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IMPACT OF NEST PREDATORS, COMPETITORS, AND ECTOPARASITES ON PEARLY-EYED THRASHERS, WITH COMMENTS ON THE POTENTIAL IMPLICATIONS FOR PUERTO RICAN PARROT RECOVERY

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Resumen. Durante los pasados 17 años, la investigación en una población de Zorzal pardo (*Margarops fuscatus*) en la sierra de Luquillo, un bosque lluvioso Neotropical en la región oriental de Puerto Rico, con observaciones adicionales de Cotorras puertorriqueñas (*Amazona vittata*) anidando en la misma montaña, ha demostrado que el éxito reproductivo de zorzales y cotorras (ver Snyder *et al.* 1987) se ven notablemente reducidas como resultado de los efectos cumulativos de un diverso grupo de depredadores, competidores y ectoparásitos. Aún cuando la pérdida de pichones y huevos debido a la depredación y a la competencia por nidos significó menos del 10%, el ectoparasitísmo de una mosca parasítica fue responsable de la pérdida del 56% de los pichones restantes. Este estudio no solo resume la prevalecencia e intensidad de la depredación y ectoparasitísmo pero además, y aún más importante, adjudica la interacción entre estas dos formas de control biológico. Tal conocimiento es apremiante en el manejo de especies en peligro de extinción y sus estresantes biológicos. Los resultados de la investigación del Zorzal pardo muestran que las tazas de depredación, competencia por territorio de reproducción, y la prevalecencia e intensidad de ectoparasitísmo por moscas en los nidos artificiales de los zorzales varia significantemente a lo largo de años y meses, incrementando según progresa la actividad reproductiva de los zorzales y se intensifica luego de una perturbación de gran escala del hábitat. Los depredadores primarios de los nidos de los zorzales y de las cotorras han desarrollado una estrategia en la que toman su presa justo antes de la edad promedio en la que mueren los pichones víctimas del ectoparasitísmo por la mosca *Philornis*, lo cual promueve un aumento en la probabilidad de éxito del depredador. En los nidos artificiales de los zorzales, sucesos de depredación, usurpación de las cavidades y la prevalecencia e intensidad de ectoparasitísmo por moscas están altamente correlacionadas con la propia época reproductiva de cada depredador, competidor, y ectoparásito los cuales una vez combinados, virtualmente expanden el período reproductivo tanto del zorzal como de la cotorra. La amplitud y grado de los hábitos parasíticos y depredativos de los cinco estresores biológicos principales de la Cotorra puertorriqueña demuestran que una constante protección de los nidos es necesaria en esfuerzos para la recuperación de estas aves. Se ofrece recomendaciones para el manejo y necesidades adicionales de investigación de la cotorra como posibles pasos para disminuir los efectos de este dañino organismo, que es tan perjudicial para el éxito reproductivo de la Cotorra puertorriqueña.

Abstract. Over the past 17 years, research on a rain forest population of the Pearly-eyed Thrasher (*Margarops fuscatus*), with additional observations on nesting Puerto Rican Parrots (*Amazona vittata*) within the Sierra de Luquillo, Puerto Rico, has shown that reproductive success of thrashers and parrots is often greatly reduced as a result of the additive effects of a diverse group of predators, competitors and ectoparasites, namely, other thrashers, Puerto Rican Screech-Owl (*Otus nudipes*), scansorial black rat (*Rattus rattus*); honeybee (*Apis mellifera ligustica* and *A. m. scutellata*), and a muscid botfly (*Philornis* sp.). Although egg and chick losses from nest predators and competitors accounted for less than 10%, botfly ectoparasitism was responsible for 56% of the remaining chick losses. This research not only summarizes the prevalence and intensity of nest predation and ectoparasitism but, more importantly, addresses the interaction between these two forms of biological control. Such knowledge is preeminent in managing endangered species and their biological stressors. Results from Pearly-eyed Thrasher research show that predation rates, nest-site competition, and the prevalence and intensity of botfly ectoparasitism at thrasher nest boxes varied significantly among years and months, increased with the progression of the thrasher breeding season, and escalated following major habitat disturbance. Primary nest predators of the thrasher and parrot have developed a strategy of taking their prey just before the hosts' average age at death resulting from Philornis ectoparasitism, thus increasing the predators' chances of success. At thrasher nest boxes, instances of predation, cavity takeovers, and the prevalence and intensity of botfly ectoparasitism are highly correlated with each predator's, competitor's, and ectoparasite's own breeding seasons which, when combined, span the entire reproductive period of both the thrasher and parrot. The breadth and extent of the predatory and parasitic habits of the Puerto Rican Parrot's five main biological stressors show that constant, intensive nest guarding, poisoning and trapping (rats), and repellents (against honeybees and botflies) are necessary in recovery efforts. Management recommendations and additional parrot research needs are offered as possible steps in ameliorating the effects of these nocuous organisms so detrimental to the Puerto Rican Parrot's recovery. *Accepted 8 May 1999.*

Key words: Amazona vittata, Apis mellifera, *biological control, black rat, botfly, ectoparasitism, honeybee,* ligustica, Margarops fuscatus*, nest predation,* Otus nudipes, *Pearly-eyed Thrasher,* Philornis, *Puerto Rican Parrot, reproductive success, Screech-Owl,* scutellata.

INTRODUCTION

Nest predators and competitors can have devastating impacts on populations of insular, often endemic, wildlife populations (see for example Engbring & Fritts 1988). Historically, these biological factors have played a role in the precipitous decline of the critically endangered Puerto Rican Parrot (*Amazona vittata*) (Snyder & Taapken 1977, Wiley 1985, Snyder *et al.* 1987, Lindsey 1992), and continue to hamper restoration efforts. The parrot's known and potential predators and competitors for nest sites include a variety of organisms from quite disparate phylogenetic taxa: (a) reptiles: Puerto Rican boa (*Epicrates inornatus*); (b) resident birds: Puerto Rican Screech-Owl (*Otus nudipes nudipes*) (also a competitor for nest cavities); Red-tailed Hawk *(Buteo jamaicensis*), Puerto Rican Broad-winged Hawk (*B. platypterus*), and Pearly-eyed Thrasher (*Margarops fuscatus*) (also a nest competitor); (c) two species of migratory birds from North America: Merlin (*Falco columbarius*) and Peregrine Falcon (*F. peregrinus*); (d) feral and exotic mammals: house cats (*Felis catus*), lesser Indian mongoose (*Herpestes auropunctatus*), and scansorial black rat (*Rattus rattus*); and (e) honeybee (*Apis mellifera ligustica and A. m. scutellata*) (nest competitors). Whereas the Red-tailed Hawk is the major avian predator on adult parrots (Santana C. & Temple 1984, Snyder *et al.* 1987), without rival the parrot's main nest predator and competitor for nest cavities is the Pearly-eyed Thrasher, which, while foraging or searching for potential nest sites, opportunistically feeds on the eggs and chicks of parrots and other forest birds (Snyder *et al.* 1987*,* Lindsey 1992, Arendt 1993, Latta *et al.* 1995).

It is the Pearly-eye's life-history traits and ecology that, not only attribute to its role as a major threat to parrot nesting, but justify its selection as a surrogate species for use in parrot research. Although taxonomically unrelated, both species share several life-history and ecological characteristics. These include habitat, several food resources, and reproductive similarities (Snyder *et al.* 1987, Arendt 1993, in press). Prime nesting habitat for both species is old-growth stands of palo colorado or swamp cyrilla (*Cyrilla racemiflora)* in the colorado forest zone of the Sierra de Luquillo. Fruit of the sierra palm (*Prestoea montana*) is a staple food of both species. Both are capable of laying 1-3 clutches per season, including replacement clutches (as many as 8 recorded for the thrasher). Typical clutches for both species contain 2–4 eggs, and parrot-thrasher breeding seasons, both lasting about eight months (January–August), greatly overlap (Snyder *et al.* 1987*,* Arendt 1993). Consequently, the thrasher is an ideal surrogate species for studying many of the parrot's biological and ecological stressors such as predators, competitors, and ectoparasites.

While monitoring parrot and thrasher nests during the late 1970s, it became evident that not only were the parrot's and thrasher's nest predators, competitors, and ectoparasites virtually the same species, their rates of predation and intensities of infestation were also quite similar (see also Snyder *et al.* 1987). Therefore, research into the impact of each species of predator and competitor was begun on the more abundant thrasher, with the objective of using results to improve the reproductive success of the parrot. To reduce parrot losses from predators and competitors, it is imperative that parrot stewards be aware of each impacting species' whole ecology, but particularly, those aspects of the predator's and competitor's life cycle most deleteriously affecting the parrot's survival and reproductive success.

Herein, the predatory habits and nest-box usurpation patterns of four prominent predators and competitors (other thrashers, screech-owl, rat, and bee) at Pearly-eyed Thrasher nest boxes will be quantified and discussed. In addition, the prevalence and intensity of dipteran ectoparasitism and its impact on nesting thrashers and parrots will be presented and evaluated. Information obtained from this study may be used to enhance management strategies involving cavity-nesting birds in general, and parrots in particular, to ameliorate nest predation and cavity usurpation, and increase survivorship, especially during critical stages of egg and chick development, and the first few post-fledging months.

STUDY AREA AND METHODS

This study took place in the Sierra de Luquillo, in eastern Puerto Rico (18º19'N, 65º45'W), mostly within the confines of the 11,500-ha Caribbean National Forest (also known as the Luquillo Experimental Forest, hereafter LEF) (Fig. 1). With average annual rainfall and temperatures ranging (respectively) from 300 cm and 25.5 ºC in the foothills to over 500 cm and 18.5 ºC on peaks higher than a 1000 m, the LEF hosts over 240 native tree species, of which 23 are endemic. It is comprised of four major vegetation associations that are altitudinally stratified. Tabonuco trees (*Dacryodes excelsa*) dominate the tabonuco forest type located in the sub-tropical wet and sub-tropical rain forest life zones (Ewel & Whitmore 1973). It is the lowest of the four forest types, and is found on foothills and slopes at elevations ranging from 200 to 600 m. Tabonuco forest is also the most extensive, covering 5585 ha or about 49% of the forest. Located between roughly 600 and 900 m and encompassing 3318 ha (30% of the LEF) is the palo colorado forest type in the lower montane wet forest zone. It is named for the palo colorado which, although rarely exceeding heights of 18 m, may reach almost 3 m in diameter and can survive more than a thousand years. Its propensity for producing natural cavities makes it a preferred nest-tree for the endangered Puerto Rican Parrot and its adversary, the Pearly-eyed Thrasher. Although associ-

