal nesting material, rob eggs, and depredate nestlings (see below and chapter 8).

About 1 percent of female abandonments, e.g., eggs that remained cold to the touch for several days were considered lost to natural causes such as death of the female and otherwise unexplained cessation of incubation. Deaths of developing embryos and hatchlings attempting to break out of their eggs accounted for only about 2 percent of egg losses. However, because no microscopic evaluation

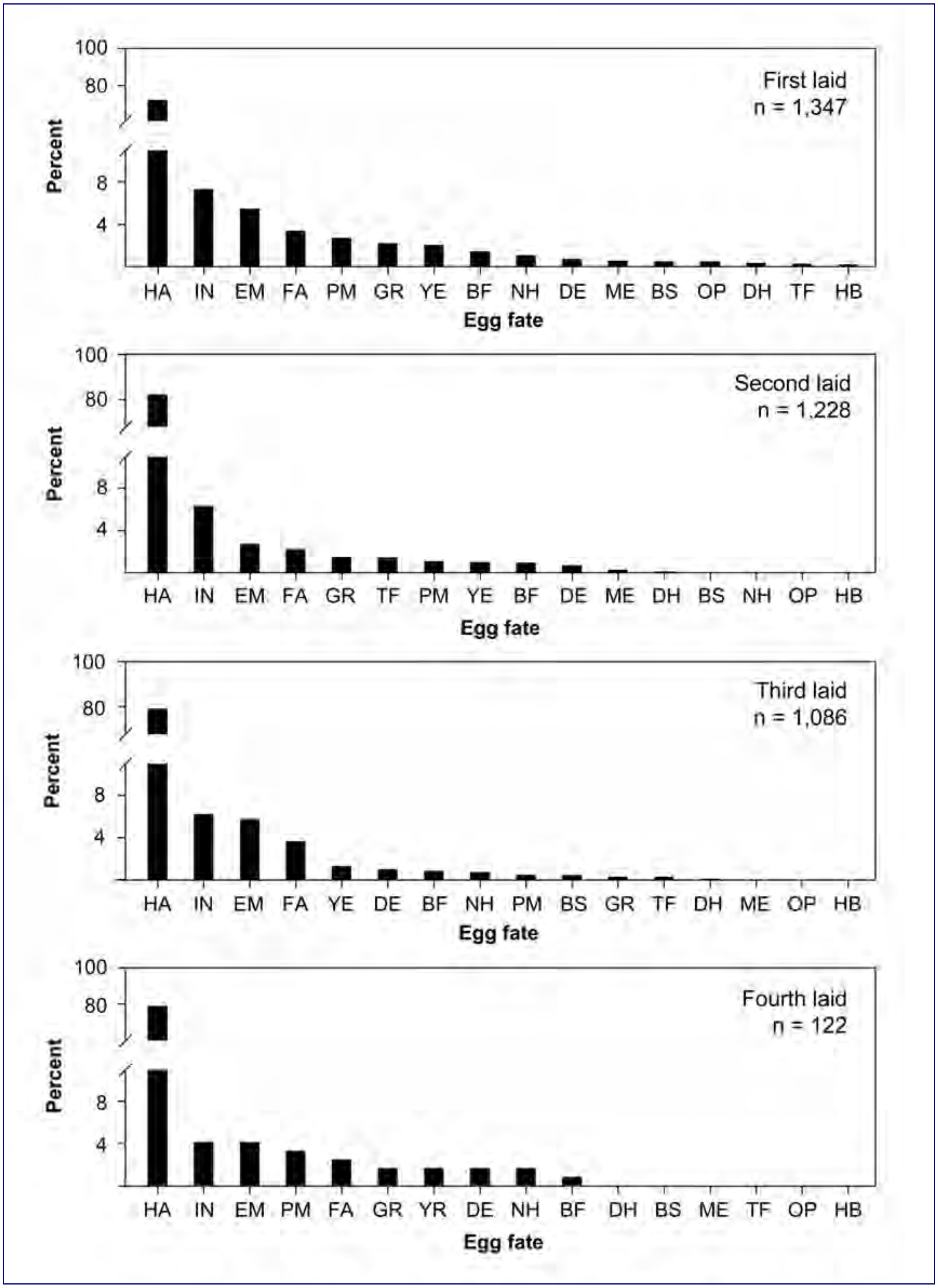

Figure 7.20—Frequency distributions of egg fates by lay order. Whereas most eggs hatched, infertility was the leading cause of hatching failure. Predation and nest abandonment by females were the second- and third-most leading causes of hatching failure among all the eggs within clutches. Specific causes of egg failure were BF (broken or cracked by female), BS (brittle shell), DE (developed embryo died), DH (died hatching), EM (egg missing), FA (female abandoned), GR (gnawed, rat predation), HA (hatched), HB (honey bees), IN (infertile), ME (malformed egg), NH (no hatch, reason unknown), OP (owl predation), PM (peck marks, bird predation), TF (tree fell), YE (young embryo died).

of addled eggs, i.e., for the presence of dead embryos was conducted, mortality owing to the death of developing embryos may be higher. During the first year of the study, in the initiatory clutches of two unknown-aged females (one clutch in March, and the other in May), malpositioned chicks within the first-laid eggs of each clutch died at hatching. Both showed abnormal tucking positions well known in the poultry sciences (Brooks 1978, Byerly and Olsen 1937, Munday 1953, Waters 1935). Normally, the well-developed embryo at the time of hatching has its legs, feet, and left wing flexed, and the neck is depressed ventrally; the head is turned to the right, its left side resting on the right pectoral muscle, and is tucked **under** the right wing (Brooks 1978). Both pearly-eye embryos were in the normal hatching position except that their bills were not tucked under the right wing, but instead rested on it (malposition VI category). Although some early authors did not consider malposition VI abnormal (Byerly and Olsen 1937, Munday 1953, Waters 1935), Brooks (1978) convincingly showed that once the head is over the wing it is free to move more extensively. Thus, the restricted focal point necessary to concentrate the pecks in order to penetrate the thick eggshell is lost and the neonate loses the ability to break out of its shell.

Of the broken eggs found during nest visits, about 1 percent was attributed to careless females, the category labeled "broken female." Not included in these analyses was an additional 1 percent of the eggs involved in egg manipulation experiments to determine (a) if the pearly-eye is a determinate or indeterminate layer[1] (it is a determinate layer); and (b) the largest clutch size that a female would accept, or at least could physically incubate. Five eggs was the maximum number accepted, whereas 6-egg clutches (or larger) were always destroyed or abandoned. Older females were generally responsible for laying brittle-shelled and malformed eggs. Human impact on hatching success was minimal. Eggs dropped during handling and forced nest abandonments accounted for less than 1 percent of hatching failures based on the original total of 3,867 eggs. A few additional eggs were lost to natural causes, e.g., when nest-box trees toppled or boxes were blown down during severe windstorms and so were included in the analyses (figs. 7.19 and 7.20).

Botfly ectoparasitism was the major cause of nestling mortality.

Nestling Mortality and Number of Fledglings

Between 1979 and 2000, 2,907 eggs produced nestlings, 46 (about 2 percent) of which were used in food provisioning experiments or died during handling

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[1] Determinate layers are species in which the number of ovarian follicles responding to the stimulation of gonadotropic hormones is equal to the number of eggs laid, and the number is determined when egg laying begins (*cf.* Klomp 1970). Indeterminate layers are species in which the number of follicles that respond to hormonal stimulation is greater than the number of eggs laid normally. If eggs are removed as laid, laying continues beyond normal clutch size.

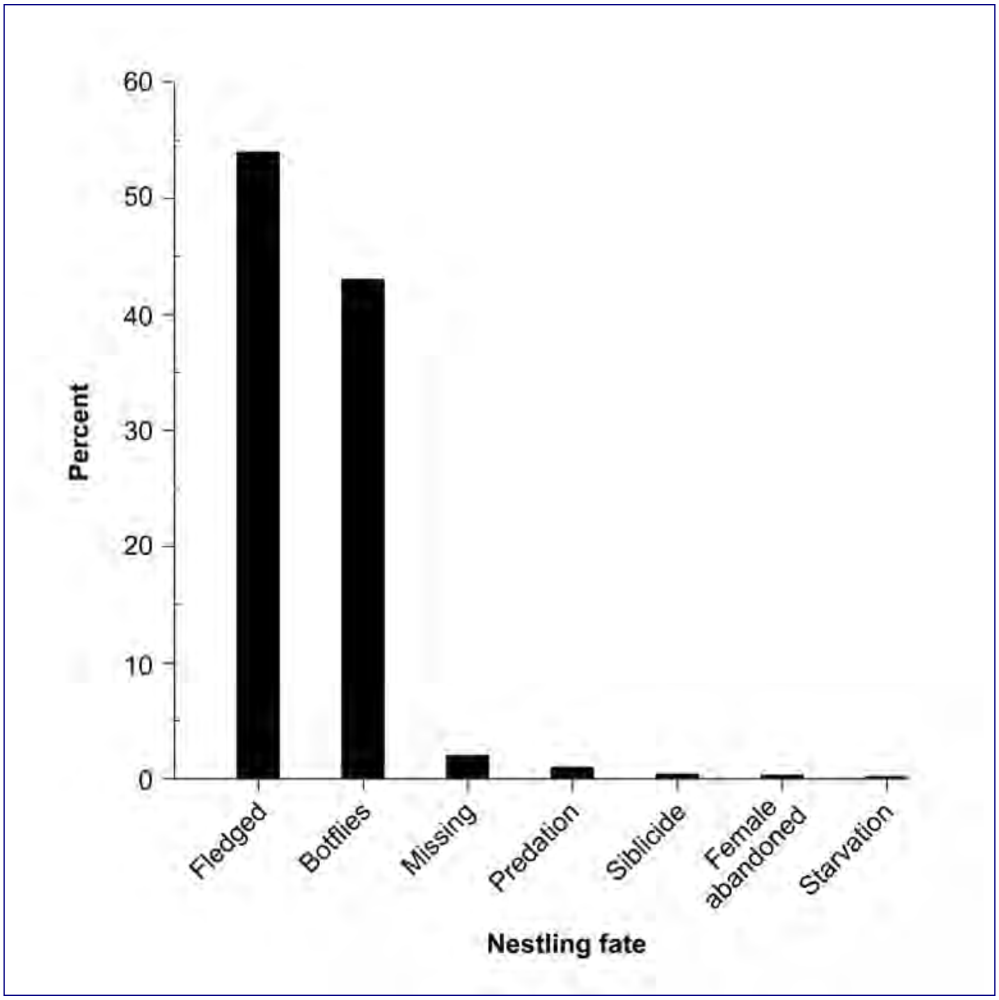

Figure 7.21—Frequency distribution of nestling fates. Philornid ectoparasitism was the prime mortality factor among thrasher nestlings, whereas siblicide, nest abandonment by females, and starvation were minimal.

and were therefore excluded from the following analyses. Of the remaining 2,861 nestlings, 1,547 (54 percent) fledged, whereas 1,314 (46 percent) died in the nest of natural causes, e.g., ectoparasitism, predation, and climatic disturbances (fig. 7.21).

Nestlings were exposed to many dangers as summarized in figure 7.22. Philornid ectoparasitism was by far the major source of nestling mortality in this rain-forest population (see also Arendt 1985a, 1985b, 2000). Mortality caused by philornid botflies was much higher than all other causes of mortality, which, when combined, accounted for only about 3 percent. Younger siblings succumbed more often to philornid ectoparasitism than did first-hatched nestlings (fig. 7.22) Although almost 60 percent of first-hatched nestlings fledged and only about 20 percent succumbed to botfly ectoparasitism, more nestlings in the remaining three positions in the hatching sequence died as a result of botfly ectoparasitism than the number of nestlings that fledged.

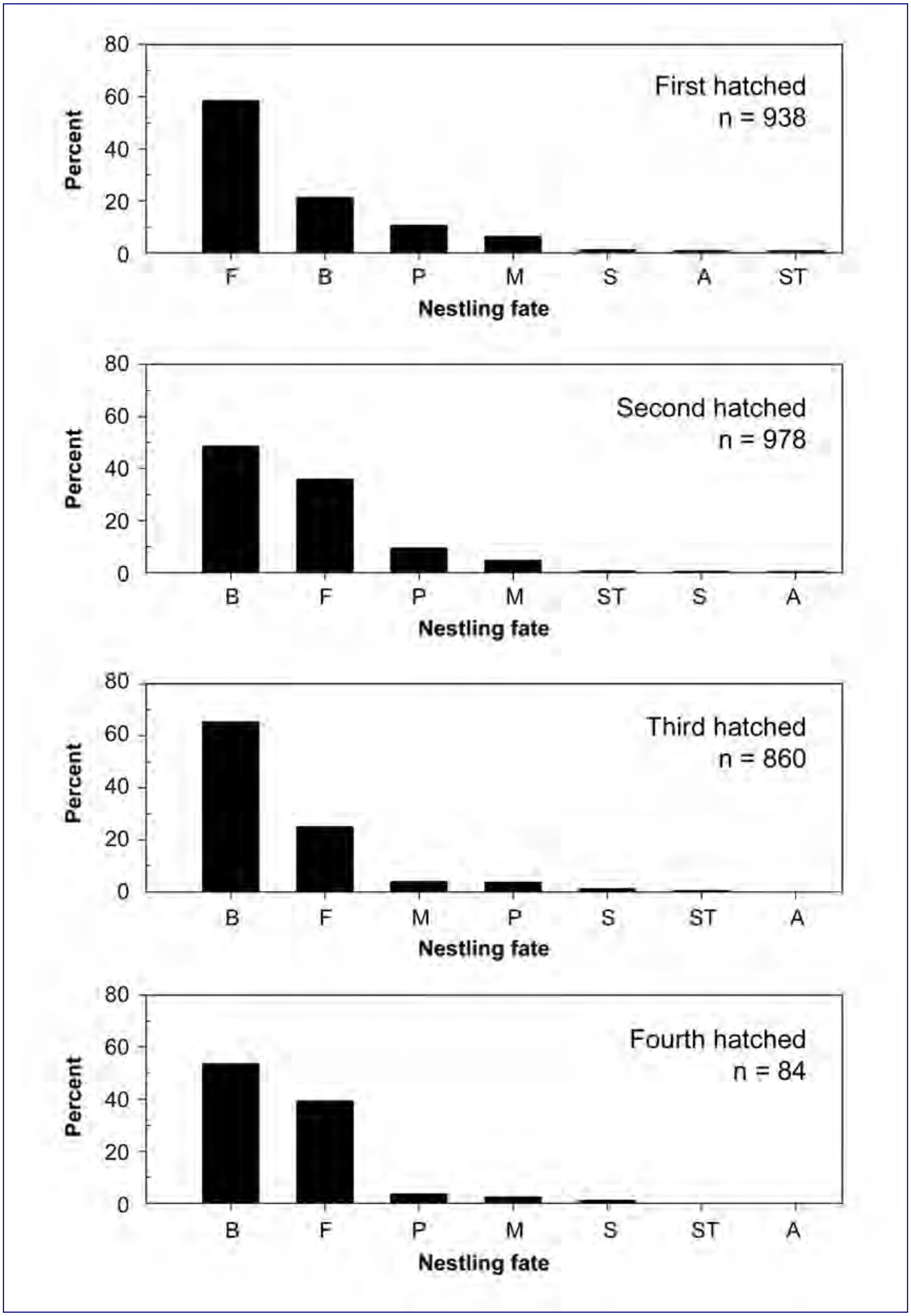

Figure 7.22—Frequency distributions of nestling fates by lay order. Philornid ectoparasitism has a greater impact on second-hatched and younger siblings than on first-hatched nestlings. Abbreviations are as follows: A = female abandoned nest, B = botfly ectoparasitism, F = fledged, M = missing from nest, P = predation, S = siblicide, ST = starvation.

Nest predation and "missing" nestlings (probably also the results of nest predation) account for the second and third greatest causes of mortality, depending on hatch order (fig. 7.22). Although red-tailed hawks are known to bring featherless nestlings plucked from open-cup nests as well as adult thrashers as prey to their aeries (E. Santana-C. 1983, pers. comm.), in the study area, hawks were rarely seen in the understory and have never been observed entering nest boxes. Therefore, they are not considered a major nest predator at thrasher boxes. Siblicide, which is often a consequence of sibling competition for food and space within the nest, although not severe, is a constant contributing factor. The fact that about three times as many third-hatched nestlings succumbed to ectoparasitism than fledged suggests that mortality caused by botfly ectoparasitism may be masking the impact of siblicide, i.e., even if more nestlings had survived the effects of ectoparasitism, they may very well have died as a result of siblicide. Many younger, and usually much smaller (runt) nestlings, died from suffocation. They were literally trampled to death by their older nest mates. Those that did not die directly from physical competition succumbed to malnutrition because the older and usually larger nestlings out maneuvered them when vying for food.

Siblicide results in brood reduction, a preadaptation in supertramps such as the pearly-eye, to ensure reproductive success even in patchy or disturbed environments. With exceptions, the pearly-eye does not normally begin incubating until the laying of the penultimate egg, which varies from the first to the third laid in two- to four-egg clutches, respectively. However, recent egg and clutch experimentation has shown that some females do not commence incubation until after the final egg is laid, regardless of clutch size (M. Cook 2003, in litt.). The pattern of commencement of incubation on the penultimate egg is common in passerines and other mimids (Brackbill 1985). Consequently, asynchronous hatching and brood reduction are prevalent (see Murray 1994, Nolan 1978, Nolan and Blank 1980, Royle and Hamer 1998, and Slagsvold et al. 1984, for discussions of brood reduction and adaptive values, including intraclutch egg-size variation; see also Clark and Wilson 1985, Harper et al. 1993, and Murray 1999, for discussions of the complexity of the subject). Combined, the remaining five sources of nestling mortality accounted for less than 2 percent of the total.

Egg Deposition Strategy and Reproductive Response to Hurricane Hugo

The effects of Hurricane Hugo on nesting phenology and number of clutches attempted subsequent to disturbance have been discussed. Commensurate with a compression of the breeding season and reduction in the number of nesting attempts was a depression in the number of eggs laid (fig. 7.23a). Excluding the 1979 breeding season when the study was just getting underway, fewer eggs were laid in the first post-Hurricane Hugo (1990) breeding season than in any other year prior to the commencement of more frequent and intense hurricane activity in the mid- to late-1990s. However, by delaying breeding and laying fewer eggs in 1990, the birds achieved a higher percentage of successful hatchings than in all but two prehurricane years. The 80-percent hatching success rate obtained in 1990 was higher than the 8-year predisturbance average of 78 percent (range: 70 to 82 percent). It is evident that the pearly-eye has adapted to ecological crunches so common on pelagic islands.

The ability of birds to increase reproductive rates and yield in response to environmental variation such as major habitat destruction has received "little rigorous quantitative scrutiny" (Ricklefs 2000a) and even has been put into question (Cooch and Ricklefs 1994, Sibly et al. 1991). The pearly-eyed thrasher attempted fewer nestings and laid fewer eggs in the first breeding seasons in the wakes of both Hurricanes Hugo and Georges (fig. 7.23a). Moreover, a higher than average annual number of eggs hatched two seasons after disturbance, thereby maintaining the average annual percentage of eggs hatched. This attests to the fact that this avian supertramp can indeed maintain its reproductive yield, if not a constant reproductive rate, in response to environmental stress.

Between 1979 and 2000, 41 percent of all eggs laid (1,547 of 3,783) and about 54 percent of all eggs hatched (1,547 of 2,861) produced fledglings, total numbers of which differed seasonally (fig. 7.23b). As in the egg stage, following Hurricane Hugo, breeders were able to increase their annual reproductive success through delayed breeding and moderate production. The percentages of nestlings fledged per eggs laid and eggs hatched were higher in the 1990 breeding season than in all but two of the eight predisturbance seasons (fig. 7.23b). The percentages of nestlings fledged per eggs laid (43 percent) and nestlings fledged per eggs hatched (54 percent) obtained during the 1990 breeding season were higher than the overall 8-year **predisturbance** fledging rate averages of 48 percent for eggs laid and 51 percent for eggs hatched. Likewise, the 1990 percentages (43 and 54 percent) were higher than the overall 19-season fledging rates of 32 and 42 percent for eggs laid and hatched, respectively. Fledging success diminished in postdisturbance breeding seasons from 1990 to 1999 owing to an increase in nest predators, competitors, and ectoparasitism (Arendt 2000) but increased again in 2000. It is possible that populations of this disparate group of organisms (mammals, birds, and insects) are once again stabilizing following the effects of two, almost back-to-back, major habitat disturbances.

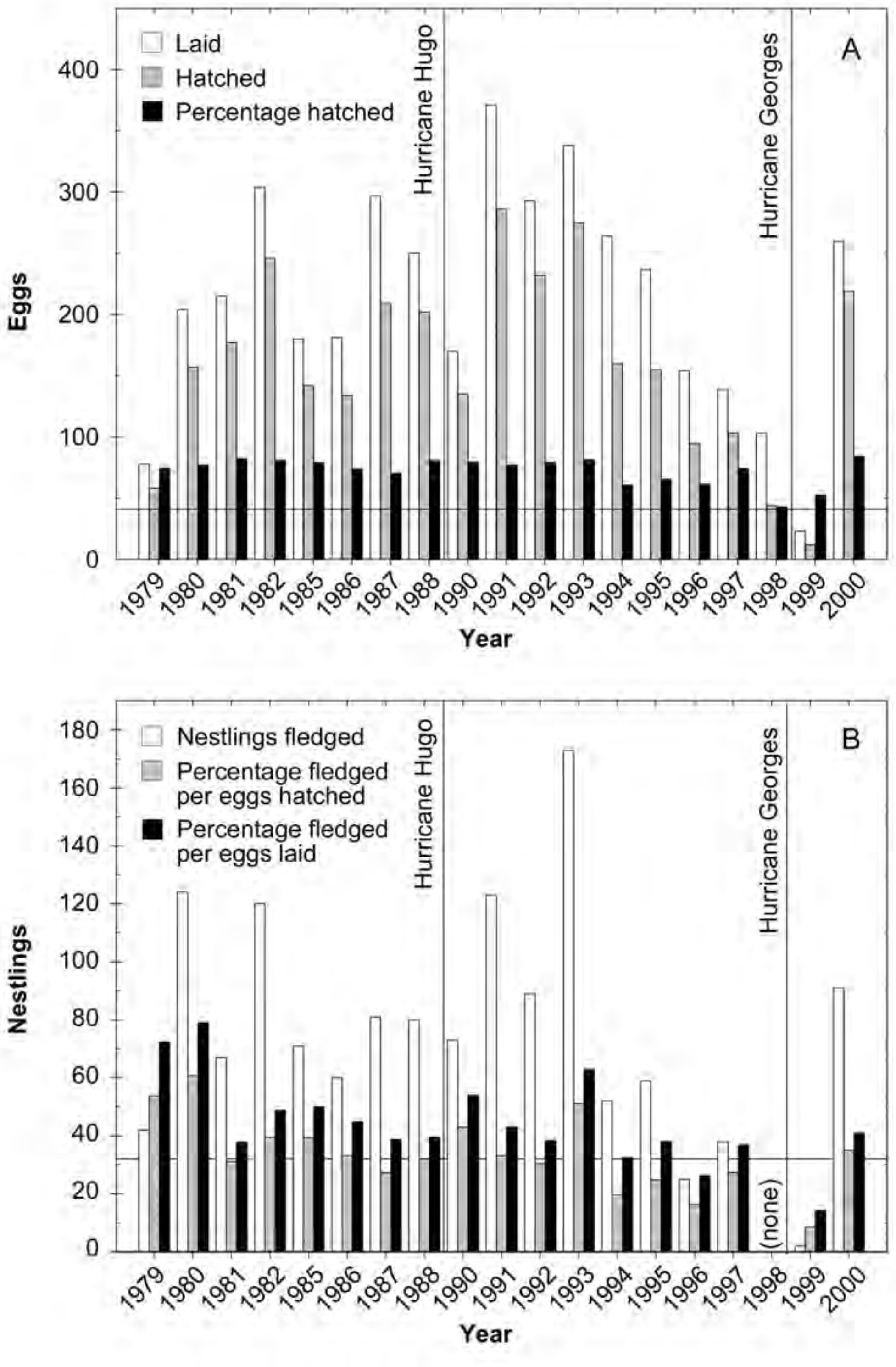

Figure 7.23—Annual reproductive success in a rain-forest population of the pearly-eyed thrasher in the Sierra de Luquillo, Puerto Rico, from 1979 to 2000. Although total numbers of eggs laid and nestlings fledged were reduced following major habitat disturbances, more importantly, the percentages of each were higher following the first hurricane, but not the second, suggesting synergistic effects of "back-to-back" major habitat disturbances.

In conclusion, after calculating the pearly-eye's annual reproductive success in terms of the number of eggs hatched and nestlings fledged over the 21-year period, there are four major revelations. First, in disturbance-free years the pearly-eye is capable of maintaining a constant and fairly high rate of success even for a tropical passerine. Second, through a number of physiological and behavioral adaptations, it is able to achieve above-average rates of reproductive success even after major habitat destruction. Third, the long-range impact of Hurricane Hugo may be more severe than previously assumed. Five years following the storm, the number of eggs hatched dropped below a 12-year predisturbance average, as did the number of nestlings fledged per eggs laid. Even the number of nestlings fledged per eggs hatched was well below average from 1994 to 1998 (prior to Hurricane Georges). The 1998 breeding season was one in which no nestlings fledged owing to heavy losses to philornid ectoparasitism, the impact of which greatly increased following major habitat disturbances. Finally, even insular species like the thrasher that have adapted to stochastic events such as periodic habitat disturbances cannot rebound as well when the disturbances become too frequent or destructive in nature.

Lifetime Reproductive Success

Evaluation of a species' reproductive success at the population level involves determining the LRS of marked, known-aged individuals. Variation of lifetime reproductive success is a function of the way a life cycle is defined, and thus comparisons across studies and taxa will be valid only if the life cycles are complete, i.e., over an entire generation (Barrowclough and Rockwell 1993). As a measure of performance, LRS reveals the full extent of individual variation in reproduction, while providing a better basis for estimating biological fitness than any other measure yet available (Newton 1989). The following section (a) covers a brief overview of some of the accumulated knowledge concerning avian LRS, (b) treats how the pearly-eye compares with other species, and (c) concludes with an evaluation of several of the pearly-eye's LRS parameters.

Newton (1989) published the results of 23 avian life-history studies comparing LRS components among a diverse group of avian taxa. From these studies, some general trends have emerged: (1) most fledglings die before they can breed, (2) a variable percentage of breeders (5 to 50 percent, depending on the species) produces no fledglings, (3) as many as 50 percent or more of the fledglings are produced by only 15 to 30 percent of the breeders (see also Thorstrom et al. 2001), (4) few individuals reproduce themselves many times over, and (5) the best predictors of the number of fledglings and recruits produced by an individual or breeding pair are (a) the number of recruits per fledgling (Balen et al. 1987), (b) offspring survival (Fitzpatrick and Woolfenden 1988); and especially (c) lifespan (Balen et al. 1987, Grant and Grant 2000, Hötker 1988, Pierotti 1991). For a review of the evolution of life history studies, see Charnov 1993; Martin 2004; Partridge and Harvey 1988; Ricklefs 2000a, 2000b, 2000c, 2004; Roff 1992).

Comparison of Lifetime Reproductive Success Parameters Among Avian Taxa

How does the pearly-eye compare with other species in terms of lifetime reproductive success? From the 23 species presented in Newton (1989), descriptive statistics of various LRS parameters are presented in table 7.7 and are compared to those of the pearly-eye. For some LRS parameters, it would be illogical to compare the pearly-eye with raptors, ducks, geese, and seabirds. However, for others, the variation among all avian groups thus far studied is so small that comparisons were justified using all 23 species.

Table 7.7—Lifetime reproductive success parameters of as many as 23 species compared to those of the pearly-eye (sexes lumped in all species)

	All species		
Parameter	**Mean or maximum**	**Range**	**Means for pearly-eye**
Body mass (g)[a]	34	9–79	112
Maximum longevity (years)[a]	9	5–14	15[b]
Mean longevity (years)[a]	1.8	1.3–4.2	6
Percentage of annual adult survival[c]	59	23–95	85
Number of clutches per season[c]	1.8	1–3	2.3
Clutch size[c]	4.4	1–11	3
Percentage fledged per egg laid[c]	59	29–86	48[d]
Number of fledglings per lifetime[c]	30	0–62	45
Percentage of recruits per lifetime[c]	7	2–12	3

[a] Pearly-eye compared to short-lived, hole- and open-nesters, and cooperative breeders.

[b] 15 years recorded in the rain-forest population; 17 years in the Guánica dry-forest population.

[c] Pearly-eye compared to all 23 species, including raptors and seabirds.

[d] Mean of 48 percent for an 8-year period (1979-1988) prior to frequent and intense hurricane activity; 41 percent from 1979 to 2000.

The pearly-eye's body mass was compared to that of other passerines and some similar-size nonpasserines. The pearly-eye is clearly a very large passerine, and it is a relatively long-lived species capable of surviving as long as some raptors and individuals in other phylogenetically distant taxa. The pearly-eye's annual adult survival rate equals that of many long-lived species of geese and even some seabirds. The pearly-eye's modal clutch size of three is relatively small for many north temperate passerines, but not for tropical species. Likewise, the percentage of fledglings per eggs laid falls short of the midway point between the lower and upper percentages of successful fledgings for the other 23 species. Nonetheless, and most importantly, many individual pearly-eyes are able to produce more than the average number of fledglings during their reproductive lifetimes. The pearly-eye's prolonged lifespan and nest-site persistence obviates a high percentage of yearly recruits into the breeding population.

Lifetime Reproductive Success Patterns Among Known- and Minimum-Aged Pearly-Eyed Thrashers

Clutch Size and Number Per Season and Egg Volume

A discussion of LRS topics involving 31 known-aged individuals would be limited because of the relatively small sample size. Therefore, data gathered for various LRS parameters involving the 18 known-aged female and 13 known-aged male pearly-eyes were compared to data gathered from 247 breeders (126 minimum-aged females and 90 minimum-aged males) to determine if results were similar. Frequency distributions of size and number of clutches per season as well as egg volume were similar for both groups of females. Therefore statistical testing was done on known- and minimum-aged individuals to determine how lay month, number of nestings per season, mean egg size (volume—see also Arendt 2004b) and clutch size, vary throughout a female's lifetime (fig. 7.24). Column A includes all years, whereas column B shows the results when hurricane-affected years (1990 to 1991 and 1999 to 2000) were eliminated from the analyses. Although there was considerable variation in the number of clutches laid per season and month, the disparity was not significant in either case. However, regarding lay month, there is a clear downward trend showing that older females tend to nest earlier than do younger females. The curve for number of clutches per season was convex with a downward trend toward young and old females (fig. 7.24). Thus, the number of clutches initiated each season ($y = 3.12 - 0.10$; $R = 0.28$; $P = 0.053$) and, to a lesser extent clutch size, reveal that productivity as measured by these two indices is lower in young and old females, and highest in middle-aged nesters (for similar results, see Fitzpatrick and Woolfenden 1988, Woog 2002). Although clutch size was small in this sampled population, and was virtually static throughout life, there was a reduction in 12-year-old-and-older females (fig. 7.24). This downward trend was also revealed in the comparison of female age vs. egg volume, in which there was a significant reduction of egg volume in older females: volume = 7.09 – (0.018 * female age); $R^2_{adj} = 0.29$; $P < 0.001$). For comparison, in a Swedish population of the rock pipit (*Anthus petrosus*), a passerine with an average clutch size of four (2 to 5), Askenmo and Unger (1986) observed that clutch size increased

Pearly-eyes exhibit the same LRS patterns as do other passerines, i.e., most fledglings die before breeding, few breeders produce fledglings or recruits, and lifespan is a major predictor of LRS.

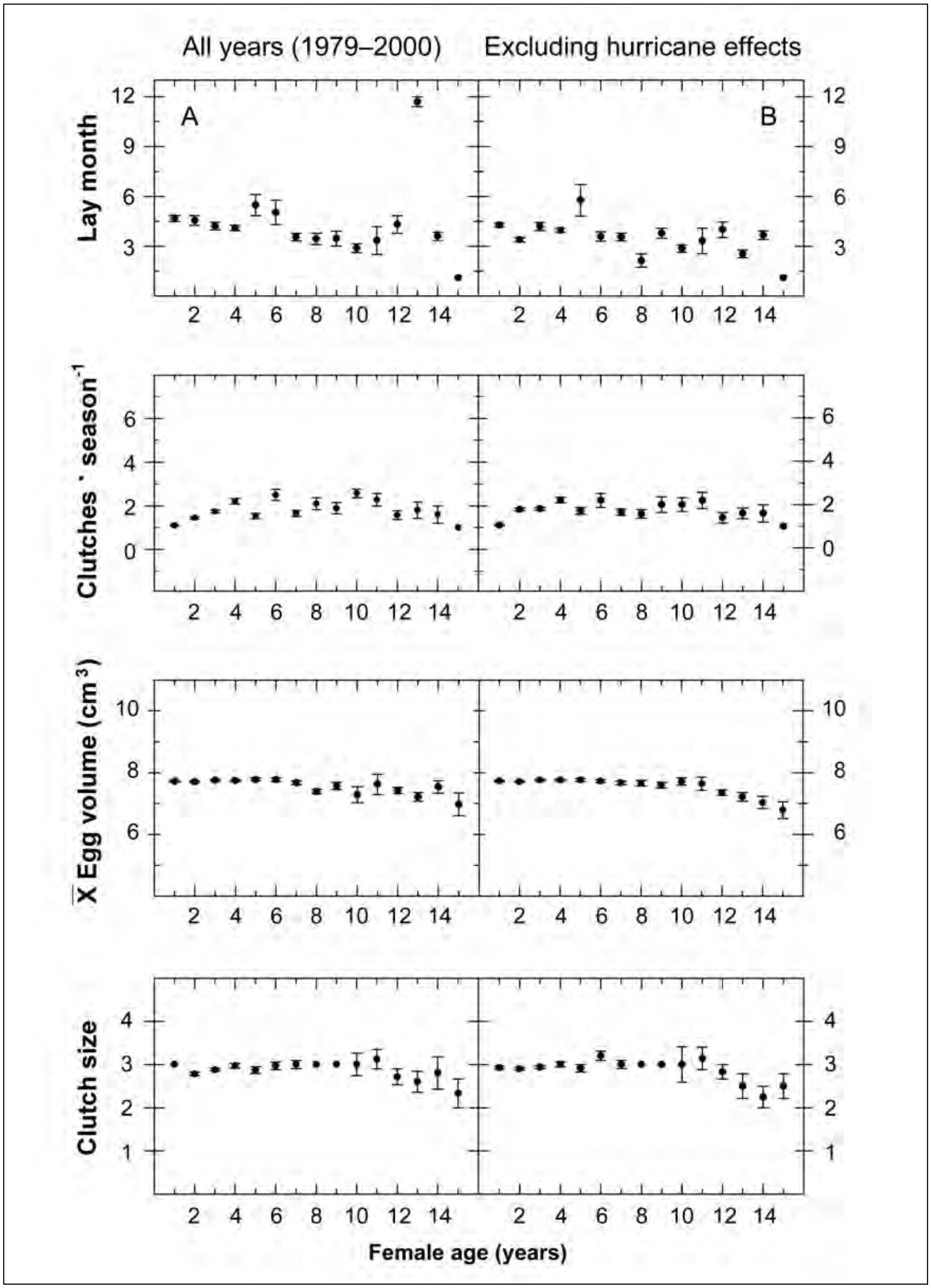

Figure 7.24—Comparisons of female ages vs. egg-laying months (first clutches only; n = 592), number of multiple clutches (1,327), mean egg volumes (3,156), and clutch sizes (1,386) between 1979 and 2000 (col. A). Results from the same analyses after hurricane-affected years (1990–1991 and 1999–2000) were eliminated are shown in column B. The convexity of the curves attests to the fact that "middle-aged" females in their prime are more productive than either novice young or aged females. Data points (filled circles) are means and capped vertical bars (⊥, ⊤) are ±1 standard errors.

slowly over most of the season but then decreased rapidly toward the end. In a Mediterranean multibrooded passerine, the black wheatear (*Oenanthe leucura*), Soler et al. (1995) found that female age and time of residency, as well as indices of parental condition such as discontinuities in feather growth or prevalence of ectoparasites did have significant effects on breeding productivity. In a Hungarian population of the great tit, Báldi and Csörgő (1994) showed that the age and dominance of males had no significant effect on clutch and egg sizes, but possibly on laying date (see, however, Potti 1993). The influence of age and dominance of females, nevertheless, was much more prominent, with dominance status being more important than age.

Body Size and Age of the Female

Intuitively, large, aggressive females should be better able to successfully defend their territories and nest boxes throughout life. Therefore, three morphological characters were tested to determine if older, more experienced (proven) female breeders are larger than younger nesters. Results were mixed. Length of the culmen (chosen for its role in competitive and predatory contexts) did not differ significantly among females. That is, on average, older females did not have longer bills than younger ones (fig. 7.25). Body mass, however, generally increased to about age five, leveled off, and then began to decrease after about 10 years of age, suggesting that very old females are lighter (and less fit?) on average. This finding is in accord with mean egg volume results (fig. 7.24). Smaller (often younger) females lay smaller eggs (see also Leeson and Summers 1987). Wing chord generally increased until about age 4, and then generally leveled off. Owing to the very small sample size of very old females (>12 years), it is impossible to make generalizations as to their body size for even minimum-aged females (fig. 7.25). However, from a study of the collared flycatcher in central Moravia, Czech Republic, from 1988 to 1993, Bureš and Král (1995) found that senescence[2] appeared in female flycatchers from about age four, after which wing length decreased and older females began to lay later in the season than did younger ones, including 3-year-old females, which was the same egg-laying trend observed in this study.

Total Number of Nestlings and Fledglings Produced

Two additional and very important LRS parameters are the number of nestlings and fledglings produced on a spatiotemporal scale. Several statistical tests were performed comparing the number of nestlings and fledglings produced per nest,

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[2] Senescence is the decline in organismic performance with age, leading to decrements in survival probabilities owing to intrinsic causes and in reproductive success (Moreno 1993).

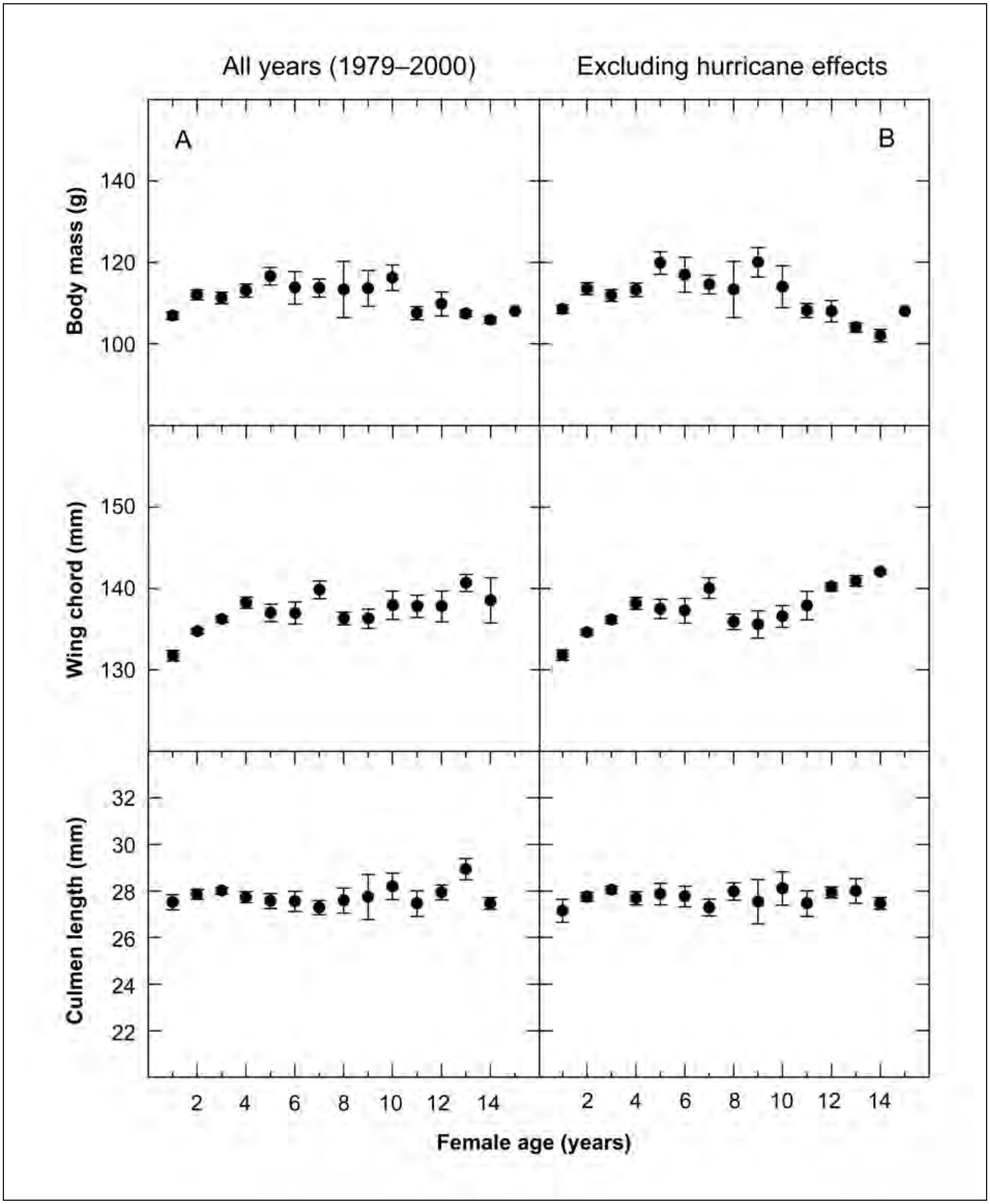


Figure 7.25—Comparison of body masses, length of wing chords, and exposed culmens of 143 known- and minimum-aged female pearly-eyes over 19 breeding seasons (col. A) and excluding the effects of Hurricanes Hugo (1990–1991 seasons) and Georges (1999–2000 seasons) (col. B). Data points (filled circles) are means, and capped vertical bars (⊥, ⊤) are ±1 standard errors. Very old females are shown to have longer (or just as long) wing chords than younger ones, but are noticeably lighter in mass.

season, and during a nest pair's reproductive lifetime. Prior to testing, results from the descriptive statistics revealed that known- and minimum-aged females produced similar numbers of nestlings and fledglings per nest and season (table 7.8). Frequency distributions of the number of nestlings and fledglings produced per nest and season were also similar between the two groups: (1) nestlings per nest: t = -0.26; P = 0.79; and nestlings per season: t = -0.72; P = 0.46; and (2) fledglings per nest: t = -1.21; P = 0.22; and fledglings per season: t = -1.23; P = 0.21. Likewise, the frequency distributions of the number of nestlings and fledglings per nest and season sired by known- and minimum-aged males were similar (figs. 7.26 through 7.29). None of the age-category comparisons resulted in a significant difference. Therefore, to increase sample sizes, further testing was conducted on the combined total of known- and minimum-aged females and males. Results were similar between both genders for the first 10 to 12 years, but diverged thereafter. During a nest pair's reproductive years, there is a general increase in the production of nestlings per nest and season to about age 4 (fig. 7.30). Production then decreases slightly but is sustained to just past midlife (8 to 9 years). It then drops off precipitously in females, but increases in males. The production of fledglings is less cyclic. For females, there is a gradual but continuous reduction in the number of fledglings produced per nest and season throughout her reproductive life, with productivity beginning to decline more abruptly after age 9 or 10 (fig. 7.30). In terms of fledgling production, the continuous decline in reproductive success among female breeders was confirmed by constructing a frequency distribution of nestling fates for known- and minimum-aged females (fig. 7.31). Clearly, fledging success is highest prior to midlife, and then continues to decline as females mature.

Table 7.8—Numbers of pearly-eye nestlings and fledglings produced per nest and season by 18 known-aged and 126 minimum-aged females

	Mean		SE		Range	
	Known-aged	**Minimum-aged**	**Known-aged**	**Minimum-aged**	**Known-aged**	**Minimum-aged**
Nestlings:						
Number per nest	1.85	1.83	0.29	0.19	0–3	0–4
Number per year	4.4	5.61	.48	.39	0–9	0–13
Fledglings:						
Number per nest	1.42	1.61	1.24	.18	0–3	0–4
Number per year	2.65	3.37	.57	.31	0–7	0–11

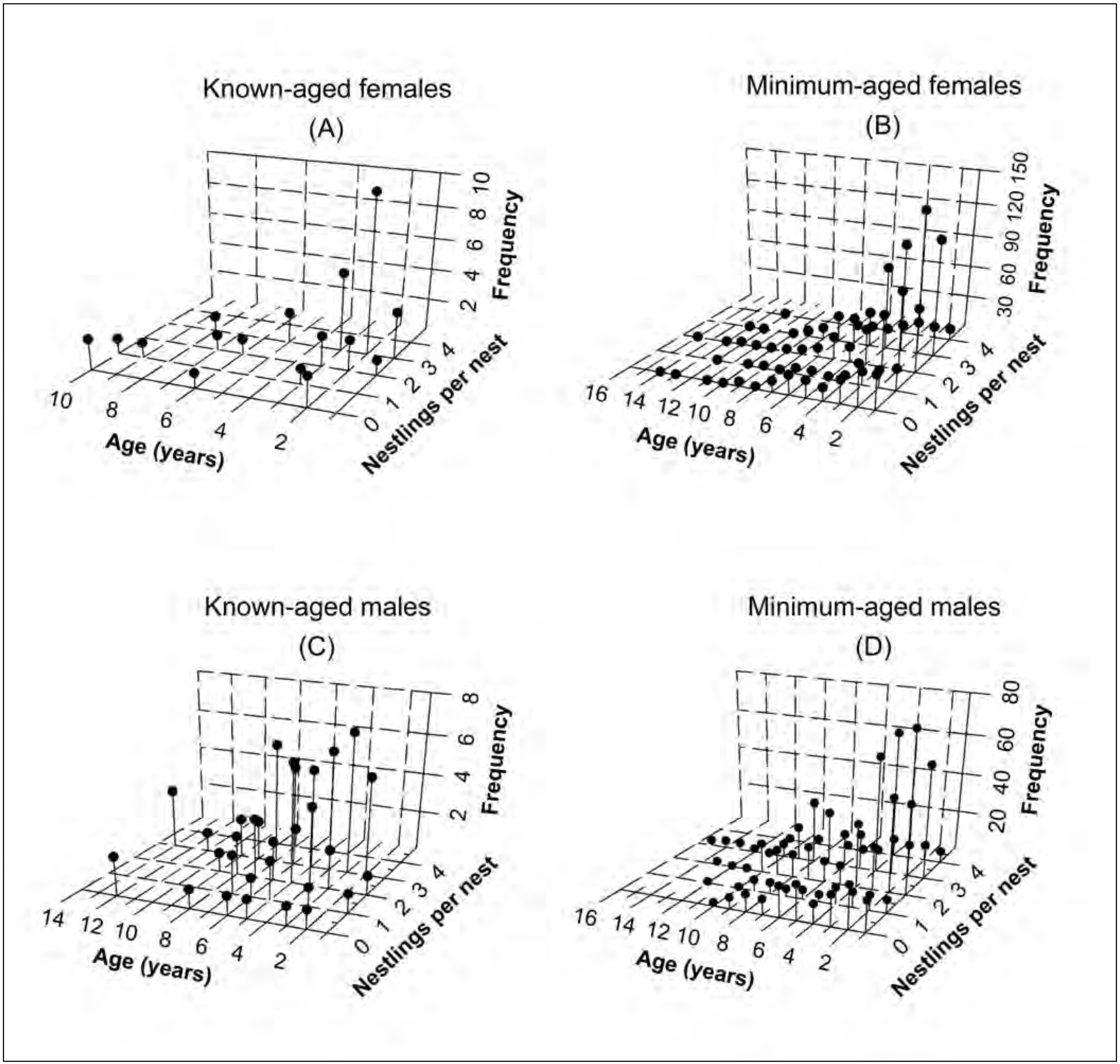


Figure 7.26—Frequency distribution of nestlings per nest of known-aged (graphs A and C) and minimum-aged (graphs B and D) female and male pearly-eyes, respectively. Although adult breeders produce nestlings from ages 1 (min. of 9 mo, thus far recorded) to at least 15 years and possibly even longer, prime productivity for the nest pair is between 2 and 6 to 8 years of age, depending on the reproductive parameter.

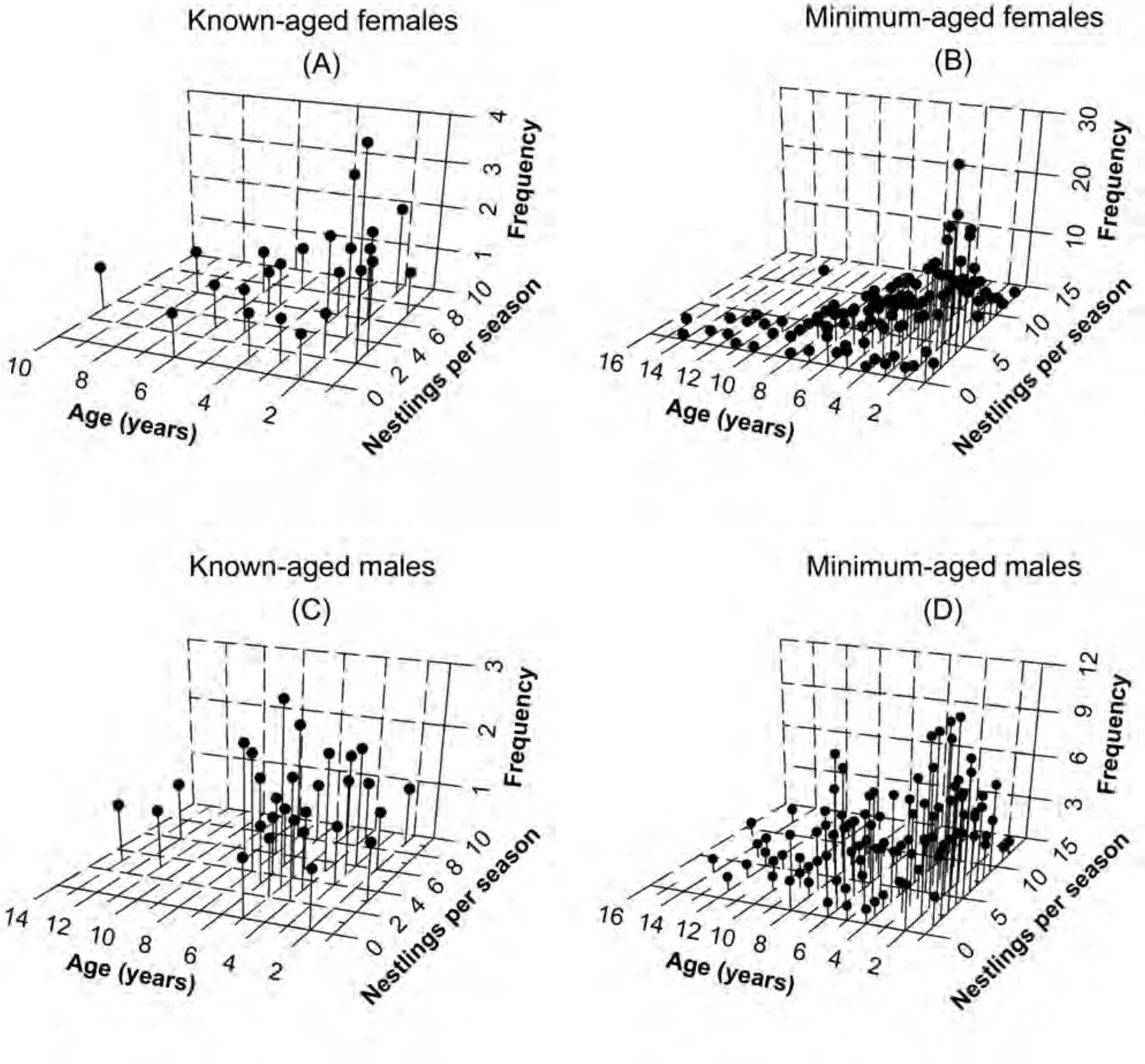


Figure 7.27—Frequency distributions of nestlings per season of known-aged (graphs A and C) and minimum-aged (graphs B and D) female and male pearly-eyes, respectively. As in the production of nestlings per nest, although female pearly-eyes from ages 1 to 15 years are capable of producing often several nestlings a year, most nestlings are produced on a seasonal basis by breeders 2 to 8 years old.

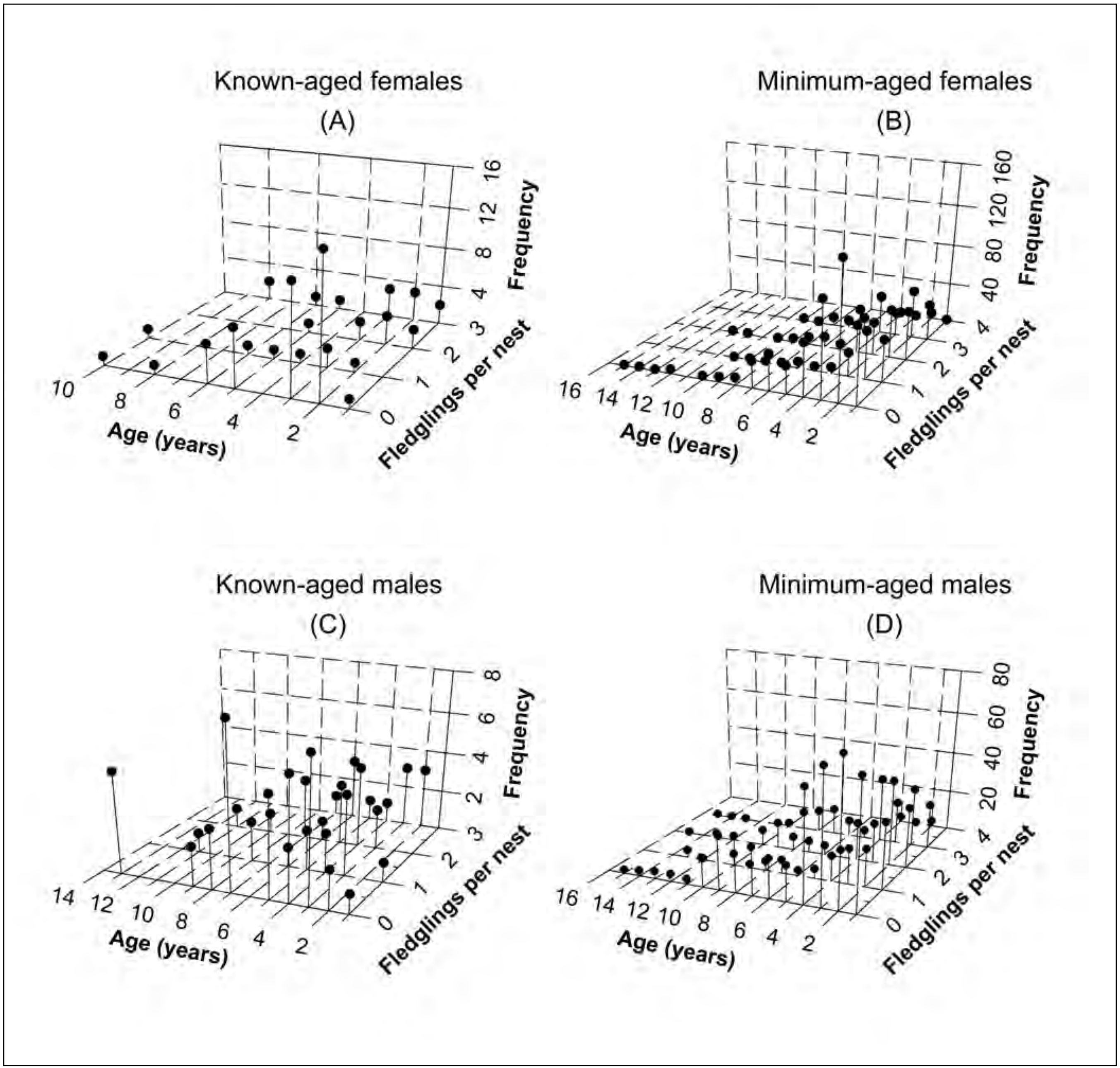


Figure 7.28—Frequency distribution of fledglings per nest of known-aged (graphs A and C) and minimum-aged (graphs B and D) female and male pearly-eyes, respectively. Most breeders capable of producing 1 to 4 fledglings per nest ranged in ages from 1 to 8 years old.

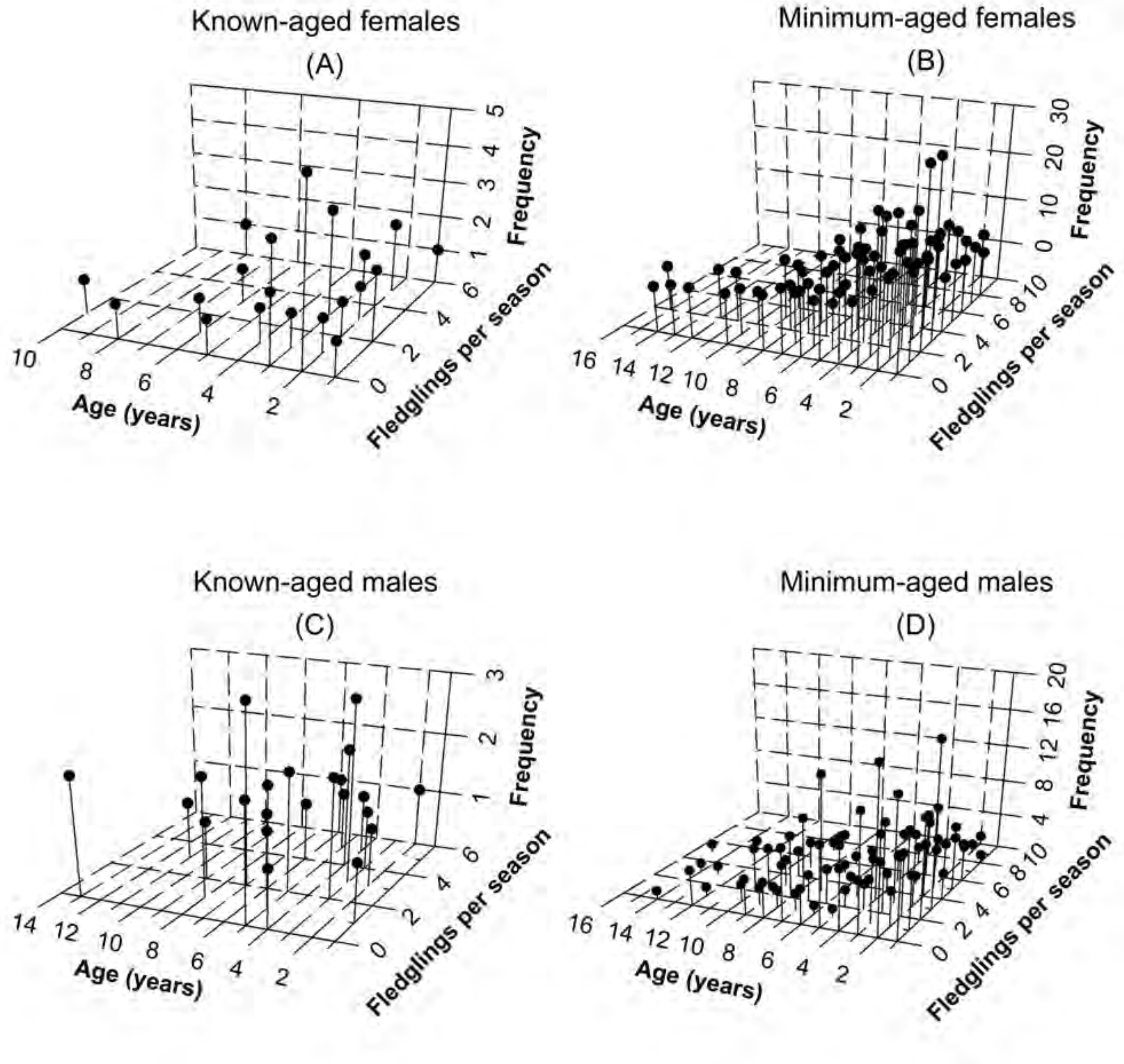


Figure 7.29—Frequency distributions of fledglings per season of known-aged (graphs A and C) and minimum-aged (graphs B and D) female and male pearly-eyes, respectively. Basing productivity on the number of fledglings produced each season, prime productivity in adult male and female breeders was between 2 and 4 years, dropping slightly but continuing steadily until ages 9 to 10, after which productivity dropped off dramatically. Older males tended to produce slightly more fledglings each season than did older females (see also fig. 7.30).

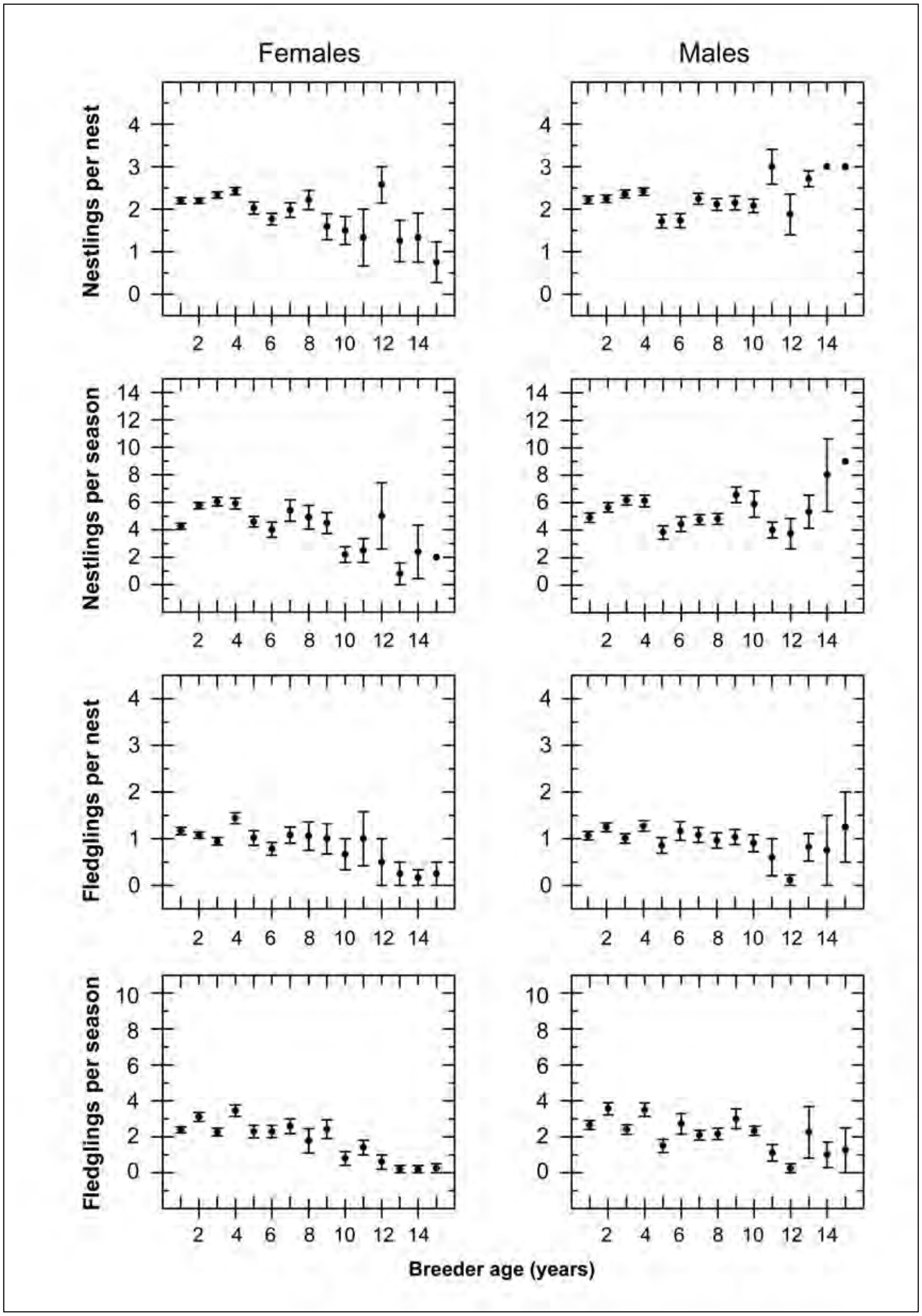
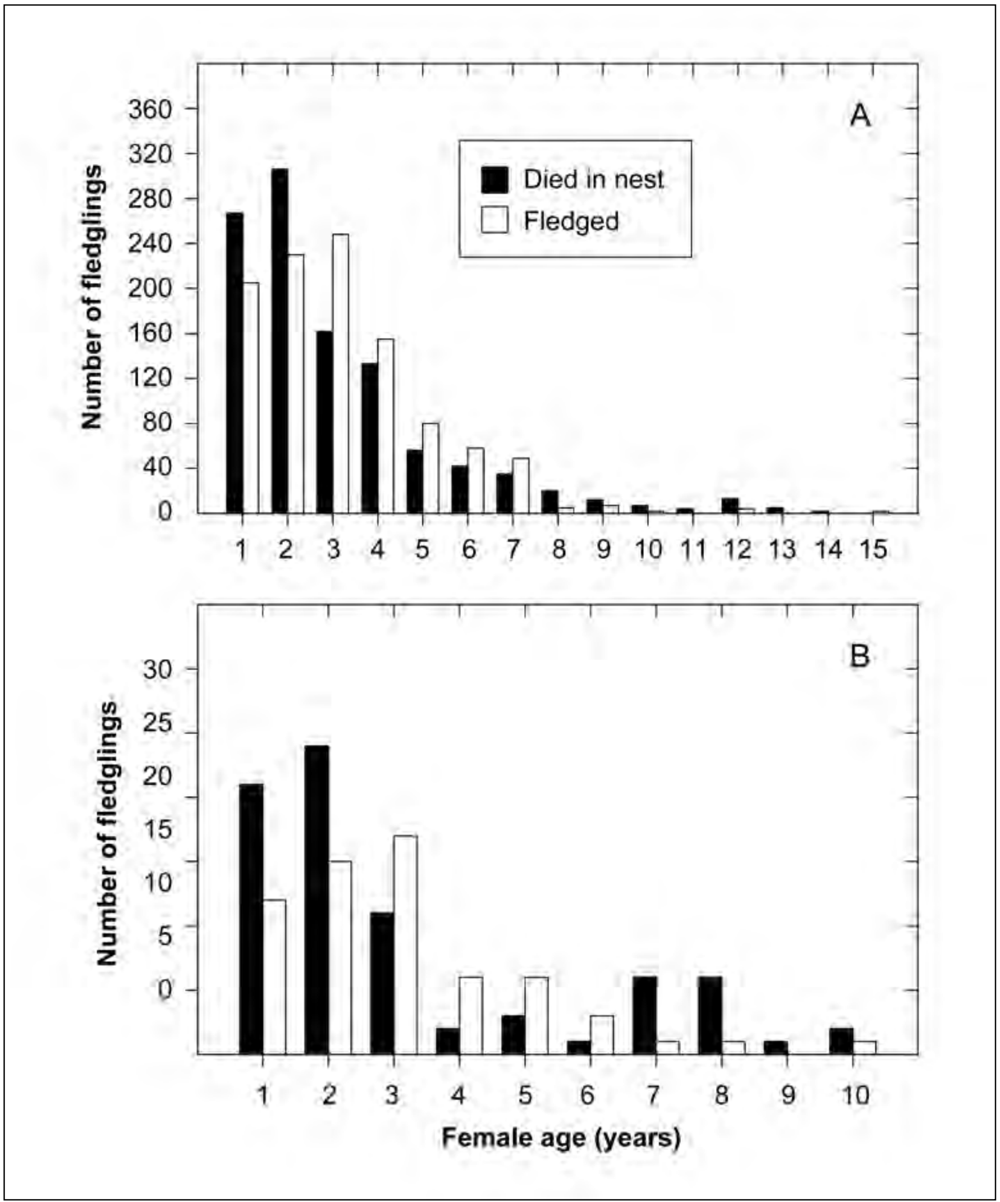


Figure 7.30—Number of nestlings and fledglings per nest and season produced by 247 known- and minimum-aged pearly-eyed thrashers, 143 banded females and 104 banded males. In every case, nesting success increased until about the fourth or fifth year of life, and then decreased as breeders aged, with the exception of very old males (explained in text). Data points (filled circles) are means and capped vertical bars (⊥, ⊤) are ±1 standard errors.



Figure—7.31. Frequency distribution of nestling fates for 126 minimum-aged (A) and 18 known-aged (B) female pearly-eyes. In both groups, nest failure is most prominent in first- and second-year breeders, as well as in older breeders. Nesting success is highest in third- and fourth-year breeders.

Although the patterns of nestling and fledgling production per nesting attempt and season were similar between the sexes for about the first 11 to 12 years, thereafter female productivity continued to decline, especially in their last two to three seasons as breeders (fig. 7.30). Conversely, male productivity increased in every case during the same period (fig. 7.30). One could easily surmise that because males simply inseminate females and subsequently may not experience such high costs of reproduction, i.e., the formation of eggs followed by 14 days of incubation, during which time the females' food intake is more limited than theirs, this might enhance the males' overall fitness, resulting in the observed apparent increased productivity during their last few breeding seasons. However, a review of the history of the five males apparently contributing to the elevated production in their boxes during their last seasons as breeders (13 to 15 years of age) revealed that (a) one male changed boxes, (b) males averaged 3.4 females during their reproductive years (*SD* = 1.14; range: 2 to 5 females per male); and (c) the average age of their mates during their last breeding season was 4.2 years (*SD* = 3.11; range: 1 to 8 years of age), i.e., the age of peak productivity. There were only two instances in which both mates were older during the males' last breeding seasons. One female was at least 7 years old when her mate was at least 14, and one female was a minimum of 8 years old when her mate was at least 12. Thus, the apparent elevated reproductive success in very old males may instead be best attributed to their generally younger mates. Similar patterns of age-related productivity were documented in two long-term studies, i.e., village weaver (Collias et al. 1986) and Florida scrub jay (Fitzpatrick and Woolfenden 1988). Both species are also passerines adapted to semitropical environments.

Because male pearly-eyes live, or at least breed, for more seasons than females, they might be expected to produce more offspring. Frequency distributions of the total number of fledglings produced by known- and minimum-aged females and males are presented for comparison (fig. 7.32). Minimum-aged males did produce significantly (M-W R S: *T* = 9202.5; *P* = 0.01) more fledglings (avg. 20.69; median 21; 25 to 75 percentiles = 6.5 to 27.5; 95 percent *CI* = ± 2.87) than did minimum-aged females (avg. 18.61; median 18; 25 to 75 percentiles = 5 to 18.75; 95 percent *CI* = ± 1.93). It is evident from figure 7.32 that although both **average** minimum-aged females and males can produce about 20 fledglings (18.6 and 20.7, respectively) during their lifetime, twice as many males than females produce more than 30 fledglings, owing mostly to their higher survival rates. Known-aged females and males produced about the same number of fledglings (9.5 and 10.3, respectively) (fig. 7.32).

In comparison with other passerines, the production by both sexes of a maximum of 45 fledglings during a lifetime of breeding is above the collective average: avg. max. number = 30, range: 0 to 62, for 23 species (Newton 1989). As further examples, during a 12-year study of meadow pipits (*Anthus pratensis*) in northwest Germany, Hötker (1988, 1989) found that both males and females produce on average about six fledglings during their reproductive lives (range: 0 to 25). From a 10-year study in southern Michigan, Payne (1989) showed that indigo

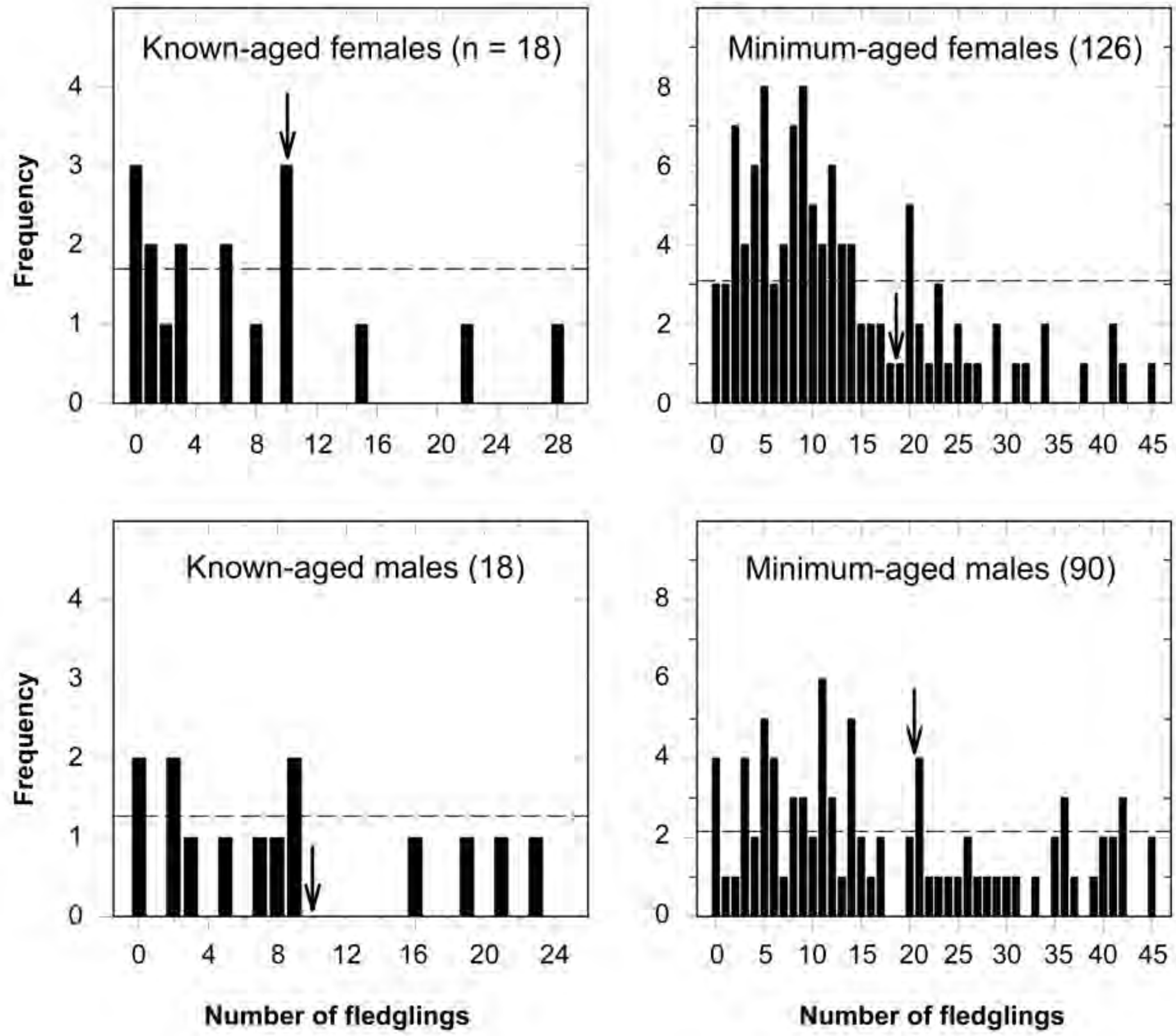


Figure 7.32—Lifetime reproductive success (expressed as number of fledglings) in 31 known-aged and 216 minimum-aged pearly-eyes between 1979 and 1997. Although frequency distributions varied considerably, there were no significant gender differences at the 95 percent level of confidence. Arrows (↓) indicate the mean number of fledglings per breeder, whereas plot-wide dashed lines represent frequency means.

buntings (*Passerina cyanea*) can produce up to 27 fledglings during their lives. During a 22-year study of a German population of the pied flycatcher, Sternberg (1989) established that the most productive females and males produced 36 and 37 fledglings, respectively. At the upper extreme, from a 10-year study in Northern Belgium, Dhondt (1989a) reported that blue tits (*Parus caeruleus*), although a relatively short-lived species, produced as many as 62 fledglings in a lifetime (see also Zeh et al. 1985).

Recruitment Into the Breeding Population

Factors Influencing the Number and Fitness of Recruits

Numerous long-term studies conducted on a variety of species from diverse avian taxa have shown that 50 percent or more of the production of fledglings and future recruits is achieved by only 15 to 30 percent of the breeders (Clutton-Brock 1988, Newton 1989). Among passerines in particular, few breeders are successful in producing new recruits. The pearly-eye is no exception to the general rule. Below, are a few direct and indirect factors affecting the number and quality of recruits.

There were no parental gender differences in the production of fledglings or recruits.

Breeding longevity of recruits' parents—

Longevity records of males that produced recruits revealed that they breed for significantly more seasons (mean = 9; *SE* = ± 1.13; range: 2 to 15; *t* = 4.37; 95 percent *CI* for diff. of means = 1.81 to 4.82; *P* <0.001) than the "typical" male breeder, which nests on average for 5.7 seasons (*SE* = 0.33; range: 1 to 11) before disappearing. Likewise, male parents of recruits breed significantly longer than female parents of recruits (fig. 7.33; see also chapter 6) (*t* = -3.69; 45 df; 95 percent *CI* for diff. of means = -5.15 to -1.20; *P* <0.001). However, female parents of recruits breed significantly longer (avg. 6.1 years; *SE* = 1.26; range: 2 to 14; *t* = -2.20; 13 df; 95 percent *CI* for diff. of means = -2.35 to -0.12; *P* = 0.02) than females that failed to produce recruits (avg. = 5 years; *SE* = ± 1; range: 1 to 9).

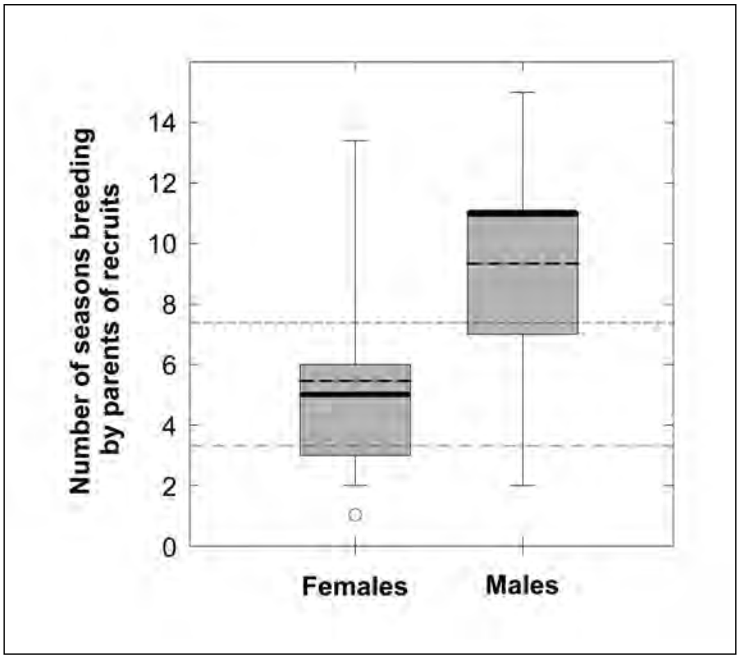


Figure 7.33—Number of seasons that adults who produced recruits were recorded breeding. Note that the median number of seasons (solid horizontal lines within rectangles) for males who sired recruits is more than double that of females (11 vs. 5, respectively), and the combined average of 7.4 breeding seasons for parents of recruits (upper plot-wide dashed line) is more than double the average of 3.2 seasons for all breeders (lower plot-wide dash-dot-dot line). Within each rectangle, dashed lines are means, lower and upper hinges 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.

Age and body mass comparisons between recruits' parents—
Several between- and within-gender age and body mass comparisons were carried out on the parents of recruits to assess any potential demographic and size similarities or differences. Parents of male and female recruits were similarly aged in the year the recruits fledged. For male recruits (*T* = 159; *P* = 0.41), the father's median age was 4 years (25 to 75 percentiles = 2 to 7.5 years; avg. = 5 years; *SD* = 3.63; range 2 to 15 years) and the mother's median age was 3 years (25 to 75 percentiles = 2 to 4.5 years; avg. = 3.54 years old; *SD* = 1.90; range: 1 to 7 years). For female recruits (*T* = 182.5; *P* = 0.23), the father's median age was 2 years (25 to 75 percentiles = 1 to 4.5 years; avg. = 3 years; *SD* = 2.36; range: 1 to 8 years), and the mother's median age was 1 year (25 to 75 percentiles = 1 to 2 years; avg. = 2.14 years old; *SD* = 1.99; range: 1 to 8 years). Although there were no significant differences in the ages of the parents of either male or female recruits, these results also reflect the higher mortality rate of resident female breeders (see chapter 6).

As expected, mothers of male recruits were significantly older than mothers of female recruits (*T* = 230; *P* = 0.02). Likewise, fathers of male recruits were significantly older than fathers of female recruits (*T* = 229; *P* = 0.04). It is not surprising that both parents of male recruits were older than parents of female recruits because males did not enter the breeding population as young as did females.

Between- and within-gender comparisons of body mass of the recruits' parents were carried out. As anticipated (see sexual dimorphism results in chapter 5), mothers of male recruits were significantly heavier than fathers of male recruits (*T* = 201.5; *P* = 0.01). The mother's median body mass was 111 g (25 to 75 percentiles = 106 to 118 g). The father's median body mass was 103 g (25 to 75 percentiles = 100 to 108 g). Conversely, and quite unexpectedly, however, mothers of female recruits were **not** significantly heavier than fathers of female recruits (*T* = 220; *P* = 0.44). The mother's median body mass was 110 g (25 to 75 percentiles = 104 to 115 g). The father's median body mass was 106 g (25 to 75 percentiles = 101 to 110 g).

Within-gender comparisons revealed that fathers of female recruits were heavier (avg. = 107 g; *SD* = 6.39; range: 100 to 118 g) than fathers of male recruits (avg. = 104.5 g; *SD* = 5.16; range: 97 to 114 g) suggesting that fathers of female recruits were older on average than those of male recruits. Contrarily, mothers of female recruits were lighter (avg. body mass = 108.9 g; *SD* = 6.8; range: 97 to 120 g) than mothers of male recruits (avg. body mass = 112.8 g; *SD* = 9.41; range: 100 to 134). These results suggest that mothers of female recruits were younger on average than mothers of male recruits because younger individuals of both genders tend to weigh less than older ones (see also chapter 5 and Curio 1983). Once again, it was not surprising that female parents of female recruits were lighter, since female recruits enter the breeding population well (often years) before male recruits, and very well could have fledged from boxes housing young, resident females. Why fathers of female recruits were heavier and older is not so easily explained, and remains a mystery.

Production of Recruits and Potential Breeders

Over a 21-year period, of 58 known-age dispersers that attempted to enter the breeding population (i.e., take up residency in nest boxes), 31 were successful. However, because all 58 were observed attempting to enter into the breeding population, e.g., as "floaters" prospecting for nest sites, I have included all 58 in the following analyses.

No individual breeder parented more than three recruits. In fact, most breeders and nest boxes produced no recruits (fig. 7.34). There was no significant gender difference in the number of unsuccessful nesters, or in the other three categories of nesters producing 1 to 3 recruits. Of 143 females, 118 (83 percent) failed to produce recruits. Similarly, of 104 males, 82 (79 percent) were unsuccessful (z-Test on proportions with Yates correction applied: $z = 0.56$; 95 percent *CI* for diff. = -0.06 to 0.13; $P = 0.57$). Only 15 percent, i.e., 21 of 143 female breeders and 17 percent (18 of 104) male breeders produced single recruits ($z = 0.38$; 95 percent *CI* for diff. = -0.11 to 0.06; $P = 0.70$). Two percent of both female and male breeders (3 of 143 and 2 of 104, respectively) produced two recruits ($z = -0.36$; 95 percent *CI* for diff. = -0.03 to 0.03; $P = 0.71$). Whereas an additional 2 percent of male breeders (2 of 104) produced three recruits, only one of 143 females (<1 percent) was successful in fledging three recruits ($z = 0.27$; 95 percent *CI* for diff. = -0.03 to 0.01; $P = 0.78$) (fig. 7.34). Similarly, in a separate study of another semitropical passerine, the Florida scrub jay, Fitzpatrick and Woolfenden (1988) reported an average LRS rate of 2.4 recruits from within a population of 37 breeders.