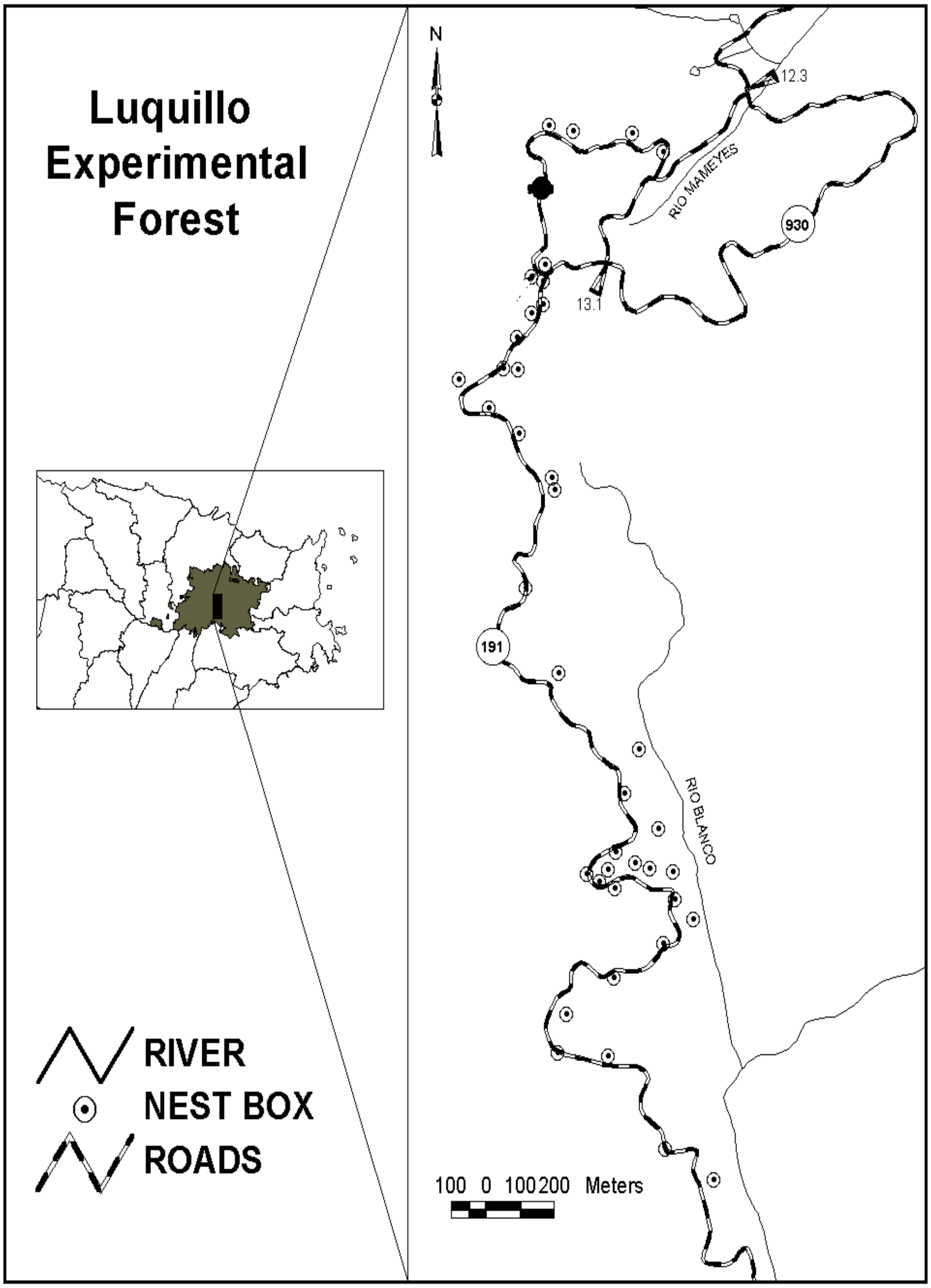

FIG. 1. Dispersion of Pearly-eyed Thrasher nest boxes within the Luquillo Experimental Forest, Puerto Rico.

ated with all life zones within the LEF, sierra palm forest is found chiefly on steep slopes and streambeds above 750 m. It forms almost pure stands along stream valleys and on steep or unstable slopes. It covers 1942 ha, and thus comprises about 17% of the forest. Cloud forest (also known as dwarf or mossy forest, and elfin woodland) is confined to higher elevations and peaks above 750 m. As a result of strong winds and high humidity, constant and heavy rainfall (> 500 cm) and thus saturated, nutrient-drained soils, cloud forest is comprised of dense stands of short, twisted trees and shrubs with diameters averaging 5–10 cm and heights rarely exceeding 5 m. The ground layer is a tangled mass of trees, roots, ferns, forbs and grasses. The trees and shrubs are often covered with mosses, liverworts, algae, bromeliads, and other epiphytes. Cloud forest covers only about 405 ha, or 4% of the LEF, but it contains more endemic trees and shrubs than do the other forest types.

The results presented below are derived from field data gathered during 17 breeding seasons (1979–1995) as part of ongoing parrot-related research. When data coverage was complete, all 17 seasons are included in the analyses. However, thrasher-related data collection was less intense in 1983, 1984, and 1989, owing to other commitments. Therefore, some thrasher analyses exclude these years.

Thrasher nest-box study

Location and monitoring of thrasher nest boxes. In December, 1978, I began monitoring about 40 thrasher nest boxes (see Snyder *et al.,* 1987, for box description and dimensions) placed 0.1 km apart at elevations ranging from about 460 to 800 m (mean = 650 m) primarily in palo colorado forest within the LEF. Although nest boxes were placed along several highways, e.g., PR 191 (Quebrada Juan Diego) to PR 9938 ("loop road") and PR 930 ("molindero loop"), and around the Puerto Rican Parrot aviary (PR 10), most boxes were placed 5–50 m inland along a closed section of PR 191 in the Icacos Valley (Fig. 1).

Nest boxes were closely monitored throughout the nesting period every two days or daily during critical periods; e.g., egg laying, hatching, and the fledging of young. At each nest visit, stage of nest building, nest completion, laying of first and subsequent eggs, hatching, fledgling, and nest predation on nest contents were recorded to calculate rates of predation, loss of nest contents, and seasonal and lifetime thrasher reproductive success. During the non-breeding season, each box was checked every two weeks for signs of activity by thrashers or other competitors for nest sites, or weekly just after or before breeding seasons.

Data collection on nest predators and competitors. Evidence of nest predation and competition for nest sites was recorded at each nest-box visit. In addition to observed owl predations, using four additional criteria, egg and chick losses were attributed directly or indirectly to owls: (1) owl feathers in the box; (2) flattened substrate—nest or twig platform; (3) raptor-style plucked remains of adult and nestling thrashers (generally partially eaten carcasses in which the brain and pectoral muscles were preferred food items; carcasses left behind by owls most often appeared shredded, with multiple talon puncture wounds); and (4) crushed or addled eggs resulting from skirmishes between owls and resident female thrashers and death of, or nest abandonment by, the resident thrasher. In all owl-depredated boxes, often daily detections (mostly vocalizations, with occasional visual contact) and monthly point-count censuses confirmed nearby owl territories and their ever presence. Nest predation was attributed to rats only when rat excreta, gnawed eggshells, or chick remains were found in the nest. Intruding thrashers left recognizable beak puncture wounds in both eggshell remains and depredated nestlings, which they often left in the nest. The prevalence, intensities, and implantation sites of dipteran ectoparasites (*Philornis* sp.) were determined upon capture of adult thrashers and, for young thrashers, during each visit to nest boxes. Implantation sites and growth of infesting larvae were recorded on diagrams of thrasher chicks and in field notebooks. For a more detailed description of measurements taken at each box, use of observation blinds, capture of adult thrashers, radio telemetry, the impact of Hurricane Hugo on nest trees, boxes, thrasher breeding pairs, and their young, see Arendt (1993).

Control of honeybees. Upon detection (audio-visual contact), swarming or recently established colonies of honeybees were extracted by either smoking them out or using a commercial "freeze" spray. Nest boxes were replaced to reduce the probability of re-colonization by the bees and potential harmful effects on nesting thrashers from the chemicals in the spray.

Population censuses

The temporal relative abundance of Pearly-eyed Thrashers inhabiting the LEF was assessed using point-count census methods. Thirty points were established every 100 m in Palo Colorado forest (prime thrasher habitat) between elevations of 600–800 m in the Icacos Valley within the LEF. At each point, all detections (visual and aural) of birds less (or greater) than 25 m were recorded (see Hutto *et al.* 1986 for more details on methods). Point-count censuses were conducted monthly following the passage of Hurricane Hugo (September 1989 to December 1995). However, to equalize sampling periods for each of the complete 6-year periods, data analyzed herein are limited to January 1990–December 1995.

Statistical analyses

All statistical analyses were conducted using SigmaStat® (Fox *et al.* 1994) and the DOS version (5.03) of SYSTAT® (Wilkinson 1990). During exploratory analyses, all variables used in the statistical analyses were checked for normality (Kolmogorov-Smirnov test with Lilliefors' correction) and equal variance (Levene median test). Standard deviations (± SD) to explain variation about the sample mean are included in textual descriptive analyses, whereas standard error (± SE) are presented in several visual analyses (illustrations). Three separate statistical procedures were used to compare frequencies, rates, and proportions for: (a) prevalence and intensities of larval infestations; (b) rates of predation and loss of nest contents; (c) thrasher reproductive success, and (d) predation rates pre- and post-disturbance). *Z*-tests were used to determine if the proportions of two groups within a single category were significantly different. Also used were contingency tables with a *chi-square* analysis and, when applicable, the Fisher exact test (to determine the exact two-tailed probability of observing a specific 2 x 2, or greater, contingency table). Yates Correction for continuity (to make tests more conservative, increase the *P* value, and reduce the chance of false positive conclusions) was applied to all *z*-tests and 2 x 2 tables with the *chi-square* distribution with one degree of freedom. Percentage data (number of egg or chick losses per total number of eggs or chicks produced) were arc-sin square-root transformed before analyses. Group comparison procedures included: (1) Pearson product-moment correlation (parametric) when the residuals (distances of the data points from the regression line) were normally distributed with constant variance; (2) Spearman rank order correlation (nonparametric) when the residuals were not normally distributed

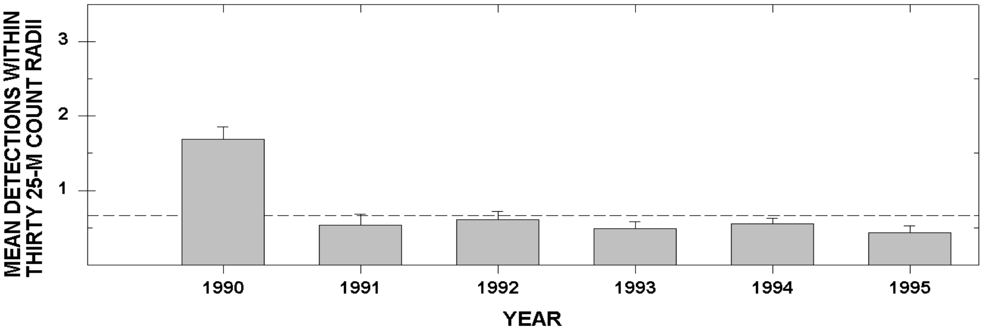

FIG. 2. Yearly comparison of Pearly-eyed Thrasher abundance in prime habitat (Palo Colorado forest) within the Luquillo Experimental Forest, Puerto Rico. Data are taken from 30 post-Hurricane Hugo fixed-radius points sampled monthly for a total of 2160 samples taken between 1990 and 1995. Note how thrasher numbers increased sharply following habitat destruction, then declined in subsequent years.

with constant variance; (3) *t*-tests (2 groups); (4) one- and two-way ANOVA tests (more than 2 groups, with one or two factors), or their nonparametric equivalents: (5) Mann-Whitney rank sum; and (6) Kruskal-Wallis ANOVA on ranks, when the assumptions of normality or equal variance were violated. Post-hoc comparisons testing involved the Student-Newman-Keuls (SNK) test and the Tuckey HSD test for multiple comparisons when neither normality nor equal variance assumptions were violated. Otherwise, the nonparametric SNK test was used when sample sizes were equal and no data were missing. Dunn's test was used whenever sample sizes were unequal or there were missing data. A 95% level of confidence ($\alpha = 0.05$) was maintained in all of the analyses.

PREDATORS AND COMPETITORS FOR NEST SITES

Pearly-eyed Thrasher

Distribution and abundance. The Pearly-eye is a habitat generalist, found from seashore to mountain pinnacle, and has a Caribbean-wide distribution (Arendt 1993). It was present in the region as early as the late Quaternary, more than 2000 years ago (Arendt in press). Historically, Pearly-eyes were scarce and only patchily distributed in the lowlands and hills of Puerto Rico. However, by 1930 thrashers were reported up to 600 m in the Sierra de Luquillo (Danforth 1931), and gained a prominent foothold by the 1950s (Snyder *et al.* 1987). As in any well-established founder population, thrasher numbers increased during the first decade after arrival (Snyder *et al.* 1987, Table 8.6). This well documented increase, together with similar increases noted on several other Caribbean islands, may be the result of habitat alterations concomitant with the ever increasing development, urbanization, and consequential species impoverishment taking place throughout the region. The relatively recent spread of the Pearly-eye in Puerto Rico is similar to that of other mimids, especially the Northern Mockingbird (*Mimus polyglottos*), during the settling of North America (Stiles 1982, David *et al.* 1990, and references therein). Nonetheless, two subsequent and widely separated follow-up population censuses (after 11 years and 22 years) in the LEF show that thrasher numbers may have reached the carrying capacity of their forest habitat and may be undergoing saturation dispersal (Arendt in press).

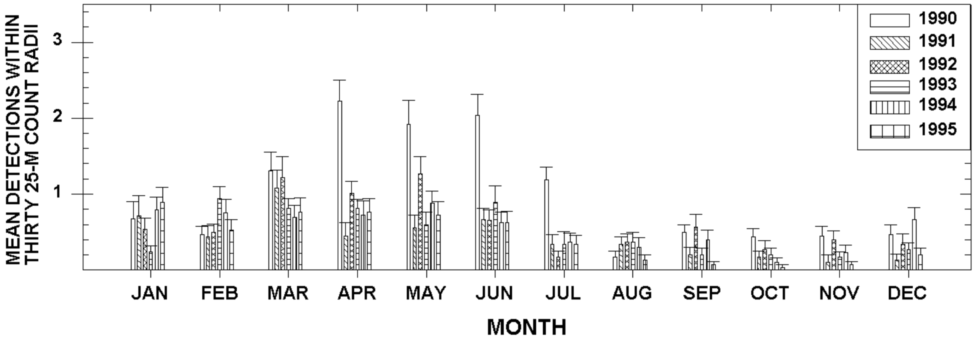

FIG. 3. Monthly comparison of Pearly-eyed Thrasher abundance in prime habitat within the Luquillo Experimental Forest, Puerto Rico. Monthly enhanced detectability corresponds to the increased calling and movements of adults associated with the breeding cycle. As with years following disturbance, monthly totals reveal how thrasher numbers rose sharply following habitat destruction, then subsequently declined.

In 1989, concern that the placement of wooden nest boxes might be artificially increasing thrasher numbers in the forest led to the establishment of monthly forest-bird population counts following major habitat destruction caused by Hurricane Hugo on September 18, 1989. If wooden nest boxes used for thrasher research were augmenting its numbers, there should have been a steady increase of thrashers with each subsequent year following habitat destruction as its population recovered from the effects of the storm. Results from six years of post-disturbance monitoring, however, show that thrasher numbers have not only leveled off, they may even be slightly declining (Fig. 2). Thrasher numbers greatly increased directly following the hurricane and then decreased as other avian populations rebounded (see also Wunderle 1995, Fig. 5), just as is predicted by Jared Diamond's (1974) theory of avian "supertramps", of which the thrasher is a prime example (Arendt 1993, in press). It is noteworthy that the mean number of thrashers per 25-m count radius (n = 30 points visited 2,160 times over a 6-year period) varied significantly among the first six post-disturbance years ($H = 25.4$, $P = 0.00$), and was significantly higher during the first year (1990) following disturbance compared with each of five subsequent years (1991–1995) ($P < 0.05$ in every one of the five comparisons) (Fig. 2).

A second trend shown by the point-count data is that the apparent (and typical) breeding season "increase" in thrasher numbers is more likely an increased detectability of breeders during the major months (January–July) of the thrasher's breeding season (Fig. 3). It is also noteworthy that, instead of a continual increase in population size, field personnel living and working within various sections of the forest recently (January 1996) have begun reporting quite noticeable decreases in thrasher numbers around their living quarters and in some traditional "parrot areas" (O. Carrasquilla, pers. comm.). In concordance with continued field observations, a comparison of previous years does show a sharp decrease in the number of thrashers detected during point-count censuses conducted over the last five months of 1995 (Fig. 3). This trend further suggests that the Pearly-eye has reached the carrying capacity of its palo colorado forest and may be undergoing saturation dispersal (Arendt in press). Thrasher numbers will be monitored throughout the forest in the coming years to assess the validity of this assumption.

Breeding phenology. The Pearly-eye is an omnivorous, secondary cavity nester. Its breeding season is extensive. Depending on the availability of food, especially the ripening of staple fruits, breeders' ages, and the proximity of major habitat disturbances, generally, older individuals begin nesting in October–January, whereas first-time breeders (often less than a year old) attempt but a single clutch in late April or May of their first breeding season. Older females lay multiple clutches, averaging 2–3 clutches per season (a record of 8, two years post-hurricane, 6 otherwise). The nesting season lasts through July and often into early August. Incubation lasts about two weeks, and nestlings remain in the nest for another three weeks, but longer if the brood suffers from botfly ectoparasitism or food shortages. Brood reduction is common in the Pearly-eye, with third- and fourth-hatched siblings succumbing to food shortages and sibling competition. The normal 8–10-month breeding season is substantially shortened following major habitat destruction, which affects the fruiting of several preferred food plants. Following major hurricanes, the Pearly-eye limits its reproductivity to 2–3 months, with most females laying only a single clutch or, less often, two (see Arendt 1980, 1993, and information presented below for more details).

Puerto Rican Screech-Owl

Distribution and abundance. A common, endemic forest raptor, the Puerto Rican Screech-Owl is found on Puerto Rico proper and, at least historically, on several satellite and neighboring islands (see Moreno, 1998, for a complete geographical and status treatment). This smallish owl is only about half the size and body mass of the parrot and is not considered a major threat in terms of interference competition or nest usurpation (Snyder *et al.* 1987). Still, the owl should be considered as a potential nest predator of unguarded parrot nests (nest pair absent at the time of predation). Thus, knowledge of the owl's predatory habits on cavity-nesting birds is essential in the design and implementation of satisfactory parrot management strategies.

Breeding phenology. The following information is taken from 18 owl nestings (total of 20 eggs and 18 chicks) studied over a 10-year period (1985–1995), 13 nests in thrasher nest boxes as described below, plus five additional nests found in natural cavities within the forest. For this sampled population, the reproductive season lasted 4–5 months (March–July). The average date of egg laying was 4 April, with extremes ranging from 19 March to 21 April, and a median lay date of 29 March. Average clutch size was 1.2 (ranging from 1–2 eggs per clutch; mode = 1). On average, incubation lasted 31 days (also a 31-day median), and ranged from 29 to 32 days. The average hatch date was 6 May (median of 5 May), and ranged from 21 April to 22 May. Hatching success was nearly 100%. On average the nestling stage lasted 34 days (median also 34 days), and ranged from 32 to 36 days. The average date of fledging was 11 June (median of 9 June), ranging from 25 May to 30 June. Interestingly, after Hurricane Hugo, a single chick remained in its nest 65 days before fledging, because of slow development, most likely resulting from a post-disturbance food shortage.

Roosts and nests. Puerto Rican Screech-Owls occasionally roost in, or usurp, nest boxes from resident thrashers to use as nest sites. If a box is chosen for consistent roosting and eventual nesting by a female owl before the breeding season (that is, she does not abandon a "roost" box to breed elsewhere), the

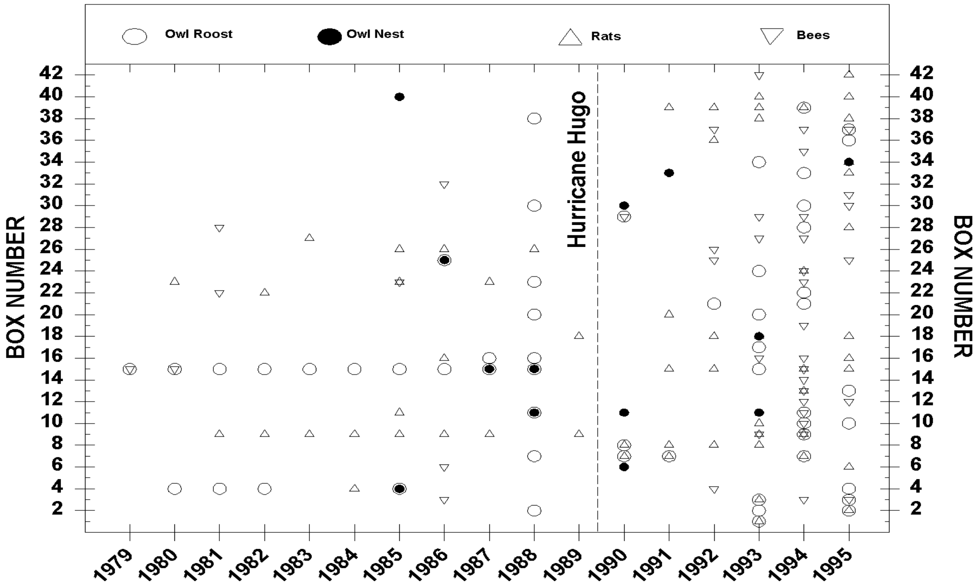

FIG. 4. Spatio-temporal patterns of competition for thrasher boxes by roosting or nesting owls, rats, and bees. Note the substantial increase in owls roosting, rats nesting, and bees invading thrasher boxes following a major habitat disturbance (Hurricane Hugo).

resident thrasher pair must wait until owlets fledge before building a nest and attempting to rear their broods. If the usurpation of the nest box occurs after the thrashers begin nesting, the owl will often eat the female thrasher and young if present. This is not the case, however, in parrot nests. Usually, adult parrots are too large and aggressive to fall prey to screech-owls. Owl predation on parrot eggs and chicks occurs only when the adult parrots are not in close attendance, usually due to injury or death of one or both of them (Snyder *et al.* 1987).

From 1979 to 1995, owls were recorded roosting in thrasher boxes on 61 occasions, 23 times during eight pre-disturbance breeding seasons before Hurricane Hugo, and 38 times during six post-disturbance breeding seasons following the disturbance. On average, about four boxes were used as owl roosts each year (Fig. 4). Comparing both the total number of roosts (n = 61) and percentages (10% vs 16%) of boxes in which owls roosted before (10%) (23 of 232 boxes--same number of boxes available each year during eight breeding seasons) versus 16% (38 of 241 boxes during six breeding seasons) after disturbance, the increase in owl predations following disturbance was not significant in either comparison (z = 1.60, P = 0.10; z = 1.76, P = 0.07, respectively). However, there were two more pre-disturbance than post-disturbance breeding seasons included in the analysis. As a result of this, plus the fact that rates of owl predation and roosting during the 1996–1999 breeding seasons continued to be high (unpubl. data), I will continue to monitor this trend to document any potential significant increases in roosting behavior.

Owls have nested in thrasher boxes 13 times over the past 16 years for an average of about one owl nest pair per year. Many boxes used by owls as roosts were never used for nesting (Fig. 4).