Although no parent produced more than three recruits, the lineage of one female breeder was followed into the third generation, i.e., she produced a recruit that in turn produced a second recruit. In 1979 at the onset of the study, an unknown-aged female produced a fledgling that bred a year later a kilometer away. This known-aged, second-generation female then produced a third-generation fledgling that, in turn, bred 2 years thereafter with a dispersal distance of only 0.4 km. The second-generation (1980) recruit bred for only 1 year. She produced three fledglings, none of which has subsequently bred in a nest box. The third-generation (1982) recruit bred for four seasons (1982 to 1985). She produced 11 fledglings, but none has yet bred in a nest box. Even though neither recruit has yet produced subsequent recruits, the original 1979 female produced

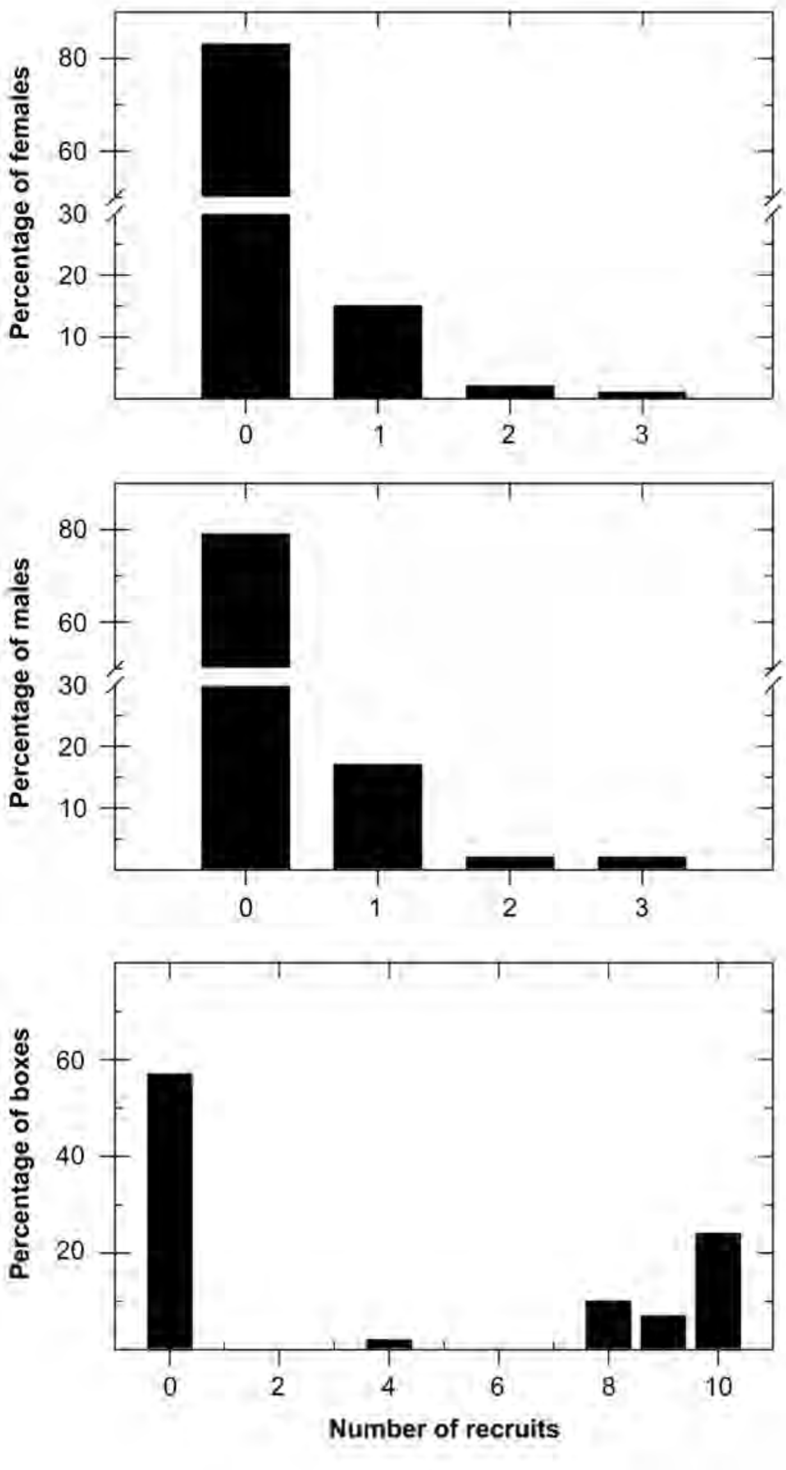


Figure 7.34—Percentage of adults and nest boxes producing recruits between 1979 and 2000. As in many species of birds, most pearly-eye breeders produce no recruits. Likewise, recruits fledged from a small percentage of nest boxes, which reflects the observed elevated productivity of just a few nest pairs.

two other fledglings, one in 1979 and another in 1980, that were subsequently observed prospecting for nest boxes. The 1979 fledgling was observed on May 5, 1984, being supplanted by the resident female. The 1980 fledgling was observed on January 12, 1981, being supplanted by the resident female about 2.5 km from its hatch site. Still, neither of these fledglings has yet successfully bred in a nest box, further attesting to the prolonged longevity and site tenacity of resident breeders.

Influence of Nest Boxes on Fledglings and Recruits

There was no subset of "preferred" boxes from which recruits fledged, or in which they bred.

Reproductive dispersal of resident breeders, location and microclimates of nest boxes, predation, and other sources of mortality affect fledging and recruitment success. Consequently, there may be a predisposition for a few productive boxes from which future recruits fledge and later breed. Of 42 available boxes, 24 (57 percent) failed to house recruits as nestlings (7.34A). The proportion of boxes housing no recruits as nestlings was significantly higher than all the proportions of boxes housing from 0 to 4 future recruits (z-Test on proportions with Yates correction applied: $z = 2.89$; 95 percent *CI* for diff. = 0.12 to 0.54; $P < 0.001$ for boxes with no recruits vs. boxes with 4 recruits, the highest possible proportion). Ten boxes (24 percent of available boxes) housed single future recruits: 10 of 31 (32 percent) of all recruits. However, the proportion was not significantly greater than that of the four boxes (10 percent of available boxes) housing two recruits each: 8 of 31 (26 percent) of all future recruits ($z = 1.48$; 95 percent *CI* for diff. = -0.01 to 0.30; $P = 0.13$). Three boxes (7 percent of available boxes) housed 3 recruits each: 9 of 31 (29 percent) of all future recruits. One box (2 percent) housed 4 future recruits: 4 of 31 (13 percent) of all future recruits (fig. 7.34). Taken collectively, 18 boxes housed future recruits, but the proportion was not significantly greater than that of the 24 boxes producing no future recruits ($z = 1.09$; 95 percent *CI* for diff. = -0.35 to 0.07; $P = 0.13$). Thus, there does not appear to be a subset of exceedingly productive thrasher nest boxes housing recruits as nestlings (fig. 7.35a). Nor is there a definite subset of boxes housing recruits as first-time breeders ($z = 0.65$; 95 percent *CI* for diff. = -0.11 to 0.30; $P = 0.51$). Although the number of nest boxes in which recruits bred (n = 23) was greater than the number from which they fledged (n = 18), the increase was not significant ($z = 0.87$; 95 percent *CI* for diff. = -0.33 to 0.09; $P = 0.38$). In contrast, however, of the 42 boxes available each year, 29 (69 percent) have fledged and/or received recruits (fig. 7.35a). Thus, the proportion of nest boxes involved in fledging **and** receiving recruits as first-time breeders is significantly greater than that of the 13 uninvolved boxes ($z = 3.26$; 95 percent *CI* for diff. = 0.16 to 0.59; $P < 0.001$). Separating recruits by gender revealed no clear subset of boxes from which either sex fledged (fig. 7.35b) or within which either

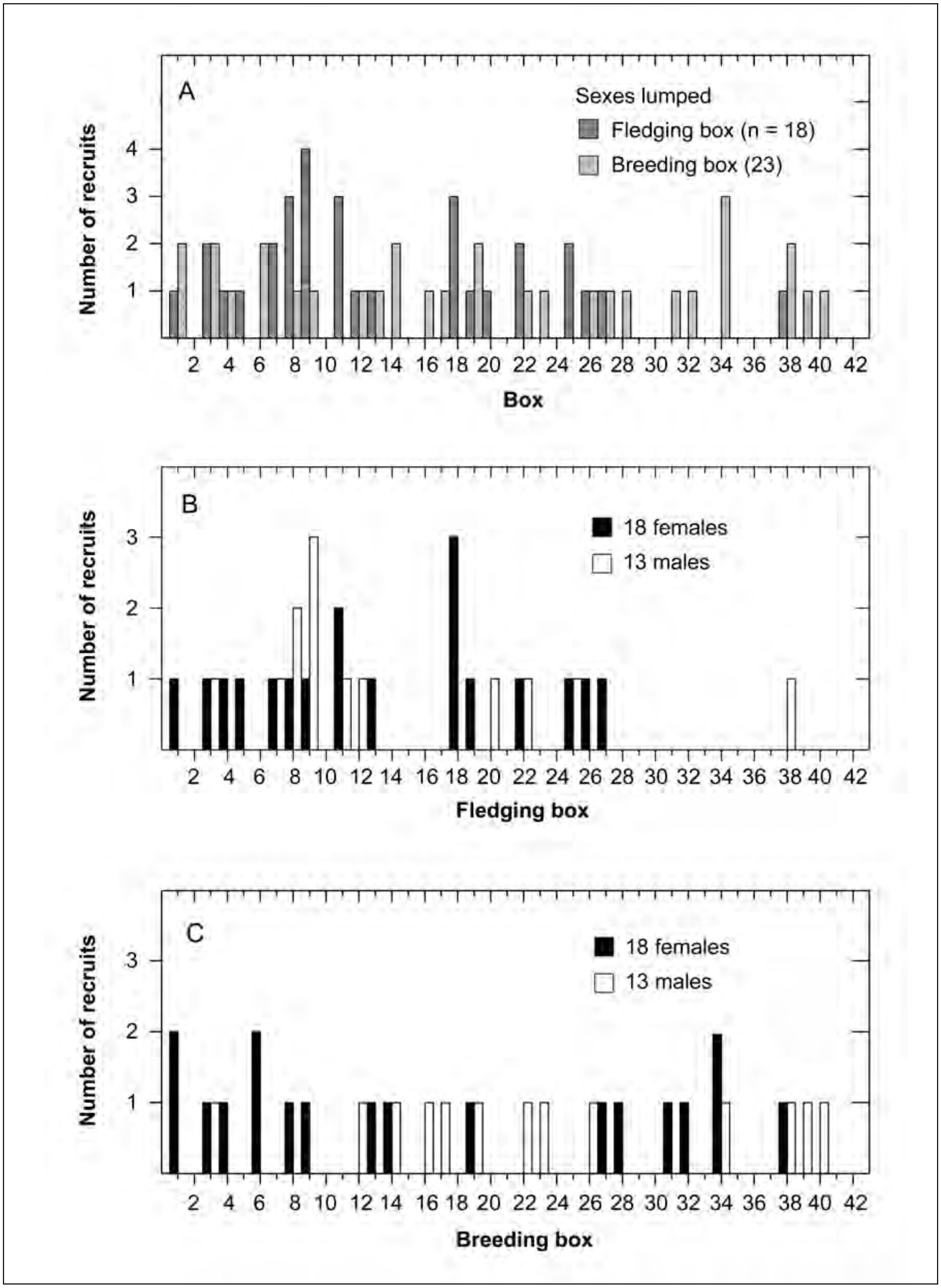


Figure 7.35—Frequency distribution of boxes from which new recruits fledged (A, B) and in which they bred (A, C) between 1979 and 2000. Whereas recruits fledged from fewer than half (n = 18) of the 42 available boxes, thus emphasizing the productivity of but a few breeders (A, B), the distribution of boxes selected for breeding (n = 23) was somewhat more uniform (A, C).

sex bred (fig. 7.35c). In figure 7.35b, the subset of boxes 28 through 42 that never housed fledging recruits exists because the oldest females bred in boxes 1 through 27. That there is probably no biological significance to the apparent exclusion of boxes 28 through 42 is corroborated in figure 7.35c, where clearly both genders are using this subset of boxes to breed.

Seasonal Influences on Fledglings and Recruits

Frequency distributions of the breeding seasons in which recruits fledged (fledging years) or entered the breeding population (breeding years) are shown in figure 7.36a. Three fledging years (1979, 1980, and 1982) produced more than half of the 31 recruits. The sampled population's overall fledging success from eggs that hatched was 54 percent over the entire study period. Fledging success for the three exemplary fledging years was 72, 79, and 49 percent, respectively or, on average, well above the population level (67 >55 percent). Thus, the fact that more recruits were produced during these years may simply reflect the large number of nestlings that successfully fledged during this period. In contrast, in the Florida scrub jay, Fitzpatrick and Woolfenden (1988) reported that about 80 percent of the recruits were produced during 5 of the 13 breeding seasons between 1970 and 1982. Although they caution that the available evidence remains somewhat circumstantial, these authors suspect that the production of jay recruits is highly correlated with predation.

As a result of botfly ectoparasitism, brood number (fledglings from early broods) was more influential in the fledging and breeding of recruits than was precipitation.

Influence of Ectoparasites on Fledglings and Recruits

The prevalence of botfly infestation and consequential nestling mortality in this rain-forest population are positively correlated with precipitation and resultant high humidity (Arendt 1985a, 2000). Therefore, the possibility of an inverse correlation between the production of future recruits and rainfall each year was explored, especially in light of the fact that most future recruits fledged from earlier broods before the heavy May rains and harbored fewer botfly larvae as nestlings (chapter 6). Total precipitation was compared to recruit production and was expressed as a mean of six weather stations surrounding the study area for an 8-month period (December to July) coinciding with the bulk of thrasher reproduction. Most (7) recruits were produced in 1980, the season with the highest fledging success thus far documented (see fig. 7.23). Yet, rainfall was higher than average in 1980 and one (1982) of the other two productive fledging years (1979, 1982). Furthermore, there was no clear inverse correlation depicted in any of the remaining years. Thus, total precipitation was replaced by departure from normal (DFN) rainfall in the analyses by using DFN totals only for the month that each

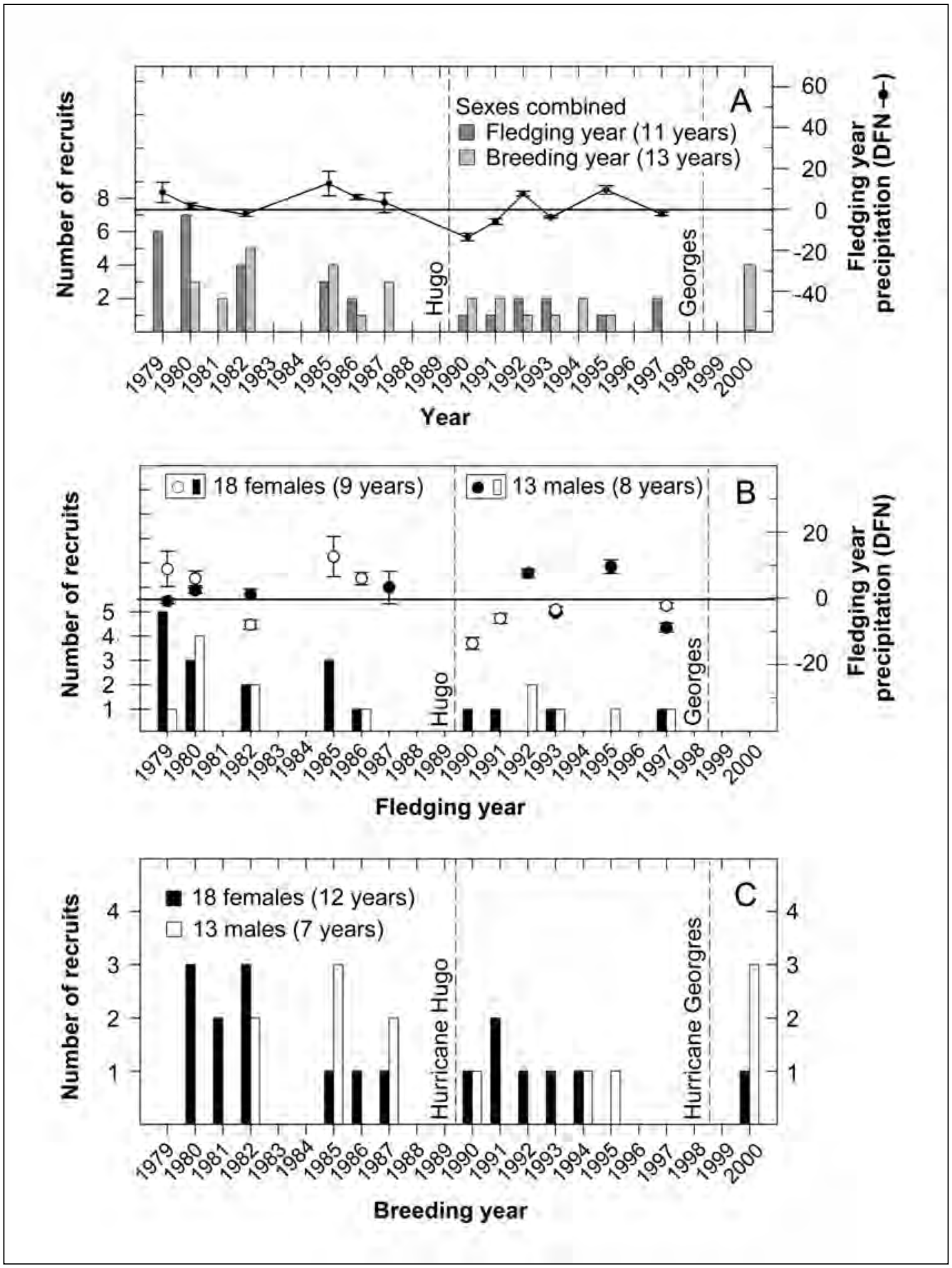


Figure 7.36—Comparison of years during which recruits fledged and entered the breeding population. Neither total rainfall nor departure from normal amounts was inversely correlated with numbers of recruits produced (A and B). However, there was a propensity for new recruits entering the sampled population, especially females, during the first 6 years following Hurricane Hugo (C). Note also the three males and one female recruited 2 years following Hurricane Georges. Data points (filled and unfilled circles) in the precipitation graph (scatter plots in graphs A and B) are 8-month (Dec.–July) mean annual rainfall totals (in cm) for six weather stations surrounding the study site. In graphs A and B, the plot-wide solid black line represents no departure from normal precipitation, and the filled and unfilled circles represent mean departures from normal precipitation to show often extreme yearly variation. Capped vertical bars (⊥, ⊤) are ±1 standard errors.

recruit fledged (fig. 7.36a and 7.36b). Still, however, there was no indication that rainfall was lighter during the period that the recruits were in the nest and most vulnerable to philornid ectoparasitism (Spearman Rank Order Correlation: $r_s^2 = 0.26$; $P = 0.38$). Thus, rainfall is less important than brood number in the production of future recruits. As a comparison, in the rock pipit study cited above, Askenmo and Unger (1986) reported that local recruitment of breeders was also highest in fledglings from early broods, a tendency correlated with female age (older, more experienced females—as observed in this study) than with clutch size or ecological or environmental influences.

Separating breeding recruits by gender (fig. 7.36b and 7.36c) further substantiated earlier dispersal and survival analyses. That is, female recruits enter the breeding population more frequently and at younger ages because of higher mortality in resident females. In addition, the lowered reproductive success previously shown for the last half of the 1990s is also evidenced in figure 7.36c. The lack of recruitment over a 4-year period (1996 to 1999) is most likely a consequence of continuous environmental stress during that period, as well as an aging population. After all, females past their prime produced fewer fledglings than younger, fitter females (fig. 7.30).

Lifespan as a Predictor of Lifetime Reproductive Success

One of the major findings of the 23 studies treated in Newton (1989) was that the overall best predictor of the number of fledglings and recruits produced is the lifespan of the parents. That is, the longer a breeder can survive, the more offspring it will produce. The pearly-eye is no exception to the rule. The number of fledglings produced is positively correlated with the breeder's age (fig. 7.37). Prolonged survival in males generally translates into more fledglings per individual; this is noted in the steeper curve and the higher asymptote. Of course, one would expect that the longer a breeder survives the more potential offspring it will produce. Yet, there are so many inherent and environmental variables (e.g., ectoparasitism) that could significantly influence this trend that confirmation is warranted. For example, in the pearly-eye as in many other species, some individuals simply do not produce as many offspring as others, regardless of age or exogenous circumstances. Similarly, botfly infestations in some nest boxes are consistently higher than in others and, consequently, fledging success is nil at worst and low at best each year in highly infested boxes regardless of the fitness or longevity of the breeders. Thus, even if nest pairs residing at heavily infested boxes survive for a decade or more, their LRS often is lower than shorter-lived individuals at more productive boxes receiving lower intensities of ectoparasites.

Annual survival, which translates directly into "lifespan," was the major predictor of LRS in the pearly-eye.

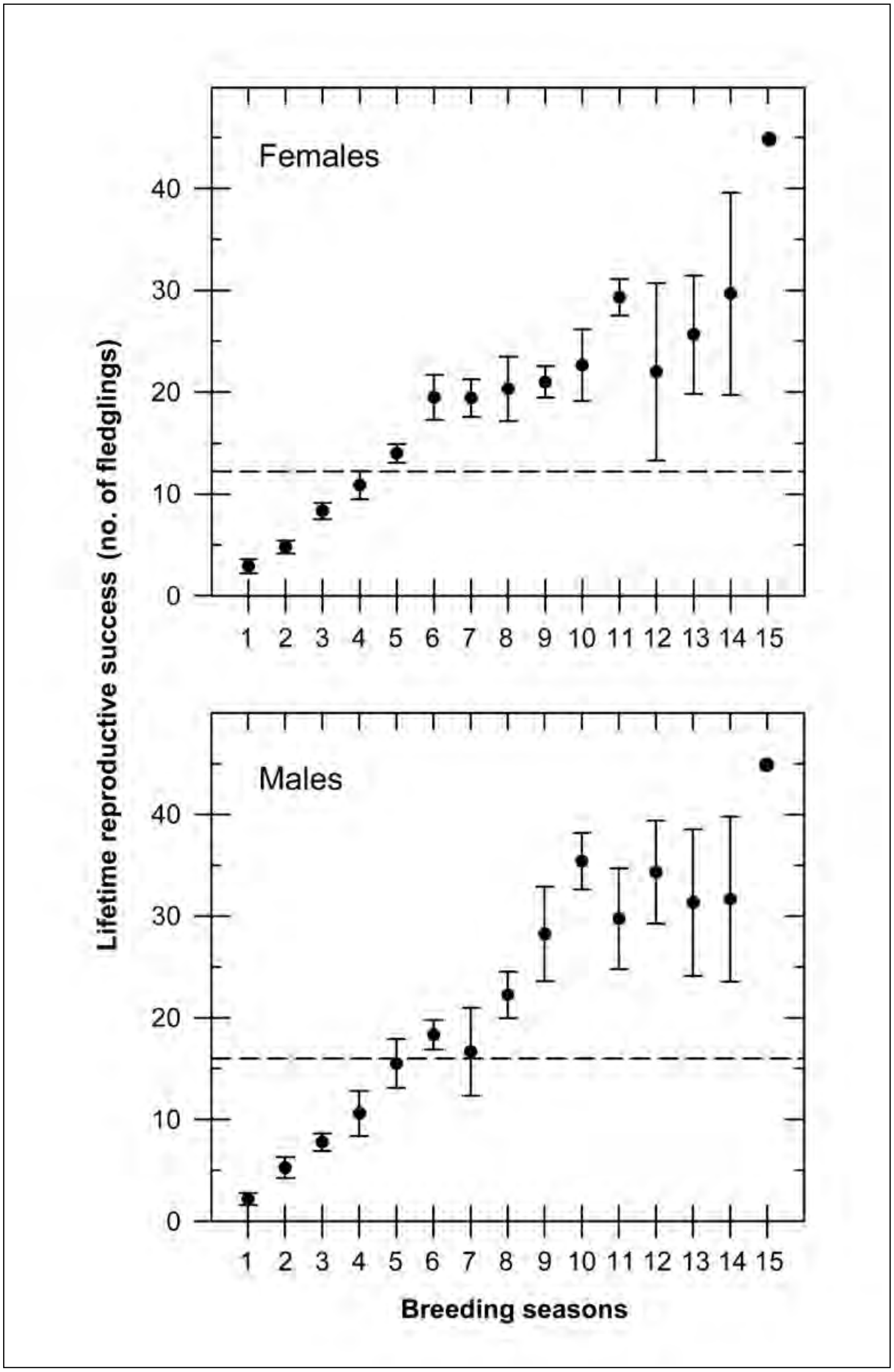


Figure 7.37—Lifetime reproductive success expressed as the total number of fledglings produced by 247 pearly-eyed thrashers as a function of the number of seasons individuals were recorded breeding. Plot-wide dashed lines are the overall lifetime mean number of fledglings produced by all breeders. Data points (filled circles) are means for each breeding season and capped vertical bars (⊥, ⊤) are ±1 standard errors.

Conclusions

In every aspect of its reproduction, the pearly-eye not only meets, but often excels in, each reproductive trait that characterizes a true supertramp. The most salient result emerging from the above analyses is that, as a supertramp, the pearly-eye is indeed resilient to major habitat disturbances and is able to reestablish depleted numbers within two breeding seasons after population decimation. Furthermore, regardless of environmental stresses, the pearly-eye is shown to surpass many species in terms of lifetime reproductive success as expressed in the total number of fledglings produced in a breeder's lifetime. In some species, as many as 50 percent of the breeders produce no fledglings in a lifetime of reproductive efforts. In the pearly-eye, none of the known-aged males failed to produce at least one fledgling, and only about 5 percent of known-aged females failed. In minimum-aged breeders, only 5 percent of the males and 3 percent of the females failed to produce at least one fledgling. If thrasher fledglings can survive the first few post-fledging months, the probability is high that they will achieve recruitment into local as well as distant breeding populations. Males produce significantly more fledglings during their reproductive years than do females. The documented maximum number of lifetime fledglings (45) is a conservative estimate because at least two of the individuals (one of each sex) were banded as unknown-aged breeders in 1979 at the onset of the study. A single breeder of either sex may very well produce more than 50 fledglings in its reproductive lifetime.

Reproductive success as measured by egg volume, clutch size, and number of clutches per season did not vary significantly as females aged, although clutch size and egg volume showed downward trends in older females. Female morphology may influence reproductive success in terms of interference competition and predation, but results remain equivocal in the characters analyzed. In contrast, reproductive success as measured by the number of nestlings and fledglings per nest and season was lowest in novice (first-year) breeders, increased to about midlife, then decreased as females neared senescence, a trend commonly found among passerines (Dhondt 1985, 1989b; Gustafsson and Pärt 1990; Moreno 1993), and often linked to increased levels of parental effort early in life. In short, the high costs of reproduction often negatively affect overall reproductive performance (e.g., Heaney and Monaghan 1995) and even longevity. Aging in the pearly-eye, together with its direct and indirect secondary effects, significantly impacts the individual's potential lifetime reproductive success.

Review of the comparative studies in this section reveals that, traditionally, most studies that treat LRS components have been conducted in Palearctic and Nearctic regions of the world. Indeed, in his review of life history evolution, Martin (1996) concluded that our understanding of life histories—and thus LRS components—of tropical birds, especially in Latin America, is weak. Worse yet, as Martin (1996) concluded, there are many perceived reproductive disparities between temperate and tropical species that may not actually exist or at least are unclear. That so many of the pearly-eyed thrasher's reproductive parameters, as well as those of the semitropical Florida scrub jay, **do** in fact bear out several significant differences in their reproductive ecologies as compared to those of temperate species, suggests that at least some traditional and contemporary tenets regarding these traits may be well founded. Still, as Martin (1996) further cautioned, this debate awaits more rigorous testing, and much more research is needed, especially on cosmopolitan species in which island, continental, and latitudinal comparisons can be made. Future life-history studies should also include phylogenetically uniform and disparate **tropical** species from a broad geographic area, especially those involved in varied reproductive strategies among diverse habitats.

Summary: Reproduction

Insight into pearly-eye reproduction has revealed several traits, e.g., nest-site persistence, strong pair bonding, prolific breeding, rapid recycling, shortened incubation period, and elevated reproductive success, that enable it to attain high densities in species-impoverished habitats and undergo rapid population growth following major habitat disturbances. *Margarops fuscatus* is a prolific breeder and is multibrooded, laying as many as six clutches during extended breeding seasons following major habitat disturbances. It was shown to reestablish itself within two breeding seasons after devastating hurricanes. Female thrashers maximize their reproductive yield by recycling faster with each subsequent clutch. The shortest and longest reproductive recycling (renesting) periods thus far documented for this thrasher population are, respectively, 3 days, and 6 months. Although some females can recycle in less than a week, most females recycle in less than 2 weeks (usually within 9 to 12 days). The thrasher's observed incubation period is almost a week shorter than that predicted when a published formula typical for many passerine species is used. This is crucial to maximizing reproductive yield on an annual and lifetime basis. Within the past three decades, this study, and a long-term study within the Guánica Biosphere Reserve, has shown that some pearly-eyes can survive a minimum of 17 years and, undoubtedly, longer. Individual breeders can produce 45 to 50 fledglings during their reproductive lifetimes, and probably more. The number of fledglings produced in a lifetime is positively correlated with a breeder's longevity. Males produced significantly more fledglings in their reproductive lifetimes than did females, owing mostly to the males' longer survival on average. Ultimately, these reproductive traits, along with the many others presented earlier in this volume, join forces to cinch the pearly-eye's rightful place as a bonafide avian supertramp.

Chapter 8: Impact on Other Vertebrates and Epilogue

Among its many other supertramp attributes, the pearly-eye has now been shown to be a prolific breeder. Presented in this chapter, are some of the behavioral, physical, and ecological characteristics that enhance the pearly-eye's success in depauperate avian communities. Such characteristics include (1) pugnacious behavior, (2) large body size, and (3) stalwart predatory habits, which often result in a significant impact, and even the potential for complete control of other vertebrate populations. Contrarily, factors that impede the pearly-eye from establishing itself on neighboring continents are its generalized food habits, and diffuse (interspecific) competition.

Pugnacity

Like its close relative, the European starling (Sibley and Ahlquist 1984), the pearly-eye is very pugnacious in general, but especially so when guarding its nest site, individual space, and breeding territory (for comparison, see Flux and Flux 1992 for a 20-year nest-box study of the starling). The pearly-eye's relentless aggression and tenacity immediately impress anyone who has ever observed it in physical combat with conspecifics or, more often, interspecifics. Oftentimes, territorial adults are so caught up in the "heat of battle" that they lock claws and beaks and plummet to the forest floor, sometimes from heights of more than 10 m. This behavior often results in the injury or even death of the opponents (pers. obs.; see also Flux and Flux, 1992, for similar behavior in *Sturnus vulgaris*). Rollé (1965a) reported the death of a nesting red-legged thrush resulting from this form of interference competition when a female pearly-eye nested within 10 m of the thrush. Both individuals may have died consequential to the intense battles that raged for more than 3 days. The thrush was found dead on the ground below her nest. The thrasher, although not located, disappeared, and eggs were never laid in her nest.

The pearly-eye's larger body size, pugnacity, and stalwart predatory habits allow it to impact and even control other vertebrate populations.

To determine whether pearly-eyes guard their nest sites on a continual basis, I placed a thrasher mount near nest boxes during the nonbreeding season (Arendt 1983; and fig. 7 in "Study Area and Methods" this volume). Both sexes of the resident nest pairs viciously attacked the mount, either by diving at it while making audible sounds with their wings or by pecking at the head, neck, and dorsal areas from nearby perches. This aggressive behavior is not unique to the pearly-eye but is common in many species of mimids, including catbirds and mockingbirds (Ficken and Ficken 1982). In an experimental study of antipredator aggression in nesting birds, Gottfried (1979) placed mounts of an avian predator, a blue jay (*Cyanocitta cristata*), and a rubber snake resembling the blue racer (*Coluber constrictor*) near the nests of various species. Exhibiting behavior very similar to that of pearly-eyed thrasher females, brown thrashers and gray catbirds attacked the predators with "rushing" flights, using their wings and claws to inflict wounds, and from nearby perches to deliver a series of hammering blows with their beaks.

Thrasher pairs, especially females, are often so aggressive that they draw blood from exposed areas of skin of any human approaching their nest boxes. Heads, especially hairless areas and dorsal portions of the neck are favorite sites, as are bare arms, elbows, and hands. Attack strategies usually involve flying to elevated perches, then diving down to the intruder at high speeds, piercing the skin with their claws and then contracting their toe muscles, ripping out small chunks of flesh as they lift off. An imprudent investigator inevitably accrues multiple puncture wounds within a very short time. I will never forget the unfortunate fate of one particularly bellicose female. She had nested for 5 years prior to Hurricane Hugo and even survived it. But during one of my nest-box visits early in the 1990 breeding season, she struck my bare elbow with such force that she died as a result. Although she managed to land on a nearby branch after striking me, she appeared dazed then simply fell to the ground, dead. In Bonaire, (the late) Fr. Candidus van der Linden (1992, in litt.) reported that during prolonged droughts, normally between April and August, the number of pearly-eyes greatly increases in and around residential areas, where they are "the terror of the village!" Pearly-eyes harass all the other birds that frequent bird feeders. In fact, Fr. Candidus had to dispatch three pearly-eyes before the year-round resident birds would return to his feeders. In a separate, published account of the birds of the Washington-Slagbaai National Park (Netherlands Antilles National Parks Foundation 1975), Fr. Candidus related the following story. A pearly-eye arrived at a feeder in which several bananaquits were feeding on fruits and sugar. The thrasher, upon alighting, pecked a nearby bananaquit, which fell to the ground. The thrasher looked down possibly to see if it was still moving, but resumed feeding on a rotten apple. When the bananaquit showed signs of reviving, the thrasher flew down, pecked it, and then brought it back to the feeder and laid it down at its side. The thrasher pecked the bananaquit a couple of more times, but then continued to feed on the apple. The thrasher alternated between feeding and pecking the prone body of the now deceased bananaquit for about 10 minutes, and then pushed its corpse from the feeder. In natural habitats away from urban situations and under apparently less stressful circumstances, the same author has never seen such "...dominant aggressive behaviour" in the pearly-eye.

In the U.S. Virgin Islands, Seaman (1961) reported similar bullying behavior by the pearly-eyed thrasher at a drinking pool on the Canaan Estate. Seaman had made the pool for pigeons and doves to use during periods of drought.

Each time a thrasher arrived, it would "drive all the other drinkers away, be they bananaquits, Zenaida doves or Quail doves [Bridled quail-dove, *Geotrygon mystacea*]." The thrashers would take their time drinking and preening with no apparent desire to depart. Single thrashers would remain motionless sipping water and picking at their feathers for half an hour or longer. If other birds attempted to alight, they were immediately dispatched. Scaly-naped pigeons (*Patagioenas squamosa*) were the only birds able to dominate and supplant the thrashers. In Seaman's words, thrashers respected the larger pigeons because they could really "knock [the thrashers] spinning" with their large and powerful wings.

Predation on Adult Birds and Other Vertebrates

The pearly-eye is an avid predator on adults of other vertebrates, some of which pose a predatory threat to the thrasher itself, e.g., mice and rats. On Puerto Rico, Rollé (1965b) documented the pearly-eye's frequent predation and caching behavior involving the house mouse (*Mus musculus*) and rats. On the island of Vieques (Puerto Rico), Sorrié (1975) cited his observation of a pearly-eye dragging a spotted sandpiper (*Actitis macularia*) to an entanglement of mangrove roots and then plucking and eating it. On tiny Guana Island, just north of Tortola in the British Virgin Islands, Robert Chipley of the Nature Conservancy (1995, in litt.) found a thrasher "....pecking at the skull of a freshly killed Mangrove Cuckoo (*Coccyzus minor*) which in turn had thrasher feathers in its bill. In addition, a quail-dove [bridled quail-dove] in an unattended net was killed, presumably by this species" (there are no mongooses on Guana Island).

More recently, in Puerto Rico on February 24, 1993, and in association with the ongoing pearly-eyed thrasher nest-box study, during his daily visits to nest boxes, Roberto Díaz (1993, pers. comm.) observed an adult pearly-eye along the roadside (PR Highway 191, Icacos Valley) eating the neck of a decapitated scaly-naped pigeon. It is not known if the pigeon had fallen prey first to a hawk or if it had lost in a battle with the thrasher (but see Seaman's 1961 account above). On another occasion, Sr. Díaz observed either cannibalism, or at least scavenging on a conspecific, by the pearly-eyed thrasher. A thrasher was observed eating on a thrasher carcass along the same roadway (no date given). As in the case of the pigeon, it is unknown if the deceased thrasher had fallen prey to some other predator or rather was the loser in a bout of conspecific interference competition, which is frequently observed in this population. I have observed thrashers eating unfeathered thrasher nestlings presumably robbed from nearby nests.

In her study of the Puerto Rican tody (*Todus mexicanus*), Kepler (1977: 160) noted that pearly-eyes devour fledglings and possibly adult todies. Snyder et al.

(1987: 193) cited several authors from the literature who reported instances of predatory attacks by pearly-eyes on other birds including a “dove” reported by Danforth (1936b) from Mona, a Puerto Rican satellite island (the “dove” was most probably a zenaida dove or common ground-dove), and a “warbler” reported by Wolcott (1942). Although the identification of the “warbler” is also unknown, it may have been a yellow warbler (*Dendroica petechia*), a species confirmed by Seaman (1961) as prey of the pearly-eyed thrasher in the U.S. Virgin Islands. In addition to yellow warblers, Seaman reported pearly-eyes also feeding upon “tree lizards” (*Anolis acutus*), frogs, centipedes, and young birds.

In the Luquillo Experimental Forest, Puerto Rico, succeeding Hurricane Hugo, pearly-eyes captured in mist nets attacked other captured birds with a frequency and intensity unseen prior to the storm (J. M. Wunderle, Jr. 1989, pers. comm.; and pers. observ.). Also after Hurricane Hugo, in Guadeloupe, Pagney Bénito-Espinal and Bénito-Espinal (1991) photographed a pearly-eye pecking apart and eating portions of a bananaquit trapped in a mist net (fig. 8.1).

Figure 8.1—Bananaquit captured in a mist net by Pagney Bénito-Espinal and Bénito-Espinal (1991) in Guadeloupe following Hurricane Hugo. While hanging helplessly in the net, the bananaquit was preyed upon by a pearly-eyed thrasher. (Photo courtesy of the Bénito-Espinals).

Nest Predation

Figure 8.2—Pearly-eyed thrasher removing nestling thrasher from a natural cavity. The pearly-eyed thrasher is an avid predator on adults, eggs, and nestlings of other birds. This photo was taken by John Taapken and appeared as fig. 8.10 in the Puerto Rican parrot monograph (Snyder et al. 1987). It has been graphically enhanced by Francisco Cedeño (http://www.sariguadesigns.com), with the exchange of the original egg for a young thrasher nestling in the bird's bill. The author has observed both eggs and young nestlings being removed from thrasher nest boxes by predatory thrashers. (Photo courtesy of Noel Snyder.)

The pearly-eye's notoriety as a nest predator is also well documented, and its prey includes a wide variety of forest and nonforest birds alike (fig. 8.2). In an unpublished progress report dated June 30, 1944, issued by the U.S. Fish and Wildlife Service in the Virgin Islands, H. A. Beatty (cited in Seaman 1961) stated that the pearly-eye is "the worst enemy of our forest and woodland birds." He reported "…innumerable instances when the thrasher was seen beating Zenaida doves from their nests and eating the contents, which in most cases were eggs. But nestlings also were devoured greedily." Beatty concluded his remarks with "…the thrasher [is] …an important predator and…its rapacity is one to be reckoned with in game bird restoration." In a separate account Seaman (1961) observed that the pearly-eye eats eggs of the bananaquit, black-faced grassquit, and zenaida dove. In a later document involving a study of the bridled quail-dove in the U.S. Virgin Islands, Seaman (1966) reported that quail-dove egg loss to the predatory pearly-eye was particularly high, which led him to state "…the Pearly-eyed Thrasher (*Margarops fuscatus*) is very likely the Quail dove's greatest enemy." More recently, during a study of the nesting biology of the bridled quail-dove on Guana Island located in the nearby British Virgin Islands, Chipley (1991) documented nest predation by an especially persistent pearly-eye, which came close to the incubating adult quail-dove 11 times within a 2-week period, once almost jumping on top of the brooding bird! Ultimately, within 24 hours of the thrasher's last observed visit, the nest was found unattended and bits of buff-colored eggshell were scattered on the ground immediately beneath it (Chipley 1995, in litt.). During avian studies on Montserrat in 1984, my wife and I also observed pearly-eyes feeding on the nest contents of the bridled quail-dove. In an earlier account referring to Mona Island, a Puerto Rican Satellite, Barnés (1946) cited pearly-eyes as feeding upon the eggs and young of the zenaida dove and common ground-dove.

In the Sierra de Luquillo, Puerto Rico, bananaquit nests and their contents are commonly preyed upon by pearly-eyed thrashers, which often knock nests to the ground before ripping them apart in search of eggs and nestlings. Elsewhere in Puerto Rico, in the Guánica Biosphere Reserve, Vilella (1995) reported the pearly-eye "...commonly...taking eggs and young of smaller passerines such as the bananaquit...." R. A. Pérez-Rivera has studied Puerto Rico's fauna and flora for several decades and has made numerous observations of nest predation by the pearly-eye. He has documented its impact on the zenaida dove and red-legged thrush (Pérez-Rivera 1978a, 1982, respectively). Although not yet published, he also has observed pearly-eye nest predation on 11 other resident species within the Carite Forest including the following species (asterisks preceding vernaculars denote species that I, too, have observed suffering from pearly-eye nest depredation within the Luquillo Experimental Forest): *common ground-dove, *ruddy quail-dove (*Geotrygon montana*), *Puerto Rican emerald (*Chlorostilbon maugaeus*), Puerto Rican tody, Puerto Rican woodpecker (*Melanerpes portoricensis*), *bananaquit, Antillean euphonia (*Euphonia musica*), Puerto Rican spindalis (*Spindalis portoricensis*) [formerly stripe-headed tanager, *S. zena*], Puerto Rican tanager (*Nesospingus speculiferus*), *Puerto Rican bullfinch (*Loxigilla portoricensis*), *black-faced grassquit, and Greater Antillean grackle (*Quiscalus niger*). More recently, during a 9-year study (1985 to 1994) of the reproductive ecology of the red-legged thrush, A. I. Arendt (1994, pers. comm.) has observed, on four separate occasions in different years, pearly-eyes pecking at, and then removing, nestling thrushes.

Barnés (1946) cited pearly-eyes as feeding upon the eggs and young of the white-crowned pigeon (*Patagioenas leucocephala*). More recently, in a comprehensive study of the breeding biology and ecology of the white-crowned pigeon, Wiley and Wiley (1979: table 6; also cited in Snyder et al. 1987) concluded that the pearly-eye was the most important of four major nest predators. For example, thrasher predation led to the failure of 43 percent of the active white-crown nests under study on the Roosevelt Roads Naval Base, Puerto Rico (fig. 8.3), and 33 percent under study on nearby Mona Island. During his 10-year study of the zenaida dove in Puerto Rico and its offshore islands, Wiley (1991) found that the pearly-eyed thrasher was the most common nest predator, being responsible for 49 percent of the egg and chick losses. Lastly, during an island-wide, long-term study of Puerto Rican columbids, Rivera-Milán (1990, 1992, 1995) documented the pearly-eye's major impact on the reproductive performance of numerous species.

Figure 8.3—Pearly-eyed thrasher depredating a nest of the white-crowned pigeon on the Roosevelt Roads Naval Base, Ceiba, Puerto Rico. Although older squabs are usually able to fend off thrashers, younger ones often die of lacerations caused by numerous pecks inflicted by the predacious thrasher. (Photo courtesy of J. W. Wiley.)

Seaman (1952) referred to the pearly-eye as an “intrepid poacher.” He suggested that much of the blame for the depleted faunas of numerous Caribbean islands, so often attributed to the introduced mongoose, should instead be accredited to the thrasher and two introduced species of *Rattus* (black rat, *R. rattus* and brown rat, *R. norvegicus*). Thrashers and rats are much more arboreal than the mongoose, although mongooses have been seen in trees at heights of 3 m near thrasher boxes (R. Díaz, 1996, pers. comm., and pers. obs.). Snyder et al. (1987) went as far as to reference the pearly-eye as the “insidious thrasher” because of its belligerent nature and rapacious habits. Indeed, any species that can potentially pose a threat to the mere existence of coinhabiting species will be looked upon disdainfully by some, and yet venerated by others.