Predatory behavior. Only female thrashers incubate, brood, and roost in their nest boxes, thus greatly increasing their exposure times to nest predators. During the past 17 seasons, with more than a thousand thrasher nestings, there have been only 19 documented instances (about one per year) of breeding adult female thrashers falling prey to screech-owls. More often, however, pioneering or nearby resident owls eat thrasher chicks (46 depredations, or about 3 per year). There was only one observation of owl predation on an adult male thrasher. Early in the morning of 6 March 1995, two thrasher chicks and the resident adult male were found dead and partially eaten within their nest box (Roberto Díaz, pers. comm.). Because male thrashers help feed the young, virtually the only times they will enter nest boxes, it is likely that predation occurred in the early morning hours just as the male began assisting the female in feeding their brood.

Black rat

The following information was taken from Weinbren *et al.* (1970), Layton (1986) and Zwank and Layton (1989) from studies conducted within the confines of the LEF, some of which were carried out in and around captive parrots (Luquillo Aviary) and wild parrot nesting areas. I have added information obtained from the thrasher nest-box study.

Distribution and abundance. Scansorial black rats are found on at least six continents and thousands of islands throughout the world (Clark 1980). Puerto Rico is no exception. Black rats are common from seashore to mountain peak, and are especially abundant within the LEF, where tree-cavity denning sites are preferred over terrestrial ones. Black rats spend most of the daylight hours in their arboreal sites, descending mostly at night to forage on the ground.

In the Icacos Valley (main thrasher study area), Zwank and Layton (1989) monitored black rat transects from March to August 1984. Rats were most abundant in July and least numerous in April (Zwank and Layton 1989, Table 2). Only adults were captured during March and April. Subsequently, the percentage of immatures increased and peaked at 70% in June, then diminished thereafter. Average longevity appears to be less than a year. In their El Verde study in which 618 black rats were captured and recaptured 1821 times, Weinbren *et al.* (1970) found that the annual probabilities of appearance for adult males and females were essentially identical (0.03). Thus, the annual probability of disappearance was 0.97. Virtually the entire sampled population died within a year.

Breeding phenology. Black rats appear to cycle annually, with a single spring breeding season. The average female produces 9.4 embryos each year. Although reproduction can last 5–6 months, peak sexual activity occurs in the months of May or June, depending on the year. Female sexual activity is first noted in April and then diminishes after a usual peak in June. Males are capable of breeding during an entire 6-month period (April-September). Most females produce about one litter (1.2) per year. Population density lows occur during late winter and early spring just before the rat breeding season, with density estimates reaching 70.1 to 280.7 rats/ha in July and August (Layton 1986).

Zwank and Layton (1989) concluded that a difference in timing between when Puerto Rican Parrots and black rats breed reduces the likelihood of rat predation on parrot eggs and young. However, data obtained from more than three decades of parrot research and two decades of thrasher research, and presented herein, negate such an assumption.

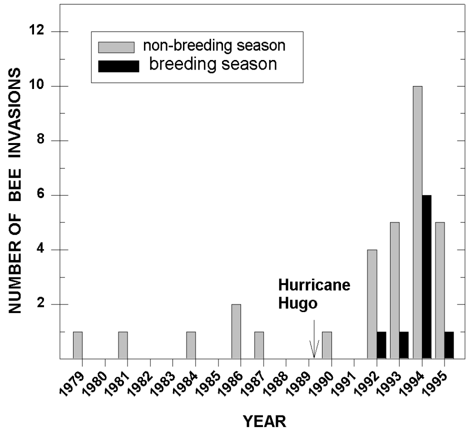

FIG. 5. Temporal pattern of honeybee invasions in thrasher nest boxes. For the first 13 years of the study, honeybee swarms and subsequent invasions of boxes occurred outside of the thrasher's breeding season. In 1994, however, the honeybee began lowering the thrasher's reproductive success.

Honeybee

Takeovers at thrasher nest boxes. Until 1992, the usurpation of thrasher nest boxes by swarming honeybees was incidental and of little consequence to the reproductive success of the thrasher. However, as with nest predation and competition for nest sites by vertebrates, invasion of thrasher nest boxes by swarming bees has greatly increased following Hurricane Hugo (Figs 4 and 5). From 1979 to 1995, there have been 40 instances of invasions by honeybees, resulting in the formation of hives within boxes (Figs 4 and 5). Of the 40 invasions, 32, or 80%, have taken place since a major habitat disturbance and the arrival of the Africanized hybrid bee. Only nine invasions occurred while a box was being used for breeding by thrashers. Yet, six of the nine invasions occurred during the 1994 thrasher breeding season (Fig. 5), substantially lowering the thrasher's seasonal reproductive success. There was one additional occurrence (July 1994) of a swarm forming near a box, but with no subsequent invasion. It is evident that within the past four years, honeybees have become a biological factor lowering the thrasher's reproductive success, and pose a health hazard to human visitors to the forest.

Cavity takeovers at parrot nests. In relation to parrot nesting, of 20 accurately dated honeybee swarms reported in the upper Sierra de Luquillo between 1973–1979 (Snyder *et al.* 1987), most swarming occurred between 1 June and 1 September, the period after which most parrot chicks had already fledged. Swarming coincided with peak flowering of sierra palm on which the bees feed heavily. Also documented during the same period were five instances of honeybees taking over parrot nests at three different sites after the young parrots had already fledged successfully. More recently (between 1990 and 1998), there has been but a single instance of a swarm taking over a parrot nest cavity while young were still present (P. Torres, USFWS, pers. comm.). In June 1993 a small swarm invaded an active parrot nest. However, the young parrots were safely transferred to temporary quarters while the bees were extinguished, and then the young parrots were returned to the nest when the danger had passed. It is likely that, in the absence of human intervention, the invading swarm would have taken over the cavity, causing nest abandonment by the adult parrots and consequential starvation of the chicks, ultimately suppressing the parrot's current and future reproductive efforts.

Arrival and impact of the Africanized honey bee. Separate, post-Hurricane Hugo research (W. J. Arendt & E. Garcia, in prep.) has shown that the Africanized strain arrived and substantially influenced the timing, frequency, and intensity of bee swarms within the LEF in the early 1990s. However, more recently (1996), the number of invasions, frequency and intensities of swarming have diminished, suggest-

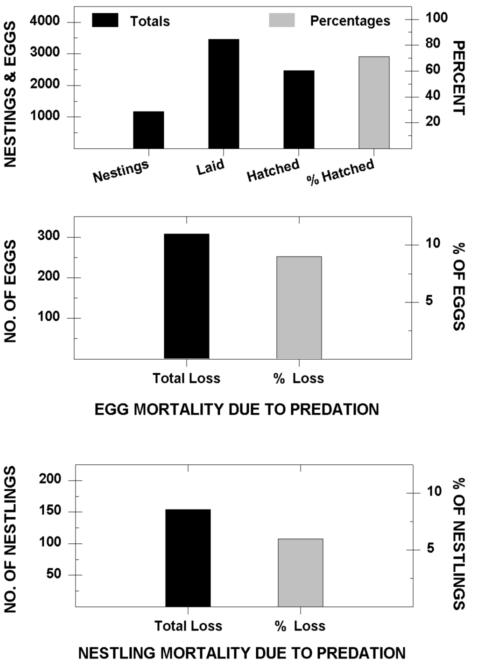

FIG. 6. Thrasher reproductive success and losses to nest predators. Less than ten percent of either eggs or chicks were lost to nest predators.

ing that the Africanized genes have been diluted among those of earlier strains of colonizers.

Nest predation and competition

Distinguishing between nest predation at thrasher nest boxes and competition for nest sites by other thrashers, owls, and rats was not always possible. Often predation on adult thrashers and nest contents occurs while predators are exploring potential nest sites for themselves. Therefore, these two subjects have been combined in the following analyses and discussion.

Thrasher reproductive success and losses. During 14 breeding seasons over the past 17 years, thrashers attempted more than a thousand documented nestings, laid 3459 eggs of which 2629 hatched for a hatching success of

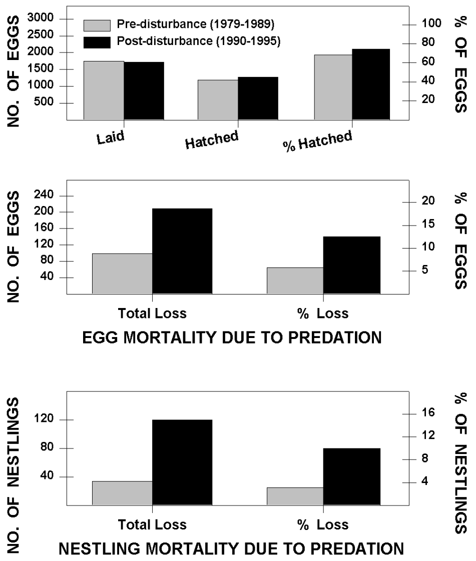

FIG. 7. Thrasher reproductive success during eight breeding seasons before Hurricane Hugo (18 September 1989) and the first six seasons following disturbance. Although reproductive parameters (totals and percentages of eggs laid and chicks hatched) remained comparable during both periods, egg and chick mortality rose substantially following disturbance.

76% (Fig. 6). During this period, 308 eggs and 154 chicks (Fig. 6) were lost to nest predators (for a summary of other sources of egg and chick mortality, see Arendt 1993).

Effects of catastrophic habitat disturbance on predation rates. I compared the Pearly-eyed Thrasher's reproductive yield during eight breeding seasons before Hurricane Hugo (18 September 1989) and during the first six seasons following disturbance to confirm basically equal reproductive yields during the two periods of comparison. There was only a 33-egg (non-significant) difference ($z = 0.58$, $P = 0.55$) in the number of eggs produced during the pre- (1979–1989) and post-disturbance (1990–1995) periods (Fig. 7). Likewise, no significant differences resulted in the number ($z = 0.24$, $P = 0.87$) or percentage

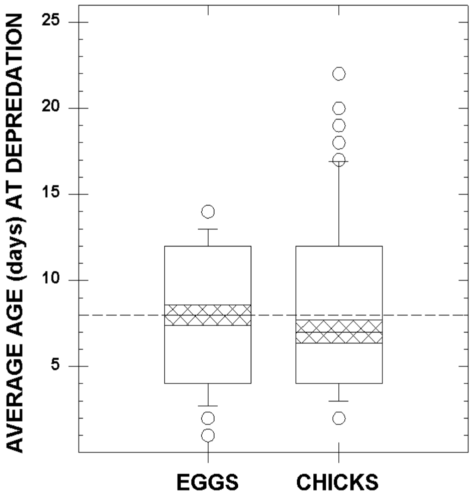

FIG. 8. Age-specific comparison of eggs and chicks in depredated thrasher nests. Though chicks remain in the nest about 21 days, whereas the egg stage is only 14 days, nest predation on eggs and chicks occurs at about the same time. Solid horizontal lines are medians. Lower and upper hinges of the boxes encompass the 25th and 75th percentiles, respectively. Lower and upper caps mark the 10th and 90th percentiles, respectively. Cross-hatched rectangles define a 95% confidence interval around the median. Non-overlapping cross-hatched rectangles imply different population medians at the 95% level of confidence. The plot-width dotted line is the average age at predation for eggs and chicks combined. Plot-width dotted lines are overall averages in subsequent box-plot figures.

(z = 0.32, P = 0.74) of eggs hatched before and after disturbance (Fig. 7). However, the number of eggs and chicks lost to predation (Fig. 7) was significantly higher following disturbance (z = 0.57, P = 0.00; z = 0.58, P = 0.00, respectively).

Age-specific comparison of eggs and nestlings in depredated nests. The ages (in days) of eggs and chicks at the time of predation were determined to evaluate whether younger or older eggs (or chicks) were preyed upon (Fig. 8). Minimum age at depredation was 2 days for both eggs and chicks, whereas maximum age was 14 days for eggs and 22 days for chicks, reflecting of course the maximum obtainable age by each group within the nest. There was no significant difference (t = -1.82, P = 0.09) between the average age of eggs (mean = 7.31 days; SD = 4.07; 95% CI = 0.89 – 1.18) and chicks (mean = 9.24 days; SD = 5.19; 95% CI = 1.39 – 1.85) at the time of predation. Still, the resulting means of 7.31 and 9.24 for eggs and chicks, respectively, represent a slight relative difference between the two groups because 7.31 days is just past the mid-point of 7 days in the egg stage, whereas 9.24 days is just before the mid-point of 10.5 days in the chick stage.

Temporal correlates of seasonal fecundity and nest predation. Temporal aspects of the prevalence (number of predations) and loss of nest contents are highly correlated with the continual increase in production of eggs and chicks (thus increasing the probability of detection and predation) commensurate with the continuation of the thrasher breeding season (Fig. 9).

Egg production, and thus egg loss, vary greatly among months because the thrasher has been recorded laying in at least 11 months of the year (Fig. 10). Monthly samples of egg depredations were large enough for statistical testing for only an 8-month period (December–July), with sufficient numbers of nests showing intra-month variation from February to July (Fig. 11). Nest predation on eggs varied significantly (G = 23.07, df = 7, P = 0.00) from month to month, and was greatest during the thrasher's main breeding months (March to June).

Nestling production spans at least 11 months of the year, with losses documented in 10 of the 11 months (Fig. 10). Chick loss due to predation also varied significantly (H = 17.6, P = 0.01) over the same 6-month period

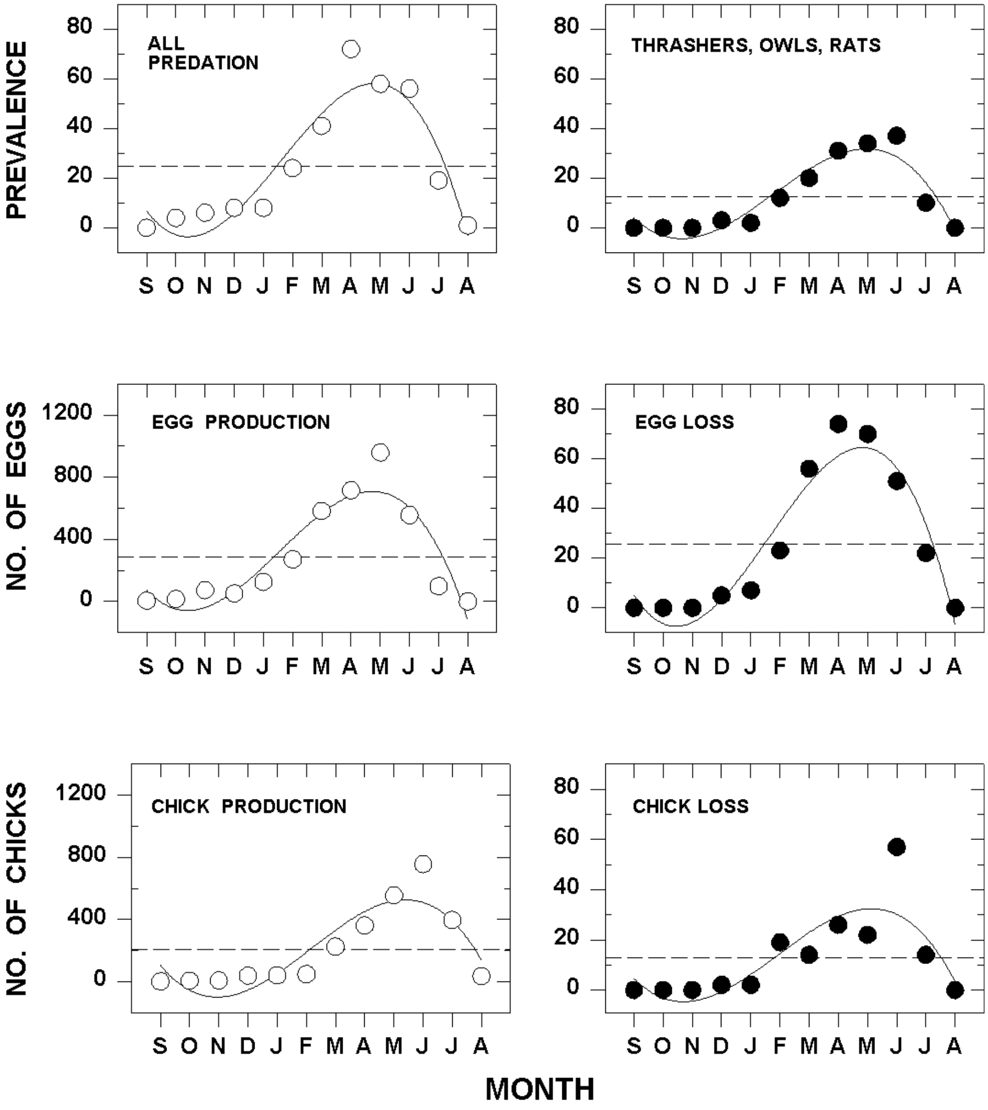

FIG. 9. Temporal correlates of seasonal fecundity and nest predation at thrasher nest boxes. Nest predation increases as the thrasher breeding season advances. Prevalence (rate) of predation, monthly fecundity, and loss of nest contents follow a third-order polynomial regression curve. For example, egg loss = 0.675 - (0.235*month) + (0.0455*month^2) - (0.00231*month^3), and chick loss = 2.540 - (1.200*month) + (0.204*month^2) - (0.00111*month^3).

(February–July), with significantly more chicks falling prey to nest predation during February and March than during later months (Fig. 11).

Impact of distinct predators on the thrasher's seasonal fecundity. Prevalence (rate) of nest predation and loss of nest contents have been shown to vary before and after a major habitat distur-

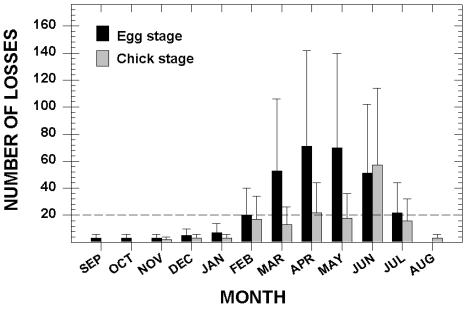

FIG. 10. Monthly variation in loss of eggs (n = 308) and chicks (n = 154) to nest predators. Prime months of nest predation are March through June, which is also the main breeding season of the thrasher and parrot, and their principal predators, competitors, and ectoparasites. Caps ("T") on bars are ± 1 standard error.

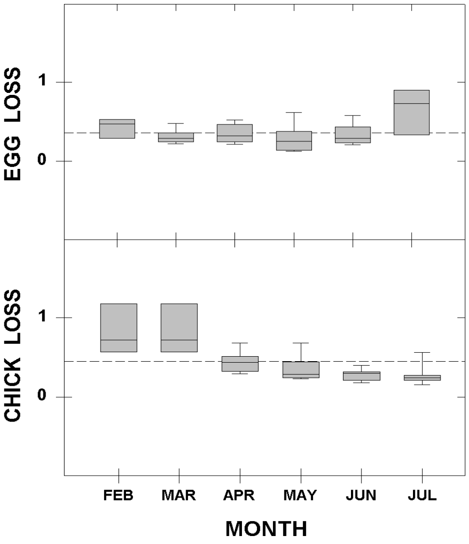

FIG. 11. Comparison of monthly variation in loss of eggs and chicks to nest predators. Substantially more chicks fall prey to nest predation early in the breeding season than in subsequent months, the period of high mortality resulting from botfly ectoparasitism. Data are percentages (arcsine, square-root transformed) represented on the y-axis as proportions of the total number of eggs and chicks produced. Box-plot parameters are described in Figure 8.

bance. Because observations of nest predation were made mostly during nest visits, the causes of the nest content losses were often undetermined and therefore are classified simply as eggs or chicks "missing from nest." However, over the past 17 years there have been enough definite determinations (e.g., rat excreta in the nest, remains of gnawed or beak puncture-wound eggshells, and raptor-style partially eaten carcasses) to allow comparative analyses.

Sources of reduced reproductive success from nest predation. From 1979 to 1995, 9% of the eggs and 6% of the chicks produced were lost to nest predators (Table 1). About half of the egg losses were categorized as "missing from nest," whereas about 20% of the documented losses were attributed to "other thrashers" (other than the nest pair) and rats (Fig. 12). The 10% of the eggs attributed to owl predation may appear to imply that the owls, like thrashers and rats, ate the eggs, but this was never documented. Eggs were lost to owls indirectly; for example, when the eggs became addled after having been left unattended following owl predation of the adult female thrasher, or when eggs were broken as a result of the owl fighting with the adult thrasher, roosting, or nesting in a box. Conversely, only 23% of the chicks were categorized as "missing," 43% were preyed upon by owls, and about 17% each were lost to other thrashers and rats (Fig. 12).

Pre- and post-disturbance comparisons were made by including each category of predation (Fig. 12). About half of the egg losses before and after disturbance were attributed to "missing" and were not significantly different ($z = 0.02$, $P = 0.17$). Egg losses attributed to owls and other thrashers did not decreased significantly ($z = -1.07$, $P = 0.29$; $z = -0.32$, $P = 0.75$, respectively) during the post-hurricane period (Fig. 12). Conversely, rat preda-

TABLE 1. Impact of nest predation on Pearly-eyed Thrasher reproductive success. Nest predators accounted for less than 10% of reproductive losses from 1979 to 1995.

Nest predator category	Eggs lost (percentage)	Chicks lost (percentage)	Total eggs & chicks lost (percentage)
Missing[1]	157 (5)	35 (1)	192 (3)
Thrashers[2]	58 (2)	25 (1)	83 (1)
Owls	31 (1)	66 (3)	97 (2)
Rats	62 (1)	28 (1)	90 (2)
Total	308 (9)	154 (6)	462 (8)

[1] "Missing" (undetermined causes of nest content losses involving every predator).
[2] Thrashers other than the nest pair.

Table 2. Temporal correlates of nest predation and the advancement of the Pearly-eyed Thrasher's breeding season. Excepting the category "missing" (undetermined causes of nest content losses involving every predator), there were significant increases in predation rates by all predators as the thrasher breeding season proceeded.

Each consecutive month vs	n[1]	r_s	P
Missing	136	0.54	0.07
Thrashers[2]	70	0.83	0.00
Owls	46	0.79	0.00
Rats	45	0.79	0.00

[1] Total number of depredations from 1979 to 1995.
[2] Thrashers other than the nest pair.

tion on eggs following disturbance increased significantly (z = 2.19, P = 0.03). Nestling losses to predation increased slightly for all predator categories except rats (Fig. 12). However, none of the pre- and post-disturbance predation rate comparisons among chicks showed significant differences: missing (z = 0.33, P = 0.73); thrashers (z = 0.26, P = 0.79); owls (z = 1.48, P = 0.14); rats (z = -0.22, P = 0.83).

To summarize, nest predation at thrasher nest boxes from unknown sources ("missing") and individual predators (other thrashers, owls, and rats) averaged about 1–3 percent. Overall, 8% of the total number of eggs and chicks were lost to nest predators.

Temporal variation among nest predators. Although there were on average about 20 nest predations per month (all 17 seasons combined), temporal patterns of predation varied greatly among the four (missing, thrashers, owls, rats) predation categories (Fig. 13). Predation rates varied significantly (Fig. 14) among years (H = 91.6, P < 0.00) and months (H = 16.6, P = 0.00), were correlated with the progression of the thrasher breeding season (Table 2), and reflected both the variable onset and duration of each predator's own breeding seasons (Table 3, Fig. 15).