Potential for Controlling Vertebrate Populations

Impact on Forest-Bird Populations in Puerto Rico

Mist-net results—

The pearly-eye's predatory habits can deleteriously impact forest birds and other vertebrate populations in Puerto Rico and elsewhere in the Caribbean. Within the palo colorado (*Cyrilla racemiflora* L.) forest zone of the Luquillo Experimental Forest (the pearly-eye's preferred habitat within the forest), each year over a 22-year period (1978 to 2000), mist-net capture rates of two species of frugivorous forest birds (Puerto Rican bullfinch and Puerto Rican spindalis) have been dwindling (Arendt, unpubl. data). During the late 1970s, on average, bullfinches constituted 57 percent (range: 43 to 64 percent) of the captures, but their numbers dropped precipitously to 15 percent (range: 9 to 26 percent) during the 1980s, and then diminished to 4 percent (range: 3 to 5 percent) during the 1990s. Similarly, capture rates for the Puerto Rican spindalis averaged 14 percent (range: 13 to 15 percent) during the 1970s and 1980s, but then declined to 4 percent (range: 3 to 5 percent) during the 1990s. Capture rates of a third species, the bananaquit, remained low in comparison to those in other forest types averaging 4 percent (range: 0 to 5 percent) from the late 1970s to the mid-1990s, suggesting that something was suppressing its numbers in colorado forest. Unexpectedly, however, their average rate of capture quadrupled, jumping to 16 percent (range: 13 to 18 percent), from 1996 to 1999, possibly owing to effects of several hurricanes, including Hurricane Georges (see also below under point-count results). These results suggest that the pearly-eye may be suppressing at least bullfinch and tanager numbers within colorado forest and, until recently, also suppressed bananaquit numbers as well in this forest type.

Point-count results—

With the passage of Hurricanes Hugo in 1989 and Georges in 1998, there arose two unique opportunities to study not only the potential recovery (or decline) of various forest-bird populations within the various forest types and at different elevations following major habitat destruction, but also the potential threat posed by the predatory pearly-eyed thrasher during intervening, "hurricane-free" years.

In late September 1989, 3 days following Hurricane Hugo, census routes were established in three different forest types over most of the forest's elevational gradient: (1) an exotic mixed-species plantation, e.g., pine (*Pinus elliottii* Engelm var. *Pinus caribaea* sensu Small), kadam (*Neolamarckia cadamba* [Roxb.] F. Bosser), and mahogany (*Swietenia macrophylla* x *mahagoni* hybrid Stehle and

Cusin) within the forest's lower boundary at about 200 m elevation; (2) palo colorado (*Cyrilla racemiflora* L.) forest from about 600 to 800 m elevation, and (3) cloud forest on the higher peaks (850 to 900^{+} m elevation). These three forest types, encompassing a broad elevational gradient, were chosen to complement avian census routes previously established by other investigators (see Waide 1991 for details). Following Hurricane Georges in late September 1998, tabonuco (*Dacryodes excelsa* Vahl.) forest, the fourth and last major forest type of the Sierra de Luquillo to be monitored in this study, was added by placing 30 points each on the eastern (between the Catalina Service Center and the Sabana Research Field Station) and western (El Verde) sides of the forest.

Five species: bananaquit (BANA), Puerto Rican bullfinch (PUEB), Puerto Rican tanager (PRTA), Puerto Rican spindalis (PRSP), and scaly-naped pigeon (SNPI) were chosen to determine if the pearly-eye might be suppressing nectarivorous- and frugivorous-bird populations in the colorado forest type, which supports the highest thrasher densities. Each species was selected because it fit at least one of the following three main criteria: (1) is a frugivore-nectarivore, and thus is also a potential food competitor of the pearly-eye; (2) is found in at least three of the four main forest types in numbers adequate for comparative analyses; and (3) is a documented victim of nest predation by the thrasher.

For each of the six species (pearly-eye included), the mean number of birds detected within 25-m point radii (30 points per habitat, except in plantation forest, which accommodated only 10 points) during monthly censuses conducted over a 12-year period (1989 to 2000) is presented in (fig. 8.4).

Most of the six frugivorous-nectarivorous species showed a peak in numbers during the months immediately following Hurricanes Hugo and Georges owing to an increase in detectability and resurgence of vegetation. Owing to extensive loss of the forest overstory, frugivores-nectarivores were forced to forage within a few meters of the forest floor. Concomitant with extensive canopy loss, came an influx of sunlight penetrating to the forest floor, resulting in abundant food supplies provided by the surge of fruiting vines, ground-cover plants, and fast-growing shrubs. The initial peak in numbers among these species was then generally followed by downward population trends in all three forest types for the first 2 years following each hurricane. Following Hurricane Hugo, frugivore-nectarivore populations began to recover by 1992. With exceptions, there was a general forest-wide reduction in bird populations in 1991 when the resurgence of flowering and fruiting that immediately followed Hurricane Hugo began to taper off by the end of 1990, but resumed once again in 1992 (see Wunderle 1999 for similar results). It is evident that the vagile scaly-naped pigeon moves out of habitats severely impacted by

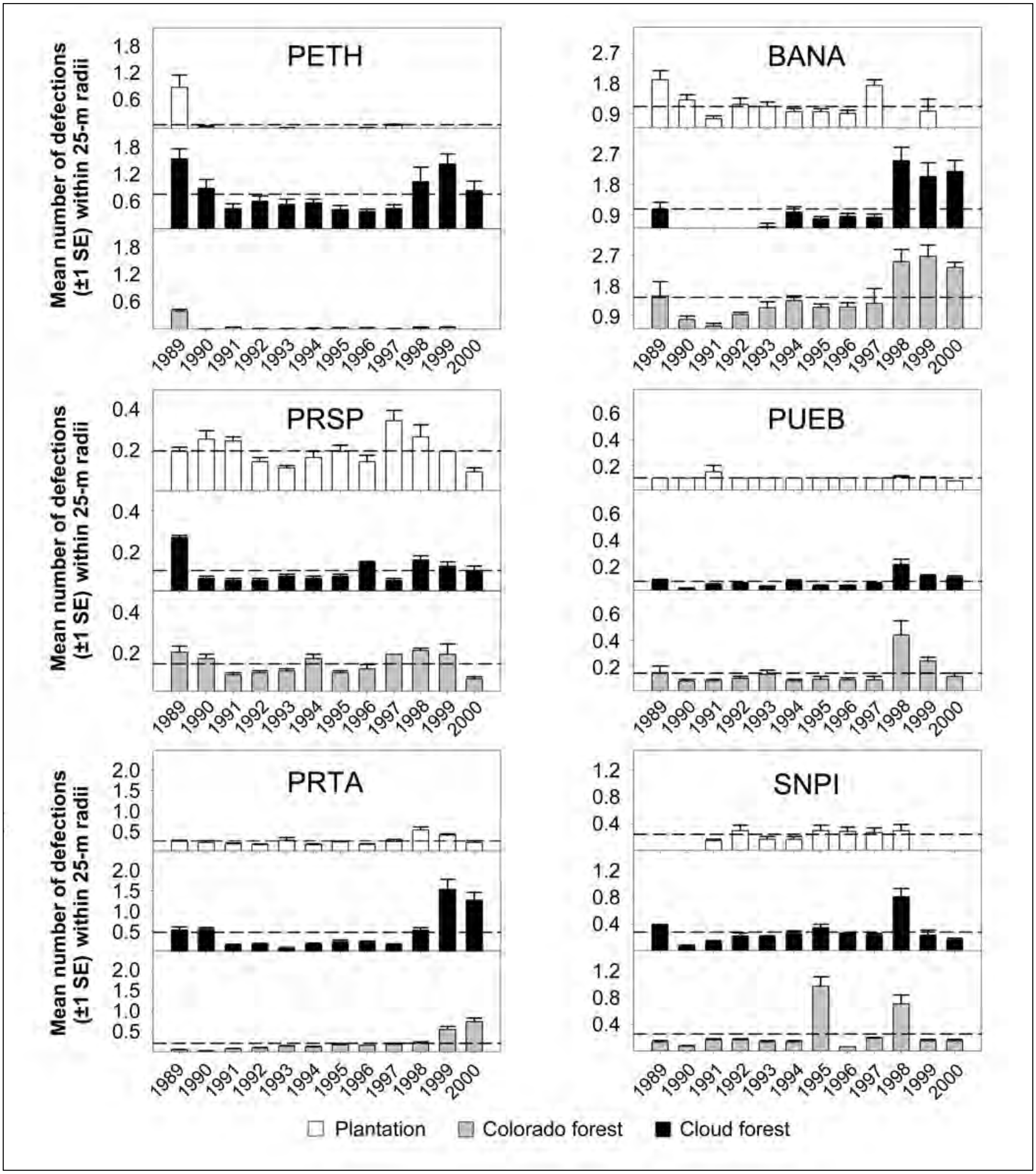


Figure 8.4—Population trends for six species of nectarivorous and frugivorous birds that are potential competitors with the pearly-eye for food and other resources. Results are derived from fixed-radius circular point counts conducted each month during the first 12 years following Hurricane Hugo. Data are shown as the overall 12-month mean number of detections within 30 25-m radii averaged each month among three forest types: exotic mixed-species plantation (no fill), colorado (*Cyrilla racemiflora* L.) (black bars), and cloud forest (gray bars). Capped vertical bars (⊤) are absolute positive error bars (±1 SE). Species abbreviations are as follows: bananaquit (BANA), pearly-eyed thrasher (PETH), Puerto Rican spindalis (PRSP), Puerto Rican tanager (PRTA), Puerto Rican bullfinch (PUEB), and scaly-naped pigeon (SNPI).

hurricanes (review plantation habitat after both hurricanes in fig. 8.4) and tends to forage widely, often aggregating in vegetation refugia scattered throughout the forest.

Interyear comparisons within three forest types—
Following procedures outlined in Hutto et al. (1986), to evaluate the confounding effects of yearly differences on single species within the same forest types including and excluding years affected by the two hurricanes (1989 to 1991 and 1998 to 2000), statistical tests (K-W ANOVA) were conducted on the mean number of detections per 25-m-radius point count. (see "Study Area and Methods" for sampling regime). Although significant interyear variation in the average number of detections within 25-m radii resulted for every species in every forest type, it disappeared completely when the effects of the two hurricanes were removed by eliminating the years 1990 and 1991 (Hugo) and 1998 to 2000 (Georges).

Throughout the 6-year interim (1992 to 1997) between the two major hurricanes, population levels of all six species were relatively stable, oscillating little around the population means in comparison to hurricane-impacted years (fig. 8.4). Although all five of the pearly-eye's potential competitor/prey species recovered in plantation and cloud forest types, numbers of three of the four smaller species (bananaquit, Puerto Rican bullfinch, and Puerto Rican spindalis) remained low in colorado forest over the entire 6-year interim period. Pearly-eyes are notorious nest predators at unguarded nests of the scaly-naped pigeon and undoubtedly impact the pigeon's population throughout the forest. However, the scaly-nape is mobile and wide-ranging, especially while foraging. If its numbers are being suppressed in colorado forest because of resource competition or nest predation by pearly-eyes, it is not evident from point counts as many pigeons detected during counts could be foragers from other areas where thrasher numbers are lower (fig. 8.4).

As the supertramp theory predicts, pearly-eye numbers increased in "hard-hit" areas of the forest (plantation and cloud forest) immediately following Hurricane Hugo, but decreased thereafter and remained low throughout the remainder of the 12-year monitoring period as populations of other resident species became reestablished. Thrashers did not invade the plantation or cloud forests immediately following Hurricane Georges as they did so promptly following Hurricane Hugo (fig. 8.4). There is, however, evidence that thrasher numbers have actually been declining in the Sierra de Luquillo over the past decade (Arendt 2000 and fig. 18, this volume). Dwindling numbers and possible lingering effects on habitat and resources in the wake of Hurricane Hugo only 9 years prior to the passage of Hurricane Georges may be major factors behind this anomaly. In its preferred colorado forest habitat, the pearly-eye showed the same general population decline as that observed in several of the other species from 1990 to 1991, recovering by 1992 in response to the abundance of small vertebrates (frogs, lizards, and baby birds) and the annual fluctuations in its preferred tabonuco and sierra palm fruit crops (see similar results in Wunderle 1999: fig. 1). Taken collectively, these results also strengthen the contemporary belief that (excluding some very specialized habitats and species) over several millennia, populations of most insular forest birds have been able to adapt to stochastic habitat disturbances and can even recover from the effects of major hurricane damage within 2 to 3 years following destruction (reviewed by Wiley and Wunderle 1993).

Comparison of frugivore-nectarivore populations—
Having eliminated confounding interyear effects on frugivore-nectarivore populations within the three forest types by excluding hurricane-impacted years (1989 to 1991 and 1998 to 2000), the same statistical test (K-W ANOVA) was conducted by using the remaining **pooled** 6-year (1992 to 1997) mean number of monthly detections within 25-m radii per point count for each of the six species to compare populations among the three forest habitats. As anticipated, the pearly-eye population in colorado forest is significantly larger than those in the exotic mixed-species plantation and cloud forest (table 8.1, fig. 8.5). Because of such a high density of thrashers in colorado forest, numbers of the usually ubiquitous bananaquit are significantly lower there than in either plantation or cloud forest (fig. 8.5). Likewise, Puerto Rican spindalis and Puerto Rican bullfinch numbers are also significantly lower in colorado forest than in either the plantation or cloud forest (fig. 8.5). Conversely, numbers of the Puerto Rican tanager and scaly-naped pigeon diminished with increasing elevation, although there were no significant differences in mean numbers of either species among the three habitats (fig. 8.5). It will be interesting to monitor avian population trends for several more years in the wake of Hurricane Georges; especially considering the cyclic pattern of the populations of most species associated with the two major habitat disturbances and interim periods in all three forest types (fig. 8.4).

Coupled with the mist-net results presented earlier, these data suggest that predation by the pearly-eyed thrasher may be suppressing populations of small, frugivorous-nectarivorous birds in the thrasher's prime habitat. This is true especially for the bananaquit, a species that is abundant in other habitats in and around the forest, in many of which the thrasher is scarce. Observations of frequent nest predation by thrashers on bananaquits nesting in colorado forest are attested by many.

Table 8.1—Results of a Kruskal-Wallis one-way analysis of variance on ranks and all pairwise multiple comparisons (Dunn's method) on the monthly mean number of detections along an elevational gradient and among three forest types[a]

	Percentile						
Species and forest type	**Median**	**25**	**75**	**Paired forest types[b]**	**Difference in ranks**	**Q**	**P <0.05**
	- - - - - - - - - - - - - *Mean number of detections* - - - - - - - - - - - - -						
Pearly-eyed thrasher							
(*H* = 12.64; *P* = 0.001)							
Plantation	0.01	0	0.01	P vs. C	10.50	3.40	Yes
Colorado	.50	.41	.57	C vs. D	7.50	2.43	Yes
Dwarf	.02	.01	.03	D vs. P	3.00	.97	No
Bananaquit							
(*H* = 9.73; *P* = 0.001)							
Plantation	1.05	.98	1.20	P vs. C	7.66	2.48	Yes
Colorado	.79	.54	.85	C vs. D	8.83	2.86	Yes
Dwarf	1.13	1.11	1.24	D vs. P	1.16	.37	No
Puerto Rican spindalis							
(*H* = 9.39; *P* = 0.001)							
Plantation	.16	.15	.20	P vs. C	9.33	3.02	Yes
Colorado	.07	.06	.08	C vs. D	7.67	2.58	Yes
Dwarf	.11	.10	.17	D vs. P	3.66	1.19	No
Puerto Rican bullfinch							
(*H* = 12.19; *P* = 0.001)							
Plantation	.15	.11	.18	P vs. C	9.50	3.08	Yes
Colorado	.05	.04	.06	C vs. D	8.50	2.75	Yes
Dwarf	.09	.06	.10	D vs. P	1.00	.32	No
Puerto Rican tanager							
(*H* = 2.41; *P* = 0.29)							
Plantation	.20	.16	.23	P vs. C	(None significant)		
Colorado	.17	.16	.23	C vs. D			
Dwarf	.15	.11	.18	D vs. P			
Scaly-naped pigeon							
(*H* = 3.89; *P* = 0.14)							
Plantation	.28	.17	.30	P vs. C	(None significant)		
Colorado	.25	.23	.27	C vs. D			
Dwarf	.15	.14	.20	D vs. P			

[a] Data encompass a 6-year interim period (1992–97) between two major hurricanes, and include six species of frugivorous-nectarivorous forest birds inhabiting the Luquillo Experimental Forest, Puerto Rico; forest types and elevational ranges are described in the "Study Area and Methods" section.

[b] Paired forest types: plantation (P), colorado (*Cyrilla racemiflora* L.) (C), dwarf (D).

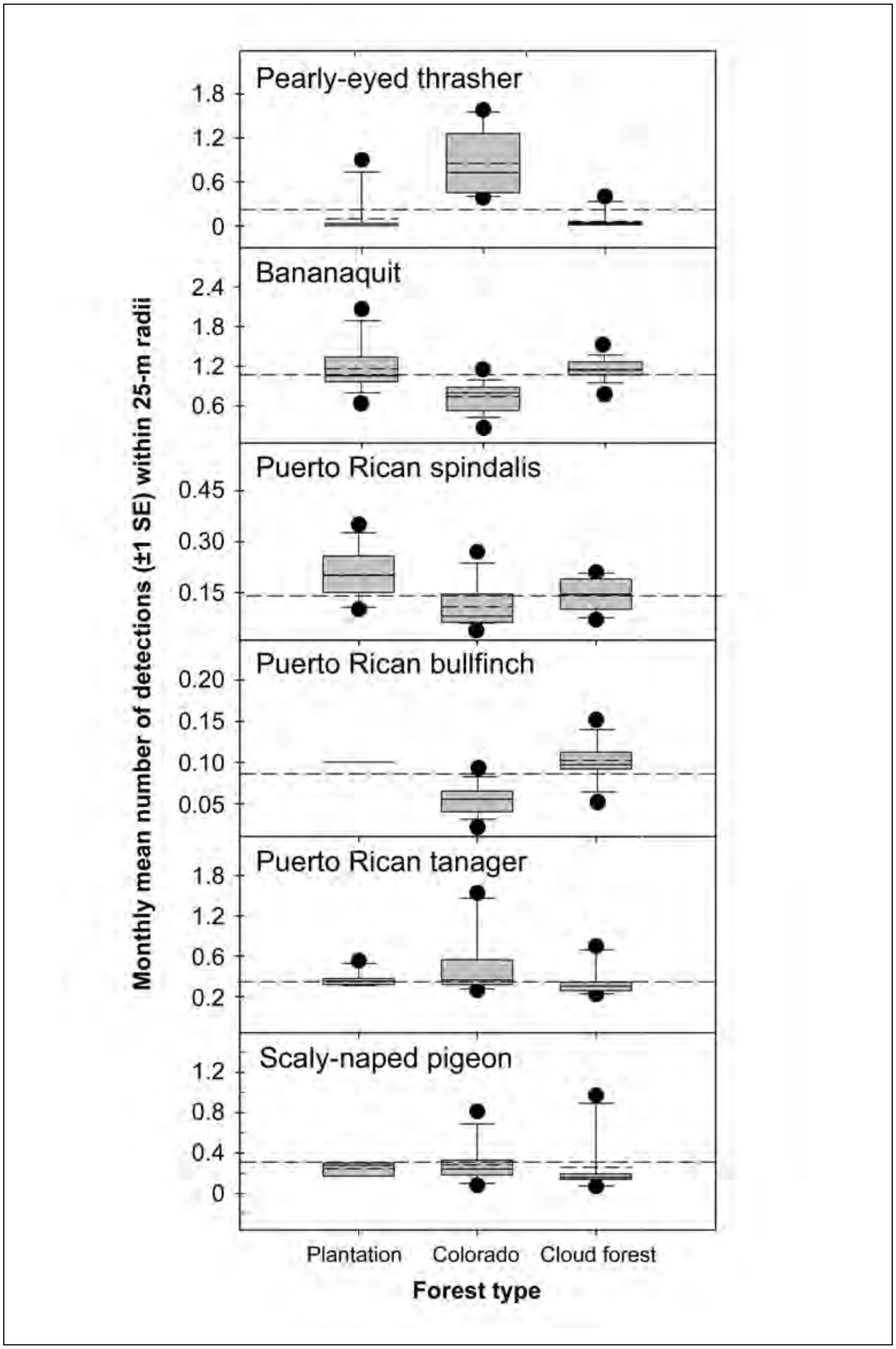


Figure 8.5—Cumulative results from a total of 216 monthly, fixed-radius circular point-count censuses (72 monthly counts × 3) conducted over 6 years (1992 to 1997) in three forest types: mixed-species plantation, colorado (*Cyrilla racemiflora* L.), and cloud forest. Whereas the thrasher abounds in colorado forest, populations of three species of nectarivorous (BANA) and frugivorous species (PUEB, PRSP) are suppressed in this forest type (see app. 1 for codes, English vernaculars, and scientific names). Plot-wide dashed lines are the overall monthly mean number of detections of each species averaged over all three forest types. Box-plot parameters are explained in fig. 4.6.

Comparison of Results With Other Studies

Results obtained during the present study are in general agreement with those reported by earlier researchers. Recher (1970: tables 2 and 3) compared forest-bird abundance at a low-elevation site (tabonuco forest near the El Verde Experimental Station, about 450 m above sea level) and a high-elevation site (transition colorado-cloud forest along the trail leading to Mt. Britton Observation Tower, about 850 m above sea level). More recently (12 February to 29 March 1993), Pagán (1995) compared avian distribution and abundance in relation to vegetational changes along an elevational gradient within the forest. As shown in the present study, both previous authors also reported that numbers of the Puerto Rican tanager and scaly-naped pigeon decreased along an elevational gradient, noting that the reduction in numbers is in concordance with the dwindling number of insects and fewer, smaller fruits and flowers at higher elevations (see Wolda 1987 for a review of insect populations related to elevation and habitat). In Pagán's study, two species (Puerto Rican spindalis and Puerto Rican bullfinch) showed an increase in numbers with increasing elevation, also being attributed to microhabitat differences and food availability. Recher also emphasized the obvious increase in the bullfinch at higher elevations. However, in Recher's study *Spindalis* numbers decreased with elevation, i.e., contrary to the results obtained by Pagán. Twelve years of constant population monitoring tends to support Recher's results, although it is noteworthy that although all three studies were carried out within the same forest, some of the forest types and especially geographic sites varied. Moreover, both previous studies were shorter in years and encompassing months. All of these factors no doubt contribute to the occasional exception to the otherwise virtual unanimity among all three studies.

It is noteworthy that during a 6-year interim period between two major hurricanes, populations of the Puerto Rican bullfinch were larger and rebounded more quickly from the effects of first (Hurricane Hugo) at higher elevations (characterized by more open-canopy cloud forest with extensive "edge" in the form of tree-fall gaps and eroded slopes) than in either of the two forest types at lower elevations (fig. 8.4). As cited previously, several authors have noted that the Puerto Rican bullfinch is more of a high-elevation, open-canopy and "edge" species (Pagán 1995, Recher 1970, Wunderle et al. 1992, Norton 1992, unpubl. data). Assuming that the cloud forest sampled in the Sierra de Luquillo is characteristic of high-elevation vegetation associations found on other islands, the results of the present study do not support the logical and well deduced hypothesis (with substantiating evidence) that, in general, Antillean bullfinch (*Loxigilla* spp.) numbers decline in postdisturbance montane habitats such as cloud forest owing to the longstanding recovery time necessary to produce sufficient seed and fruit crops at high elevations (see, e.g., the discussion in Wunderle et al. 1992). The now apparently extinct bullfinch of St. Kitts known as the mountain blacksmith (*Loxigilla portoricensis grandis*) may very well have met its demise owing to a combination of factors (see also Olson 1984) such as forest fragmentation (Norton), nest predation (Bond 1956b), parasitism, and disease, forcing it into its last, scant stronghold in montane forest on that island, only to be "carried over the brink" by the passage of two hurricanes in 1899 (Raffaele 1977). That the Puerto Rican bullfinch fared better in cloud forest than at lower elevations during a 6-year period following major habitat destruction suggests that other factors besides highland food shortages govern the size of bullfinch populations, not only in cloud forest, but in all three of the forest types under study. Note for example that, when compared to the other five species, Puerto Rican bullfinch detections are substantially lower in all three forest types (fig. 8.5).

In conclusion, the fact that populations of three of the five species under study (bananaquit, Puerto Rican bullfinch, and Puerto Rican spindalis) remained significantly lower in colorado forest than in other forest types over a 6-year interim period between two major hurricanes adds credence to the notion that the pearly-eye is indeed impacting interspecific frugivorous-nectarivorous bird populations inhabiting colorado forest in the Luquillo Experimental Forest.

Comparison of Wet- and Dry-Forest Frugivore-Nectarivore Populations

Whereas pearly-eyes exert control over other vertebrate populations in species-depauperate wet forest, it has no such effect in species-rich dry forests, in which thrasher populations are small.

To compare rain forest with dry-forest populations of the pearly-eyed thrasher and three other species (bananaquit, Puerto Rican bullfinch, and Puerto Rican spindalis), 32 years of banding data (1973 to 2005) from the Guánica Biosphere Reserve (Faaborg et al. 2000) were summarized (fig. 8.6a). In dry-forest habitat, all four species declined following severe drought conditions in the mid-1970s (Faaborg 1982a) and have fluctuated similarly for more than two decades in relation to rainfall (Dugger et al. 2000, Faaborg and Arendt 1992, Faaborg et al. 1984). In the Guánica reserve, thrasher numbers are not thought to be great enough to significantly impact other species unless they are already suffering significant losses from other causes (e.g., avian brood parasitism—see Woodworth 1997 for details). Correspondingly, the percentage of immatures (potential recruit breeders) in the yearly captures of bananaquits and Puerto Rican spindalis is also cyclic, with both species showing similar patterns (fig. 8.6b). As demonstrated by total captures, the yearly number of immatures in both populations is also undoubtedly closely related to local rainfall patterns. The dramatic drop in the

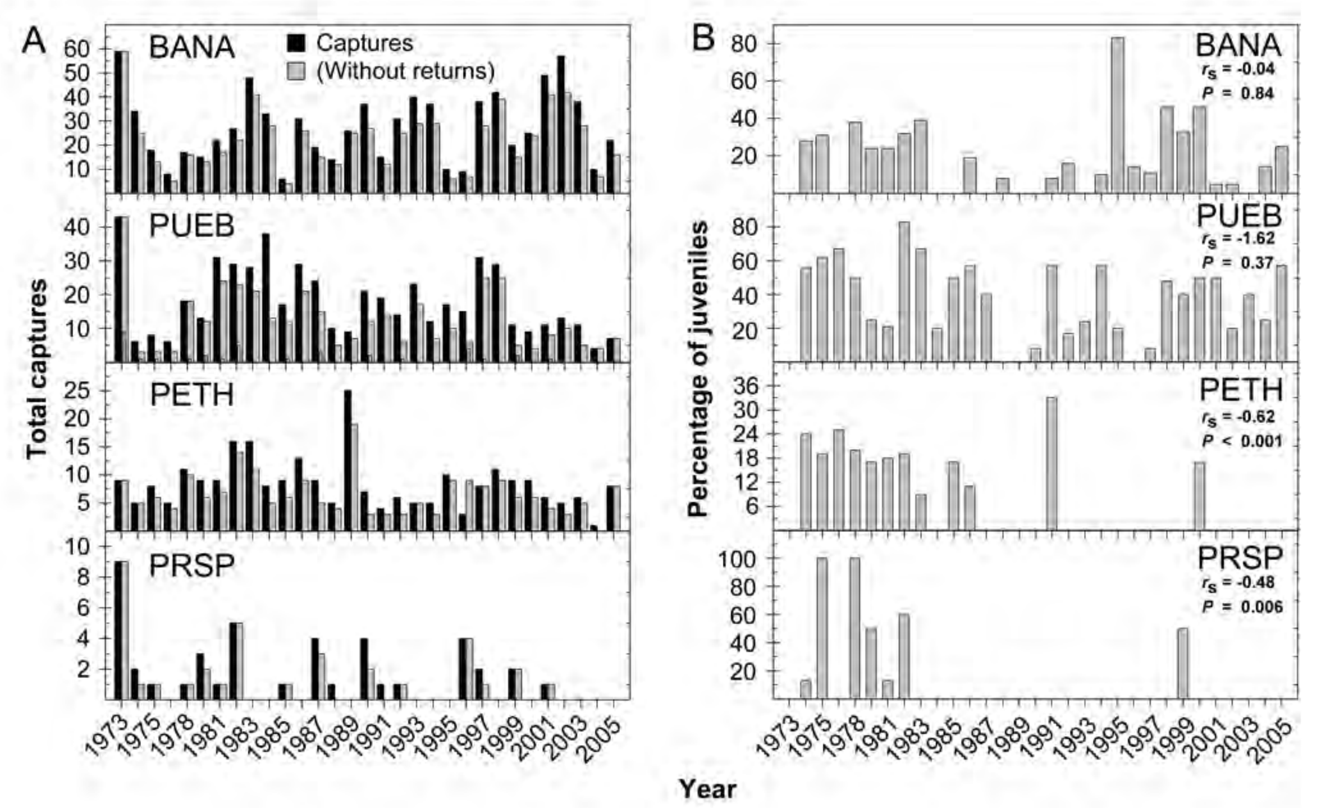


Figure 8.6—Thirty-two years of banding results for populations of the bananaquit, Puerto Rican bullfinch (PUEB), Puerto Rican spindalis (PRSP), and pearly-eyed thrasher (PETH) inhabiting coastal dry forest, a habitat in which the thrasher is much less common. In contrast to their suppressed populations in upland colorado (*Cyrilla racemiflora* L.) forest where the thrasher abounds, dry forest populations of at least the bananaquit and bullfinch are thriving (A). Dry forest does not appear to be preferred habitat for the Puerto Rican spindalis (A). With the exceptions of the bananaquit and bullfinch, the proportion of immatures in yearly captures of the thrasher and tanager has dropped precipitously since the mid 1980s (B); thus, the latter two species should be closely monitored.

number of immature pearly-eyes and Puerto Rican spindalis after the mid-1980s also has been observed in other resident birds and is currently under investigation (Faaborg et al., in preparation). The significant decline in potential recruits among several resident species over the past two decades clearly demonstrates that, just as with the Puerto Rican vireo (see Faaborg et al. 1997), monitoring efforts for several of Guánica's forest birds should be strengthened.

In summary, the pearly-eye may be suppressing populations of at least three coinhabiting frugivorous-nectarivorous species within the colorado forest zone of the Luquillo Experimental Forest. However, it is probably not suppressing any species in the Guánica reserve simply because the thrasher is not as common, owing to the increased species richness found in dry forests in general. Undeniably, in addition to the pearly-eye's real or potential threat to other forest-bird populations, many other unresearched climatic, edaphic, and ecological factors are involved.

Impact on Forest-Bird Populations in Montserrat

During wildlife assessments on Montserrat in 1984 (Faaborg and Arendt 1985), mist netting and line transects (Emlen 1971, 1977) revealed that populations of the bananaquit and Lesser Antillean bullfinch (*Loxigilla noctis*) were reduced in forested areas where the thrasher abounded. Mist-net capture rates of bananaquits at five banding sites in dry, wet, and cloud forest were negatively correlated with those of the pearly-eye (Spearman Rank Order Correlation: $r_s = -0.90$; $P < 0.001$). Bullfinches, usually caught in large numbers in most habitats, were almost extirpated in these areas (fig. 8.7). Bananaquits and bullfinches persisted in substantial numbers only in xeric scrub vegetation where they built their nests deep in crevices of columnar cacti, often out of reach of marauding thrashers. In contrast, however, in March 1990, only 6 months following the passage of Hurricane Hugo, bananaquits and bullfinches were found in numbers often equaling those of the pearly-eye in many of the same areas where they were previously suppressed (fig. 8.7; see also Arendt et al. 1999 after volcanic eruptions). Bullfinches and bananaquits are, respectively, C- and D-tramps and, like the thrasher, were able to respond quickly to the widespread habitat destruction and prolific vegetative regeneration resulting from the passage of the hurricane and subsequent volcanic eruptions. With time, and barring any immediate major disturbances, bullfinch and bananaquit numbers should once again diminish in areas where the pearly-eye will undoubtedly recover and become prevalent once more.

Impact on Other Caribbean Vertebrates

Resident and migratory birds representing diverse taxa and foraging guilds found throughout the Caribbean and adjacent regions are known to include lizards in their diets (Aborn and Froehlich 1995, Adolph and Roughgarden 1983, Arendt 1980, McLaughlin and Roughgarden 1989, Snyder et al. 1987, Waide and Reagan 1983, Wunderle 1981). Moreover, many of the aforementioned authors contend that predation is as likely a candidate as competition in affecting the distribution and diversity of anoles and birds in the West Indies.

The pearly-eyed thrasher feeds extensively on anolid lizards (Arendt 1980). Although fruits are a staple in the pearly-eye's diet, especially during the nonbreeding season, thrashers prey on lizards and frequently feed them to their young (J.W. Wiley—cited in Waide and Reagan 1983; and this study). R. Díaz (1996, pers. comm.) once observed a young female pearly-eye attack and attempt to carry off a ground lizard (*Ameiva exsul*). However, she was unable to either kill or remove the lizard from the immediate area. On a regional scale, Adolph and Roughgarden (1983), working on St. Eustatius, Netherlands Antilles, found

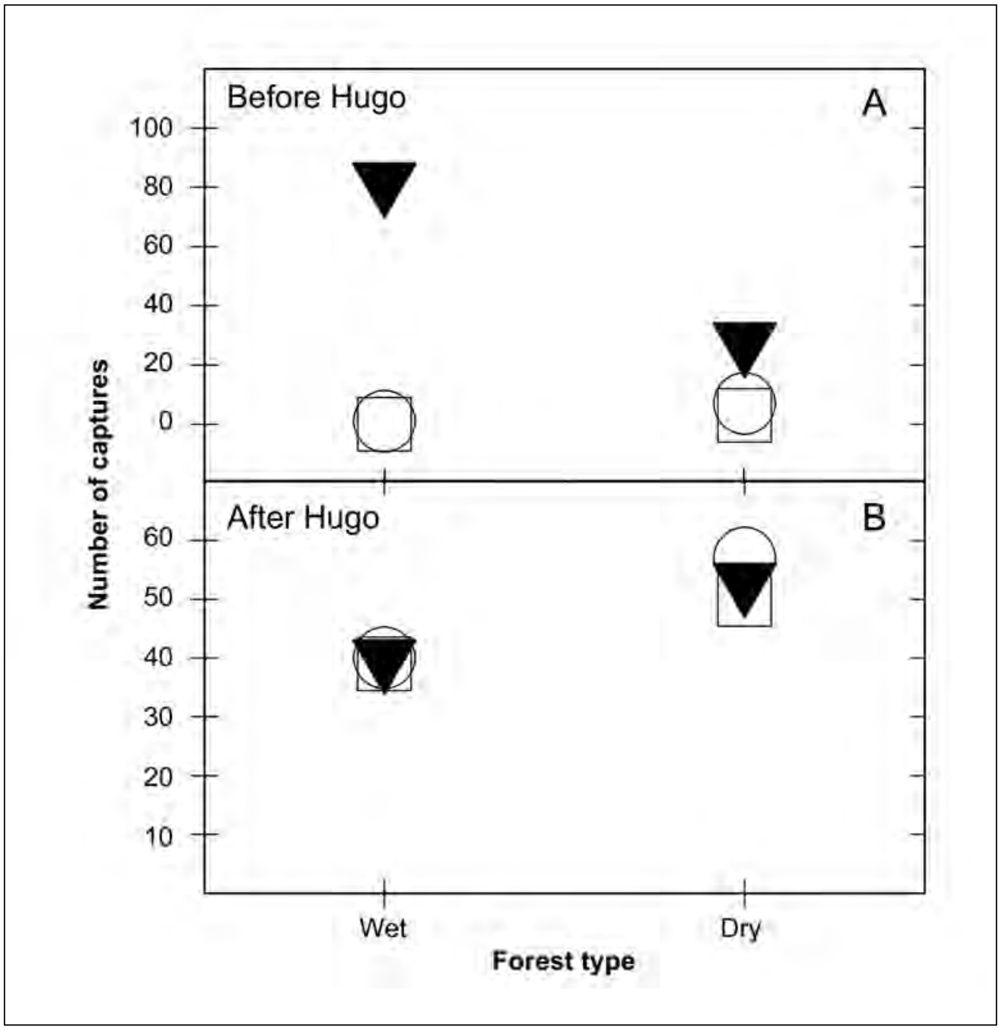


Figure 8.7—Capture rates of pearly-eyes (▼), bananaquits (○), and Lesser Antillean bullfinches (□) in wet and dry forest on Montserrat, West Indies. In June 1984, pearly-eyed thrashers were observed suppressing predisturbance populations of bananaquits (D-Tramps) and bullfinches (C-Tramps) (graph A). Conversely, in March 1990, 6 months subsequent to the passage of Hurricane Hugo, their numbers rivaled those of the pearly-eye, a characteristic of C- and D-tramps responding rapidly to major habitat destruction (graph B). See appendix 1 for avian scientific names.

the pearly-eye to be not only a prime predator of anolid lizards but also one of its major competitors. The pearly-eye's predation on anoles can be so intense that it has even been found to reduce their populations on other small islands in the northeastern Caribbean. McLaughlin and Roughgarden (1989) reported that in moist habitats on St. Martin, the pearly-eye potentially accounted for a well-documented anole decline during the dry season. Taking a different view, however, Schoener and Adler (1991) showed that habitat affinities and interactions might be more important than species' interactions in determining lizard and bird distributions in the West Indies.

Impact on Endemic and Endangered Species

In the U.S. Virgin Islands, the pearly-eyed thrasher may have played a major role in the endangerment and apparent extirpation of the subspecific form of the Puerto Rican screech-owl (*Megascops nudipes newtoni*) (Moreno 1998; see also Raffaele et al. 1998—table of critically endangered species on p. 36, and text on p. 321).

The pearly-eye's impact can be devastating on already endangered, often endemic species.

In nearby Puerto Rico, the pearly-eye is a major nest predator of at least four species of endemic forest birds: Puerto Rican tody (Kepler 1977), Puerto Rican nightjar, *Caprimulgus noctitherus* (Vilella 1989), yellow-shouldered blackbird, *Agelaius xanthomus*, (Pérez-Rivera 1978b, Post and Wiley 1976), and Puerto Rican parrot (Rodríguez-Vidal 1959, Snyder and Taapken 1978, Snyder et al. 1987, Wiley 1985b). Snyder et al. (1987) state that the pearly-eye is "Without any serious rivals, the [parrot's] most remarkable natural enemy..." However, it is noteworthy that the additional mortality caused by ectoparasitic philornid flies on nestlings and fledglings of already critically endangered species within the Sierra de Luquillo should not be underestimated (Arendt 2000). Numerous management steps have been taken, and others proposed (Arendt 2000), to mitigate thrasher nest predation on the parrot (Snyder and Taapken 1978, Snyder et al. 1987). Yet, thrasher attacks continue. Between 1989 and 1993, thrashers depredated 3 of 27 (about 11 percent) of the active parrot nests (F. Vilella 1993, U.S. Fish and Wildlife Service, pers. comm.). Until the critical mass of breeding parrots is greatly augmented in the Sierra de Luquillo, or until the parrot can be successfully reintroduced into parts of its former range where thrashers may be less common, pearly-eyes will continue to be a contributing factor in lowering parrot nesting success.

Two subspecies of endangered forest raptors within the Sierra de Luquillo are also known to suffer from pearly-eye nest predation, namely the broad-winged hawk, *Buteo platypterus brunnescens*, and sharp-shinned hawk, *Accipiter striatus venator* (Delannoy 1984, 1997, Wiley 1985c, 1986a). As Delannoy (1997) pointed out, not only does the pearly-eye pose a direct threat to the sharp-shinned hawk as a nest predator, it further impacts it indirectly by reducing populations of small forest birds, which form a substantial portion of the hawk's diet. Snyder et al. (1987) reported that the abundance of small birds is in general significantly and negatively correlated with abundance of the pearly-eye in Puerto Rico. Avian population censuses conducted by J.W. Wiley in the Sierra de Luquillo through 1986 indicated a steadily increasing thrasher population, but steadily declining populations of other forest birds (cited in Delannoy 1997). Wiley (1985c) also documented that from 1973 to 1984, 29 percent of the nest failures in the sharp-shinned hawk were attributed to thrasher predation.

The pearly-eye also has been implicated in the endangerment of the Puerto Rican plain pigeon, *Patagioenas inornata wetmorei* (Pérez-Rivera and Collazo Algarín 1976b, 1976c; Wiley 1985a), and the extirpation of the island's population of the white-necked crow (Snyder et al. 1987, Wiley 1985a). Whereas the pigeon has been extirpated from most of its historical range throughout the island, a remnant population remains near the town of Cidra in an area where thrashers are generally scarce (about 0.5 per km., J.W. Wiley 2001, in litt.). Fewer than one pearly-eye per kilometer is considered scarce because as many as 118 per kilometer have been reported in Puerto Rico and the Virgin Islands (Snyder et al. 1987, app. 29: 338). White-necked crows disappeared from the Sierra de Luquillo at about the same time that thrashers are thought to have invaded the area (Snyder et al. 1987: 193). Could the pearly-eye have expedited the extirpation of the crow from its last foothold in Puerto Rico? Owing to the substantial amount of evidence amassed over the past several decades demonstrating the thrasher's predatory prowess, it is likely that indeed the pearly-eye was, at least in part, responsible for the crow's demise, once its population was severely reduced owing to other unknown causes (e.g., botfly ectoparasitism?). Nonetheless, this question remains open to debate, and the extent of the thrasher's role in historical and contemporary extinctions (or at least significant reduction in numbers) of Puerto Rico's native fauna will probably always remain open to question. What is certain, though, is that in areas of dense populations, the pearly-eyed thrasher can, and does, deleteriously impact coexisting populations, including those of already threatened or endangered species. As one last case in point, following volcanic eruptions in Montserrat that began in the 1990s and persisted for several years, numbers of its only endemic bird, the Montserrat oriole (*Icterus oberi*), continue to decline (Hilton et al. 2003). A major cause of reproductive loss has been nest predation by pearly-eyed thrashers, which now appear to be more prevalent than even *Rattus rattus* (G. Hilton 2004, in litt.).

Interspecific Competition and the Supertramp Strategy

As shown in chapters 4 and 5, the pearly-eye, like other island colonists, is continually constrained by many diverse and often subtle ecological factors such as versatility in habitat occupancy, trophic status, and body size in relation to its guild neighbors (for more examples, see Faaborg 1982b, 1985; Terborgh et al. 1978). The pearly-eye has been shown to be a potentially good competitor in terms of versatility in habitat occupancy as it is a habitat generalist and can be found in every major habitat type, even on mountain summits of the highest relief islands. In terms of trophic status, the pearly-eye is omnivorous and can "fit into" species-poor avian communities on small islands by replacing similar-sized passerine and nonpasserine guild members, and sometimes even species from different foraging guilds (Faaborg 1985).