Spatial variation among nest predators. If predator populations were evenly dispersed, and individual predators possessed the same inherent extent of aggressiveness and predatory instinct (and thus had the same probability of preying upon the nest contents of any given box), predation rates among all boxes would have been about equal. But, because most

Table 3. Comparative results of predation rates at Pearly-eyed Thrasher nests among years, months, and boxes (Kruskal-Wallis one-way ANOVAS on ranks). Tabular entries are post-hoc results from all pairwise multiple procedures (Dunn's method). There was more variation in rates of nest predation by specific predators in different years than among months or boxes.

Comparisons	Years		Months		Boxes	
	Q	$P < 0.05$	*Q*	$P < 0.05$	*Q*	$P < 0.05$
Thrashers vs Missing[1]	6.69	Yes	2.97	Yes	6.21	Yes
Thrashers vs Owls	0.95	Yes	3.49	Yes	1.68	No
Thrashers vs Rats	4.54	Yes	2.50	No	5.24	Yes
Owls vs Missing	5.79	Yes	0.27	No	4.53	Yes
Owls vs Rats	5.17	Yes	0.41	No	3.55	Yes
Rats vs Missing	9.51	Yes	0.59	No	0.97	No

[1] "Missing" denotes contents missing from nest, but predator's identity is unknown.

predator populations are comprised of clusters of individuals, owing to resource patchiness (see Bowman and Harris 1980), and because predatory habits and aggression vary greatly among species and even individuals, naturally some boxes were exploited more than others (Fig. 16). However, although the number of nest predations at some boxes was well above, or below, the average number of predations per box (mean = 7.1; SD = 3.41; range = 1–17) (Fig. 16), predation rates among boxes did not differ $F = 0.95$, $P = 0.56$). Contrarily, however, distribution of individual species of predators among boxes (Table 3, Fig. 17) did differ significantly ($F = 8.59$, $P < 0.00$). Whereas loss of nest contents attributed to "missing from nest" and other thrashers was more evenly dispersed among all nest boxes, owl and rat predation was more clumped. Among boxes receiving heavy predation by thrashers and owls (boxes 24–35), rat predation was generally nil (Fig. 17).

PHILORNIS ECTOPARASITISM

Taxonomy and distribution of *Philornis*

The genus *Philornis* was erected by Meinert (1889, p. 304—cited in Aldrich 1923) and was placed in the family Anthomyiidae after larvae were first collected from the Hispaniolan Woodpecker in Santo Domingo by Macquart (1853) (see LaRue, 1987, for a more detailed history of the taxonomy of this group). More than 30 species of *Philornis* botflies (Aldrich 1923, Skidmore 1985) are known to parasitize some 100 species of tropical birds (Pont 1972; LaRue 1987—see his Appendix A). Flies of this genus range throughout the Neotropics from Florida (Dodge 1955), through Mexico (Héctor 1982, Winterstein & Raitt 1983) and Central America, e.g., Costa Rica, (Young 1993) and Panama (Smith 1968), and throughout South America from Venezuela (Thomas 1977) and Guyana (Aiken 1913), across Brazil (Couri 1984, 1985), and down to Argentina (Nielsen 1913, Fraga 1984); the genus is also common throughout the Caribbean Basin from Jamaica (Ventura 1968), Hispaniola (Macquart 1853, Engel 1920), and Puerto Rico (Wolcott 1948, Arendt 1985a, 1985b; LaRue 1987, Rivera Irizarry 1990, Delannoy & Cruz 1991), south to Trinidad (Dodge & Aiken 1968).

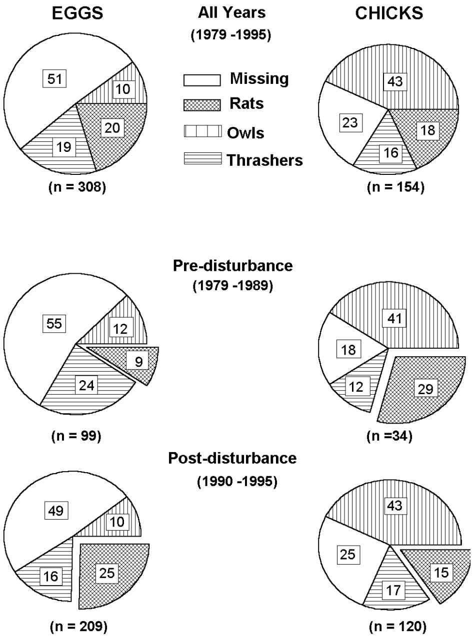

FIG. 12. Sources of reduced reproductive success from nest predation throughout (1979–1995) the study (upper diagrams), before (1979–1989) major habitat disturbance (center diagrams), and during the first six (1990–1995) post-disturbance breeding seasons (lower diagrams). Sample sizes (n) are shown below each diagram, whereas percentage data are given within each. Rat predation varied the most. Rat predation on eggs increased following Hurricane Hugo, whereas predation on chicks decreased.

Because several species of botflies in the genus *Philornis* are polytypic and have a wide host specificity (Dodge & Aitken 1968), the taxonomy of this group remains extremely difficult. This has been reflected among the above-cited studies done within recent decades in Puerto Rico. To date, four species of philornid botflies have been identified by various taxonomists and systematists contacted through avian researchers involved in various bird-related studies. Botflies collected in the western portion of the island have been identified as *P. obscura* (Van der Wulp)

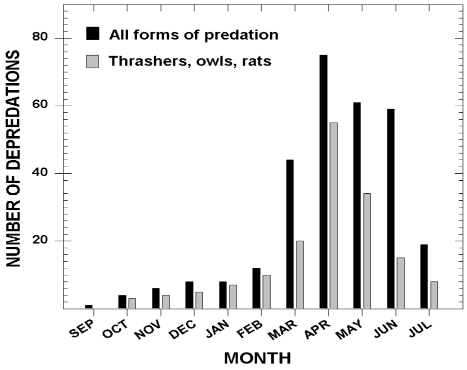

FIG. 13. Predation rates each month among various categories of nest predators. Though nest predation spans virtually an entire calendar year, most losses occur from March to June, the principal breeding period for many species.

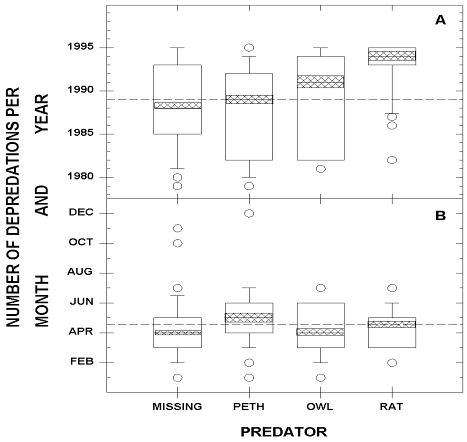

FIG. 14. Comparison of yearly (A) and monthly (B) activity among nest predators. On a yearly scale, "missing" equally spans the entire study period, with its median (1988) close to the average year (1987) for this period. Likewise, the thrasher's (PETH) rate of predation has been prominent throughout the 17-year study, with its median (1989) just slightly above that of "missing." Owl predation has increased slightly in recent years (median = 1991). Rat predation has increased significantly during the past few years (median = 1994), and continues to be increasing at thrasher boxes. Box-plot parameters and statistical inferences are described in Figure 8.

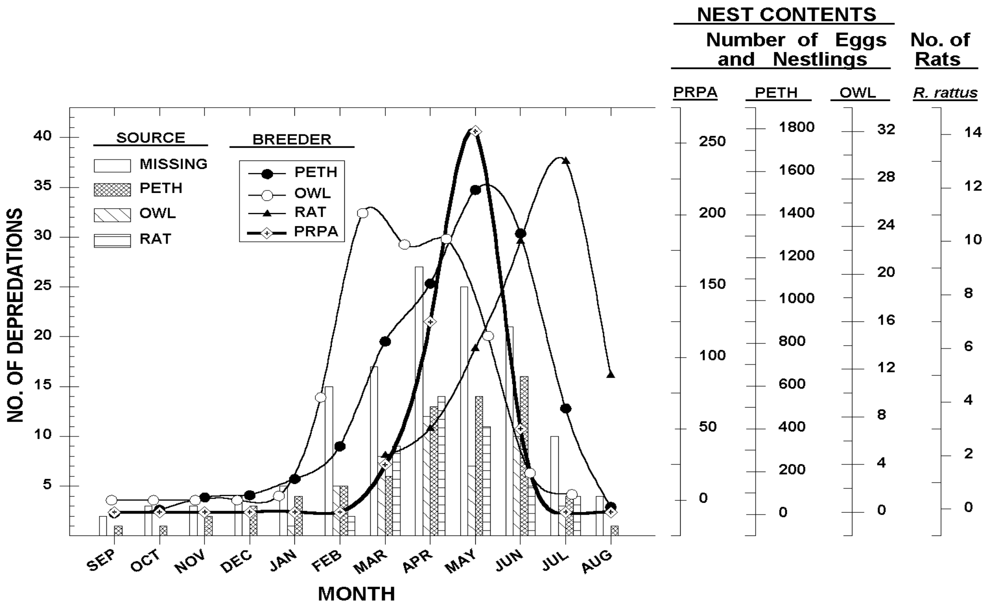

FIG. 15. Monthly predatory activity among nest predators reflecting the breeding season of each. Note how breeding seasons vary among predators, but closely follow those of the parrot and thrasher (PRPA = Puerto Rican Parrot — data from 1946–1998, and PETH = Pearly-eyed Thrasher). Monthly totals for "nest contents" (right ordinate) are not independent, i.e., the same eggs and chicks were recounted as long as they remained in the nest and vulnerable to predation).

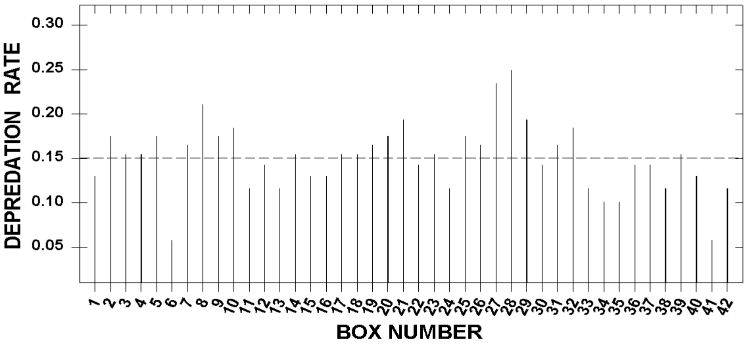

FIG. 16. Prevalence of nest predation among thrasher nest boxes. Data for each box are percentages (arcsine, square-root transformed) represented on the y-axis as proportions of the total number of predations at all boxes. On average, each box was depredated about seven times from 1979 to 1995.

from specimens taken at Ponce by Wolcott (1948), *P. pici* (Macquart) by D.G. Hall in Mayagüez (Wolcott 1948), and *P. angustifrons* (Loew) on the University of Puerto Rico campus at Mayagüez by an unreported source cited in Rivera Irizarry (1991). In Eastern Puerto Rico, within the Sierra de Luquillo, botflies infesting Puerto Rican Parrots and

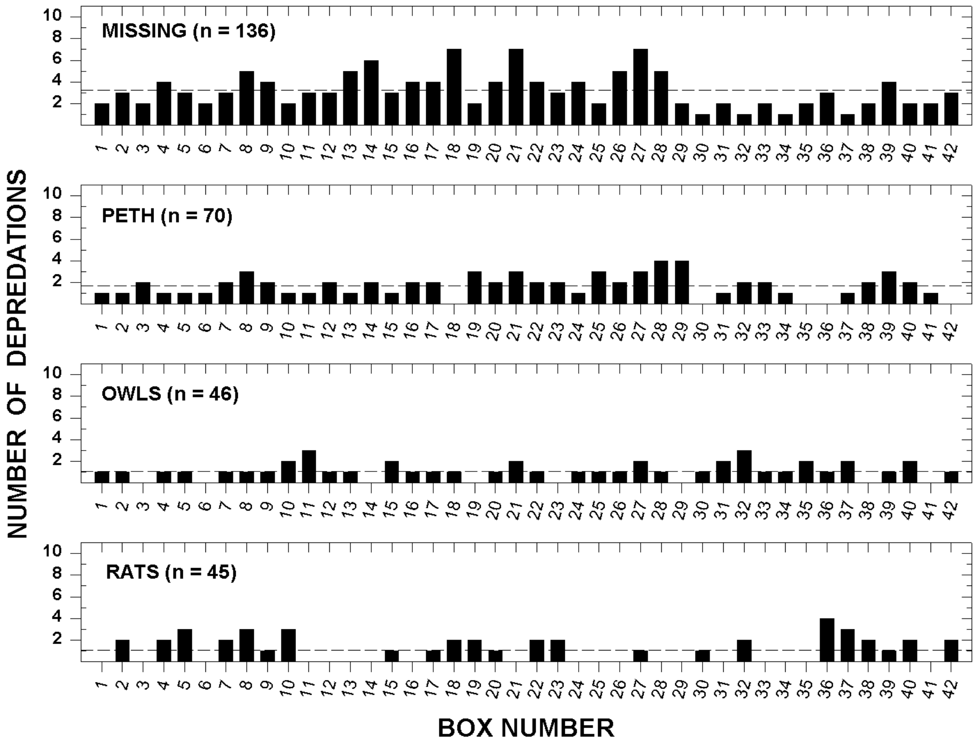

FIG. 17. Comparison of frequencies of nest predation at thrasher nest boxes among four predation categories (each species, plus "missing"). On average, at each box about 1–5 losses (plot-wide horizontal dashed lines) were attributed to predators in each of the four categories.

Pearly-eyed Thrashers have been identified as *P. pici* (Macquart) by R. J. Gagne (Snyder *et al.* 1987), and M. S. Couri (LaRue 1987); and also as *P. deceptivus* (Dodge and Aitken) by M. S. Couri (*in litt.*) and cited by Arendt (1985b). LaRue (1987) questioned the *P. deceptivus* designation given by Couri because she later identified flies from some of the same nest boxes used by Arendt (1983, 1985a, 1985b) as *P. pici* from specimens sent to her by LaRue in 1986. Yet, regarding several specimens sent to the UK by Arendt in the mid-1980s to A. C. Pont, an authority on the Diptera, his reply (A. C. Pont *in litt.*) was that none of the specimens were like any *P. pici* he had ever seen. Therefore, it is evident that much more research into the number of species and distributions of the philornid flies inhabiting Puerto Rico is necessary before any resolute conclusions can be made.

Mechanisms of *Philornis* ectoparasitism

Parasite-host relationships and their underlying mechanisms are known for less than half (21 of 49) of the described species of *Philornis* botflies (Couri 1985, 1991; Teixeira *et al.* 1990). Most species live intradermically, three live freely in the nest (two of which are semi-hematophagous), and only one (*P. aitkeni*) has adapted coprophagous habits (Dodge 1963). Within the Sierra de Luquillo, Puerto Rico, *Philornis* botflies parasitize more than 20 avian species in diverse taxa including Falconiformes, Columbiformes, Psittaciformes, Cuculiformes, and many species of Passeriformes (Snyder *et al.* 1987, Rivera Irizarry 1990, R. Pérez-Rivera *in litt.*, pers. observ.). Larvae of the philornid botflies discovered to date live subcutaneously for about a week, situated in furuncles with their caudal spiracles visible through the dermal openings of their avian hosts. Infesting larvae feed upon their host's erythrocytes, mononuclear cells, necrotic cellular debris, and body fluids. At pupation, via modified salivary glands, the larvae secrete a frothy cocoon that anchors the puparia to twigs under of the nest cup and relative safety (and warmth) from the brooding bird. In the rain forest, the effects of *Philornis* ectoparasitism are of less consequence to adult thrashers than to their young, in which most mortality (often as high as 80% in the first year) is caused by infesting fly larvae. Many heavily infested thrasher young that leave the nest subsequently die as a result of ectoparasitism. Larval infestation rates vary seasonally, with the chick's ontogeny and rainfall. Larval implantation sites vary with the chick's growth and development, especially within the feather pterylae. Whereas thrasher growth rates vary little among unparasitized chicks, growth and development are retarded in heavily parasitized young, especially during the first 1.5 weeks post-hatching, the period of maximum growth in four of five sampled growth characters (body mass, culmen, ulna, tarsus). Body mass and tarsus lengths are the most affected by ectoparasitism. Heavily parasitized chicks weigh significantly less than unparasitized young after larval removal. Pathogenesis associated with philornid myiasis appeared to significantly debit an energy budget responsible for chick development and growth, and played a major role in lowering post-fledging survivorship (preceding information taken mostly from Arendt (1983, 1985a, 1985b, 1993), Uhazy & Arendt (1986), and LaRue (1987).

Effects of botflies on nesting parrots

In addition to their effects on Pearly-eyed Thrashers, ectoparasites and the resulting myiasis involving *Philornis* botflies are major biological stresses impacting young parrots in the remaining wild population (Snyder *et al.* 1987). From 1973 to 1979, 6 of 21 nests and 11 of 44 parrot chicks experienced *Philornis* ectoparasitism, for a prevalence of 29% of the nests and 25% among chicks (Snyder et. al. 1987). Within the last six seasons (1990–1995), there has been a prevalence of 15% among nestings (5 of 34). Similarly, 12 of 14 chicks from 5 nests were parasitized out of 93 chicks produced in the wild during that period, for a prevalence of 13% among chicks (information from USFWS monthly reports). A comparison of the two periods (1973–1979 and 1990–1995) showed no significant differences in the prevalence of *Philornis* ectoparasitism among nests ($z = 0.90$, $P = 0.36$) or chicks ($z = 1.52$, $P = 0.12$). The decade spanning 1980–1989 was omitted because of insufficient available information (only one inclusion of a post-1979 instance of botfly ectoparasitism in Appendices 32 and 33 of Snyder *et al.* (1987).

Until recently, philornid larvae had not been reported in captive Puerto Rican parrots. In April, 1995, Anne Smith (*in litt.*) documented for the first time larval infestations (species unknown) in both adult and young parrots in the Río Abajo Aviary (one of two federally- and state-sponsored parrot captive-breeding facilities in Puerto Rico). She reports that on 11 April 1995 two Hispaniolan Amazon chicks, aged 11 and 9 days, were found harboring nine and six larvae, respectively. The larvae were immediately removed, including an additional first-instar larva from the youngest chick two days later. Both chicks recovered. The parrot's nest was placed in a palm log (*Roystonea* sp.) with palm core as nesting material. On 15 April 1995, eleven botfly larvae (species unknown), ranging in

Table 4. Seventeen-year (1979–1995), fourteen-season (1983, 1984, and 1989 seasons excluded), summary of the prevalence and intensity of botfly ectoparasitism at 42 Pearly-eyed Thrasher nest boxes. Whereas first- and second-hatched nestlings suffered about a 50% rate of mortality resulting from botfly ectoparasitism, 60–80% of the third- and fourth-hatched siblings succumbed.

Per box or chick	Minimum	Maximum	Average	Total or %
Years active	6	17	14	473[1]
Total number of nestings	12	38	23	1170
Average number of nestlings per year	1.64	2.85	2.14	—
Prevalence (no. of nests infested)	12	36	21.57	1112
Percent prevalence	80	100	95	—
Total number of chicks	29	97	58	2467
Number of chicks died[2]	9	58	31.81	1391
Number of chicks fledged	4	73	26.05	1073
Percentage of chicks fledged	8	78.5	44.5	56
Number of first-hached chicks	10	33	19.3	842
Intensity[3]	0	217	48.7	34,467
Number died	3	21	10.3	450
Percent mortality	30	64	53.4	53
Age (days) at death	0	31	11.6	—
Number fledged	2	20	8.95	392
Number of second-hatched chicks	4	35	19.1	835
Intensity	0	220	46.5	35,642
Number died	2	19	10.7	444
Percent mortality	50	54	56	53
Age (days) at death	0	25	11.5	—
Number fledged	1	26	9.5	391
Number of third-hatched chicks	5	30	16.45	723
Intensity	0	224	40.6	25,233
Number died	2	19	9.5	445
Percent mortality	40	63	58	62
Age (days) at death	0	26	10.8	—
Number fledged	1	25	7.19	278
Number of fourt-hatched chicks	1	6	2.09	67
Intensity	0	122	40.2	2011
Number died	0	6	1.63	52
Percent mortality	0	100	78	78

Table 4. Continued.

Per box or chick	Minimum	Maximum	Average	Total or %
Age (days) at death	0	25	9.36	—
Number fledged	0	3	0.47	15

[1] Total number of nest-box years (on average, about 34 boxes were available each year).
[2] Mortality resulting from ectoparasitism only.
[3] Total number of botfly larvae per chick.

size from first- to third-instars, were found on an adult Puerto Rican Amazon. She was about to lay her first egg of the season when nine larvae were discovered near the vent, with an additional two larvae in the patagial membrane of the right wing. Both anatomical regions are prime botfly infestation sites in adult birds (see Arendt 1985b, Table 4). Although the female recovered, she did not lay additional eggs during the 1995 breeding season. There is no published information available on the botfly's effect on free-flying, adult Puerto Rican Parrots.

Need for parrot nest monitoring

Aspects of the botfly's life history and impact on the growth, development, and survival of parrots and other forest birds have been known for more than two decades. Thus, the results and information obtained from these studies have been used periodically and effectively to minimize the infesting larvae's impact on parrot chicks. Ironically, however, parrot chicks needlessly continue to die as a result of botfly ectoparasitism. Within a 5-year period (1990–1995), 12 parrot chicks were infested by *Philornis* larvae, and half succumbed as a result of the ectoparasitism (USFWS, monthly reports). Therefore, it is my intent, after analyzing the results of 17 breeding seasons of ectoparasite data on a surrogate host species, the Pearly-eyed Thrasher, to offer management prescriptions that would ameliorate the effects of infesting larvae on the growth, development, and survival of parrots in both wild and captive flocks.

Philornis ectoparasitism in thrasher nests

One of the best ways to analyze ectoparasite data to obtain quantitative results is by comparing the spatio-temporal components of the ectoparasitism; i.e., prevalence (number of nests parasitized per box each year) and intensity (number of larvae per chick). Results of the prevalence and intensity of botfly ectoparasitism at thrasher nest boxes (range = 27 boxes in 1979 to 42 boxes from 1990 to 1995, mean = 34 boxes per season) during 14 of the past 17 seasons are summarized in Table 4. The prevalence of *Philornis* ectoparasitism was alarmingly high. No fewer than 80% of all nestings within a given nest box were parasitized. Moreover, although the overall average number of parasitized nestings was 95% (1112 of 1170), 100% of all nesting attempts experienced ectoparasitism in half (21 of 42) of the nest boxes (n = 430 broods of the 1112 broods infested, or about 39%). Likewise, the intensity of *Philornis* ectoparasitism was substantial. Older (1st- and 2nd-hatched) chicks tended to live longer and averaged more larvae per individual (*c.* 48/ind.) than their younger (3rd- and 4th-hatched) siblings (*c.* 40/ind.). More than half (56%) of all the chicks (1391 of 2467) succumbed as a result of *Philornis* ectoparasitism, whereas about 32% (range = 9–58) per nest box succumbed. With an average of 23 nestings per box (range = 12–38), only about 26 chicks fledged per box (range = 4–73), or about 1 chick/box/year

Table 5. Summary of the intensity of botfly ectoparasitism (total number of larvae per nest) among broods at 42 Pearly-eyed Thrasher nest boxes during 14 breeding seasons, 8 pre- and 6 post-disturbance (Hurricane Hugo) years between 1979 and 1995, excluding 1983, 1984, and 1989. Multiple broods (two or more per season) suffered significantly higher numbers of infesting larvae after, rather than before, habitat disturbance.