If the pearly-eye can impact, or even limit, populations of other vertebrates to the point of accelerating the extinction of already threatened or endangered species, why then cannot the thrasher compete in all avian communities everywhere within its range? After all, the pearly-eye undergoes density overcompensation in species-poor communities consequential to competitive release (Buden 1990; Diamond 1974; Faaborg 1980c, 1988; Hernández-Prieto 1993; MacArthur 1972; MacArthur et al. 1972; Terborgh and Faaborg 1973). Furthermore, as a supertramp, it responds quickly to "ecological crunches" (sensu Wiens 1977) as shown throughout this and other studies. Also to the pearly-eye's advantage, it is endowed with a high degree of morphological plasticity and large, overall body size, which often allows it to overpower and defeat opponents in bouts of physical combat (interference competition) over food resources and nest sites. For example, in the Sierra de Luquillo, Puerto Rico, during the breeding season, the pearly-eye excludes from within its nesting and foraging territories all other potential competitors, ranging from tiny hummingbirds that take insects from bromeliad water as do thrashers, to a much larger frugivore, the scaly-naped pigeon, which (among other species) competes for the seeds of the sierra palm, one of the thrasher's staple foods. The thrasher is able to successfully exclude interspecific competitors from its nest sites and food resources because it is a very large and aggressive passerine. Unquestionably, the pearly-eye has adapted well to the "interference" component of interspecific competition through the evolution of its pugnacious personality and large body size. And, there are still other advantages to being large.

Attributes of Large Body Size in Birds

Noting that several West Indian foraging guilds (frugivores, nectarivores, insectivores) are reduced to a single member on small islands, Faaborg (1975) presented three advantages to being large. The first is related to the relative range of resource sizes that birds of various dimensions can use. The mean and variance of food size increase as avian body size increases (Faaborg 1982b, 1985). Thus, a large bird can ingest a wider range of food resources than a small one. In the absence of competitors, whereas small species are limited to food resources of diminutive dimensions, large species extend their foraging niche to include large and small food items.

A second component of the large-versus-small body size adaptive strategy involves the role of metabolic rates and biomass in species survival. Avian metabolic rates decrease on a per-gram basis with increasing body size (Kendeigh 1970). A 100-g thrasher is about three times the size of a 32-g finch but needs only twice the daily energy intake. Requiring only twice the daily energy of a finch, the thrasher has developed a body size and morphology that allow it to harvest a wider range of food resources thus enhancing its long-term survival, especially on small islands where food and other resources are often scarce.

A third advantage to being large is evident if there exists skewness in the overall dimensions of food resources on islands of varying size. Faaborg (1988) presented data that invoke such size skewness in the resource base for three Neotropical islands. On the tiny island of Santa Fe in the Galápagos Archipelago, food resources are highly skewed toward small fruits and seeds. Not surprisingly, the island is inhabited mainly by several species of small, closely studied fringillids, known collectively as Darwin's finches (see Bowman et al. 1983, Grant and Grant 1999). In contrast, on the very small West Indian island of Mona, near Puerto Rico, fruits and seeds, although skewed toward the smaller dimensions, show a much larger mean and range of sizes than those on Santa Fe. On Mona, the pearly-eye is able to persist, even to the point of dominating the avian community, because of its aggressiveness, predatory habits, and large size, taking full advantage of the wide range of food resources. To compare with Mona's food resource base, Faaborg and colleagues measured fruit and seed size in the Guánica Biosphere Reserve, a dry forest with a similar climate and vegetation, located only about 100 km to the east in southwestern Puerto Rico. Fruits and seeds in the Guánica reserve had a size distribution similar to that found on Mona. Given a similar set of potential competitors and resource base, intuitively, the thrasher should be a prominent member of Guánica's avian community just as it is on Mona. Yet, as shown in chapter 4, the pearly-eye is quite uncommon in the Guánica Biosphere Reserve. But, why?

The pearly-eye's large body and supertramp atributes, both pluses in terms of interference competitiion and colonization, are nullified through community competition, barring its gaining a "foothold" on neighboring continents unless species impoverishment and habitat degradation continue.

Generalized Food Habits and Diffuse Competition

Why does the pearly-eye not compete on larger islands such as Cuba or Hispaniola or, more specifically, in species-rich avian communities? Part of the answer may lie in the adverse effects caused by diffuse competition. To its disadvantage, the pearly-eye is a "jack-of-all-trades, master-of-none" generalist. Although able to physically expel competitors from nesting and foraging territories in habitats in which it abounds on a year-round basis, the pearly-eye cannot utilize the food resource base as efficiently as many foraging specialists in the community as a whole (see discussion in Schoener 1969). As Faaborg (1975) pointed out, "Under the constraints of an insular situation, a high density of small birds may make it impossible for larger species to exist." He offers the large island of Hispaniola as a case in point. The relatively numerous, small frugivorous specialists inhabiting Hispaniola may deplete food resources to an extent that makes it impossible for *Margarops fuscatus* to survive on the main island, thus limiting the thrasher to its smaller, species-poor satellites such as Beata.

Similar interspecific competitive pressures are likely to keep the pearly-eye from gaining a foothold in Cuba and Jamaica. Puerto Rico on the other hand has fewer frugivorous species and, not surprisingly, there the pearly-eye can compete, at least in species-poor habitats. One final example is given to corroborate the notion that small, foraging specialists may in fact be excluding large foraging generalists from some island communities. Terborgh et al. (1978) present and discuss avian communities and species composition on the Îslès les Saintes, a group of very small satellite islands with a combined landmass of <26 km^2 located about 11 km south of Guadeloupe. Because they are satellite islands, they have more bird species than their small area would suggest. The Îslès les Saintes are also among a very few islands in the Lesser Antilles where neither *M. fuscatus* nor *M. fuscus* is resident. Within the constraints of diffuse competition, the relatively diverse, small bird fauna found on these islands allow both *Margarops* species to exist only at low densities, apparently densities too low to sustain viable populations. Whereas being large is advantageous in some isolated situations, e.g., small species-poor islands, diffuse competition from a set of smaller competitors may limit the distribution of larger species.

In summary, the pearly-eye is excluded from species-rich communities where niches are mainly delineated by diffuse interspecific competition (Faaborg 1988, Terborgh and Faaborg 1980).

The Pearly-Eye's Future

Over the past few centuries, the pearly-eye has undergone numerous population and range contractions and expansions (review chapters 3, 4, and app. 3). What might the future hold for this highly vagile Caribbean supertramp? The pearly-eye's future depends on its ability to adapt to the ever changing conditions in natural and anthropogenic environments throughout the region. *Margarops fuscatus* is expanding its range northward on islands in both the Greater and Lesser Antilles (chapter 4, and app. 3). An increase in tourism, establishment of businesses and exclusive vacation resorts, as well as rapid and, in many cases, poorly planned urbanization, continue unchecked throughout the region and in coastal areas along both the North and South American continents. Furthermore, the pearly-eyed thrasher, a habitat generalist like many other mimids, is able to adapt to many natural, disturbed, and human-induced environments. For example, even in its prime colorado forest habitat in Puerto Rico, thrashers are three times as abundant (avg. = 16 individuals per km) in cutover sections than in virgin colorado forest (avg. = 5 individuals per km) (see app. 29 in Snyder et al. 1987). Thus, one is tempted to suggest an expansion of populations and range for the species. One could even go as far as proposing continental invasions via chains of small cays and colonization of numerous land-bridge islands. But, as attractive as this scenario is, it may not be realistic, at least for the near future. One must not forget the pearly-eye's history. For hundreds of years, the pearly-eyed thrasher has proven its capabilities of dispersing to and colonizing islands throughout the greater Caribbean Basin. Yet, it has been unsuccessful in establishing continental populations in spite of its long-time residence on islands and cays not too distant from the shorelines of both North and South America. Why then has *Margarops fuscatus* not been able to colonize continental habitats in the past? Relying on the information presented herein, I contend that, historically, the pearly-eyed thrasher has not been able to establish itself either on the continents or on most large Caribbean islands simply because habitat degradation has not yet advanced, nor has avian diversity decreased, sufficiently to allow it. In the more distant future, however, given the current and projected socioeconomic levels and environmental conditions existing in the Caribbean's major islands and coastal areas of the adjacent continents, pearly-eye populations may reach the critical mass necessary for the establishment of the species in these areas. If the pearly-eye does secure a foothold on one of the continents, its large size, pugnacity, and predatory habits would certainly enhance its chances of success. These intrinsic competitive traits, together with a continual reduction of species richness in avian communities through constant degradation of natural habitats to accommodate evergrowing human populations, would certainly enhance the thrasher's probability of success. Ultimately, the pearly-eye could conceivably compete with native and introduced species adapted to urban life, at least in species-impoverished environments. After all, the pearly-eyed thrasher **is** the Caribbean's premier avian supertramp.

Summary: Impact on Other Vertebrates and Epilogue

The pearly-eye undergoes density overcompensation on small islands and in species-poor communities owing to competitive release and is able to successfully exclude interspecific competitors from its nest sites and food resources because of its large size and pugnacity. It is an avid predator on adults and nest contents of many species of insular birds and other vertebrates. It impacts herpetofaunal populations and forest birds, including several threatened and endangered species in Puerto Rico and elsewhere in the Caribbean. As the supertramp theory predicts, pearly-eye numbers increased in "hard-hit" areas of the Sierra de Luquillo immediately following habitat disturbance, but continue to decrease as other resident species reestablish themselves. In terms of trophic status, the pearly-eye is omnivorous and can "fit into" species-poor avian communities on small islands by replacing similar-size passerine and nonpasserine guild members, and sometimes even species from different foraging guilds. Why, then, does the pearly-eye not compete on larger islands, or more specifically, in species-rich avian communities? Part of the answer is diffuse competition. To its disadvantage, the pearly-eye is a "jack-of-all-trades, master-of-none" generalist. Within insular habitats, a high density of small, avian specialists makes it impossible for this larger generalist to exist. Interspecific competitive pressures are among the key factors keeping the pearly-eye from gaining a foothold on the large islands of Hispaniola, Cuba, and Jamaica, as well as the continents. On Puerto Rico, a smaller island with fewer frugivorous species, the pearly-eye can compete in species-poor habitats. The pearly-eye's future depends on its ability to adapt to the ever-changing conditions in natural and anthropogenic environments. It is unlikely that the pearly-eyed thrasher will ever expand its range onto the continents, at least in the near future. However, if the pearly-eye secures a foothold on either nearby continent, its large size, combative nature, and predatory habits would certainly enhance its chances of success, especially in species-impoverished environments resulting from today's burgeoning human populations.

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Figure 15 (photomicrograph) was produced by Leslie S. Uhazy during a cooperative IITF and university study completed at the University of Missouri-Columbia. He presently teaches at Antelope Valley College, Lancaster, CA.

English Equivalents

When you know:	Multiply by:	To get:
Centimeters (cm)	0.394	Inches
Millimeters (mm)	.039	Inches
Meters (m)	1.094	Yards
Hectares	2.47	Acres
Kilometers (km)	.6215	Miles
Grams (g)	.022	Pounds
Square kilometers (km^2)	.386	Square miles

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Appendix 1: Competitive Strategies Classification[a], Distribution[b], and Habitats[c] of 224 Species of West Indian Landbirds[d]

The West Indian faunal region encompasses all the islands of the Greater Antilles (eastward from Cuba and the Bahamas to the United States and British Virgin Islands) and the Lesser Antilles (southward from Anguilla and Saba to Grenada, the latter of which represents the extreme southeastern border of the region). Swan Island, together with Old Providence, and St. Andrew, form the southwestern extreme of the West Indian faunal region. Land-bridge islands (e.g., Trinidad, Tobago, Margarita, and the southern Netherlands Antilles) have been excluded from this analysis because of the continental affinities of their avifauna.

In the West Indies, 224[e] species of landbirds (Falconiformes, and Columbiformes through Passeriformes) inhabit 177 selected islands from which the number of breeding species was determined by literature review and personal study. Although regional endemism is high, many species occur on several islands. Many of the habitats listed for certain species may not appear in conventional reference texts (e.g., AOU Checklist 1998) because island populations often undergo extensive niche shifts in the absence of competitors. As an example, the habitat for continental populations of the American kestrel (*Falco sparverius*) is listed in the AOU Checklist (1998) as "Open and partly open country with scattered trees, cultivated lands and urban areas." On Montserrat for example, where other raptors are absent, the kestrel is found in all major habitats ranging from sea level to the highest point (Chance's Peak, 915-m elev. prior to recent volcanic eruptions). It hover-hunts in open areas and above closed-canopy forests similar to insular buteos, and either perch-hunts or actively pursues small birds and bats in forest edge and closed-canopy habitats similar to forest falcons and accipiters.

Recent taxonomic revisions and additions to the number of regional endemics, e.g., six species of *Contopus* (see Raffaele et al. 1998, Reynard et al. 1993), four species of *Spindalis* (Garrido et al. 1997), three species of Adelaide's warbler, and two each of trembler and chat-tanagers (AOU 1998) do not significantly affect the results. Indeed, the number of Caribbean endemics was substantially higher than that of the Pacific avifauna even before the 12 to 13 recent additions.

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[a] Species incidence functions. Criteria used in placing each West Indian bird species into Diamond's high-S and tramp categories, as well as one additional category, are outlined below. Many of the seven competitive strategy categories were greatly affected by species found in species-poor communities on satellite islands near the main islands with the stated number of breeding landbird species.

High-S species (HS): Endemics and/or species generally restricted to one, or a few islands and habitats with ≥40 species of breeding landbirds.

A-Tramps (A): Endemics, and/or species restricted to single, or a few, islands and habitats with 30 or more species of breeding landbirds.

B-Tramps (B): Species restricted to a few islands and habitats with 30 or more species of breeding landbirds; generally, these species are somewhat more widely distributed than A-tramps.

C-Tramps (C): Species with a wider geographical and habitat distribution, e.g., throughout the Greater or Lesser Antillean islands, but not found throughout the region; these species often do not occur on more than 60 percent of the islands with 20 or more species of breeding landbirds.

D-Tramps (D): Widely distributed species, i.e., throughout the region, including both the Greater and Lesser Antilles, found in a variety of habitats; these species often occur on 80 to 100 percent of the islands with 10 or more species of breeding landbirds.

Supertramps (S): Species with an extensive geographical and habitat distribution and/or restricted to small islands with few species of breeding landbirds or on large islands in species-poor habitats; these species often occur on fewer than 50 percent of the species-poor islands.

Anomalous species (AS): species that do not readily ‘fit’ into any of the previous six categories: (a) generally thought to be introduced by man; (b) relict species that did not radiate following isolation resulting from past, dramatic climatic changes; or (c) mainland species naturally occurring on landbridge and extralimital islands near continental source populations.

[b] **Islands.** 1. Acklins (Bf), 2. Ambergris Cay Big (C), 3. Ambergris Cay Little (C), 4. Andros (B), 5. Anegada (BVI), 6. Anguilla (LI), 7. Antigua (LI), 8. Barbados (WI), 9. Barbuda (Antigua), 10. Bay Cay (C), 11. Beata (H), 12. Beef (BVI), 13. Bellamy Cay (BVI), 14. Bequia (Gr), 15. Big Flat Cay (USVI), 16. Big Sand Cay (T), 17. Biminis (B), 18. Bird Rock (B), 19. Booby Cay (B), 20. Bovoni Cay (USVI), 21. Bass Inner (USVI), 22. Bass, Outer (USVI), 23. Buck (BVI), 24. Buck (USVI), 25. Carriacou (Gr), 26. Carval (BVI), 27. Cas Cay (USVI), 28. Castle (B), 29. Cat (B), 30. Catalina (H), 31. Cay Sal (Bah.), 32. Cayemites (H), 33. Cayman Brac 34. Cinnamon Cay (USVI), 35. Cockroach Cay (USVI), 36. Cockroach (BVI), 37. Cocoloba Cay (USVI), 38. Congo Cay (USVI), 39. Cooper (BVI), 40. Cotton Cay (T), 41. Crooked (B), 42. Cuba 43. Culebra (PR), 44. Dead Chest (BVI), 45. Dellis Cay (C), 46. Desecheo (PR), 47. Dog (USVI), 48. Dominica 49. Dutch Cap (USVI), 50. East Caicos 51. East Cay (T), 52. East Seal Dog (BVI), 53. East Six Hill (C), 54. Eleuthera (B), 55. Eustatia (BVI), 56. Fish Cay (B), 57. Fortune (B), 58. French Cap (USVI), 59. French Cay (C), 60. Ft. George (C), 61. George Dog (BVI), 62. Gibbs Cay (T), 63. Ginger (BVI), 64. Gonâve (H), 65. Grand Bahama 66. Grand Cayman 67. Grand Turk 68. Grass Cay (USVI), 69. Great Abaco (B), 70. Great Camanoe (BVI), 71. Great Dog (BVI), 72. Great Exuma (B), 73. Great Inagua (B), 74. Great St. James (USVI), 75. Great Tobago (BVI), 76. Green Cay (BVI), 77. Green Cay (USVI), 78. Grenada 79. Guadeloupe 80. Guana (BVI), 81. Guana Cay (B), 82. Hans-Lollick, Big (USVI), 83. Hans-Lollick Little (USVI), 84. Harbour (B), 85. Hassel (USVI), 86. Henley Cay (USVI), 87. Hispaniola 88. Île-à-vache (H), 89. Îslès les Saintes (G), 90. Jamaica 91. Jost Van Dyke (BVI), 92. Kalkun Cay (USVI), 93. La Désirade (G), 94. La Juventud (Cu), 95. Little Abaco (B), 96. Little Camanoe (BVI), 97. Little Cayman 98. Little Exuma (B), 99. Little Inagua (B), 100. Little Jost Van Dyke (BVI), 101. Long Cay (C), 102. Long Cay (T), 103. Long (B), 104. Lovango Cay (USVI), 105. Marie Galante (G), 106. Marina Cay (BVI), 107. Martinique 108. Mayaguana (B), 109. Middle Caicos 110. Mingo Cay (USVI), 111. Mona (PR), 112. Montserrat (LI), 113. Mosquito (BVI), 114. Necker (BVI), 115. Nevis (LI), 116. New Providence (B), 117. Norman (BVI), 118. North Caicos 119. Parrot Cay (C), 120. Patricia Cay (USVI), 121. Pear Cay (T), 122. Penniston Cay (T), 123. Perkins Cay (USVI), 124. Peter (BVI), 125. Pine Cay (C), 126. Plana Cay East (B), 127. Plana Cay West (B), 128. Prickly Pear (BVI), 129. Providencia (Co.), 130. Providenciales (C), 131. Puerto Rico 132. Ragged Islands (B), 133. Ramgoat Cay (USVI), 134. Rotto Cay (USVI), 135. Rum Cay (B), 136. Saba (NNA), 137. Saba Cay (USVI), 138. Salt Cay (BVI), 139. Salt Cay (T), 140. Salt Cay (USVI), 141. Samana Cay (B), 142. San Andrés (Co.), 143. Sandy Cay (BVI), 144. San Salvador (B), 145. Saona (H), 146. Savannah (USVI), 147. Scrub (BVI), 148. Shark Rock (USVI), 149. Sheep Cay (B), 150. South Caicos 151. St. Barthelemy (LI), 152. St. Croix (USVI), 153. St. Eustatius (NNA), 154. St. John (USVI), 155. St. Kitts (LI), 156. St. Lucia 157. St. Martin (NNA), 158. St. Thomas (USVI), 159. St. Vincent 160. Steven Cay (USVI), 161. Stubbs Cay (C), 162. Swan (Ho.), 163. Thatch Cay (USVI), 164. Tortola (BVI), 165. Tortue (H), 166. Trunk Cay (USVI), 167. Turtledove Cay (USVI), 168. Union (Gr.), 169. Vieques (PR), 170. Virgin Gorda (BVI), 171. Water Cay (C), 172. Water (USVI), 173. West Caicos 174. West Cay (USVI), 175. West Dog (BVI), 176. West Seal Dog (BVI), 177. Whistling Cay (USVI).

[c] Habitat distribution and abbreviations. Habitats refer to resident populations of species on islands in which migrant individuals exist.

T: habitat and vegetation type: 1. strand vegetation; 2. mangroves; 3. marsh (saline); 4. swamp (freshwater); 5. lakes and/or rivers (including riparian vegetation); 6. arid vegetation; 7. semiarid vegetation; 8. grassland; 9. savanna; 10. scrub; 11. woodland; 12. deciduous forest; 13. "mixed" forest, e.g., deciduous-coniferous or evergreen-coniferous; 14. coniferous forest; 15. evergreen forest.

S: vegetation structure: 1. open country, 2. scattered trees, 3. shrubbery, 4. brush, 5. thickets, 6. undergrowth, 7. open canopy, 8. closed canopy, 9. clearings, 10. edge.

E: Elevation: 1. coast, 2. lowlands, 3. hills, 4. mountains, 5. aerial.

HI: Human-induced environments: 0. none, 1. cultivations, 2. gardens, 3. hedgerows, 4. orchards, 5. parks, 6. pastures, 7. plantations, 8. settlements.

[d] **Sources:** B. Aldridge (1991, in litt. Grand Turk, North Caicos, Parrot and Pine Cays); American Ornithologists' Union 1998 (region); Arendt 1988, 1990, 1993, 1995, 1997a,b; Arendt and Arendt 1988, Arendt et al. 1999; (Bahamas, and Dominican Republic east through Barbados); Atwood (1791); Barbour 1943 (Cuba); Beatty 1930, 1931, 1941 (Puerto Rico, U.S. Virgin Islands); Biaggi 1974 (Puerto Rico); Bond 1945, 1950, 1956a (regional checklist); Bond 1979a (regional guide); Bond 1982a (Hispaniola); Bond (regional checklist's 24 Supplements: 1956—1982); Bradley 1985 (Cayman Islands); Brudenell-Bruce 1975 (Bahamas); Buden 1987a, 1987b, 1987c, 1990, 1992b, 1992c (Bahamas); Buden and Schwartz 1986 (Cay Sal Bank); Collazo and Bonilla Martínez 1988 (Puerto Rico); Cory 1889 (Region); Cruz 1977, 1987, 1988 (Jamaica, Puerto Rico); Diamond 1973a (St. Lucia); Dod 1978, 1981 (Dominican Republic); Emlen 1977 (Grand Bahama I.); Evans 1990 ("eastern Caribbean"); Faaborg 1980b (Hispaniola: Beata and Saona Islands); Faaborg 1985; Faaborg and Arendt 1985 (Lesser Antilles); Garrido et al. 1997 (region—one species); Hilty and Brown 1986 (Providence and St. Andrew Island); Holland and Williams 1978 (Antigua); Howard and Moore 2003 (region); Johnston 1975, Johnston et al. 1971 (Cayman Island); LaBastille and Richmond 1973 (Anegada, BVI); Lack and Lack 1973 (Grenada); Miller 1978 (San Salvador); Mirecki et al. 1977 (British Virgin Islands); Nichols 1943 (U.S. Virgin Islands); Norton 1980, 1981, 1982, 1983, 1989 (U.S. Virgin Islands); Paulson 1966 (Bahamas); Paynter 1956 (Swan I.); Pérez-Rivera and Bonilla 1983 (Mona, Puerto Rico); Peters 1927 (Anguilla); Peters 1960 (region); Pinchón 1963 (French West Indies); Post and Wiley 1977 (region—one species); Raffaele 1983 (Puerto Rico and U.S. Virgin Islands); Raffaele et al. 1998 (West Indies region); Read 1912 (La Juventud); Recher and Recher 1966 (Puerto Rico); Reynard et al. 1993 (region—one species); Robertson 1962 (U.S. Virgin Islands); Rollé 1963 (Puerto Rico); Russell et al. 1979 (Providence and St. Andrew Islands); Schwartz 1970 (Saona, Dominican Republic); Schwartz and Klinikowski 1963, 1965 (region); Siegel 1983 (Montserrat); Sladen 1987 (St. Croix, U.S. Virgin Islands); Sorrié 1975 (Vieques, Puerto Rico); Stahl 1882 (Puerto Rico); Steadman et al. 1997 (St. Kitts); Voous 1983 (Netherlands Antilles); Wells 1902 (Carriacou, Grenadines); Wetmore 1916a, 1917 (Culebra, Puerto Rico), 1918 (Desecheo, Puerto Rico); Wetmore and Lincoln 1933 (Hispaniola); Wetmore and Swales 1931 (Hispaniola); Wiley 1984, 1985a, 1985b, 1985c, 1986a, 1986b (Puerto Rico and the region); Wiley and Wiley 1981 (Hispaniola); Willis 1973 (Puerto Rico); Woods and Ottenwalder 1983, 1986 (Haiti); Wunderle 1985 (Grenada).

[e] Postanalysis taxonomical revisions increased the original total number of Caribbean landbird species (see "Study Area and Methods" and tabular text, as well as the American Ornithologists' Union 1998 and supplements) but did not affect the results or conclusions of the analyses.

[f] Island abbreviations. (B) Bahamas; (BVI) British Virgin Islands; (C) Caicos Islands; (Co) Colombia, South America; (Cu) Cuba; (G) Guadeloupe; (Gr) Grenadines; (H) Hispaniola; (Ho) Honduras; (LI) Leeward Islands; (NNA) Northern Netherlands Antilles; (PR) Puerto Rico; (T) Turks); (USVI) United States Virgin Islands; (WI) Windward Islands.

1. *Cathartes aura* (turkey vulture) (TUVU) (A-tramp) (number of islands = 7)
   Islands: 4, 42, 65, 87, 90, 94, 131
   Habitat: T: 1–15 S: 1, 2, 7, 9, 10 E: 1–5 HI: 1–8
2. *Pandion haliaetus* (osprey) (OSPR) (C-tramp) (n = 16)
   Islands: 5, 42, 67, 73, 87, 90, 94, 99, 118, 125, 126, 130, 131, 135, 152, 171
   Habitat: T: 1–5, 9, 11, 12 S: 1, 2, 7, 9, 10 E: 1–3 HI: 5, 6, 8
3. *Chondrohierax uncinatus* (hook-billed kite) (HBKI) (Anom.) (n = 2)
   Islands: 42, 78
   Habitat: T: 3, 4, 6, 7, 11, 12, 13, 15 S: 7, 8, 10 E: 1–2 HI: 0
4. *Rostrhamus sociabilis* (snail kite) (SNKI) (high-S) (n = 2)
   Islands: 42, 94
   Habitat: T: 4 S: 7, 9, 10 E:1–3 HI: 0
5. *Accipiter striatus* (sharp-shinned hawk) (SSHA) (high-S) (n = 3)
   Islands: 42, 87, 131
   Habitat: T: 11–15 S: 4–8 E: 2–4 HI: 7
6. *A. gundlachi* (Gundlach's hawk) (GUHA) (high-S) (n = 1)
   Island: 42
   Habitat: T: 1–5, 11–15 S: 4–8 E: 1–4 HI: 7
7. *Buteogallus anthracinus* (common black-hawk) (COBH) (high-S) (n = 3)
   Islands: 42, 94, 159
   Habitat: T: 1–7, 10–12, 15 S: 4–10 E: 1–5 HI: 0
8. *Buteo ridgwayi* (Ridgway's hawk) (RIHA) (high-S) (n = 5)
   Islands: 11, 32, 64, 87, 88
   Habitat: T: 6–12 S: 1, 2, 7, 9, 10 E: 2, 3, 5 HI: 1, 5, 6, 7
9. *B. platypterus* (broad-winged hawk) (BWHA) (C-tramp) (n = 10)
   Islands: 7, 14, 42, 48, 78, 107, 131, 156, 159, 168
   Habitat: T: 11–13, 15 S: 7, 8 E: 2–5 HI: 0
10. *B. jamaicensis* (red-tailed hawk) (RTHA) (C-tramp) (n = 27)
    Islands: 4–6, 11, 42, 43, 46, 64, 65, 69, 87, 88, 90, 95, 115, 131, 136, 137, 152–155, 157, 158, 164, 169, 170
    Habitat: T: 1–15 S: 1, 2, 7–10 E: 1–5 HI: 1, 4–8
11. *Polyborus plancus* (crested caracara) (CRCA) (high-S) (n = 2)
    Islands: 42, 94
    Habitat: T: 6–12 S: 1, 2, 10 E: 2–3 HI: 1, 5, 6
12. *Falco sparverius* (American kestrel) (AMKE) (D-tramp) (n = 58)
    Islands: 1, 5–7, 9, 11, 29, 41–43, 46, 48, 50, 64, 67, 72, 73, 79, 87–90, 93–95, 98, 99, 103, 105, 107–109, 111, 112, 115, 118, 125, 127, 130, 131, 135, 136, 144, 145, 150–158, 164, 165, 169, 170, 173
    Habitat: T: 1–4, 6–15 S: 1, 2, 7–10 E: 1–5 HI: 1, 2, 4–8
13. *Patagioenas squamosa* (scaly-naped pigeon) (SNPI) (D-tramp) (n = 43)
    Islands: 5, 7, 8, 11, 12, 31, 42, 43, 48, 64, 70, 78–81, 87, 89–91, 105, 107, 111, 112, 115, 117, 124, 131, 136, 143, 145, 147, 152–159, 164, 169, 170, 173
    Habitat: T: 1–3, 5–7, 11–13, 15 S: 7–10 E: 1–4 HI: 1, 2, 4, 5, 7, 8

14. *P. leucocephala* (white-crowned pigeon) (WCPI) (D-tramp) (n = 75)
Islands: 1, 4, 6, 7–9, 11–13, 17, 29, 31–33, 38, 41–43, 48, 50, 54, 56, 59, 64–67, 69, 72, 73, 78, 79, 81, 84, 87, 88, 90, 91, 93–95, 97–99, 103, 105, 107–109, 111, 116, 118, 119, 125, 127, 129–132, 136, 142, 144, 145, 150, 152, 154, 156, 157, 159, 162, 165, 168, 169, 171, 173
Habitat: T: 1–3, 5–7, 11–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 5, 8
15. *P. inornata* (plain pigeon) (PLPI) (A-tramp) (n = 6)
Islands: 42, 87, 90, 94, 131, 165
Habitat: T: 1, 2, 4, 7, 11–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 5–8
16. *P. caribaea* (ring-tailed pigeon) (RTPI) (high-S) (n = 1)
Island: 90
Habitat: T: 11, 13, 15 S: 7–10 E: 2, 4 HI: 0
17. *Zenaida asiatica* (white-winged dove) (WWDO) (C-tramp) (n = 29)
Islands: 1, 11, 30, 32, 40, 42, 50, 64, 66, 67, 73, 87, 88, 90, 97, 109, 111, 118, 119, 125, 129–131, 139, 142, 145, 150, 169, 173
Habitat: T: 1, 2, 4, 6, 7, 9–11 S: 2–5, 9, 10 E: 1–3 HI: 1, 2, 5, 6, 8
18. *Z. aurita* (*zenaida* dove) (ZEND) (D-tramp) (n = 134)
Islands: 1, 2, 4–9, 11, 12, 14, 15, 17, 20–26, 29–33, 35, 36, 38, 39, 41–43, 46, 48, 50, 54–58, 60, 61, 63–76, 78–85, 87–93, 95–100, 103, 105–109, 111, 112, 114–120, 124, 125, 127, 128, 130–132, 135–138, 140, 141, 143–148, 150–158, 163–165, 167–171, 173–177
Habitat: T: 1, 2, 4, 6–15 S: 1–7, 9, 10 E: 1–3 HI: 1, 2, 5–8
19. *Z. auriculata* (eared dove) (EADO) (B-tramp) (n = 7)
Islands: 8, 14, 25, 78, 156, 159, 168
Habitat: T: 6–12 S: 2, 3, 9, 10 E: 1–3 HI: 1, 2, 5–8
20. *Z. macroura* (mourning dove) (MODO) (C-tramp) (n = 39)
Islands: 1, 2, 4, 17, 18, 29, 31, 41, 42, 50, 54, 64, 65, 67, 69, 72, 73, 84, 87, 88, 90, 95, 98, 99, 103, 108, 109, 111, 116, 118, 119, 125, 130, 131, 139, 145, 150, 169, 173
Habitat: T: 1–3, 6–9, 11, 13–15 S: 1–3, 7, 9, 10 E: 1–4 HI: 1, 2, 5–8
21. *Columbina passerina* (common ground-dove) (COGD) (D-tramp) (n = 148)
Islands: 1–9, 11–15, 17, 18, 21–25, 27–39, 41–45, 47–50, 54, 55, 57, 60, 61, 63–91, 93, 95–112, 114–120, 124–128, 130, 131, 133, 134, 136–140, 143–148, 150–160, 163–171, 173–177
Habitat: T: 1–3, 6–13, 15 S: 1–3, 9, 10 E: 1–4 HI: 1, 2, 4, 5–8
22. *Leptotila wellsi* (Grenada dove) (GRDO) (high-S) (n = 1)
Island: 78
Habitat: T: 6, 7, 10 S: 4–6 E: 2, 3 HI: 0
23. *L. jamaicensis* (Caribbean dove) (CADO) (B-tramp) (n = 4)
Islands: 33, 66, 90, 142
Habitat: T: 6, 7, 9, 11 S: 2, 3, 9, 10 E: 2, 3 HI: 1, 2, 5–8
24. *Geotrygon chrysia* (Key West quail-dove) (KWQD) (C-tramp) (n = 19)
Islands: 4, 29, 30, 42, 54, 64, 65, 69, 87, 94, 111, 116, 118, 131, 135, 144, 145, 165, 169
Habitat: T: 6, 7, 10–12 S: 4–6, 8–10 E: 2, 3 HI: 7

25. *G. mystacea* (bridled quail-dove) (BRQD) (C-tramp) (n = 26)
    Islands: 6, 7, 9, 43, 48, 79–82, 89, 93, 105, 107, 112, 115, 131, 136, 151, 153–156, 158, 159, 164, 169
    Habitat: T: 6, 7, 11, 12, 15 S: 4–6, 8–10 E: 2–4 HI: 7
26. *G. caniceps* (gray-headed quail-dove) (GHQD) (high-S) (n = 3)
    Islands: 42, 87, 94
    Habitat: T: 11, 12 S: 3, 6, 10 E: 2–4 HI: 0
27. *G. montana* ruddy quail-dove (RUQD) (B-tramp) (n = 14)
    Islands: 7, 42, 48, 64, 78, 79, 87, 90, 105, 107, 131, 156, 159, 169
    Habitat: T: 7, 11–13, 15 S: 4–10 E: 2–4 HI: 7
28. *G. versicolor* (crested quail-dove) (CRQD) (high-S) (n = 1)
    Islands 90
    Habitat: T: 13, 15 S: 3, 5–10 E: 3, 4 HI: 1, 4
29. *Starnoenas cyanocephala* (blue-headed quail-dove) (BHQD) (high-S) (n = 1)
    Island: 42
    Habitat: T: 6, 7, 11, 12, 15 S: 5, 9, 10 E: 2–4 HI: 0
30. *Aratinga chloroptera* (Hispaniolan parakeet) (HIPK) (high-S) (n = 1)
    Island: 87
    Habitat: T: 7, 9, 11, 12, 15 S: 1–3, 7–10 E: 2–4 HI: 1–5, 8
31. *A. euops* (Cuban parakeet) (CUPK) (high-S) (n = 1)
    Island: 42
    Habitat: T: 7, 9, 11, 12, 15 S: 1–3, 7–10 E: 1–4 HI: 1, 2
32. *A. nana* (olive-throated parakeet) (OTPK) (high-S) (n = 1)
    Island: 90
    Habitat: T: 1, 2, 5, 7, 10, 11, 13, 15 S: 1–3, 7–10 E: 1–3 HI: 1–8
33. *Amazona leucocephala* (Cuban parrot) (CUPA) (B-tramp) (n = 6)
    Islands: 33, 42, 66, 69, 73, 94
    Habitat: T: 1, 7, 11–13, 15 S: 3, 7–10 E: 1–4 HI: 1, 2, 4, 5, 7, 8
34. *A. collaria* (yellow-billed parrot) (YBPA) (high-S) (n = 1)
    Island: 90
    Habitat: T: 7, 11, 13, 15 S: 1, 2, 7–10 E: 2–4 HI: 1, 2, 4, 5, 6, 8
35. *A. ventralis* (Hispaniolan parrot) (HIPA) (high-S) (n = 5)
    Islands: 11, 32, 64, 87, 145
    Habitat: T: 2, 4, 7, 11–13, 15 S: 7–10 E: 1–4 HI: 1, 2, 4, 7, 8
36. *A. vittata* (Puerto Rican parrot) (PRPA) (high-S) (n = 1)
    Island: 131
    Habitat: T: 7, 11, 12, 15 S: 7–10 E: 1–4 HI: 1, 2, 7, 8
37. *A. agilis* (black-billed parrot) (BBPA) (high-S) (n = 1)
    Island: 90
    Habitat: T: 11, 13, 15 S: 2, 7–10 E: 2–4 HI: 1, 4
38. *A. arausiaca* (red-necked parrot) (RNPA) (high-S) (n = 1)
    Island: 48
    Habitat: T: 15 S: 7–10 E: 4 HI: 1, 7

39. *A. versicolor* (St. Lucia parrot) (SLPA) (high-S) (n = 1)
Island: 156
Habitat: T: 15 S: 7–10 E: 4 HI: 1, 2, 7

40. *A. guildingii* (St. Vincent parrot) (SVPA) (high-S) (n = 1)
Island: 159
Habitat: T: 7, 11, 12, 15 S: 7–10 E: 1–4 HI: 1, 2, 7, 8

41. *A. imperialis* (imperial parrot) (IMPA) (high-S) (n = 1)
Island: 48
Habitat: T: 15 S: 8 E: 4 HI: 1, 7

42. *Coccyzus americanus* (yellow-billed cuckoo) (YBCU) (C-tramp) (n = 23)
Islands: 1, 6, 11, 17, 41, 42, 64, 72, 73, 84, 87, 90, 95, 98, 101, 108, 111, 131, 145, 151, 152, 155, 169
Habitat: T: 1, 6, 7, 10–12 S: 2–6 E: 1, 2 HI: 2, 3

43. *C. minor* (mangrove cuckoo) (MACU) (D-tramp) (n = 88)
Islands: 1, 4, 5, 7, 9, 11, 12, 14, 17, 21, 25, 29, 33, 39, 41–43, 48, 50, 54, 64–67, 69, 70, 72, 73, 78–85, 87–91, 93, 95, 97–99, 103, 105, 107–109, 111, 112, 114, 116–119, 124, 125, 128–132, 137, 140, 142, 144–147, 150–152, 154–156, 158, 159, 162–164, 168–171, 173
Habitat: T: 1, 2, 4, 6, 7, 9–13, 15 S: 3–8 E: 1–3 HI: 3, 7, 8

44. *C. [Saurothera] merlini* (great lizard-cuckoo) (GRLC) (A-tramp) (n = 6)
Islands: 4, 42, 54, 84, 94, 116
Habitat: T: 1, 2, 4, 6, 7, 10–15 S: 3–8 E: 1–4 HI: 0

45. *C. vieilloti* (Puerto Rican lizard-cuckoo) (PRLC) (high-S) (n = 1)
Island: 131
Habitat: T: 1, 2, 4, 6, 7, 10–15 S: 3–8 E: 1–4 HI: 1–4, 7, 8

46. *C. longirostris* (Hispaniolan lizard-cuckoo) (HILC) (high-S) (n = 4)
Islands: 64, 87, 145, 165
Habitat: T: 1, 2, 4, 6, 7, 10–15 S: 3–8 E: 1–4 HI: 1–4, 7, 8

47. *C. vetula* (Jamaican lizard-cuckoo) (JALC) (high-S) (n = 1)
Island: 90
Habitat: T: 5–7, 11, 13, 15 S: 3–8, 10 E: 2–4 HI: 2

48. *Hyetornis pluvialis* (chestnut-bellied cuckoo) (CBCU) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 11, 13, 15 S: 5, 7–10 E: 2–4 HI: 2, 4, 6

49. *H. rufigularis* (bay-breasted cuckoo) (BBCU) (high-S) (n = 2)
Islands: 64, 87
Habitat: T: 6, 7, 10–12, 15 S: 3–7 E: 2–4 HI: 3, 7

50. *Crotophaga ani* (smooth-billed Ani) (SBAN) (D-tramp) (n = 81)
Islands: 1, 4, 5, 17, 25, 29–33, 39, 41–44, 48, 50, 54, 55, 57, 63–67, 69, 70, 72, 73, 78–81, 84, 87–91, 93, 95–99, 104, 105, 107–109, 111–114, 116–118, 124, 125, 128, 129, 131, 132, 135, 138, 142, 144, 145, 147, 152–156, 158, 159, 162, 164, 169, 170
Habitat: T: 1–4, 6–11 S: 1–7, 9, 10 E: 1–4 HI: 1, 2, 4, 5–8

51. *Tyto alba* (common barn-owl) (COBO) (D-tramp) (n = 38)
Islands: 1, 4, 14, 25, 29, 33, 41, 42, 48, 50, 54, 61, 65–67, 69, 73, 78, 87, 90, 97, 103, 108, 109, 116, 118, 119, 125, 130, 132, 144, 145, 150, 156, 159, 165, 168, 173
Habitat: T: 3, 4, 6–11 S: 1–3, 9, 10 E: 1–4 HI: 1, 2, 4–8
52. *Megascops nudipes* (Puerto Rican screech-owl) (PRSO) (B-tramp) (n = 9)
Islands: 43, 131, 152, 154, 157, 158, 164, 169, 170
Habitat: T: 4, 6, 7, 11–13, 15 S: 7, 8 E: 2–4 HI: 4, 5, 7, 8
53. *Gymnoglaux lawrencii* (bare-legged owl) (BLOW) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 11, 12, 14, 15 S: 2, 7, 8, 9 E: 2, 3 HI: 4, 5, 7
54. *Glaucidium siju* (Cuban pygmy-owl) (CUPO) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 7, 9, 11, 12, 14, 15 S: 7, 9, 10 E: 1–4 HI: 2, 4, 5, 7
55. *Athene cunicularia* (burrowing owl) (BUOW) (C-tramp) (n = 14)
Islands: 4, 11, 17, 29, 31, 42, 54, 64, 65, 69, 87, 94, 103, 116, 155 (extirpated)
Habitat: T: 6–10 S: 1, 2, 9, 10 E: 2 HI: 1, 6, 8
56. *Asio stygius* (stygian owl) (STOW) (high-S) (n = 4)
Islands: 42, 64, 87, 94
Habitat: T: 11, 12, 13, 15 S: 7, 8, 10 E: 2–4 HI: 0
57. *A. flammeus* (short-eared owl) (SEOW) (A-tramp) (n = 5)
Islands: 42, 43, 87, 131, 151
Habitat: T: 3, 6–11 S: 1–3, 6, 9, 10 E: 2 HI: 6–8
58. *Pseudoscops grammicus* (Jamaican owl) (JAOW) (high-S) (n = 1)
Island: 90
Habitat: T: 6–11, 13, 15 S: 2, 5, 7–10 E: 2, 3 HI: 1–3, 5–8
59. *Chordeiles gundlachii* (Antillean nighthawk) (ANNI) (C-tramp) (n = 53)
Islands: 1, 4, 5, 11, 17, 18, 29, 31, 33, 41, 42, 50, 54, 60, 64–67, 69, 72, 73, 84, 87, 90, 94, 95, 97–99, 103, 108, 109, 116, 118, 119, 125, 127, 130–132, 135, 139, 141, 144, 145, 150, 152, 158, 164, 165, 169, 171, 173
Habitat: T: 3, 4, 6–12 S: 1, 2, 9, 10 E: 1–3, 5 HI: 5, 6, 8
60. *Siphonorhis brewsteri* (least pauraque) (LEPA) (high-S) (n = 3)
Islands: 64, 87, 90
Habitat: T: 6, 7, 10–12 S: 2, 3, 7, 9, 10 E: 1, 2, 3, 5 HI: 0
61. *Caprimulgus rufus* (rufous nightjar) (RUNI) (high-S) (n = 1)
Island: 156
Habitat: T: 6, 7, 10–12 S: 2, 3, 7, 9, 10 E: 1–3, 5 HI: 0
62. *C. cubanensis* (Greater Antillean nightjar) (GANI) (high-S) (n = 3)
Islands: 42, 87, 94
Habitat: T: 4, 11, 12 S: 2, 6, 7, 9, 10 E: 1–5 HI: 0
63. *C. noctitherus* (Puerto Rican nightjar) (PRNI) (high-S) (n = 1)
Island: 131
Habitat: T: 6, 7, 11, 12 S: 7–10 E: 1–3, 5 HI: 7

64. *C. cayennensis* (white-tailed nightjar) (WTNI) (high-S) (n = 1)
    Island: 107
    Habitat: T: 8, 9 S: 1, 2, 3, 9 E: 2–5 HI: 1, 2, 5, 8
65. *Nyctibius jamaicensis* (northern potoo) (NOPO) (high-S) (n = 3)
    Islands: 64, 87, 90
    Habitat: T: 4, 6, 7, 9, 11, 12, 15 S: 1–3, 7, 9, 10 E: 2–5 HI: 5, 7, 8
66. *Cypseloides niger* (black swift) (BLSW) (B-tramp) (n = 13)
    Islands: 6, 7, 42, 48, 79, 87, 90, 107, 112, 131, 155, 156, 159
    Habitat: T: 3–9, 11, 12, 15 S: 1, 2, 7–10 E: 1–5 HI: 1, 2, 4–8
67. *Streptoprocne zonaris* (white-collared swift) (WCSW) (A-tramp) (n = 4)
    Islands: 42, 87, 90, 165
    Habitat: T: 15, S: 10 E: 2–5 HI: 0
68. *Chaetura brachyura* (short-tailed swift) (STSW) (high-S) (n=1)
    Island: 159
    Habitat: T: 1–12 S: 1, 2, 7–10 E: 1–3, 5 HI: 1–8
69. *C. cinereiventris* (gray-rumped swift) (GRSW) (high-S) (n = 1)
    Island: 78
    Habitat: T: 1–12, 15 S: 1, 2, 7–10 E: 1–5 HI: 1–8
70. *C. martinica* (Lesser Antillean swift) (LASW) (high-S) (n = 5)
    Islands: 48, 79, 107, 156, 159
    Habitat: T: 1–15 S: 1, 2, 7–10 E: 1–5 HI: 1–8
71. *Tachornis phoenicobia* (Antillean palm swift) (ANPS) (A-tramp) (n = 7)
    Islands: 11, 42, 87, 88, 90, 94, 145
    Habitat: T: 1–12 S: 1–3, 9, 10 E: 1–3, 5 HI: 1, 2, 4–8
72. *Glaucis hirsuta* (rufous-breasted hermit) (RBHE) (high-S) (n = 1)
    Islands: 78
    Habitat: T: 11, 12, 15 S: 4, 5, 6, 7, 9, 10 E: 3, 4 HI: 3, 4, 7, 8
73. *Anthracothorax prevostii* (green-breasted mango) (GBMA) (Anom.) (n = 2)
    Islands: 129, 142
    Habitat: T: 1–4, 6–11 S: 1–3, 7, 9, 10 E: 1–3 HI: 1, 2, 5–8
74. *A. mango* (Jamaican mango) (JAMA) (high-S) (n = 1)
    Island: 90
    Habitat: T: 1, 2, 5–7, 9–11, 13, 15 S: 1–4, 7, 9, 10 E: 1–4 HI: 1–5, 8
75. *A. dominicus* (Antillean mango) (ANMA) (C-tramp) (n = 17)
    Islands: 5, 11, 30, 32, 64, 74, 82, 85, 87, 88, 131, 137, 145, 146, 158, 165, 171
    Habitat: T: 1–4, 6, 7, 9–15 S: 1–3, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8
76. *A. viridis* (green mango) (GRMA) (high-S) (n = 1)
    Island: 131
    Habitat: T: 6, 7, 10–12, 15 S: 3, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8
77. *Eulampis jugularis* (purple-throated carib) (PTCA) (C-tramp) (n = 13)
    Islands: 7, 48, 79, 105, 107, 112, 115, 136, 137, 153, 155, 156, 159
    Habitat: T: 7, 10, 11–13, 15 S: 3, 6, 7, 9, 10 E: 2–4 HI: 1–5, 7, 8

78. *E. holosericeus* (green-throated carib) (GTCA) (D-tramp) (n = 81)
Islands: 5–9, 12, 14, 20–25, 34, 35, 38, 39, 43, 47–49, 55, 70, 71, 74–76, 78–83, 85, 86, 89, 91, 93, 96, 104–107, 110, 112–115, 117, 120, 124, 128, 131, 133, 134, 136–138, 140, 143, 146, 147, 151–160, 163, 164, 167–171, 174, 177
Habitat: T: 2, 6, 7, 10–13, 15 S: 3, 6, 7, 9, 10 E: 1–4 HI: 1–5, 7, 8

79. *Orthorhyncus cristatus* (Antillean crested hummingbird) (ACHU) (C-tramp) (n = 43)
Islands: 5–9, 12, 14, 25, 39, 43, 48, 70, 74, 78–81, 89, 91, 93, 105, 107, 112, 113, 115, 124, 128, 131, 136, 147, 151–159, 164, 168–170
Habitat: T: 1–7, 9–13, 15 S: 3, 6, 7–10 E: 1–4 HI: 1–5, 7, 8

80. *Chlorostilbon ricordii* (Cuban emerald) (CUEM) (A-tramp) (n = 5)
Islands: 4, 42, 65, 69, 94
Habitat: T: 3–7, 9–15 S: 1–10 E: 1–4 HI: 1–5, 7, 8

81. *C. swainsonii* (Hispaniolan emerald) (HIEM) (high-S) (n = 1)
Island: 87
Habitat: T: 5, 7, 10–15 S: 3, 6, 7, 9, 10 E: 2–4 HI: 1–5, 7, 8

82. *C. maugaeus* (Puerto Rican emerald) (PREM) (high-S) (n = 1)
Island: 131
Habitat: T: 5, 7, 10–15 S: 3, 6, 7, 9, 10 E: 2–4 HI: 1–5, 7, 8

83. *Cyanophaia bicolor* (blue-headed hummingbird) (BHHU) (high-S) (n = 2)
Islands: 48, 107
Habitat: T: 9, 11–13, 15 S: 2, 3, 6, 7–10 E: 3–4 HI: 1–5, 7, 8

84. *Trochilus polytmus* (streamertail) (STTL) (high-S) (n = 1)
Island: 90
Habitat: T: 1, 2, 5–7, 10, 11, 13, 15 S: 1–4, 7–10 E: 1–4 HI: 1–5, 7, 8

85. *Calliphlox evelynae* (Bahama woodstar) (BAWO) (C-tramp) (n = 36)
Islands: 1, 2, 4, 17, 29, 40, 41, 50, 54, 57, 65, 67, 69, 72, 73, 84, 95, 98, 99, 103, 108, 109, 116, 118, 119, 125, 126, 130, 132, 135, 139, 141, 144, 150, 171, 173
Habitat: T: 1, 2, 6, 7, 9–14 S: 2, 3, 6, 7, 9, 10 E: 1–3 HI: 1–5, 7, 8

86. *Mellisuga minima* (vervain hummingbird) (VEHU) (B-tramp) (n = 8)
Islands: 30, 32, 64, 87, 88, 90, 145, 165
Habitat T: 1–7, 9–15 S: 2–7, 9, 10 E: 1–4 HI: 1–5, 7, 8

87. *M. helenae* (bee hummingbird) (BEEH) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 1, 4–7, 10–13 S: 2–7, 9, 10 E: 1–4 HI: 1–5, 7, 8

88. *Priotelus temnurus* (Cuban trogon) (CUTR) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 1, 15 S: 4–6, 8 E: 1–4 HI: 0

89. *P. roseigaster* (Hispaniolan trogon) (HITR) (high-S) (n = 1)
Island: 87
Habitat: T: 6, 7, 10–15 S: 4–6, 8 E: 2–4 HI: 0

90. *Todus multicolor* (Cuban tody) (CUTO) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 0

91. *T. subulatus* (broad-billed tody) (BBTO) (high-S) (n = 2)
Islands: 64, 87
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–5, 7, 8

92. *T. angustirostris* (narrow-billed tody) (NBTO (high-S) (n = 1)
Island: 87
Habitat: T: 5, 11–15 S: 3–10, E: 3, 4 HI: 1–5, 7, 8

93. *T. todus* (Jamaican tody) (JATO) (high-S) (n = 1)
Island: 90
Habitat: T: 1, 2, 5–7, 10, 11, 13, 15 S: 3–10 E: 1–4 HI: 1, 2, 4

94. *T. mexicanus* (Puerto Rican tody) (PRTO) (high-S) (n = 1)
Island: 131
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–5, 7, 8

95. *Ceryle torquata* (ringed kingfisher) (RIKI) (high-S) (n = 3)
Islands: 48, 79, 107
Habitat: T: 1–5 S: 9, 10 E: 1–4 HI: 0

96. *Nesoctites micromegas* (Antillean piculet) (ANPI) (high-S) (n = 2)
Islands: 64, 87
Habitat: T: 1–7, 10–15 S: 2, 7, 8 E: 1–4 HI: 4, 5, 7

97. *Melanerpes herminieri* (Guadeloupe woodpecker) (GUWO) (high-S) (n = 1)
Island: 79
Habitat: T: 5–7, 9–12, 15 S: 2, 7, 9, 10 E: 2–4 HI: 1, 2, 4–8

98. *M. portoricensis* (Puerto Rican woodpecker) (PRWO) (high-S) (n = 2)
Islands: 131, 169
Habitat: T: 1–7, 9–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 4–8

99. *M. striatus* (Hispaniolan woodpecker) (HIWO) (high-S) (n = 1)
Island: 87
Habitat: T: 1–7, 9–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 4–8

100. *M. radiolatus* (Jamaican woodpecker) (JAWO) (high-S) (n = 1)
Island: 90
Habitat: T: 1, 2, 5–7, 9–11, 13–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 4–7

101. *M. superciliaris* (West Indian woodpecker) (WIWO) (A-tramp) (n = 6)
Islands: 42, 65, 66, 69, 94, 144
Habitat: T: 1–7, 9–15 S: 2, 7–10 E: 1–4 HI: 1, 2, 4–8

102. *Xiphidiopicus percussus* (Cuban green woodpecker) (CGWO) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 1, 2, 4, 5, 7, 10–13, 15 S: 2, 7–10 E: 1–4 HI: 2, 4, 5

103. *Picoides villosus* (hairy woodpecker) (HAWO) (A-tramp) (n = 4)
Islands: 4, 65, 69, 116
Habitat: T: 1–7, 9–14 S: 2–10 E: 1–3 HI: 1, 2, 4, 5, 7, 8

104. *Colaptes auratus* (northern flicker) (YSFL) (high-S) (n = 3)
Islands: 42, 66, 94
Habitat: T: 11–15 S: 2, 7, 9–14 E: 1–3 HI: 1, 2, 4–8

105. *C. fernandinae* (Fernandina's flicker) (FEFL) (high-S) (n = 1)
Islands: 42, 94
Habitat: T: 1–7, 9–11 S: 2, 7, 9, 10 E: 1–3 HI: 2

106. *Campephilus principalis* (ivory-billed woodpecker) (IBWO) (high-S) (n = 1)
Island: 42
Habitat: T: 7, 11–14 S: 7–10 E: 2–4 HI: 7

107. *Myiopagis cotta* (Jamaican elaenia) (JAEL) (high-S) (n = 1)
Island: 90
Habitat: T: 5–7, 10, 11, 13, 15 S: 7–10 E: 2–4 HI: 1, 2

108. *Elaenia martinica* (Caribbean elaenia) (CAEL) (C-tramp) (n = 52)
Islands: 5–9, 12, 21, 23, 25, 27, 33, 43, 48, 66, 70, 71, 74, 78, 79, 82, 83, 85, 89, 91, 93, 97, 105, 107, 112, 114, 115, 124, 129, 131, 136, 140, 142, 146, 147, 151–159, 163, 164, 169, 170
Habitat: T: 6, 7, 9–13, 15 S: 2, 3, 4, 6, 7, 9, 10 E: 2–4 HI: 1–8

109. *E. flavogaster* (yellow-bellied elaenia) (YBEL) (B-tramp) (n = 4)
Islands: 14, 78, 159, 168
Habitat: T: 6, 7, 9–12 S: 2–7, 9, 10 E: 2–3 HI: 1–8

110. *E. fallax* (Greater Antillean elaenia) (GAEL) (high-S) (n = 2)
Islands: 87, 90
Habitat: T: 11, 13–15 S: 2–7, 9–10 E: 3, 4 HI: 1–5, 7, 8

111. *Contopus caribaeus* (Greater Antillean pewee) (GREP) (A-tramp) (n = 11)
(now 6 species: see Reynard et al. 1993 and Raffaele et al. 1998 for particulars)
Islands: 4, 29, 42, 54, 64, 65, 69, 87, 90, 94, 116
Habitat: T: 1–7, 9–15 S: 2–7, 9, 10 E: 1–4 HI: 1–8

112. *C. latirostris* (Lesser Antillean pewee) (LAPE) (A-tramp) (n = 5)
Islands: 48, 79, 107, 131, 156
Habitat: T: 7, 9–12, 15 S: 2–7, 9, 10 E: 2–4 HI: 1–8

113. *Empidonax euleri* (Euler's flycatcher) (EUFL) (high-S) (n = 1)
Island: 78
Habitat: T: 11, 12, 15 S: 2, 3, 7, 9, 10 E: 3–4 HI: 4, 6, 7

114. *Myiarchus barbirostris* (sad flycatcher) (SAFL) (high-S) (n = 1)
Island: 90
Habitat: T: 2, 5–8, 10, 11, 14, 15 S: 2–7, 9, 10 E: 1–4 HI: 1, 2, 4, 6, 7

115. *M. nugator* (Grenada flycatcher) (GRFL) (B-tramp) (n = 4)
Islands: 14, 78, 159, 168
Habitat: T: 1–7, 9–12, 15 S: 2, 3, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8

116. *M. validus* (rufous-tailed flycatcher) (RTFL) (high-S) (n = 1)
Island: 90
Habitat: T: 2, 5–7, 11, 13, 15 S: 7–10 E: 2–4 HI: 1, 4

117. *M. sagrae* (La Sagra's flycatcher) (LSFL) (A-tramp) (n = 11)
Islands: 1, 4, 41, 42, 54, 65, 66, 69, 73, 94, 116
Habitat: T: 7, 10–14 S: 2, 7, 9, 10 E: 1–3 HI: 0

118. *M. stolidus* (stolid flycatcher) (STOF) (B-tramp) (n = 8)
Islands: 11, 32, 64, 87, 88, 90, 145, 165
Habitat: T: 1, 2, 6, 7, 9–12 S: 3–7, 9, 10 E: 1–3 HI: 4, 5, 7

119. *M. antillarum* (Puerto Rican flycatcher) (PRFL) (A-tramp) (n = 7)
Islands: 43, 131, 154, 158, 164, 169, 170
Habitat: T: 1, 2, 6, 7, 9–12 S: 3–7, 9, 10 E: 1–3 HI: 4, 5, 7

120. *M. oberi* (Lesser Antillean flycatcher) (LESF) (B-tramp) (n = 7)
Islands: 9, 48, 79, 107, 115, 155, 156
Habitat: T: 6, 7, 9–12 S: 3–7, 9, 10 E: 1–3 HI: 4, 5, 7

121. *Tyrannus melancholicus* (tropical kingbird) (TRKI) (high-S) (n = 1)
Island: 78
Habitat: T: 6, 7, 9–12 S: 2, 3, 7, 9, 10 E: 1–3 HI: 1, 2, 4–8

122. *T. dominicensis* (gray kingbird) (GRAK) (D-tramp) (n = 138)
Islands: 1, 4–9, 11–14, 17, 18, 20–25, 27–34, 38–44, 47, 48, 50, 54, 55, 57, 60, 63–65, 67–70, 72–74, 77–101, 103–120, 123–125, 127, 128, 130–132, 135–140, 143–147, 150–161, 163–171, 173–175, 177
Habitat: T: 1–7, 9–15 S: 2, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8

123. *T. caudifasciatus* (loggerhead kingbird) (LOKI) (B-tramp) (n = 10)
Islands: 4, 33, 42, 65, 66, 69, 87, 90, 116, 131
Habitat: T: 6, 7, 9–15 S: 2–7, 9, 10 E: 2–4 HI: 0

124. *T. cubensis* (giant kingbird) (GIKI) (B-tramp) (n = 6)
Islands: 42, 50, 73, 94, 109, 118
Habitat: T: 5, 11–15 S: 2–7, 9, 10 E: 1–4 HI: 0

125. *Pachyramphus niger* (Jamaican becard) (JABE) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 7, 11, 13–15 S: 2, 7–10 E: 2–4 HI: 6, 7

126. *Progne cryptoleuca* (Cuban martin) (CUMA) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 1–5, 8, 9 S: 1, 2, 9, 10 E: 1–5 HI: 1, 2, 6, 8

127. *P. dominicensis* (Caribbean martin) (CAMA) (D-tramp) (n = 44)
Islands: 6–9, 14, 25, 39, 42, 43, 48, 52, 70, 78, 79, 87–91, 93, 105, 107, 111, 112, 115, 124, 131, 137, 145, 146, 152–159, 164, 168–170, 175, 176
Habitat: T: 1–5, 8, 9 S: 1, 2, 9, 10 E: 1–5 HI: 1, 2, 5, 6, 8

128. *Tachycineta euchrysea* (golden swallow) (GOSW) (high-S) (n = 2)
Islands: 87, 90
Habitat: T: 8, 11, 13–15 S: 1, 2, 7–10 E: 3–5 HI: 1, 6, 7

129. *T. cyaneoviridis* (Bahama swallow) (BAHS) (high-S) (n = 3)
Islands: 4, 65, 69
Habitat: T: 2–10, 13, 14 S: 1, 2, 9, 10 E: 1–3, 5 HI: 1, 2, 5–8

130. *Hirundo fulva* (cave swallow) (CASW) (B-tramp) (n = 10)
Islands: 42, 64, 87, 88, 90, 94, 111, 115, 131, 169
Habitat: T: 1–15 S: 1, 2, 9, 10 E: 1–5 HI: 1, 2, 4–8

131. *Corvus palmarum* (palm crow) (PACR) (high-S) (n = 2)
Islands: 42, 87
Habitat: T: 8–15 S: 2, 3, 7–10 E: 1–4 HI: 1, 2, 4–8

132. *C. nasicus* (Cuban crow) (CUCR) (A-tramp) (n = 5)
Islands: 42, 94, 109, 118, 125
Habitat: T: 1, 4, 5, 7, 9–15 S: 2–4, 7–10 E: 1–4 HI: 1, 2, 42–8

133. *C. leucognaphalus* (white-necked crow) (WNCR) (high-S) (n = 3)
Islands: 64, 87, 145
Habitat: T: 1–7, 9–15 S: 2–4, 7–10 E: 1–4 HI: 1–8

134. *C. jamaicensis* (Jamaican crow) (JACR) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 7, 8, 11, 13, 15 S: 1, 2, 7–10 E: 3 HI: 1, 2, 4, 6–8

135. *Sitta pusilla* (brown-headed nuthatch) (BHNU) (high-S) (n = 1)
Island: 65
Habitat: T: 6, 7, 9–14 S: 2–10 E: 2–3 HI: 2–8

136. *Ferminia cerverai* (zapata wren) (ZAWR) (high-S) (n = 1)
Island: 42
Habitat: T: 3–4 S: 3–6 E: 1, 2 HI: 0

137. *Troglodytes aedon* (southern house wren) (SHWR) (A-tramp) (n = 5)
Islands: 48, 78, 79, 156, 159
Habitat: T: 6, 7, 10–12, 15 S: 3–6, 8 E: 2–4 HI: 1–5, 7, 8

138. *Polioptila caerulea* (blue-gray gnatcatcher) (BGGN) (C-tramp) (n = 27)
Islands: 1, 4, 17, 18, 41, 50, 57, 65, 67, 69, 72, 73, 84, 95, 98, 99, 108, 109, 118, 119, 125, 127, 130, 139, 141, 150, 173
Habitat: T: 1–7, 10–14 S: 3–6, 8 E: 1–3 HI: 2–5, 7, 8

139. *P. lembeyei* (Cuban gnatcatcher) (CUGN) (high-S) (n = 1)
Island: 42
Habitat: T: 6, 7, 9, 10 S: 3–6 E: 2 HI: 0

140. *Myadestes elisabeth* (Cuban solitaire) (CUSO) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 11, 12, 13, 15 S: 7, 8, 10 E: 3–4 HI: 0

141. *M. genibarbis* (rufous-throated solitaire) (RTSO) (high-S) (n = 6)
Islands: 48, 87, 90, 107, 156, 159
Habitat: T: 5, 13–15 S: 2–10 E: 3–4 HI: 7

142. *Turdus fumigatus* (cocoa thrush) (COTH) (A-tramp) (n = 2)
Islands: 78, 159
Habitat: T: 15 S: 7–10 E: 3–4 HI: 4, 7

143. *T. nudigenis* (bare-eyed [thrush] robin) (BERO) (B-tramp) (n = 7)
Islands: 14, 25, 78, 107, 156, 159, 168
Habitat: T: 6, 7, 10–12, 15 S: 3–6, 7, 9, 10 E: 1–3 HI: 1–5, 7, 8

144. *T. jamaicensis* (white-eyed thrush) (WETH) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 11, 13, 15 S: 5–10 E: 3, 4 HI: 1, 2, 4, 6, 7

145. *T. swalesi* (La Selle thrush) (LSTH) (high-S) (n = 1)
Island: 87
Habitat: T: 5, 13–15 S: 3–6, 8 E: 3, 4 HI: 2, 3, 7

146. *T. aurantius* (white-chinned thrush) (WCTH) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 10, 11, 14, 15 S: 1–10 E: 1–4 HI: 1, 2, 4–8

147. *T. plumbeus* (red-legged thrush) (RLTH) (C-tramp) (n = 20)
Islands: 4, 17, 29, 33, 42, 48, 54, 64, 65, 69, 72, 73, 84, 87, 94, 98, 116, 131, 145, 165
Habitat: T: 1–7, 10–15 S: 2, 3, 7–10 E: 1–4 HI: 1, 2, 4, 5, 7, 8

148. *Cichlherminia lherminieri* (forest thrush) (FOTH) (A-tramp) (n = 4)
Islands: 48, 79, 112, 156
Habitat: T: 15 S: 3–6, 8 E: 3–4 HI: 1, 3, 4, 7

149. *Mimus polyglottos* (northern mockingbird) (NOMO) (C-tramp) (n = 73)
Islands: 1, 4, 5, 12, 17, 21, 22, 24, 29, 32, 33, 41–43, 45, 50, 54, 55, 57, 63–67, 69, 70, 72, 73, 80–85, 87, 88, 90, 95, 97–99, 103, 104, 106, 108–110, 114, 116, 118, 119, 124, 125, 127, 128, 130, 131, 137, 139, 144, 145, 147, 150, 152, 154, 158, 163–165, 169–171, 173
Habitat: T: 1–15 S: 1–7, 9, 10 E: 1–4 HI: 1–8

150. *M. gilvus* (tropical mockingbird) (TRMO) (C-tramp) (n = 11)
Islands: 14, 25, 48, 78, 79, 93, 107, 142, 156, 159, 168
Habitat: T: 3, 4, 6–12 S: 1–7, 9, 10 E: 1–3 HI: 1–8

151. *M. gundlachii* (Bahama mockingbird) (BAMO) (C-tramp) (n = 40)
Islands: 1, 4, 17, 18, 29, 31, 40–42, 50, 54, 56, 57, 65, 67, 69, 72, 73, 84, 90, 95, 98, 99, 103, 108, 109, 116, 118, 119, 125–127, 130, 132, 135, 141, 144, 150, 171, 173
Habitat: T: 6, 7, 10 S: 3–6 E: 1–3 HI: 1–8

152. *Ramphocinclus brachyurus* (white-breasted thrasher) (WBTH) (high-S) (n = 2)
Islands: 107, 156
Habitat: T: 6, 7, 10–11 S: 3–6 E: 2–3 HI: 0

153. *Margarops fuscus* (scaly-breasted thrasher) (SBTH) (C-tramp) (n = 18)
Islands: 7–9, 25, 48, 78, 79, 93, 105, 107, 112, 115, 136, 153, 155–157, 159
Habitat: T: 5–7, 10–12, 15 S: 2–10 E: 1–4 HI: 1–5, 7, 8

154. *M. fuscatus* (pearly-eyed thrasher) (PETH) (Supertramp) (n = 80*)
Islands: 1, 5–7, 9, 11, 12, 18, 21, 22, 24, 38, 39, 41, 43, 46, 48–50, 61, 63, 67, 68, 70, 71, 73–75, 79, 80, 82, 83, 85, 88, 91, 93, 99, 100, 104, 105, 107–113, 115, 117, 118, 119, 124, 125, 128, 131, 135–137, 140, 144, 146, 147, 151–158, 163, 164, 169–172, 174, 175, 177 (*also resident on Bonaire, Southern Netherlands Antilles, an island not included in this analysis)
Habitat: T: 1–7, 9–15 S: 2–10 E: 1–4 HI: 1–8

155. *Cinclocerthia ruficauda* (trembler) (TREM) (C-tramp) (n = 10)
(American Ornithologists' Union 1998 now recognizes 2 species: brown trembler, *C. ruficauda*—10 islands—see Raffaele et al. 1998 for island list; and gray trembler, *C. gutturalis*—Martinique and St. Lucia; however, recent mitochondrial DNA studies suggest 3 species—see Hunt et al. 2001 for particulars)
Islands: 48, 79, 107, 112, 115, 136, 153, 155, 156, 159
Habitat: T: 7, 10–12, 15 S: 3–10 E: 1–4 HI: 3, 4, 7

156. *Dulus dominicus* (palmchat) (PALM) (high-S) (n = 3)
Islands: 64, 87, 145
Habitat: T: 1–7, 9–13, 15 S: 2, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8

157. *Vireo crassirostris* (thick-billed vireo) (TBVI) (C-tramp) (n = 39)
Islands: 1, 4, 17, 29, 31, 33, 41, 50, 54, 57, 65–67, 69, 72, 73, 84, 95, 98, 99, 103, 108, 109, 116, 118, 119, 125, 127, 129, 130, 132, 135, 141, 142, 144, 150, 165, 171, 173
Habitat: T: 2–7, 10–14 S: 3–6, 8 E: 1–3 HI: 3, 4, 7, 8

158. *V. caribaeus* (St. Andrew vireo) (SAVI) (Anom.) (n = 1)
Island: 142
Habitat: T: 1–4, 6, 7, 10–12 S: 3–6, 8 E: 1–3 HI: 0

159. *V. modestus* (Jamaican vireo) (JAVI) (high-S) (n = 1)
Islands: 90
Habitat: T: 1, 5–7, 10, 11, 13 S: 3–10 E: 1–4 HI: 0

160. *V. gundlachii* (Cuban vireo) (CUVI) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 6, 7, 10–13, 15 S: 3–6, 8 E: 1–4 HI: 0

161. *V. latimeri* (Puerto Rican vireo) (PRVI) (high-S) (n = 1)
Island: 131
Habitat: T: 2–7, 10–12 S: 3–8 E: 1–3 HI: 1–4, 7, 8

162. *V. nanus* (flat-billed vireo) (FBVI) (high-S) (n = 2)
Islands: 64, 87
Habitat: T: 1–7, 10–13, 15 S: 3–10 E: 1–4 HI: 3, 7

163. *V. osburni* (Blue Mountain vireo) (BMVI) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 11, 13–15 S: 3–10 E: 3, 4 HI: 0

164. *V. altiloquus* (black-whiskered vireo) (BWVI) (D-tramp) (n = 88)
Islands: 1, 4–9, 11, 12, 14, 17, 18, 20, 25, 27, 29, 30, 32, 33, 41–43, 48, 50, 54, 57, 64, 65, 67, 69, 72–74, 78, 79, 82, 84, 85, 87–90, 93, 95, 97–99, 103, 105, 107–109, 112, 115, 116, 118–120, 125, 129–132, 134, 136, 137, 139–142, 145, 150–159, 163, 165, 168, 169, 171, 173, 177
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–8

165. *V. magister* (Yucatan vireo) (YUVI) (high-S) (n = 1)
Island: 66
Habitat: T: 1–4, 6, 7, 10, 11 S: 3–8 E: 1–3 HI: 0

166. *Dendroica petechia* (yellow warbler) (YWAR) (D-tramp) (n = 115)
Islands: 1, 3–9, 12, 17, 18, 20, 23, 27–29, 33, 39–44, 47, 48, 50, 54–57, 60, 61, 64–67, 69, 71–74, 79–82, 84, 85, 87–91, 93–95, 97–99, 101, 103, 105–109, 112–120, 124–132, 135, 137–144, 146, 147, 150–158, 161, 163, 164, 168–171, 173, 177
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–8

167. *D. dominica* (yellow-throated warbler) (YTWA) (high-S) (n = 2)
Islands: 65, 69
Habitat: T: 14 S: 3–8 E: 2, 3 HI: 7

168. *D. adelaidae* (Adelaide's warbler) (ADWA) (A-tramp) (n = 4)
(American Ornithologists' Union 1998 now recognizes 3 species: Adelaide's warbler, *D. adelaidae*, [Puerto Rico], Barbuda warbler, *D. subita*, and St. Lucia warbler, *D. delicata*)
Islands: 9, 131, 156, 169
Habitat: T: 6, 7, 10–12, 15 S: 3–8 E: 1–4 HI: 0

169. *D. pityophila* (olive-capped warbler) (OLIW) (high-S) (n = 3)
Islands: 42, 65, 69
Habitat: T: 13, 14 S: 7, 8, 10 E: 3 HI: 0

170. *D. pinus* (pine warbler) (PIWA) (A-tramp) (n = 5)
Islands: 4, 65, 69, 87, 116
Habitat: T: 14 S: 3–8 E: 2, 3 HI: 0

171. *D. vitellina* (vitelline warbler) (VIWA) (B-tramp) (n = 4)
Islands: 33, 66, 97, 162
Habitat: T: 6, 7, 10, 11 S: 3–8 E: 2–3 HI: 0

172. *D. plumbea* (plumbeous warbler) (PLWA) (high-S) (n = 3)
Islands: 48, 79, 105
Habitat: T: 6, 7, 10–12, 15 S: 3–8 E: 2–4 HI: 0

173. *D. pharetra* (arrowhead warbler) (AHWA) (high-S) (n = 1)
Island: 90
Habitat: T: 5, 11, 13, 15 S: 4–10 E: 3–4 HI: 0

174. *D. angelae* (elfin-woods warbler) (EWWA) (high-S) (n = 1)
Islands: 131
Habitat: T: 15 S: 3–8 E: 3, 4 HI: 0

175. *Catharopeza bishopi* (whistling warbler) (WHWA) (high-S) (n = 1)
Island: 159
Habitat: T: 15 S: 3–8 E: 3, 4 HI: 0

176. *Geothlypis rostrata* (Bahama yellowthroat) (BAYE) (A-tramp) (n = 6)
Islands: 4, 29, 54, 65, 69, 116
Habitat: T: 1–4, 6, 7, 10–12–14 S: 3–8 E: 1–3 HI: 2, 3, 7, 8

177. *Microligea palustris* (green-tailed [ground] warbler) (GRTW) (high-S) (n = 3)
Islands: 11, 87, 88
Habitat: T: 1–7, 10–13–15 S: 3–6, 8 E: 1–4 HI: 7

178. *Teretistris fernandinae* (yellow-headed warbler) (YHWA) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 2, 4, 6, 7, 10–12 S: 3–6, 8 E: 1–4 HI: 0

179. *T. fornsi* (oriente warbler) (ORWA) (high-S) (n = 1)
Island: 42
Habitat: T: 6, 7, 9–12, 15 S: 3–6, 8 E: 1–4 HI: 0

180. *Leucopeza semperi* (Semper's warbler) (SEWA) (high-S) (n = 1)
Islands: 156
Habitat: T: 15 S: 3–6, 8 E: 4 HI: 0

181. *Xenoligea montana* (white-winged warbler) (WWWA) (high-S) (n = 1)
Island: 87
Habitat: T: 15 S: 3–10 E: 4 HI: 0

182. *Coereba flaveola* (bananaquit) (BANA) (D-tramp) (n = 131)
Islands: 1, 4–9, 11, 12, 14, 17, 20–25, 27, 29, 32, 33, 38–41, 43, 44, 47–50, 54–57, 60, 61, 64–67, 69–76, 78–85, 87–91, 93, 95–100, 103–105, 107–110, 112–120, 124–132, 135–147, 150–161, 163–165, 168–171, 173–177
Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–5, 7, 8

183. *Tangara cucullata* (Lesser Antillean tanager) (LATA) (A-tramp) (n = 2)
Islands: 78, 159
Habitat: T: 2–7, 10–12, 15 S: 7–10 E: 1–4 HI: 1, 2, 4, 5, 7, 8

184. *Cyanerpes cyaneus* (red-legged honeycreeper) (RLHO) (high-S) (n = 1)
Island: 42
Habitat: T: 11–15 S: 2–6, 7, 9, 10 E: 3, 4 HI: 2, 4, 5

185. *Euphonia jamaica* (Jamaican euphonia) (JAEU) (high-S) (n = 1)
Islands: 90
Habitat: T: 1, 2, 5–8, 10, 11, 13, 15 S: 2, 7, 9, 10 E: 1–4 HI: 1, 2, 4, 5, 7, 8

186. *E. musica* (Antillean euphonia) (ANEU) (C-tramp) (n = 15)
Islands: 7, 9, 14, 48, 64, 78, 79, 87, 107, 112, 131, 136, 151, 155, 156, 159
Habitat: T: 6, 7, 11, 12, 13, 15 S: 7, 8 E: 2–4 HI: 4, 7

187. *Spindalis zena* (stripe-headed tanager) (SHTA) (C-tramp) (n = 28)
(AOU 1998 now recognizes 4 species: Western spindalis, *S. zena* [Cuba, Bahamas, Grand Cayman, Cozumel I., Mexico]; Jamaican spindalis, *S. nigricephalus* [Jamaica]; Hispaniolan spindalis, *S. dominicensis* [Hispaniola]; and Puerto Rican spindalis, *S. portoricensis*)
Islands: 1, 4, 17, 29, 41, 42, 54, 64–66, 69, 72, 73, 84, 87, 90, 94, 95, 98, 99, 103, 108, 116, 119, 125, 127, 130, 131
Habitat: T: 6, 7, 11–15 S: 7–10 E: 2–4 HI: 1, 2, 4, 5, 7, 8

188. *Phaenicophilus palmarum* (black-crowned palm-tanager) (BCPT) (high-S) (n = 2)
Islands: 87, 145
Habitat: T: 1–7, 10–13, 15 S: 2, 3–10 E: 1–4 HI: 1–5, 7, 8

189. *P. poliocephalus* (gray-crowned palm-tanager) (GCPT) (high-S) (n = 4)
Islands: 32, 64, 87, 88
Habitat: T: 1–7, 10–13, 15 S: 2, 3–10 E: 1–4 HI: 1–5, 7, 8

190. *Calyptophilus frugivorus* (chat-tanager) (CHTA) (high-S) (n = 2) (American Ornithologists' Union 1998 now recognizes 2 species: Western chat-tanager, *C. tertius*, and the Eastern chat-tanager, *C. frugivorus*; both are found on Hispaniola; Gonâve I. population may be extirpated [Raffaele et al. 1998])
    Islands: 64, 87
    Habitat: T: 7, 10, 13–15 S: 3–6, 8 E: 4 HI: 0
191. *Nesospingus speculiferus* (Puerto Rican tanager) (PRTA) (high-S) (n = 1)
    Island: 131
    Habitat: T: 11, 12–15 S: 3–10 E: 3, 4 HI: 7
192. *Saltator albicollis* (Lesser Antillean saltator) (LASA) (high-S) (n = 4)
    Islands: 48, 79, 107, 156
    Habitat: T: 6, 7, 10–12 S: 3–7 E: 1–3 HI: 1–3, 8
193. *Volatinia jacarina* (blue-black grassquit) (BBGR) (high-S) (n = 1)
    Island: 78
    Habitat: T: 8–10 S: 1–3, 9, 10 E: 2 HI: 1, 2, 5, 6, 8
194. *Sporophila nigricollis* (yellow-bellied seedeater) (YBSE) (Anom.) (n = 2)
    Islands: 25, 78
    Habitat: T: 6–12 S: 1–3, 9, 10 E: 2–3 HI: 1, 2, 5, 6, 8
195. *Melopyrrha nigra* (Cuban bullfinch) CUBF) (high-S) (n = 3)
    Islands: 42, 66, 94
    Habitat: T: 6, 7, 10, 11 S: 3–6, 7, 8 E: 2, 3 HI: 3, 7, 8
196. *Tiaris canora* (Cuban grassquit) (CUGR) (high-S) (n = 2)
    Islands: 42, 94
    Habitat: T: 6, 7, 9–15 S: 3–7, 9, 10 E: 1–4 HI: 3, 4, 7, 8
197. *T. olivacea* (yellow-faced grassquit) (YFGR) (C-tramp) (n = 11)
    Islands: 33, 42, 43, 64, 66, 87, 88, 90, 97, 131, 169
    Habitat: T: 6–11, 13, 14 S: 1–6, 9, 10 E: 1–4 HI: 1, 2, 4–8
198. *T. bicolor* (black-faced grassquit) (BFGR) (D-tramp) (n = 113)
    Islands: 1, 4–9, 12, 14, 15, 17, 20–25, 28, 29, 38, 39, 41, 43, 44, 47, 48, 50, 54, 57, 61, 64, 65, 68–75, 78–85, 87–91, 93, 95, 96, 98–100, 103–105, 107–110, 112–120, 124–132, 135–138, 140–142, 144, 146, 150–160, 163, 164, 168–171, 173–175, 177
    Habitat: T: 6–15 S: 1–3, 7, 9, 10 E: 1–4 HI: 1, 2, 5, 6, 8
199. *Loxipasser anoxanthus* (yellow-shouldered grassquit) (YSGR) (high-S) (n = 1)
    Island: 90
    Habitat: T: 1, 2, 5–7, 10, 11, 13, 15 S: 2–6, 9, 10 E: 1–4 HI: 1, 2, 4, 7, 8
200. *Loxigilla portoricensis* (Puerto Rican bullfinch) (PUEB) (high-S) (n = 1)
    Islands: 131 155 (extirpated)
    Habitat: T: 1–4, 6, 7, 10–15 S: 3–10 E: 1–4 HI: 1–4, 7, 8
201. *L. violacea* (Greater Antillean bullfinch) (GABU) (C-tramp) (n = 29)
    Islands: 1, 4, 11, 17, 29, 30, 32, 41, 50, 54, 64, 65, 69, 72, 73, 84, 87, 88, 90, 95, 98, 99, 103, 108, 109, 116, 117, 145, 165
    Habitat: T: 1–7, 10–15 S: 3–10 E: 1–4 HI: 1–5, 7, 8

202. *L. noctis* (Lesser Antillean bullfinch) (LESB) (C-tramp) (n = 22)
Islands: 6–9, 48, 78, 79, 89, 93, 95, 105, 107, 112, 115, 136, 151, 153–157, 159
Habitat: T: 1–7, 10–13, 15 S: 3–10 E: 1–4 HI: 1–5, 7, 8

203. *Euneornis campestris* (orangequit) (ORAN) (high-S) (n = 1)
Island: 90
Habitat: T: 5–7, 11, 13, 15 S: 2, 3, 7, 9, 10 E: 2–4 HI: 1, 2, 4, 5, 7

204. *Melanospiza richardsoni* (St. Lucia black finch) (SLBF) (high-S) (n = 1)
Island: 156
Habitat: T: 6, 7, 10–13, 15 S: 3–10 E: 2–4 HI: 7

205. *Torreornis inexpectata* (zapata sparrow) (ZASP) (high-S) (n = 1)
Island: 42
Habitat: T: 4, 6, 7, 10, 13 S: 3–6, 10 E: 1, 2 HI: 0

206. *Ammodramus savannarum* (grasshopper sparrow) (GRSP) (A-tramp) (n = 4)
Islands: 87, 90, 131, 169
Habitat: T: 7–9 S: 1, 2, 9, 10 E: 1–3 HI: 1, 6

207. *Zonotrichia capensis* (rufous-collared sparrow) (RCSP) (high-S) (n = 1)
Islands: 87
Habitat: T: 5, 13–15 S: 3–8 E: 3, 4 HI: 7

208. *Agelaius phoeniceus* (red-winged blackbird) (RWBL) (B-tramp) (n = 9)
Islands: 4, 17, 42, 54, 65, 69, 84, 94, 116
Habitat: T: 2–7 S: 3–6, 9, 10 E: 1, 2 HI: 2, 8

209. *A. humeralis* (tawny-shouldered blackbird) (TSBL) (high-S) (n = 2)
Islands: 42, 87
Habitat: T: 1–11 S: 1, 2, 9, 10 E: 1, 2 HI: 1, 2, 4–8

210. *A. xanthomus* (yellow-shouldered blackbird) (YSBL) (high-S) (n = 2)
Islands: 111, 131
Habitat: T: 1–7, 10–12 S: 2–4, 7, 9, 10 E: 1–3 HI: 1, 2

211. *Nesopsar nigerrimus* (Jamaican blackbird) (JABL) (high-S) (n = 1)
Island: 90
Habitat: T: 13, 15 S: 7–10 E: 3, 4 HI: 0

212. *Sturnella magna* (eastern meadowlark) (EAME) (high-S) (n = 2)
Islands: 42, 94
Habitat: T: 4, 6–9 S: 1, 2, 9, 10 E: 1–4 HI: 1, 2, 4–6, 8

213. *Dives atroviolacea* (Cuban blackbird) (CUBL) (high-S) (n = 1)
Island: 42
Habitat: T: 1, 4–15 S: 1–4, 7, 9, 10 E: 1–4 HI: 1–8

214. *Quiscalus niger* (Greater Antillean grackle) (GAGR) (B-tramp) (n = 14)
Islands: 11, 33, 42, 64, 66, 87, 88, 90, 94, 97, 131, 145, 165, 169
Habitat: T: 1–15 S: 1–4, 7, 9, 10 E: 1–4 HI: 1–8

215. *Q. lugubris* (Carib grackle) (CAGR) (C-tramp) (n = 17)
Islands: 7–9, 14, 25, 48, 78, 79, 105, 107, 112, 136, 155–157, 159, 168
Habitat: T: 1–12, 15 S: 1–4, 7, 9, 10 E: 1–4 HI: 1–8

216. *Molothrus bonariensis* (shiny [glossy] cowbird) (SHCO) (D-tramp) (n = 23)
Islands: 7–9, 14, 25, 42, 43, 78, 87, 105, 107, 111, 131, 145, 152, 154, 156, 158, 159, 162, 164, 168, 169
Habitat: T: 1–7, 9–13, 15 S: 2, 7, 9, 10 E: 1–4 HI: 1, 2, 4–8

217. *Icterus dominicensis* (Greater Antillean oriole) (GAOR) (B-tramp) (n = 11)
Islands: 4, 42, 64, 69, 87, 88, 94, 95, 131, 145, 165
Habitat: T: 1–7, 9–13, 15 S: 2–10 E: 1–4 HI: 1–8

218. *I. laudabilis* (St. Lucia oriole) (SLOR) (high-S) (n = 1)
Island: 156
Habitat: T: 1, 2, 5–7, 10–12, 15 S: 2–10 E: 1–4 HI: 1–5, 7, 8

219. *I. oberi* (Montserrat oriole) (MTOR) (high-S) (n = 1)
Island: 112
Habitat: T: 1–7, 10–12, 15 S: 2–10 E: 1–4 HI: 1–5, 7, 8

220. *I. bonana* (Martinique oriole) (MAOR) (high-S) (n = 1)
Island: 107
Habitat: T: 1, 2, 5–7, 10–12, 15 S: 2–10 E: 1–4 HI: 1–5, 7, 8

221. *I. icterus* (troupial) (TROU) (Anom.) (n = 5)
Islands: 8, 9, 131, 158, 172
Habitat: T: 1–7, 9–12, 13, 15 S: 2–7, 9, 10 E: 1–4 HI: 1–8

222. *I. leucopteryx* (Jamaican oriole) (JAOR) (high-S) (n = 1)
Island: 90
Habitat: T: 1, 2, 5–7, 10, 11, 13, 15 S: 1–10 E: 1–4 HI: 1, 2, 4–8

223. *Loxia leucoptera* (white-winged crossbill) (WWCR) (high-S) (n = 1)
Island: 87
Habitat: T: 13 S: 7–10 E: 4 HI: 7

224. *Carduelis dominicensis* (Antillean siskin) (ANSI) (high-S) (n = 1)
Island: 87
Habitat: T: 13–15 S: 2, 3, 7, 9, 10 E: 3, 4 HI: 7

Appendix 2

Table 1—Comparison of resident status ("+" denotes breeding) of the two *Margarops* thrashers and the red-legged thrush among 177 Caribbean islands

Island	Island size	Number of breeding landbirds	Pearly-eyed thrasher	Scaly-breasted thrasher	Red-legged thrush	References[a]
	Square kilometers					
1. Acklins (Bahamas)	388	22	+			6, 7
2. Ambergris Cay, Big (Caicos)	4.3	4				7
3. Ambergris Cay, Little (Caicos)	3.3	2				7
4. Andros (Bahamas)	5,957	36			+	3,7
5. Anegada (BVI[b])[c]	68	17	+			18, 19, 22
6. Anguilla (Leeward Islands)	91	18	+			13, 19, 34
7. Antigua[c] (Leeward Islands)	280	25	+	+		13, 15, 19
8. Barbados[c] (Windward Islands)	430	20		+		13, 19, 34
9. Barbuda[c] (Antigua)	160	20	+	+		9, 13, 19
10. Bay Cay (Caicos)	0.1	3				7
11. Beata Island[c] (Hispaniola)	47	30	+			12, 13, 37
12. Beef[c] (BVI)	4	14	+			20
13. Bellamy Cay (BVI)	0.006	2	+			20
14. Bequia[c] (Grenadines)	17	21				13,19
15. Big Flat Cay (USVI)	0.01	3				21
16. Big Sand Cay (Turks)	0.5	1				7
17. Biminis (Bahamas)	23	21			+	3,6
18. Bird Rock (Bahamas)	0.03	9	+			7
19. Booby Cay (Bahamas)	0.5	3				7
20. Bovoni Cay (USVI)	0.2	7				21
21. Bass, Inner (USVI)	0.5	10	+			21
22. Bass, Outer (USVI)	0.4	9	+			21
23. Buck[c] (BVI)	0.2	8				20
24. Buck (USVI)	0.3	8	+			21
25. Carriacou[c] (Grenadines)	34	21		+		19, 35
26. Carval (BVI)	0.008	1				20
27. Cas Cay (USVI)	0.06	6				21
28. Castle (Bahamas)	2.1	4				7
29. Cat (Bahamas)	389	24			+	16
30. Catalina (Hispaniola)	18	11				28
31. Cay Sal (Bahamas)	10	9				6, 8
32. Cayemites (Hispaniola)	45	20				28
33. Cayman Brac (Greater Antilles)	33	20			+	5, 19
34. Cinnamon Cay (USVI)	0.004	3				21
35. Cockroach Cay (USVI)	0.08	3				21
36. Cockroach (BVI)	0.006	2				20
37. Cocoloba Cay (USVI)	0.004	1				21
38. Congo Cay (USVI)	0.1	8	+			21
39. Cooper (BVI)	1	11	+			20
40. Cotton Cay (Turks)	1.1	7				7
41. Crooked (Bahamas)	277	21	+			6,7
42. Cuba	114,524	84			+	13, 19, 34
43. Culebra[c] (Puerto Rico)	47	20	+			9, 19
44. Dead Chest (BVI)	0.1	7				20
45. Dellis Cay (Caicos)	1.5	3				7
46. Desecheo (Puerto Rico)	1.4	12	+			17, 36

Table 1—Comparison of resident status (“+” denotes breeding) of the two *Margarops* thrashers and the red-legged thrush among 177 Caribbean islands (continued)

Island	Island size *Square kilometers*	Number of breeding landbirds	Pearly-eyed thrasher	Scaly-breasted thrasher	Red-legged thrush	References^a
47. Dog (USVI)	0.05	7				21
48. Dominica^c (Leeward Islands)	751	41	+	+	+	13,19,34
49. Dutch Cap (USVI)	0.1	4	+			21
50. East Caicos (Greater Antilles)	178	18	+			1,7
51. East Cay (Turks)	0.5	1				7
52. East Seal Dog (BVI)	0.008	1				20
53. East Six Hill (Caicos)	0.1	1				7
54. Eleuthera (Bahamas)	518	27			+	3,7
55. Eustatia (BVI)	0.1	8				20
56. Fish Cay (Bahamas)	0.7	5				7
57. Fortune (Bahamas)	34.7	14				7
58. French Cap (USVI)	0.04	1				21
59. French Cay (Caicos)	0.1	1				7
60. Ft. George (Caicos)	0.3	7				7
61. George Dog (BVI)	0.2	6	+			20
62. Gibbs Cay (Turks)	0.1	1				7
63. Ginger (BVI)	1	6	+			20
64. Gonâve (Hispaniola)	660	43			+	13,19
65. Grand Bahama	1,373	38			+	3,7
66. Grand Cayman	180	25				5,19,23
67. Grand Turk	18.2	19	+			1,7
68. Grass Cay (USVI)	0.2	4	+			21
69. Great Abaco (Bahamas)	1,681	37			+	3,7
70. Great Camanoe (BVI)	3	13	+			20
71. Great Dog (BVI)	0.3	8	+			20
72. Great Exuma (Bahamas)	169	22			+	6,19
73. Great Inagua (Bahamas)	1,544	25	+		+	3,6
74. Great St. James (USVI)	0.6	12	+			21
75. Great Tobago (BVI)	0.9	6	+			20
76. Green Cay (BVI)	0.1	4				20
77. Green Cay (USVI)	0.003	2				21
78. Grenada (Windward Islands)	310	34		+		13, 19, 34
79. Guadeloupe^c (Leeward Islands)	1,780	37	+	+		13, 19
80. Guana^c (BVI)	3	13	+			20
81. Guana Cay (Bahamas)	0.2	4				7
82. Hans-Lollick, Big (USVI)	2	14	+			21
83. Hans-Lollick, Little (USVI)	0.4	10	+			21
84. Harbour (Bahamas)	5	22			+	6,38
85. Hassel (USVI)	0.6	13	+			21
86. Henley Cay (USVI)	0.1	3				21
87. Hispaniola^c	76,484	78			+	11, 13, 19, 34
88. Île-à-vache (Hispaniola)	52	29				28
89. Îslès les Saintes^c (Guadeloupe)	13	≤12	+			13, 32
90. Jamaica	10,989	71				13, 19
91. Jost Van Dyke (BVI)	8	14	+			20
92. Kalkun Cay (USVI)	0.01	2				21
93. La Désirade^c (Guadeloupe)	27	19	+	+		13,19
94. La Juventud (= Pinos, Cuba)	3,000	57			+	2,4,19

Table 1—Comparison of resident status ("+" denotes breeding) of the two *Margarops* thrashers and the red-legged thrush among 177 Caribbean islands (continued)

Island	Island size	Number of breeding landbirds	Pearly-eyed thrasher	Scaly-breasted thrasher	Red-legged thrush	References[a]
	Square kilometers					
95. Little Abaco (Bahamas)	59.1	22				6, 17
96. Little Camanoe (BVI)	0.2	7				20
97. Little Cayman (Cayman Islands)	24	17				6, 19
98. Little Exuma (Bahamas)	26.8	21			+	6, 17
99. Little Inagua (Bahamas)	127	22	+			6
100. Little Jost Van Dyke (BVI)	0.6	6	+			20
101. Long Cay (Caicos)	1	3				7
102. Long Cay (Turks)	0.2	1				7
103. Long (Bahamas)	448	22				3, 7
104. Lovango Cay (USVI)	0.5	8	+			21
105. Marie Galante[c] (Guadeloupe)	160	21	+	+		13, 19
106. Marina Cay (BVI)	0.01	6				20
107. Martinique[c]	1,102	39	+	+		13, 19
108. Mayagüana (Bahamas)	293	21	+			6, 7
109. Middle Caicos	288	18	+			1, 7
110. Mingo Cay (USVI)	0.2	7	+			21
111. Mona[c] (Puerto Rico)	50	16	+			19, 24, 25
112. Montserrat[c] (Leeward Islands)	106	27	+	+		13, 19, 29, 34
113. Mosquito (BVI)	0.5	7	+			20
114. Necker[c] (BVI)	0.3	11				20
115. Nevis	130	20	+	+		10, 19
116. New Providence[c] (Bahamas)	207	31			+	3, 7
117. Norman (BVI)	2	11	+			20
118. North Caicos	204	20	+			1, 7
119. Parrot Cay (Caicos)	5.5	17	+			1, 7
120. Patricia Cay (USVI)	0.1	8				21
121. Pear Cay (Turks)	0.1	1				7
122. Penniston Cay (Turks)	0.04	1				7
123. Perkins Cay (USVI)	0.002	1				21
124. Peter (BVI)	4	14	+			20
125. Pine Cay (Caicos)	3.6	19	+			1,7
126. Plana Cay, East (Bahamas)	10	7				7
127. Plana Cay West (Bahamas)	8.8	14				7
128. Prickly Pear (BVI)	0.7	10	+			20
129. Providencia (Colombia, SA)	40	12				14, 19, 23, 27
130. Providenciales (Caicos)	117	20				1
131. Puerto Rico[c]	8,903	61	+		+	19, 26
132. Ragged Islands (Bahamas)	23	11				3, 7
133. Ramgoat Cay (USVI)	0.01	2				21
134. Rotto Cay (USVI)	0.008	3				21
135. Rum Cay (Bahamas)	78	11	+			3, 22
136. Saba (NNA)	13	20	+	+		19, 33
137. Saba Cay (USVI)	0.1	13	+			21
138. Salt Cay (BVI)	0.8	8				20
139. Salt Cay (Turks)	6.7	11				7
140. Salt Cay (USVI)	0.2	11	+			21
141. Samana Cay (Bahamas)	33.2	10				7

Table 1—Comparison of resident status ("+" denotes breeding) of the two *Margarops* thrashers and the red-legged thrush among 177 Caribbean islands (continued)

Island	Island size	Number of breeding landbirds	Pearly-eyed thrasher	Scaly-breasted thrasher	Red-legged thrush	References[a]
	Square kilometers					
142. San Andrés (Colombia, SA)	52	15				14, 19, 27
143. Sandy Cay (BVI)	0.05	7				20
144. San Salvador (Bahamas)	163	19	+			3, 7
145. Saona[c] (Hispaniola)	110	31			+	12, 13
146. Savannah (USVI)	0.7	12	+			21
147. Scrub (BVI)	1	12	+			17, 20
148. Shark Rock (USVI)	0.005	1				21
149. Sheep Cay (Bahamas)	0.2	1				7
150. South Caicos	21.2	18				1
151. St. Barthélemy (Leeward Islands)	25	17	+			13, 19
152. St. Croix[c] (USVI)	210	22	+			19, 30
153. St. Eustatius (Leeward Islands)	21	21	+	+		19, 33
154. St. John[c] (USVI)	50	25	+			13, 19
155. St. Kitts[c] (= St. Christopher)	170	23	+	+		10, 13, 19
156. St. Lucia[c]	616	45	+	+		9, 13, 19
157. St. Martin (Leeward Islands)	85	18	+	+		19, 33
158. St. Thomas (USVI)	70	24	+			19
159. St. Vincent[c]	350	39		+		13, 34
160. Steven Cay (USVI)	0.008	5				21
161. Stubbs Cay (Caicos)	0.5	3				7
162. Swan (Honduras, SA)	4	5				19, 23
163. Thatch Cay[c] (USVI)	0.9	12	+			21
164. Tortola[c] (BVI)	55	18	+			19
165. Tortue, Île de la (Hispaniola)	180	29			+	28
166. Trunk Cay (USVI)	0.009	2				21
167. Turtledove Cay (USVI)	0.02	4				21
168. Union[c] (Grenadines)	10	18				13, 38
169. Vieques[c] (Puerto Rico)	162	33	+			19, 31
170. Virgin Gorda[c] (BVI)	21	16	+			20
171. Water Cay (Caicos)	3.6	13	+			7
172. Water (USVI)	2	15	+			21
173. West Caicos	22.8	18				1
174. West Cay (USVI)	0.2	7	+			21
175. West Dog (BVI)	0.1	7	+			20
176. West Seal Dog (BVI)	0.02	3				20
177. Whistling Cay (BVI)	0.08	9	+			21

[a] Reference sources: 1. B. Aldridge, (1991, in litt.); 2. American Ornithologists' Union (1998); 3. Atlas: Ministry of Education, Commonwealth of the Bahamas (1976), and [addendum]: Van Tyne and Mayfield (1952); 4. Barbour (1943); 5. Bradley (1985); 6. Brudenell-Bruce (1975); 7. Buden (1987a, 1987b, 1987c, 1990, 1992a, 1992b); 8. Buden and Schwartz (1986); 9. Danforth (1935a, 1935b, 1935c); 10. Danforth (1936b); 11. Dod (1978, 1981); 12. Faaborg (1980c); 13. Faaborg (1985); 14. Hilty and Brown (1986); 15. Holland and Williams (1978); 16. W. Howe, (1999 pers. comm. (singing, territorial male); 17. I.C. Jones (Island Resources Foundation), pers. comm.; 18. LaBastille and Richmond (1973); 19. Lack (1976); 20. Mirecki et al. (1977); 21. Nichols (1943); 22. R.L. Norton, pers. comm.; 2. Paynter (1956); 23. Fisher and Wetmore (1931); 24. Pérez-Rivera and Bonilla (1983); 25. Raffaele (1973); 26. Raffaele (1983); 27. Russell et al. (1979); 28. Schwartz (1970); 29. Siegel (1983); 30. Sladen (1987); 31. Sorrié (1975); 32. Vaurie (1961); 33. Voous (1957, 1983); 34. Webster's Geographical Dictionary (1984); 35. Wells (1902); 36. Wetmore (1927); 37. Wiley and Ottenwalder (1990). 38. World of Information (1986).

[b] Islands' political affiliations in alphabetical order: (BVI) British Virgin Islands; (NNA) Northern Netherlands Antilles; (SA) South America; (USVI) United States Virgin Islands.

[c] Thirty-four islands on which Arendt and/or Faaborg conducted avifaunal assessments from 1972 to 2000.

Table 2—Nineteen islands, including banding sites, treated in various tables and figures. Islands with no banding site designated are those in which assessments encompassed the entire island, or no prominent land mark was known

Island	Forest type
7. Antigua (Leeward Islands)	
a. Shirley Heights	Dry
b. Wallings Reservoir	Moist
9. Barbuda (Antigua) Trail to Darby Cave	Dry
11. Beata Island (Hispaniola) NE near defunct prison	Dry
48. Dominica (Leeward Islands)	
a. Morne Plaisance	Wet
b. Syndicate	Wet
79. Guadeloupe	
a. Basse Terre, 350 m elev. 1 km W of the Grand Etang	Wet
b. Grande Terre, coastal scrub, 5 km NNE of Saint François	Dry
80. Guana (BVI)	Dry
87. Hispaniola	
89. Îslès les Saintes (Guadeloupe)	
a. Terre de Bas, 1 km SW of Grand Anse	Dry
b. Terre de Haut, 1.5 km WSW of Terre de Haut	Dry
93. La Désirade (Guadeloupe) 1 km NW of Grand Anse	Dry
105. Marie Galante (Guadeloupe) 2 km N of Pointe des Basses	Dry
111. Mona (Puerto Rico) plateau	Dry
112. Montserrat (Leeward Islands)	
a. Bamboo Forest	Cloud forest
b. Chances Peak, summit near fresh water pond (Soufriere Hills)	Cloud forest
c. Dannenborg estate, road between Blackburne Field and Plymouth (Soufriere Hills)	Wet
d. Fogerty Spring (Centre Hills)	Wet
e. Garibaldi Hill (trail to Fox's Bay)	Dry
f. Gingoes Ghaut (Soufriere Hills)	Wet
g. Jubilee Heights (Centre Hills)	Wet
h. Killiekrankie Spring (Centre Hills)	Wet
i. Lawyers Mountain (Centre Hills)	Wet
j. Mosquito Ghaut (Soufriere Hills)	Wet
k. Runaway Ghaut (Centre Hills)	Wet
l. Tuitt's Ghaut (Soufriere Hills)	Wet
m. Upper Pond (South Soufriere Hills)	Cloud forest
n. Wilkes Ghaut (Centre Hills) (above chicken ranch)	Moist
131. Puerto Rico (Caribbean National Forest)	
a. Cloud forest, East Peak, Mt. Britton Trail	Cloud forest
b. Colorado forest (*Cyrilla racemiflora* L.) Icacos Valley	Colorado forest
c. Tabonuco forest (*Dacryodes excelsa* Vahl.)	Tabonuco forest
131. Puerto Rico (island-wide)	
a. Cabezas de San Juan light house, Fajardo	Mangrove
b. Community Beach, Roosevelt Roads Naval Base, Ceiba	Mangrove
c. Guánica	Dry
d. Jayuya	Wet
e. Maricao Forest	Wet
f. Pig Point, Roosevelt Roads Naval Base, Ceiba	Moist
g. Río Abajo Forest	Pine (PF), wet
h. Safe Harbor Servicemen's Center, Ceiba	Moist

Table 2—Nineteen islands, including banding sites, treated in various tables and figures. Islands with no banding site designated are those in which assessments encompassed the entire island, or no prominent land mark was known (continued)

Island	Forest type
154. St. John (USVI) Virgin Islands National Park (Askins and Ewert 1991)	
a. 35 count points in extensive forest tracts	Dry evergreen woodland
b. 95 count points in extensive forest tracts	Moist
155. St. Kitts	
a. Lodge's Estate (500 m elev. NE slope of the South East Range)	Wet
b. Southeastern Peninsula (Friar's Bay, Great Salt Pond)	Dry, mangrove
156. St. Lucia	
a. Bois d' Orange	Mangrove
b. Cas-en-Bas	Dry
c. Edmond Forest	Wet
d. Forestière	Wet
e. Louvet	Dry
f. Moule-a-Chique	Dry
g. Pitón Flore	Wet
h. Quilesse	Wet
158. St. Thomas (Ewert and Askins 1991, Askins et al. 1992)	
a. forest fragments	Dry
b. forest fragments	Moist
159. St. Vincent	
a. Cumberland	Wet
b. Will-be-Free	Wet

Appendix 3

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1]

Island	Year	Source	Status
Bahamas:			
Cay Sal Bank and Ragged Islands	1968	Buden and Schwartz	No records
	1987b	Buden	No records
Great Abaco	1990	Norton	One was seen by E. VanderWerf, 20 March 1990
New Providence	1995	A.W. White (pers. comm.)	Two records: one seen by A. Sprunt IV "in Lynn Holowesko's garden years ago;" one was seen by A.W. White and Aileen Bainton at Paradise Island ponds, 1 March 1995
Harbour Island	1978	Bond	Decomposed remains of one individual found on unspecified date; possible straggler from Cat Island
	1975	Brudenell-Bruce	Both authors stated that the pearly-eye is thought to be spreading northward
	1988	Buden (in litt.)	
Eleuthera	1964	Bond	Unspecified number observed at Tarpum Bay from 10 April to early May 1956 (see section on "Dispersal" in this volume)
Cat Island	1966	Paulson	One was seen at Tea Bay, late November 1963
	1987a	Buden	None were seen 23 May–28 July 1986
	1989	Howe et al.	One was seen 13 March 1986, possibly a straggler from Rum Cay where abundant—Buden 1990 (see section on "Dispersal" in this volume)
San Salvador (= Watling Island)	1886	NMNH[2]	One collected
	1891	FMNH[2]	Sixty-six specimens collected at several locations
	1891	Ridgway	Four collected 29 March 1891
	1892b	Cory	Listed among specimens[2] collected 28 September–9 November 1891
	1905b	Riley	"Not uncommon" 11–13 July 1903
	1966	Paulson	One of the most common residents
	1978	Miller	Dense resident populations; abundant breeder (1973–76)
	1990	Olson et al.	153 bones from 9 individuals found in owl pellets, although no fossilized material was present; authors believe deposits are too scanty to predict species' early status on the island
Rum Cay	1886	NMNH[2]	Eight study skins
	1891	Ridgway	Ten collected, 1–6 March 1891
	1905b	Riley	"Not uncommon," 10 July 1903
	1990	Buden	Most common landbird; breeding in summer of 1989
Exumas	1964	Bond	One was seen February 1964 (see section on "Dispersal" in this volume) [Note: bones from the Exumas identified by Wetmore (1937) as those of the pearly-eye have been reassigned to *Sturnella magna* by Olson and Hilgartner (1982)]
	1980	Bond	Cites J.R. Miller as stating the species is not resident (J.R. Miller et al. 1976 unpublished sight records)

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1991	Buden (in litt.)	Not found on more than 70 islets and cays visited 14–19 December 1990; 20 May–4 August 1991
Long Island	1905b	Riley	Rare (mid-June 1903, gave no information as to number of birds seen, no other firsthand records—Buden 1992c)
	1980	Bond	Cites J.R. Miller as stating the species is not resident (J.R. Miller et al. 1976 unpublished sight records)
	1991	Buden (in litt.)	None were seen 28 April–13 May and 6 July–12 August 1990
Bird Rock	1903a,b	Bonhote	One struck the lighthouse, 14 November 1901 at 2150 hours (possible night dispersal; see section under "Homing Experiments" in this volume)
Crooked Island	1923	NMNH[2]	One specimen collected by P. Bartsch in the northeastern region
	1930	Bartsch (unpublished field notes)	One collected near Pittsdown Point 14 July 1930
	1972	Buden (1988, in litt.)	"Fairly common" in early April 1972; most numerous in fruit trees, e.g., sapodilla (*Manilkara* sp.) near settlements
Mayagüana (= Maragüana)	1891	FMNH[2]	One specimen collected at Betsey Bay
	1892b	Cory	Listed among specimens collected 5 August–14 September 1891
	1972–76	Buden (1988, in litt.)	None were seen 7–14 May 1972 and 29 September–2 October 1976
Great Inagua	1879	FMNH[2]	Three specimens collected on the "northeastern point"
	1880	Cory	Uncommon, summer 1879
	1890b	Cory	Uncommon; locals said common in the interior
	1891	Cory	Listed among specimens[2] collected during January and February 1891; and listed among specimens[2] collected, 1 May–10 July 1891
	1911	Todd and Worthington	Specimens[2] collected at Alfred Sound, 28 December 1908—8 May 1909
	1970s	Buden (1988, in litt.)	Observed regularly in woodlands north of Matthewtown during several visits from early to mid 1970s
	1982	Snyder et al.	Not common, restricted to northwestern region, 26–31 March 1979
Little Inagua	1974–77	Buden (1988, in litt.)	Seen regularly in more heavily wooded areas, last week of December 1974 and 8–11 April 1977
Caicos Islands	1891	FMNH[2]	Twelve study skins
	1891	Cory	Listed among 12 specimens[2] collected by C.S. Winch during January and February 1891; unspecified as to island, but reported from North, Grand (= Middle), and East Caicos Islands by Cory (1892a)
	1930	Bartsch (unpublished field notes)	Observed on Pine Cay and Water Cay 24 July 1930
	1970s	Buden (1988, in litt.)	Common on North Caicos during early 1970s in the vicinity of Kew
	1970	Buden (1988, in litt.)	Several seen on Parrot Cay 23 May 1970
	1971	LSU[2]	Seven specimens collected at Kew
	1979	Buden 1987b	Nest with three eggs, Pine Cay, summer 1979

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1987	Aldridge (1991, in litt.)	Resident on Pine and Parrot Cays
Grand Turk	1982	Norton	Sight records 6 March and 1 May 1982, possibly same individual; reported as accidental or recent invader by Buden (1987c); also seen on Grand Turk by B. Aldridge (1991, in litt.)
Jamaica	1865	NMNH[2]	One specimen collected by W.T. March
	1978	Bond	One specimen[2] collected at Phoenix Park, Spanish Town, 22 July 1865
	1881	Newton and Newton	Not included in a list of 189 species
	1920	Bangs and Kennard	Not included in a list of 219 species
Hispaniola	1807	Vieillot (correct date = 1808)	Inhabitant of “Saint-Dominique” (Hispaniola) type locality, nominate race (shared with Puerto Rico) [Note: Vieillot specifically states observing the species in Haiti]
	1891	Cory	Listed, “San Domingo”
	1927	Beebe	Listed among 13 species from Haiti; exhibited alive in the New York Zoological Park [Note: Wetmore and Swales (1931) state that Beebe’s specimen had no information as to collection locality; also, *M. fuscatus* was not listed a year later in Beebe’s bird list for Haiti]
	1928a	Bond	Not listed in his birds inhabiting Haiti
	1979a	Bond	Listed as occurring only on a single satellite island (Beata)
	1990	Wiley and Ottenwalder	One netted near Guaraguao, Boca de Yuma Forest (Parque Nacional del Este) in 1984 by T.A. Vargas Mora and C.S. Robbins
Beata	1931	USNM[2]	Four specimens collected by A. Wetmore and F.C. Lincoln
(Hispaniola)	1933	Wetmore and Lincoln	Found in “fair numbers” [= “common”?] in dense scrub
	1965	Schwartz and Klinikowski	Extremely common
	1980b	Faaborg	Common, but only 8 of 133 mist netted
	1990	Wiley and Ottenwalder	Most abundant landbird (mean = 12.4 per km)
Mona (Puerto Rico)	1901	FMNH[2]	Twelve specimens collected by B.S. Bowdish
	1903	Bowdish	Most abundant landbird (August 9–21, 1901)
	1923 and 1927	Struthers	One of the island’s most“ characteristic” [= common?] birds
	1936b	Danforth	Inhabits all parts of the island
	1946	Barnés	Most abundant landbird; widely distributed, coastal plains and plateau
	1946	Bond	Commonest landbird; Beatty estimated 1,000 individuals
	1961a	Rollé	Common on the plateau
	1964	Rollé et al.	Only a “few” individuals observed (5–7 November 1960)

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1972–84	Faaborg and Arendt (unpublished data)	Abundant; 214 of 619 (35 percent) of all birds mist netted during visits between 1972 and 1984
	1973	Raffaele	Most common resident landbird
Caja de Muertos (Puerto Rico)	1935	NMNH[2]	Two specimens collected by S.T. Danforth
Monito (Puerto Rico)	1964	Rollé et al.	No landbirds observed 31 May 1963
Desecheo (Puerto Rico)	1900a	Bowdish	Heard one individual
	1901	NMNH[2]	Four specimens collected by B.S. Bowdish
	1903	Bowdish	Abundant among rocks in "scraggy growth" [= scrub?] July 6 and 9, 1900; only landbird observed
	1918	Wetmore	About 1,200 from 13 to 16 June, 1912; only landbird observed; common in 1918
	1931	Danforth	"Rather scarce" [?] (May 1927) [see chapter 4 for discussion of temporal fluctuations in Mona Island thrashers]
	1989	Meier et al.	Abundant resident, especially in heavily forested valleys
Puerto Rico	1807 (correct date = 1808)	Vieillot	Type locality and specimen, nominant race (shared with Hispaniola); Bond (1973) states Vieillot found the species "numerous" in 1807
	1810	Ledrú	Almost 100 species listed, but pearly- eye not mentioned [?]
	1869	AMNH[2]	One study skin
	1869a	Sundevall	Included in checklist of island birds
	1878	Gundlach	Uncommon, from Quebradillas and Utuado
	1899	NMNH[2]	One specimen collected by A.B. Baker in Caguas
	1903	Bowdish	"Never met with this bird on the main island" [?]
	1907	Ridgway	Eleven collected
	1916a and 1922	Wetmore	"Rare...on the main island...", but common on the satellites
	1922	Danforth and Danforth	Not listed on Christmas Bird Count, Mayagüez (western coast)
	1923	Struthers	Common in Maricao (montane forest) (29 December 1921)
	1926	Danforth	Uncommon resident in vicinity of the Cartagena Lagoon in bamboo, but "fairly common" on Tinaja Hill
	1927	Wetmore	"Quite plentiful" Upper Toro Negro Valley (P.A. Potts)
	1927	Danforth	Not listed on Christmas Bird Count, Guánica (southwestern coast)
	1928	Danforth	Not listed on Christmas Bird Count, Cartagena Lagoon (SW)
	1929	Danforth and Bond	Not listed on Christmas Bird Count, Boquerón Valley (SW)
	1931	Danforth	Becoming more abundant and generally distributed, within recent years more common in the west, but observed in the eastern interior, e.g., Trujillo Alto, Naguabo, and El Yunque, up to 2,000 ft
	1931	Beatty	Not included in year-long avian study along southwestern coast [?]

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1931	Danforth	Becoming more abundant and widespread (repeated by Bond 1945)
	1936b	Danforth	Patchy distribution more common in coastal scrub and dry forest in the hills
	1958	McCandless	“Fairly common” in picnic areas and coastal palm groves
	1961	Burden	Not included in list of birds observed at Cartagena Lagoon
	1963	Leopold	Locally “fairly common,” common in the Virgin Islands
	1974	Biaggi	Abundant, especially along the coast
	1983	Raffaele	Common resident, thickets, woodlands, forests, coastal palm groves to mountaintops
	1998	Raffaele et al.	“Common,” including Virgin Islands ranges from uncommon to abundant in a variety of habitats from seashore to mountain pinnacle
Isla Piñeros (Puerto Rico)	1965	LSU[2]	Three study skins
Vieques (Puerto Rico)	1900	AMNH[2]	One study skin
	1900	NMNH[2]	One specimen collected by C.W. Richmond
	1900b	Bowdish	“Not uncommon”
	1916b	Wetmore	Common in dense thickets in stream beds and ravines (March-Apr 1912)
	1937	Danforth	“Fairly common” in brush-covered hills, in eastern sectors
	1975	Sorrié	Remains common in most habitats
	1990s	(various visitors)	Common
Culebra (Puerto Rico)	1899	NMNH[2]	Seven specimens collected; three by A.B. Baker and four by J.D. Milligan
	1917	Wetmore	Common resident, brushy growth, borders of mangroves (20 species of landbirds); Wetmore collected seven specimens in 1922 (measured by the author)
	1935c	Danforth	Rare (one individual was seen in January 1935)
	2000	M. I. Cook (pers. comm.)	Common throughout, especially around human habitation
Culebrita (Puerto Rico)	1912	NMNH[2]	Wetmore collected four specimens
	1917	Wetmore	Resident (13 species of landbirds)
	2000	M. I. Cook (pers. comm.)	Common
Luís Peña (Puerto Rico)	1917	Wetmore	Resident (10 species of landbirds)
	1934	NMNH[2]	One specimen collected by S.T. Danforth
St. Thomas	1859	Newton and Newton	Common resident
	1861	Cassin	Common
	1864	MCZ[2]	Five specimens collected, three by R. Swift and two by F.A. Ober
	1890a	Cory	Listed
	1930b	Danforth	“Fairly common”
	1943	Nichols	Common resident

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
Jost Van Dyke (British Virgin Islands)	1934	NMNH[2]	One specimen collected by S.T. Danforth at White Bay
St. John	18??	NMNH[2]	Three specimens collected by F.A. Ober in the late 1800s
	1927	NMNH[2]	One specimen collected by S.T. Danforth at Cruz Bay
	1930b	Danforth	Very common, in the hilly interior, less so near the coast
	1943	Nichols	Common resident
	1962	Robertson	Most abundant bird from seashore to 360 m elevation
St. Croix	1810	Ledrú	Of almost 100 species, not listed [?]
	1859	Newton and Newton	Common resident
	1862	Sclater	Two collected
	1890	AMNH[2]	One study skin
	1890	MCZ[2]	One study skin
	1891	Cory	Listed
	1916	Noble	Common in the streets of Christiansted
	1930	Beatty	Very common among fruit gardens
	1930b	Danforth	Common at Prosperity
	1987	Sladen	Very common resident
Tortola	1890a	Cory	Listed
	1917	MCZ[2]	Four specimens collected by J.L. Peters
	1930b	Danforth	Very common on the wooded, brushy hills
	1977	Mirecki et al.	Most numerous species especially in coconut plantations and middle slopes
Virgin Gorda	1890a	Cory	Listed
	1917	MCZ[2]	Two specimens collected by J.L. Peters
Anegada	1943	Nichols	Found in Anegada (J.B. Nichols)
	1973	LaBastille and Richmond	One observed in early May 1970 at fresh water pond, no other records
	1994	Arendt	None observed during a 2-day search
Sombrero	1863	AMNH[2]	Two study skins
	1867	Lawrence	One straggler [?]; shot by A.A. Julien (28 September 1863)
Anguilla	1891	Cory	Listed
	1892	Sclater	Rare by late 1800s, one collected by W.R. Elliott (March 1891)
	1922	MCZ[2]	Two skins (22 February; collector J.L. Peters)
	1927	Peters	Uncommon in dense thickets
	1989	McLaughlin and Roughgarden	Common (nine pairs per hectare, Katouche Canyon)
	2000	J. Hughes	"Locally common throughout the island in scrub and around human settlements; most common in the northern and western regions"

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
St. Martin	1927	NMNH[2]	One specimen collected by S.T. Danforth at Grand Cause
	1930a	Danforth	Locally common, in denser, higher brushy woods
	1989	McLaughlin and Roughgarden	Common (10.7 pairs per hectare, Pic du Paradis)
	1957	Voous	Common in all scrub and forest vegetation, also in gardens
	1983	Voous	Retiring, variety of vegetation types
St. Barthélemy	1869b	Sundevall	Not mentioned in checklist of island birds
	1945 to 1950	Bond	Listed
	1990	Evans	Listed as "nester," p. 153
	1998	Raffaele et al.	Listed as "common," p. 482
Saba	1937	NMNH[2]	Four specimens collected by S.T. Danforth at Spring Bay
	1938	Danforth	Most common bird, wooded and brushy areas
	1957	Voous	Common, gardens, scrub, montane forests to 500 m elevation
	1983	Voous	One of the most abundant landbirds, also in cloud forest
St. Eustatius	1891	Cory	Listed
	1922	MCZ[2]	Six specimens were collected by J.L. Peters
	1930a	Danforth	No status account given; "Two were heard on the volcano..."
	1957	Voous	Uncommon, only in desert scrub and forest of the Little Mountains on the slope of the Quill, not found near human habitation [over hunted?]
St. Kitts	1891	Cory	Not listed [?]
	1922	MCZ[2]	Two specimens collected by J.L. Peters
	1936a	Danforth	Abundant in the high forests on the Crater and observed at Monkey Hill and Olivees Mountain
Nevis	1936a	Danforth	Only common species in montane forest
	1962	LSU[2]	Four specimens collected on the eastern slope of Nevis Peak
Barbuda	1903	AMNH[2]	Ten specimens collected by H.G.S. Branch
	1905a	Riley	Five specimens[2] collected by Mr. H.G.S. Branch in 1903
	1935a	Danforth	Five observed at Highlands (1933)
	1985	Faaborg and Arendt	Uncommon, only 4 individuals of about 500 birds netted (3–5 February 1984)
Southwest Cay (Barbuda)	1935a	Danforth	One of the most abundant species in the denser woods
Antigua	1877	NMNH[2]	One specimen collected by F.A. Ober in September; museum tag reads "not plentiful; found near streams"
	1890	AMNH[2]	Two museum skins
	1891	Cory	Listed
	1879 a,c	Lawrence	Rather rare and local, found only in valleys with rivulets and trees
	1905a	Riley	Four specimens[2] collected by H.G.S. Branch in 1903

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1934	Danforth	"Fairly common" mostly in mesophytic woods, but observed near English Harbour
	1978	Holland and Williams	Uncommon and local, confined to SW forested hills above Wallings and Christian Valleys
	1985	Faaborg and Arendt	Uncommon, local, wet forest, SW hills; SE coast (1 of 159 birds netted in dry forest near Shirley Heights)
	1988	Pregill et al.	Confined to forested hills in SW region; fossilized bones present
Montserrat	1879	Sclater	Listed
	1880	NMNH[2]	Seven specimens collected by F.A. Ober between March and August
	1886b	Cory	Listed
	1891	Cory	Listed
	1937	NMNH[2]	Four specimens collected by S.T. Danforth; one at Elbertson Pond, two at Plymouth, and one on Soufrière Mountain
	1939b	Danforth	Common in lower wooded hills and densely wooded ravines in the coastal region
	1945	Bond	Common resident
	1978	Terborgh et al.	41 of 209 (20 percent) of birds captured in mist nets in wet forest on the Dannenborg Estate in 1975
	1984b	Steadman et al.	Most common forest bird observed; fossilized bones present; first prehistoric record for Lesser Antilles
	1985	Faaborg and Arendt	Abundant, composed 152 of 389 (39 percent) of the birds netted at six forested sites
	1990	Arendt	Abundant following Hurricane Hugo; 286 of 619 (46 percent) of the birds detected in 90 point-count censuses
	1999	Arendt et al.	Third most abundant forest bird (estimated pop. of 25,000) following volcanism
Guadeloupe	1879c	Lawrence	Listed
	1886b	Cory	Listed
	1890	FMNH[2]	One specimen collected by C.S. Winch
	1891	AMNH[2]	One study skin
	1891	Cory	Listed
	1916	Noble	Scarce, very retiring, found only in highest forests, very arboreal [coveted gamebird]
	1939a	Danforth	In rain forest, common on Morne Folie and the Soufrière
	1945	Bond	Common in mountain forest
	1953	Westermann	Almost extirpated, owing to mongoose predation [hunting pressure is more probable]
	1998	Feldmann et al.	Common in forests on Basse-Terre

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
La Désirade	1886	FMNH[2]	Eleven specimens collected by W.E. Richardson
	1886a	Cory	Listed
	1939a	Danforth	Common in the mountains
	1963	Pinchón	Listed
	1975	Faaborg	Uncommon, dry forest only 4 percent (19 of 442 captures) were pearly-eyes; however, 216 captures were bananaquits and 107 were black-faced grassquits, composing 73 percent, thus pearly-eyes made up 16 percent of the remaining 119 captures
Marie Galante	1965	Schwartz and Klinikowski	Uncommon, one individual observed
	1975	Faaborg	Uncommon, 1 of 134 birds netted
Îslès les Saintes	1961	Vaurie	None seen on Terre-de-Haute (2–5 July 1960)
	1975	Faaborg	None mist netted out of 326 captures on Terre-de-Bas and Terre-de-Haute (13–16 January 1974)
Dominica	1791	Atwood	"Thrushes" in the forests [probably includes the pearly-eye]
	1879b,c	Lawrence	Listed, first specimens[2] for island [F.A. Ober was the collector]
	1883	FMNH[2]	Seven specimens collected by C.J. Maynard
	1886b	Cory	Listed
	1889a	Sclater	Listed, five specimens[2] collected by George A. Ramage
	1892	Verrill	Not common, but well distributed; range has decreased
	1928a	Bond	Common; more numerous than on St. Lucia
	1945	Bond	Common in mountain forest
	1975	Swank and Julien	Scarce and local, observed only at the higher elevations in rain forest
	1976	Lack	At higher elevations in rain forest
	1980	Zamore	Confined to high elevation in rain forest
	1985	Faaborg and Arendt	Uncommon and local; only 4 individuals of 537 (<1 percent) netted at two sites in montane forest
Martinique	1864	Taylor	Specimen of *Margarops* sp. "nicely mounted by Verreaux" in a collection exhibited by M. Belanger, Director of Botanical Garden, St. Pierre
	1879c	Lawrence	Listed
	1886	FMNH[2]	Four specimens collected by W.E Richardson
	1886b	Cory	Listed
	1887	Cory	Unspecified number (n = 4, see above) collected by W.B. Richardson
	1945 and 1950	Bond	Rare and local owing to hunting pressure
	1953	Westermann	Rare, owing to mongoose predation [hunting pressure is more probable]
	1965	Schwartz and Klinikowski	Rare, owing to hunting
St. Lucia	1844	Breen	"Thrushes" taken as gamebirds [includes the pearly-eye]
	1871	Sclater	Listed, along with *M. fuscus*

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1872	Semper	Not included in his article [?]
	1879	MCZ[2]	Four specimens collected by J. Semper
	1880	Allen	Listed, first specimen[2] (+ 5 more), sent by Rev. John E. Semper [possibly "discovered" by him between 1872 and 1880]
	1886b	Cory	Listed
	1889b	Sclater	Listed, specimens[2] collected by George A. Ramage
	1928a	Bond	Common
	1935b	Danforth	Uncommon and local
	1950	Bond	Rare and local
	1953	Westermann	Rare
	1973b	Diamond	Patchy, found only in highland forests
	1977	Bond	Increasing in number
	1985	Faaborg and Arendt	Uncommon and local, only 7 (<1 percent) of 1,000 individuals mist-netted at 3 of 5 sites from coast to montane forest
St. Vincent	1957	Bond	First specimen [were there others?— none found by author in U.S. museums] collected 23 April 1890 in "thick forest at 2,000 ft in the middle of the island;" examined by D.W. Smith (date unknown) [and by the author in May 2000 at the British Museum]
	1956a	Bond	Not listed [?] in his checklist
	1960–71	Bond	Listed in guides
	1970	Devas	Not mentioned in his book
	1973	Lack et al.	Not observed
	1977	Bond	Extirpated
	1985	Faaborg and Arendt	None in almost 300 birds netted at two sites in montane forest
	1990	Evans	Absent
	1998	Raffaele et al.	No longer included in its range
Barbados	1750	Hughes	Lists two "thrushes" the "quaking thrush" [trembler] and one resembling the English thrush [most probable *Margarops* sp.]
	1763	Ligon (cited and 1764 in Clark 1905)	Lists "councellor" (1763, p. 60) and "conseiller" (1764, p. 102) [most likely one of *Margarops* spp.]
	1848	Schömburgk	Lists (p. 681) "*Turdus mustelinus*" as the "common thrush" (cited in Clark 1905) [most probable is *Margarops* sp.]
	1859	Sclater	No mention of *Margarops* spp. From the island
	1889	Feilden	None observed during visit in 1888, but specimen collected by C.J. Manning at Bagatelle on 2 March 1889 [now thought to be *M. f. Klinikowskii*, a disperser from St. Lucia—see discussion in chapter 5]
	1891	Cory	Listed

Table 1—Historical accounts of the distribution, abundance, and population fluctuations of the pearly-eyed thrasher throughout its range[1] (continued)

Island	Year	Source	Status
	1985	Faaborg and Arendt	No *Margarops* spp. observed during wildlife assessment
	1989	D.W. Buden (1991, in litt.)	No *Margarops* spp. observed
	1990	Evans	Absent
	1998	Raffaele et al.	Vagrant
	1999	M. Frost (in litt.)	Photograph and description first seen by D. Archer (14 June 1999, Gregg Farm, St. Andrew, elevation about 270 m), then by M. Frost (photographer) (19 June 1999, same locale, *Ficus* sp. tree) [most likely a disperser]
Grenada	1998	AOU	Absent from Grenada and the Grenadines
	1993–96	M. Frost (1999, in litt.)	“Four sightings between 1993 and 1996” [most likely dispersers]
Bequia (Grenadines)	1975	Faaborg	None out of 66 birds of 8 species netted in dry forest
Bonaire	1892	AMNH[2]	Five study skins
	1893b	Hartert	Five specimens[2] collected
	1893a	Hartert	Restricted to Fontein Plantation
	1948	Phelps and Phelps	Found only at the Fontein Plantation among fruit trees near brook and its spring
	1957	Voous	Restricted to Fontein Plantation and vicinity (e.g., Tras Montagne)
	1988	Frater Candidus van der Linden (in litt.)	Evenly dispersed over island in hilly, rocky areas, absent in SE; (see text and fig. 4.1 in chapter 4)
	1997b	Arendt (see text chapter 4, this vol.)	Common at Fontein Plantation (19 percent of 68 captures of 15 species); rare in Washington-Slagbaai National Park (3 percent of 215 birds detected during point-count census)
Curaçao	1983	Voous	One sight record
La Horquilla (Los Hermanos Islands, Venezuela)	1909	Lowe	Three collected on 9 January 1908 at 400–600 ft elevation [author reviewed and measured all 3 skins in 2000 at the British Museum in Tring]
	1909	Cory	Cites Lowe’s three specimens; none were seen by Ferry during a 1-day visit (8 February 1909)
	1986	Hilty and Brown	Although listed in the AOU Checklist (1998) as inhabiting the islands “north of Venezuela from Bonaire east to Los Hermanos,” now probably extirpated from La Horquilla Islands, Los Hermanos group (see also Phelps 1948, Phelps and Phelps 1963)
Margarita Island (Venezuela)	1999	M. Lentino (in litt.)	No published sightings from this island
	1999	C. Bosque (in litt.)	Not present on well-studied Paraguaná Peninsula (Estado Falcón)

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[1] Islands appear in geographical order along the Caribbean Archipelago from Northwest to Southeast. The present-day status of the pearly-eye on islands in which it is well established may not be included for the most recent decades because pertinent status information can be found in several comprehensive, contemporary field guides.

[2] Specimens measured by the author; only the earliest specimens collected on each island are included; museum abbreviations are as follows: American Museum of Natural History (AMNH), New York, NY, USA; Field Museum of Natural History (FMNH), Chicago, IL, USA; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, USA; Museum of Natural Science (LSU), Louisiana State University, including the Schwartz collection, Baton Rouge, LA, USA; National Museum of Natural History (NMNH), Washington, DC, USA; Natural History Museum (NHM), Tring, Hertz, UK.

Appendix 4

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**[a]
Wing length (mm)											
Vieques	*M. f. fuscatus*	12	135.0–142.3	138.23	2.19	7	130.0–134.8	131.86	1.40	1	4.72
St. Croix	*M. f. fuscatus*	2	144.2–145.0	144.60	.57	8	130.2–142.0	138.17	4.61	1	4.55
Caicos Islands	*M. f. fuscatus*	18	129.4–144.0	139.03	2.93	9	123.4–142.0	133.12	5.95	2	4.34
St. John	*M. f. fuscatus*	2	140.4–143.0	141.70	1.84	2	136.9–137.3	137.10	.28	1	3.30
Mona	*M. f. fuscatus*	9	134.1–142.2	137.64	2.43	8	128.4–135.9	133.23	2.37	0	3.26
St. Eustatius	*M. f. fuscatus*	9	136.8–150.0	140.39	3.86	5	133.4–138.6	136.46	2.03	2	2.84
St. Thomas	*M. f. fuscatus*	12	131.3–146.0	138.11	5.07	14	127.1–142.0	134.81	4.62	1	2.42
Great Inagua	*M. f. fuscatus*	22	129.3–146.0	138.84	4.97	6	130.1–142.5	135.95	4.39	3	2.10
Saba	*M. f. fuscatus*	4	136.9–142.2	139.33	2.33	2	135.5–137.6	136.55	1.48	2	2.02
St. Kitts	*M. f. fuscatus*	6	130.0–140.6	136.32	3.69	6	130.6–137.0	133.72	2.92	2	1.93
Barbuda	*M. f. fuscatus*	8	134.2–143.1	139.56	3.09	4	133.7–140.5	136.98	2.78	1	1.87
Desecheo	*M. f. fuscatus*	5	135.5–140.5	137.82	2.03	5	131.7–137.4	135.38	2.32	0	1.79
San Salvador	*M. f. fuscatus*	25	128.3–145.2	137.39	3.69	37	127.3–139.8	135.17	2.94	2	1.63
Caja de Muertos	*M. f. fuscatus*	4	137.1–139.8	138.08	1.25	4	130.4–138.5	135.88	3.71	1	1.61
Puerto Rico	*M. f. fuscatus*	22	126.8–146.0	136.49	4.41	17	127.3–141.6	134.47	4.37	2	1.49
Antigua	*M. f. fuscatus*	6	130.5–142.0	137.23	4.48	11	126.9–140.8	135.25	3.74	2	1.45
Culebra	*M. f. fuscatus*	11	130.3–140.0	136.98	3.12	5	128.4–139.9	135.40	5.14	1	1.16
Beata	*M. f. fuscatus*	4	136.8–140.4	138.58	1.84	3	131.8–143.0	137.37	5.60	2	.88
Tortola	*M. f. fuscatus*	4	140.4–143.0	142.10	1.23	1	—	141.00	—	1	.78
Rum Cay	*M. f. fuscatus*	10	130.7–143.0	134.97	3.72	8	126.3–140.0	133.95	4.64	1	.76
Nevis	*M. f. fuscatus*	3	129.4–139.0	133.93	4.82	1	—	133.00	—	2	.70
Piñeros Island	*M. f. fuscatus*	1	—	137.90	—	2	134.8–141.4	138.10	4.67	0	-.14
St. Martin	*M. f. fuscatus*	2	133.3–139.0	136.15	4.03	2	134.3–138.4	136.35	2.90	1	-.15
Culebrita	*M. f. fuscatus*	3	138.5–140.4	139.70	1.04	1	—	140.50	—	0	-.57
Anguilla	*M. f. fuscatus*	2	140.0–143.0	141.50	2.12	—	—	—	—	0	—
Crooked Island	*M. f. fuscatus*	2	132.3–136.4	134.35	2.90	—	—	—	—	3	—
Jamaica	*M. f. fuscatus*	1	—	140.00	—	—	—	—	—	—	—
Jost Van Dyke	*M. f. fuscatus*	—	—	—	—	1	—	127.20	—	0	—
Luís Peña	*M. f. fuscatus*	1	—	140.50	—	—	—	—	—	0	—
Mayagüana	*M. f. fuscatus*	1	—	132.00	—	—	—	—	—	2	—
Sombrero	*M. f. fuscatus*	1	—	133.60	—	—	—	—	—	—	—
Virgin Gorda	*M. f. fuscatus*	2	134.0–140.0	137.00	4.24	—	—	—	—	1	—
Number and averages for *M. f. fuscatus*		214	134.1–142.4	138.07	3.00	169	130.4–139.6	135.48	3.47	1.23	1.86

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher (continued)

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**^{a}
Martinique	*M. f. densirostris*	2	137.5–142.0	139.75	3.18	3	129.4–133.0	131.05	2.33	6	6.43
Montserrat	*M. f. densirostris*	8	133.9–142.8	138.99	3.47	6	127.1–138.3	133.02	4.92	3	4.39
Guadeloupe	*M. f. densirostris*	11	122.0–146.0	140.48	5.93	16	130.4–143.0	135.43	3.77	4	3.66
Dominica	*M. f. densirostris*	21	130.0–141.7	135.26	3.45	12	126.0–138.3	131.88	3.93	6	2.53
La Désirade	*M. f. densirostris*	9	128.6–137.8	134.23	3.38	9	130.2–138.8	134.30	3.14	2	-.05
Number and averages for *M. f. densirostris*		51	130.4–142.1	137.74	3.88	46	128.6–138.3	133.14	3.62	4.20	3.39
St. Lucia	*M. f. klinikowskii*	10	141.1–148.2	145.02	2.26	11	124.0–144.9	139.73	5.94	7	3.72
Bonaire	*M. f. bonariensis*	18	125.2–137.2	132.68	3.47	14	120.4–133.5	126.41	4.18	1	4.84
Tail length (mm)											
Vieques	*M. f. fuscatus*	12	109.1–118.8	115.24	2.76	7	104.3–111.9	107.96	2.75	1	6.52
St. Kitts	*M. f. fuscatus*	6	105.2–120.1	114.08	5.21	6	105.0–113.4	107.53	3.41	2	5.91
St. Croix	*M. f. fuscatus*	2	120.0–125.0	122.50	3.54	8	105.7–121.0	115.53	5.28	1	5.86
Saba	*M. f. fuscatus*	4	112.0–117.4	115.18	2.49	3	105.0–113.7	110.33	4.67	2	4.30
St. John	*M. f. fuscatus*	2	116.2–120.0	118.10	2.69	2	110.2–116.1	113.15	4.17	1	4.28
Great Inagua	*M. f. fuscatus*	22	100.3–120.4	113.39	5.41	6	106.7–112.9	109.35	2.30	3	3.63
Tortola	*M. f. fuscatus*	4	117.0–120.2	119.05	1.46	1	—	115.00	—	1	3.46
Caicos Islands	*M. f. fuscatus*	17	110.6–119.5	114.74	2.63	9	102.4–116.3	111.30	4.37	2	3.04
St. Thomas	*M. f. fuscatus*	12	102.0–120.2	113.37	5.14	14	104.0–118.0	110.64	3.92	1	2.44
Piñeros Island	*M. f. fuscatus*	1	—	120.00	—	2	114.9–119.7	117.30	3.39	0	2.28
St. Eustatius	*M. f. fuscatus*	9	106.0–120.0	113.96	4.26	5	109.3–115.6	111.58	2.51	2	2.11
Culebra	*M. f. fuscatus*	12	106.9–121.9	114.23	5.39	5	107.2–114.4	111.88	3.33	1	2.08
Culebrita	*M. f. fuscatus*	3	117.5–121.9	119.30	2.31	1	—	117.10	—	0	1.86
Antigua	*M. f. fuscatus*	6	107.0–119.0	113.55	4.39	11	107.2–115.5	111.57	2.98	2	1.76
Caja de Muertos	*M. f. fuscatus*	4	112.6–116.8	114.08	1.96	4	109.3–117.0	112.88	3.16	1	1.06
Rum Cay	*M. f. fuscatus*	10	105.5–122.4	112.49	5.07	8	98.9–118.0	111.59	5.59	1	.80
Mona	*M. f. fuscatus*	9	109.2–116.9	112.71	2.84	8	103.7–118.6	111.85	6.15	0	.77
Desecheo	*M. f. fuscatus*	5	110.6–118.0	114.48	3.44	5	109.4–118.1	113.66	3.62	0	.72
Puerto Rico	*M. f. fuscatus*	21	104.3–124.0	114.37	4.58	17	106.4–118.8	113.64	3.73	2	.64
Beata	*M. f. fuscatus*	4	111.9–119.8	113.63	2.29	3	111.0–116.8	113.03	4.39	1	.53
San Salvador	*M. f. fuscatus*	20	102.8–117.3	111.87	2.99	43	104.7–119.8	111.31	3.58	2	.50
Barbuda	*M. f. fuscatus*	8	113.5–119.1	115.69	2.02	4	109.1–119.4	115.25	4.80	1	.38
St. Martin	*M. f. fuscatus*	2	109.8–113.6	111.70	2.69	2	112.8–113.8	113.30	.71	1	-1.42
Nevis	*M. f. fuscatus*	3	105.4–107.4	106.53	1.03	1	—	108.60	—	2	-1.92
Anguilla	*M. f. fuscatus*	2	114.0–119.0	116.50	3.54	—	—	—	—	0	—
Crooked Island	*M. f. fuscatus*	2	111.1–116.0	113.55	3.46	—	—	—	—	2	—
Jamaica	*M. f. fuscatus*	1	—	103.80	—	—	—	—	—	—	—

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher (continued)

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**[a]
Jost Van Dyke	*M. f. fuscatus*	—	—	—	—	1	—	100.10	—	0	—
Luís Peña	*M. f. fuscatus*	1	—	112.20	—	—	—	—	—	0	—
Mayagüana	*M. f. fuscatus*	1	—	110.70	—	—	—	—	—	2	—
Sombrero	*M. f. fuscatus*	1	—	113.60	—	—	—	—	—	—	—
Virgin Gorda	*M. f. fuscatus*	2	109.0–117.0	113.00	5.66	—	—	—	—	1	—
Number and averages for *M. f. fuscatus*:		208	109.6–118.9	114.12	3.43	176	107.0–116.6	111.82	3.75	1.17	2.15
Martinique	*M. f. densirostris*	2	108.7–110.1	109.40	.99	2	98.7–102.0	100.35	2.33	6	8.63
Montserrat	*M. f. densirostris*	8	112.2–121.6	116.08	3.74	5	102.5–113.6	107.94	4.10	3	7.27
Guadeloupe	*M. f. densirostris*	12	111.0–118.8	114.48	2.72	16	103.0–110.0	106.59	2.30	4	7.14
Dominica	*M. f. densirostris*	21	100.3–117.8	110.47	5.43	12	100.7–116.7	106.58	4.90	6	3.58
La Désirade	*M. f. densirostris*	9	101.0–115.8	109.39	4.87	9	100.5–118.1	109.77	6.60	2	-.35
Number and averages for *M. f. densirostris*		52	106.6–116.8	112.0	3.6	44	101.1–112.1	106.25	4.05	4.20	5.25
St. Lucia	*M. f. klinikowskii:*	10	112.2–122.6	116.52	2.96	11	105.5–120.1	115.12	4.48	7	1.21
Bonaire	*M. f. bonariensis:*	18	100.1–119.0	110.95	4.49	14	100.4–114.8	105.61	4.24	1	4.93
Tarsus length (mm)											
Desecheo	*M. f. fuscatus*	5	36.0–38.2	37.38	1.05	5	34.7–37.8	36.08	1.21	0	3.54
St. John	*M. f. fuscatus*	2	38.4–39.0	38.69	.44	2	37.4–38.0	37.68	.40	1	2.65
Antigua	*M. f. fuscatus*	7	37.6–40.0	38.56	.91	11	36.5–38.2	37.61	.57	2	2.49
Culebra	*M. f. fuscatus*	12	36.4–38.2	37.25	.73	5	35.0–38.0	36.35	1.23	1	2.45
St. Eustatius	*M. f. fuscatus*	9	37.2–40.0	38.94	.99	5	37.0–40.0	38.11	1.16	2	2.15
Saba	*M. f. fuscatus*	4	37.0–38.3	37.87	.56	3	36.3–38.2	37.24	.97	2	1.68
Barbuda	*M. f. fuscatus*	8	36.2–38.3	37.51	.78	4	36.3–38.2	37.15	.96	1	.96
Vieques	*M. f. fuscatus*	12	35.1–39.7	38.08	1.11	7	36.4–38.1	37.72	.74	1	.95
Piñeros Island	*M. f. fuscatus*	1	—	36.82	—	2	36.3–36.7	36.50	.28	0	.87
Nevis	*M. f. fuscatus*	3	36.5–38.3	37.65	.98	1	—	37.40	—	2	.67
St. Thomas	*M. f. fuscatus*	13	34.5–39.0	37.15	1.41	14	34.0–39.0	37.24	1.50	1	-.24
San Salvador	*M. f. fuscatus*	26	33.1–38.5	36.21	1.18	34	33.3–40.0	36.37	1.43	2	-.44
St. Kitts	*M. f. fuscatus*	6	36.7–39.1	37.79	.79	6	37.3–39.0	38.09	.73	2	-.79
Puerto Rico	*M. f. fuscatus*	21	35.0–39.6	37.04	1.03	17	34.7–39.4	37.36	1.35	2	-.86
Rum Cay	*M. f. fuscatus*	10	36.1–38.3	37.35	.86	8	36.0–39.4	37.71	.99	1	-.96
Mona	*M. f. fuscatus*	9	33.0–39.4	37.21	1.84	8	35.9–39.6	37.72	1.10	0	-1.36
Beata	*M. f. fuscatus*	4	38.0–39.7	38.47	.81	3	37.7–40.0	39.13	1.25	1	-1.70
Culebrita	*M. f. fuscatus*	3	36.6–38.1	37.48	.80	1	—	38.18	—	0	-1.85
Caja de Muertos	*M. f. fuscatus*	4	36.3–37.8	37.01	.81	4	37.0–38.6	37.78	.69	1	-2.06
St. Martin	*M. f. fuscatus*	2	36.6–37.8	37.18	.85	2	36.7–39.6	38.13	2.04	1	-2.52

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher (continued)

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**[a]
Great Inagua	*M. f. fuscatus*	22	35.7–38.3	37.23	.86	6	36.1–39.8	38.24	1.25	3	-2.68
Caicos Islands	*M. f. fuscatus*	16	34.1–38.6	36.70	.98	9	35.7–38.8	38.06	.95	2	-3.64
Tortola	*M. f. fuscatus*	4	38.0–39.4	38.36	.72	1	—	40.00	—	1	-4.19
St. Croix	*M. f. fuscatus*	2	36.6–37.5	37.04	.66	8	35.0–41.0	38.93	2.13	1	-4.98
Anguilla	*M. f. fuscatus*	2	38.0–41.0	39.50	2.12	—	—	—	—	0	—
Crooked Island	*M. f. fuscatus*	2	35.2–36.2	35.70	.74	—	—	—	—	2	—
Jamaica	*M. f. fuscatus*	1	—	34.70	—	—	—	—	—	—	—
Jost Van Dyke	*M. f. fuscatus*	—	—	—	—	1	—	37.90	—	0	—
Luís Peña	*M. f. fuscatus*	1	—	37.78	—	—	—	—	—	0	—
Mayagüana	*M. f. fuscatus*	1	—	36.66	—	—	—	—	—	2	—
Sombrero	*M. f. fuscatus*	1	—	36.30	—	—	—	—	—	—	—
Virgin Gorda	*M. f. fuscatus*	2	39.0–40.0	39.50	.71	—	—	—	—	1	—
Number and averages for *M. f. fuscatus*		215	36.1–38.7	37.54	.92	167	36.0–38.9	37.70	1.09	1.25	-.41
Dominica	*M. f. densirostris*	22	34.0–38.0	35.75	1.01	12	34.7–37.1	35.84	.69	6	-.25
Guadeloupe	*M. f. densirostris*	13	36.2–40.0	37.68	1.14	16	34.0–39.0	37.51	1.67	4	.45
La Désirade	*M. f. densirostris*	9	34.2–39.0	36.73	1.61	9	36.3–38.5	37.03	.66	2	-.81
Martinique	*M. f. densirostris*	2	36.8–39.5	38.16	1.90	2	36.3–36.8	36.55	.35	6	4.31
Montserrat	*M. f. densirostris*	8	34.9–38.2	37.16	1.05	5	35.5–38.6	37.38	1.34	3	-.59
Number and averages for *M. f. densirostris*		54	35.2–38.9	37.1	1.3	44	35.4–38.0	36.86	.94	4.20	.60
St. Lucia	*M. f. klinikowskii:*	10	38.5–40.6	39.61	.67	11	38.10–41.7	40.03	1.09	7	-1.07
Bonaire	*M. f. bonariensis:*	18	33.9–38.3	37.05	1.10	14	34.8–39.5	36.89	1.12	1	.43
Exposed culmen length (mm)											
Culebrita	*M. f. fuscatus*	3	26.4–26.7	26.50	.14	1	—	25.20	—	0	5.03
St. John	*M. f. fuscatus*	2	26.6–30.5	28.53	2.79	2	26.3–28.3	27.30	1.41	1	4.41
St. Martin	*M. f. fuscatus*	2	25.9–27.0	26.45	.72	2	25.2–26.1	25.62	.65	1	3.19
Vieques	*M. f. fuscatus*	12	24.7–28.2	26.95	1.29	7	25.1–28.2	26.21	1.25	1	2.78
St. Eustatius	*M. f. fuscatus*	9	25.8–30.0	28.12	1.48	5	26.0–29.0	27.38	1.19	2	2.67
Saba	*M. f. fuscatus*	4	26.9–29.6	27.82	1.28	3	26.1–27.9	27.10	.88	2	2.62
St. Thomas	*M. f. fuscatus*	12	24.8–30.0	27.25	1.58	14	24.6–29.0	27.15	1.24	1	.37
Mona	*M. f. fuscatus*	9	25.3–28.1	27.12	.98	8	25.8–29.4	27.25	1.20	0	-.48
Desecheo	*M. f. fuscatus*	5	24.8–29.7	27.35	1.84	8	26.3–29.7	27.64	1.15	0	-1.05
Caja de Muertos	*M. f. fuscatus*	4	24.1–29.6	26.90	2.40	4	26.1–29.0	27.31	1.27	1	-1.51
Culebra	*M. f. fuscatus*	11	24.9–28.0	26.78	1.36	5	25.0–28.0	27.21	1.51	1	-1.59
Barbuda	*M. f. fuscatus*	8	24.8–28.0	26.19	1.12	4	25.0–28.2	26.62	1.73	1	-1.63
San Salvador	*M. f. fuscatus*	27	23.4–28.0	25.65	1.17	36	23.9–30.0	26.12	1.52	2	-1.82

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher (continued)

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**[a]
Piñeros Island	*M. f. fuscatus*	1	—	25.54	—	2	25.3–26.8	26.05	1.06	0	-1.98
Great Inagua	*M. f. fuscatus*	22	21.4–27.9	25.52	1.23	6	25.0–27.9	26.14	1.12	3	-2.40
Beata	*M. f. fuscatus*	4	26.5–28.4	27.45	.90	3	27.0–29.6	28.30	1.32	1	-3.05
Antigua	*M. f. fuscatus*	7	24.1–29.6	25.97	1.80	11	25.0–28.2	26.79	1.15	2	-3.11
Nevis	*M. f. fuscatus*	3	25.0–26.2	25.77	.69	1	—	26.70	—	2	-3.54
Tortola	*M. f. fuscatus*	4	26.5–29.0	27.83	1.03	1	—	29.00	—	1	-4.12
Puerto Rico	*M. f. fuscatus*	23	21.6–28.3	26.10	1.41	17	24.7–29.5	27.37	1.31	2	-4.75
Caicos Islands	*M. f. fuscatus*	14	22.9–27.5	25.34	1.06	9	25.4–28.0	26.58	.84	2	-4.78
St. Kitts	*M. f. fuscatus*	6	25.6–28.2	26.47	1.05	6	26.6–29.6	28.03	1.12	2	-5.72
St. Croix	*M. f. fuscatus*	2	26.0–27.0	26.51	.69	8	26.4–30.0	28.31	1.12	1	-6.57
Rum Cay	*M. f. fuscatus*	10	21.6–27.9	25.90	1.95	8	26.4–29.5	27.68	1.16	1	-6.64
Anguilla	*M. f. fuscatus*	2	28.0–29.0	28.25	.35	—	—	—	—	0	—
Crooked Island	*M. f. fuscatus*	2	25.0–25.5	25.26	.37	—	—	—	—	2	—
Jamaica	*M. f. fuscatus*	1	—	27.91	—	—	—	—	—	—	—
Jost Van Dyke	*M. f. fuscatus*	—	—	—	—	1	—	28.08	—	0	—
Luís Peña	*M. f. fuscatus*	1	—	26.53	—	—	—	—	—	0	—
Mayagüana	*M. f. fuscatus*	1	—	27.48	—	—	—	—	—	2	—
Sombrero	*M. f. fuscatus*	1	—	23.34	—	—	—	—	—	—	—
Virgin Gorda	*M. f. fuscatus*	2	27.0–29.0	28.00	1.41	—	—	—	—	1	—
Number and averages for *M. f. fuscatus*		214	24.8–28.4	26.67	1.30	172	25.6–28.7	27.04	1.20	1.25	-1.40
Martinique	*M. f. densirotris*	2	25.3–27.1	26.22	1.30	2	25.2–25.4	25.29	.16	6	3.61
La Désirade	*M. f. densirotris*	9	25.9–28.2	27.07	.91	9	24.9–29.0	27.24	1.23	2	-.63
Dominica	*M. f. densirotris*	20	23.6–27.0	24.92	.71	11	22.1–26.8	25.30	1.31	6	-1.51
Guadeloupe	*M. f. densirotris*	12	23.0–28.0	26.15	1.37	16	24.8–28.5	26.69	1.34	4	-2.04
Montserrat	*M. f. densirotris*	8	24.5–27.1	25.91	.89	5	26.4–28.0	26.97	.63	3	-4.01
Number and averages for *M. f. densirostris*		51	24.5–27.5	26.05	1.04	43	24.7–27.5	26.30	.93	4.20	-.90
St. Lucia	*M. f. klinikowskii*	10	25.5–28.3	26.85	.98	11	25.40–29.5	27.14	1.14	7	-1.08
Bonaire	*M. f. bonariensis*	18	26.4–29.6	27.57	.93	14	26.4–30.5	28.60	1.22	1	-3.67
Bill length from nares											
St. John	*M. f. fuscatus*	2	19.7–19.9	19.82	.12	2	18.4–18.5	18.48	.06	1	7.00
Culebrita	*M. f. fuscatus*	3	18.3–19.7	18.84	.76	1	—	18.10	—	0	4.01
St. Eustatius	*M. f. fuscatus*	4	18.1–19.9	19.11	.77	4	18.5–19.6	18.94	.46	2	.89
Caja de Muertos	*M. f. fuscatus*	4	17.5–20.1	18.88	1.32	4	18.0–19.6	18.83	.66	1	.27
San Salvador	*M. f. fuscatus*	38	16.8–19.9	18.27	.77	38	16.3–20.1	18.33	.94	2	-.33
Vieques	*M. f. fuscatus*	12	17.0–19.6	18.32	.78	7	18.0–19.7	18.45	.75	1	-.71

Table 1—Interisland descriptive statistics of measurements of museum specimens, number of mimid and thrush competitors, and sexual dimorphism indices for the four subspecies of the pearly-eyed thrasher (continued)

		Male				Female					
Island	**Subspecies**	**N**	**Min.–Max**	**Mean**	**SD**	**N**	**Min.–Max**	**Mean**	**SD**	**Number of competitors**	**Dimorphism index**[a]
Desecheo	*M. f. fuscatus*	5	18.2–19.9	18.96	.77	8	18.2–20.3	19.12	.87	0	-.84
St. Martin	*M. f. fuscatus*	2	17.3–18.4	17.84	.74	2	17.7–18.4	18.02	.47	1	-1.00
St. Croix	*M. f. fuscatus*	2	18.3–18.5	18.38	.17	4	18.3–19.6	18.68	.25	1	-1.62
Mona	*M. f. fuscatus*	9	17.9–20.3	18.70	.81	8	17.9–20.1	19.14	.86	0	-2.33
Saba	*M. f. fuscatus*	4	18.2–20.0	18.73	.87	3	18.2–19.7	19.18	.81	2	-2.37
Piñeros Island	*M. f. fuscatus*	1	—	18.44	—	2	18.7–19.1	18.89	.30	0	-2.41
Culebra	*M. f. fuscatus*	12	17.0–19.9	18.50	.83	5	17.9–19.9	18.98	1.05	1	-2.56
Nevis	*M. f. fuscatus*	3	17.5–18.3	17.80	.43	1	—	18.28	—	2	-2.66
Barbuda	*M. f. fuscatus*	8	18.3–19.9	18.91	.73	4	18.3–19.9	19.45	.76	1	-2.82
Antigua	*M. f. fuscatus*	7	17.5–20.1	18.37	.82	11	18.3–20.2	18.95	.67	2	-3.11
St. Thomas	*M. f. fuscatus*	13	17.3–19.8	18.30	.72	13	17.0–19.9	19.03	.96	1	-3.91
Puerto Rico	*M. f. fuscatus*	27	15.2–20.2	18.29	1.25	17	17.8–20.2	19.05	.81	2	-4.07
St. Kitts	*M. f. fuscatus*	6	17.3–18.5	18.00	.47	4	18.2–20.2	18.86	.89	2	-4.67
Beata	*M. f. fuscatus*	4	17.6–19.9	18.84	1.07	2	19.7–19.9	19.80	.09	1	-4.97
Rum Cay	*M. f. fuscatus*	10	18.0–19.4	18.32	.39	12	18.2–20.0	19.29	.68	1	-5.16
Tortola	*M. f. fuscatus*	4	17.0–18.0	17.67	.45	1	—	18.63	—	1	-5.29
Caicos Islands	*M. f. fuscatus*	18	16.5–18.6	17.79	.55	9	17.3–19.9	18.87	.72	2	-5.89
Great Inagua	*M. f. fuscatus*	25	13.5–19.2	17.69	1.08	6	16.7–18.9	18.82	.69	3	-6.19
Anguilla	*M. f. fuscatus*	2	19.0–19.0	18.75	.35	—	—	—	—	0	—
Crooked Island	*M. f. fuscatus*	2	17.9–18.2	18.01	.20	—	—	—	—	2	—
Jamaica	*M. f. fuscatus*	1	—	18.28	—	—	—	—	—	—	—
Jost Van Dyke	*M. f. fuscatus*	—	—	—	—	1	—	19.56	—	0	—
Luís Peña	*M. f. fuscatus*	1	—	18.10	—	—	—	—	—	0	—
Mayagüana	*M. f. fuscatus*	1	—	19.13	—	—	—	—	—	2	—
Sombrero	*M. f. fuscatus*	1	—	16.38	—	—	—	—	—	—	—
Virgin Gorda	*M. f. fuscatus*	2	18.0–19.0	18.50	.71	—	—	—	—	1	—
Number and averages for *M. f. fuscatus*		223	17.4–19.5	18.45	.72	169	18.0–19.7	18.84	.65	1.25	-2.11
Martinique	*M. f. densirostris*	2	17.8–19.0	18.41	.83	2	17.3–17.6	17.45	.21	6	5.35
Guadeloupe	*M. f. densirostris*	8	17.1–19.8	18.37	.76	4	17.0–18.1	17.77	.53	4	3.32
La Désirade	*M. f. densirostris*	9	17.1–19.4	18.25	.70	9	16.7–19.9	18.68	.88	2	-2.33
Montserrat	*M. f. densirostris*	8	17.5–18.7	18.20	.39	5	18.1–19.6	18.78	.62	3	-3.14
Dominica	*M. f. densirostris*	20	16.2–17.9	17.34	.53	11	16.5–18.9	18.20	.73	6	-4.84
Number and averages for *M. f. densirostris*		47	17.1–19.0	18.11	.64	31	17.1–18.8	18.18	.59	4.20	-.33
St. Lucia	*M. f. klinikowskii*	10	18.1–20.2	19.06	.64	11	18.1–19.8	19.10	.61	7	-.23
Bonaire	*M. f. bonariensis*	18	17.9–20.5	19.26	.82	14	18.0–21.2	19.62	.83	1	-1.85

— = no data.

[a] Dimorphism index derived by dividing the difference between the means for the sexes (male–female) by the overall mean and multiplying by 100.

Table 2—Distribution of potential mimid and thrush competitors of the pearly-eyed thrasher for islands on which the potential competitor and the pearly-eye coinhabit (species' scientific names are in app. 1)

Mimid and thrush species	Bahamas	Turks and Caicos	Beata	Puerto Rico	Virgin Islands	Anguilla	St. Martin	Saba	St. Eustatius	St. Kitts	Antigua	Barbuda	Montserrat	Guadeloupe	Dominica	Martinique	St. Lucia	St. Vincent	Total all islands
Rufous-throated solitaire															1	1	1	1	4
Cocoa thrush																		1	1
Bare-eyed robin																1	1	1	3
Red-legged thrush	1			1											1				3
Forest thrush													1	1	1		1		4
Northern mockingbird	1	1	1	1	1														5
Tropical mockingbird											1	1		1	1	1	1	1	7
Bahama mockingbird	1	1																	2
White-breasted thrasher																1	1		2
Scaly-breasted thrasher								1	1	1			1	1	1	1	1		8
Pearly-eyed thrasher	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		17
Brown trembler								1		1			1	1	1		1	1	7
Gray trembler																1	1		2
Total species per island:	4	3	2	3	2	1	1	3	2	3	2	2	4	5	7	7	9	5	[a]

[a] Excluding the 17 islands inhabited by the pearly-eyed thrasher, on average each competitor inhabits 4 islands (SD = 2.29; range: 1—8)

Appendix 5

Table 1—Adult breeders that changed nest boxes between 1979 and 2000

Adult code	Years	Pre- and postmove boxes	Clutches	Eggs laid	Chicks fledged	Reproductive success[a]	Success[b] in postmove box	Sources of lowered productivity[c] [d]
Males			- - - - - *Number* - - - - -			*Percent*		
9003	1979–84	23	8	22	10	46		BF, CM
9003	1985–89	32	13	38	16	42	Lower	BF, CM, EDO, EM, FAE, IE, PE
9030	1979–84	3	13	36	13	36		BF, EM, HIE, IE
9030	1985	3.1	2	6	2	33	Lower	BF, EDY
9030	1986	3	2	6	2	33	No change	BF, EDY, EM
7868	1980–83	27	11	31	12	39		BF, CM, EDO, FAC, FAE, IE
7868	1984–89	28	6	16	9	56	Higher	BF, EDY, IE, PE
7817	1982–86	18	6	17	7	41		BF, IE
7817	1987–92	16	12	33	9	18	Lower	BF, CM, EDO, FAE, IE, PE
7497	2000	12	1	3	1	33		BF
7497	2000	15	1	4	0	0	Lower	EM
5 males		10 boxes	75	212	81	34% (pre- 38%; post- 30%)		
Females			- - - - - *Number* - - - - -			*Percent*		
7816	1979	9	1	2	2	100		SF
7816	1979	7[e]	1	3	0	0	Lower (0)	BF, EDO
7816	1979–82	7	13	38	14	37	Higher	BF, CM, EDO, FAE, HIE, IE, PE, S
7809	1980	28	1	3	0	0		OR
7809	1981	27[e]	1	3	3	100	Higher	
7809	1981–82	27	7	17	4	24	Higher	ED, FAE, EDO, IE, OC
0875	1982–84	7.1	8	22	5	23		BF, HIE, TF
0875	1985	7[e]	3	10	5	50	Higher	BF
0875	1985–93	7	19	64	18	28	Higher	BF, CM, EM, EDO, EDY, FAE, HIE, HIC, IE, PE, RE, S
7721	1982	38	2	6	2	33		BF, EM, OR
7721	1982–84	39	2	6	2	33	No change	BF
9062	1982–85	16	7	20	11	55		BF, IE, TF
9062	1986–90	11	6	15	6	40	Lower	BF, EDY, OC
9062	1991–92	6	6	17	0	0	Lower (0)	BF, EDO, EDY, HIE, PE
9086	1982	28	2	5	3	60		BF, HIE, TF
9086	1982–83	24	3	9	0	0	Lower (0)	CM
9086	1984–87	26	8	24	11	46	Higher	BF, EDO, EM, CM, IE
9086	1988–94	24	10	29	9	31	Lower	BF, FAE, HIC, HIE, IE, NH
8930	1985	27	2	6	0	0		BF
8930	1986	25[e]	2	6	1	17	Higher	BF, CM, IE
8930	1986–88	25	8	25	8	32	Higher	BF, CM, EDO, IE
8986	1986	8.1	2	7	0	0		BF, OR
8986	1987–89	8	6	14	0	0	No change (0)	BF, S
7258	1987–89	6	6	16	5	31		BF, HIE
7258	1990–93	33	4	13	8	62	Higher	BF, EDY, PE
9177	1987	30	2	6	6	100		OR
9177	1988	26[e]	2	7	4	57	Lower	
9177	1988–94	26	15	39	22	56	Lower	BF, CM, EM, HIE, IE, OC
7070	1990	10	1	3	0	0		BF
7070	1991	39[e]	1	3	0	0	No change (0)	BF, FAE
7070	1991–93	39	7	22	0	0	No change (0)	BF, FAE, HIC, IE, OC
7070	1993	10	2	6	0	0	No change (0)	BF, EDY
7070	1994	16	3	10	2	20	Higher	BF, RC, RE

Table 1—Adult breeders that changed nest boxes between 1979 and 2000 (continued)

Adult code	Years	Pre- and postmove boxes	Clutches	Eggs laid	Chicks fledged	Reproductive success[a]	Success[b] in postmove box	Sources of lowered productivity[c d]
Females				----- *Number* -----		*Percent*		
7429	1990–92	22	7	20	9	45		BF, CM, EDY, PE
7429	1993	32	2	7	3	43	Lower	OC
7429	1994–95	22	3	9	6	67	Higher	BF
7449	1990–92	16	8	21	3	14		BF, FAE, IE
7449	1993	17	3	9	8	89	Higher	
7449	1994	1	4	12	2	17	Lower	BF, CM
7449	1995–96	17	9	29	9	31	Higher	BF, EDO, HIE, IE
7449	1997	38	1	3	3	100	Higher	
7449	1997	39	2	5	0	0	Lower (0)	BF, IE, RC
7403	1991–92	1	4	11	4	36		BF, IE, PE
7403	1993–94	34	4	12	4	33	Lower	BF, EDO, HIC, IE
9041	1991	34	2	5	0	0		BF
9041	1992	11	1	3	0	0	No change (0)	BF, OC
7237	1992–93	13	6	20	16	80		BF, PE
7237	1994	12	3	9	3	33	Lower	OC, OF
7273	1992	32	2	6	2	33		CM, PE
7273	1993	37	2	6	3	50	Higher	BF, IE
7293	1992–94	19	5	16	5	31		BF, EM, PE, RE, NH
7293	1994	33	1	3	0	0	Lower (0)	BF, NH
7293	1994–97	19	9	35	0	0	No change (0)	BF, EDO, EDY, HIE, IE, PE, RE
7297	1992	10	2	6	0	0		BF, PE
7297	1993	9	1	3	3	100	Higher	HB (after first brood fledged)
7297	1994	10	2	7	0	0	Lower (0)	EM, PE, OC
7297	1994–97	9	9	30	9	30	Higher	BF, EM, IE, PE
7199	1994–95	31	2	6	0	0		BF, PE, OC
7199	1995	37[e]	2	7	0	0	No change (0)	PE, RE
7199	1995–97	37	9	24	0	0	No change (0)	CM, PE, RE, TF
7541	1996	16	2	4	1	25		ED, RE
7541	1996	39	1	3	0	0	Lower (0)	RE
7541	1996	38	1	4	0	0	No change (0)	BF
7541	1997	17	1	3	0	0	No change (0)	BF
7541	1998	11	3	7	2	29	Higher	EM
7541	1998	18	1	4	3	75	Higher	HIE
21 females		27 boxes	265	786	236	30% (pre– 29%; post– 31%)		

[a] Percentage of chicks fledged per eggs laid.

[b] Comparison of reproductive success in pre- and postmove nest boxes: "lower" and "higher" denote decreased and increased productivity in postmove boxes; a zero (0) denotes a complete nest failure (no fledgings).

[c] BF botfly ectoparasitism; CM chick missing, reason unknown; EDO embryonic death, old (embryo 11 to 21+ days old); EDY embryonic death, young (embryo ≤10 days old); EM egg missing, reason unknown; FAE female abandons eggs; FAC female abandons chicks; HA hatching abnormality (incorrect tucking position and chick died trying to break out of shell); HB honey bee invasion; HIE, human–induced mortality, egg stage (cracked and broken eggs, or female abandonment as a consequence of a nest visit); HIC human–induced mortality, chick stage (negligent handling); IE infertile egg; NH no hatch—reason unknown; OC owl eats chicks; OF owl eats resident female; OR owl roost; PE pearly-eye eats eggs; RC rat eats chicks; RE rat eats eggs; S siblicide; SF supplanted female; TF tree and box fell as a result of heavy winds.

[d] Total egg and chick loss tallies for males (n = 128 losses): 49 BF (38 percent), 15 CM (12 percent), 15 IE (12 percent), 12 FAE (9 percent), 9 PE (7 percent), 7 FAC (5 percent), 6 EDO (5 percent), 6 EM (5 percent), 5 EDY (4 percent), 4 HIE (3 percent); total egg and chick loss tallies for females (n = 550 losses): 298 BF (59 percent), 34 IE (7 percent), 32 RE (6 percent), 29 HIE (6 percent), 28 PE (5 percent), 20 OC (4 percent), 24 EM (5 percent), 17 CM (3 percent), 11 EDY (2 percent), 10 EDO (2 percent), 10 FAE (2 percent), 8 HIC (2 percent), 6 HA (1 percent), 6 NH (1 percent), 4 OR (0.8 percent), 4 RC (0.8 percent), 3 S (0.6 percent), 3 TF (0.6 percent); 1 OF (0.2 percent); 1 SF (0.2 percent).

[e] Within nest boxes in which the numbers of clutches are considerably different before and after the move, the same numbers of pre- and postlaid clutches are compared; then the total number of clutches laid in the post-move boxes (including the subsets just described) are presented.

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