Broods per season	Number of infesting larvae per nest											
	Total			Average			Minimum[4]			Maximum[5]		
	All[1]	Before[2]	After[3]	All	Before	After	All	Before	After	All	Before	After
ONE												
All nestings	11,283	5,107	6,176	—	—	—	—	—	—	344	316	344
Avg. per nesting	101	104	97	101	104	97	41	41	41	54	52	56
(n)	(113)	(49)	(64)									
TWO												
All nestings	40,469	19,973	20,496	10,151	10,061	10,241	5,547	5,547	5,711	14,552	14,412	14,552
Avg. per nesting	226	208	244*	114	105	122*	51	50	51	72	69	73
(n)	(180)	(96)	(84)									
THREE												
All nestings	35,398	17,637	17,761	5,909	5,880	5,937	2,233	2,244	2,373	10,403	9,866	10,403
Avg. per nesting	348	309	386*	116	103	129*	48	40	58	77	57	104*
(n)	(104)	(57)	(47)									
FOUR												
All nestings	7,817	2,480	5,337	970	621	1,318	136	136	435	1,202	1,202	2,279
Avg. per nesting	474	413	534*	118	103	132	42	33	47	85	81	92
(n)	(16)	(6)	(10)									

[1]All years (1979–1995, excluding 1983, 1984, 1989); [2]Before Hurricane Hugo (1979–1988, excluding 1983 and 1984); [3]After Hurricane Hugo (1900–1995); [4,5]Among years; *$P < 0.05$ (Mann-Whitney rank sum).

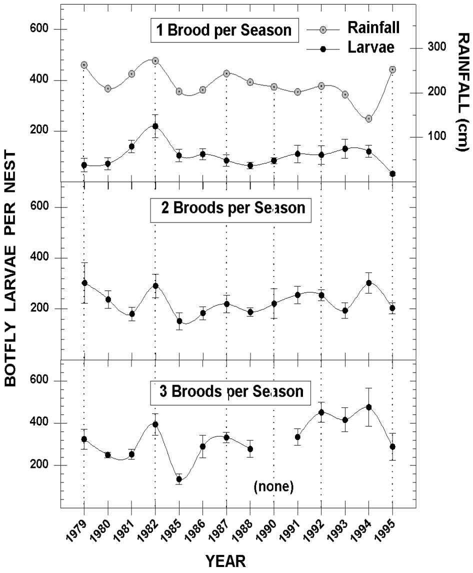

FIG. 18. Comparison of yearly fluctuations in numbers of botfly larvae per nest among multiple broods. The direct correlation (more rainfall resulting in heavier ectoparasitism) broke down during the years following a major habitat disturbance (note especially 1995).

over the 17-year period.

Although the prevalence and intensity of *Philornis* ectoparasitism were shown to be high, to ameliorate the impact of ectoparasitism on cavity-nesting birds such as the parrot and thrasher, the spatio-temporal components of the ectoparasitism must be delineated and understood. Following are a series of analyses to elucidate critical periods and areas of heavy concentrations of *Philornis* ectoparasitism.

Botfly larvae per nest among years. The intensity of botfly ectoparasitism at thrasher nests varied from year to year (Fig. 18). Inter-year comparisons (Kruskal-Wallis one-way ANOVA on ranks) were made for the first three broods per season (no analyses were done on fourth or fifth broods per season because of insufficient yearly sample sizes). Botfly larval loads per nest varied significantly among numerous inter-year comparisons for each of the three brood categories. The Student-Newman-Keuls method (Fox *et al.* 1994) was used in obtaining the following post-hoc all pairwise multiple comparisons results: (1) single broods: H = 106.0, df = 13, P <0.00; 91 possible comparisons: 4 = “no,” 12 = “do not test,” and 75 = “yes” (82%); (2) double broods: H = 60.8, df = 13, P <0.00; 91 possible comparisons: 3 = “no,” 14 = “do not test,” and 74 = “yes” (81%); (3) triple broods: H = 150.6, df = 12, P <0.00; 78 possible comparisons: 2 = “no,” and 76 = “yes” (97%).

Early in this study (1979–1984), the frequency and intensity of botfly ectoparasitism was closely correlated with rainfall (Arendt 1985b). With the addition of 10 more years, this correlation becomes more evident (Fig. 18). There was a correlation among rainfall and each of the three brood categories. However, none was significant. The correlation broke down after major habitat disturbance (Fig. 18; note especially 1994 and 1995 breeding seasons, during which an inverse correlation is observed).

Botfly larvae per nest among multiple broods. Larval loads within thrasher nests were compared among multiple broods per season (Fig. 19A) because botfly population growth is exponential, and rainfall increases from the onset of the parrot-thrasher breeding seasons, with a peak in May. There is a substantial temporal increase in the average number of infesting larvae per nest (mean = 287, range = 101–474) (Table 5, col. 2, “All years” category). With the exception of single broods per season, pre- and post-habitat disturbance (= hurricane) comparisons show that larval loads per nest increased following the storm (Table 5, Fig. 19B), significantly so among various descriptive statistics categories for two and three broods (insufficient samples for fourth

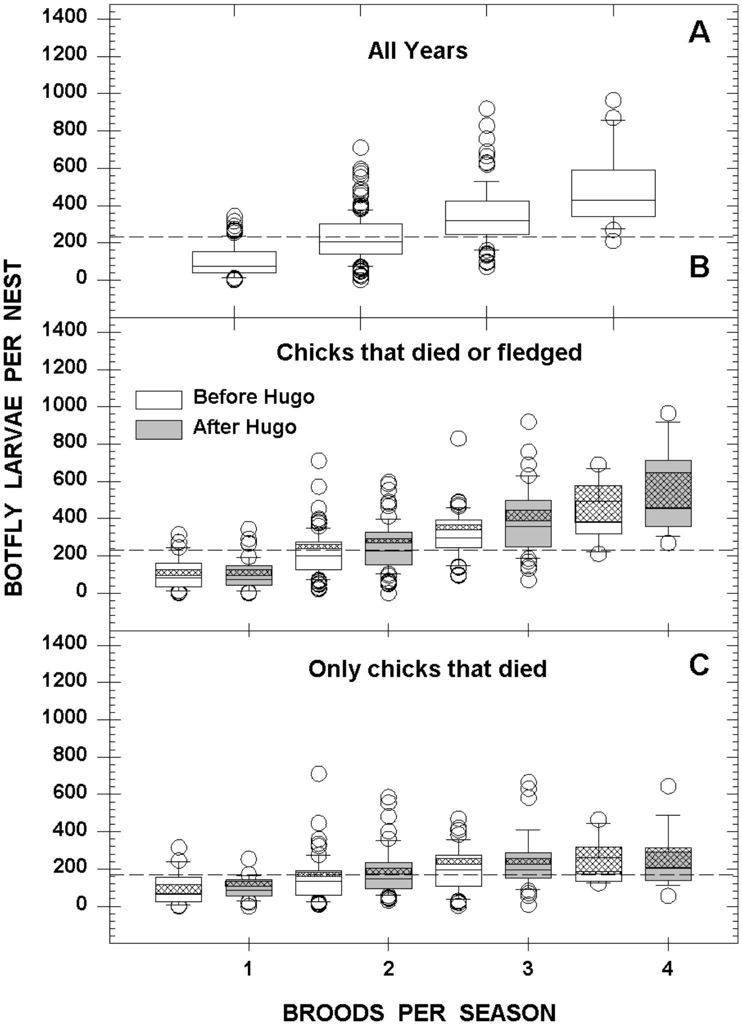

FIG. 19. Comparison of the intensity of botfly larval infestations in nests among multiple broods (A), including before and after habitat destruction (B–C). In all but first broods (often laid early in the season during periods of less rainfall), botfly ectoparasitism markedly increased in post-disturbance nests (B) of subsequent broods (2–4), even when the analyses were restricted to only chicks that succumbed to ectoparasitism (C). Box-plot parameters and statistical inferences are described in Figure 8.

broods) per season (Table 5). The previous results (Fig. 19B) included all infested chicks, namely those that died and the ones that fledged. Additional pre- and post-disturbance analyses were performed on only chicks that died (Fig. 19C). No significant differences resulted in total number of larvae per nest among any of the four brood categories.

Botfly larvae per chick among multiple broods. Average numbers of infesting larvae varied greatly among chicks from multiple broods, but sig-

Table 6. Summary of the intensity of botfly ectoparasitism among siblings in multiple broods at 42 Pearly-eyed Thrasher nest boxes during 14 breeding seasons, 8 pre- and 6 post-disturbance (Hurricane Hugo) years between 1979 and 1995, excluding 1983, 1984, and 1989. None of the four pre- vs post-disturbance brood comparisons was significant at the 95% level of confidence (Mann-Whitney rank sum test). Lumping all four brood categories, the average number is about 50 larvae per chick.

Broods per season	Number of infesting larvae per chick								
	Average			Minimum			Maximum		
	All[1]	Before[1]	After[3]	All	Before	After	All	Before	After
One	42.6	42.1	43.1	0	4	0	201	201	123
Two	53.9	50.6	57.7	4	4	9	185	149	185
Three	48.7	45.1	52.8	2	2	8	150	150	138
Four	54.2	43.8	59.8	6	10	6	172	90	172
Combined average	49.9	45.4	53.4	3	5	6	177	148	155

[1] All years (1979–1995, excluding 1983, 1984, 1989).

[2] Before Hurricane Hugo (1979–1988).

[3] After Hurricane Hugo (1990–1995).

Table 7. Age (days old) at death, of chicks by hatch order and among multiple broods at 42 Pearly-eyed Thrasher nest boxes over 17 seasons (1979–1995, excluding 1983, 1984, and 1989 seasons). Median ages at death from first- to fourth-hatched young were, respectively, 11, 11, 10, 9 days. Median ages of chicks from first to fourth broods were, respectively, 12, 11, 9, 10 days. For both hatch order and brood number, there were no significant differences between first and second siblings or nestings. However, because of size differences (owing to asynchronous hatching) and temporal differences (fewer infesting larvae early in the season), the nestlings' ages at death varied significantly among all remaining comparisons (see Table 3 for explanation of statistical procedures and results).

Category	Hatch order		Brood number	
	Q	$P < 0.05$	Q	$P < 0.05$
First vs second	0.24	No	1.93	No
First vs third	2.67	Yes	6.11	Yes
First vs fourth	2.74	Yes	2.89	Yes
Second vs third	2.98	Yes	4.66	Yes
Second vs fourth	2.65	Yes	2.65	Yes
Third vs fourth	1.78	No	1.33	No

nificantly so only among chicks from single broods (median = 35 larvae/chick) compared to chicks from two (median = 49), three (median = 44), and four (median = 46) broods per season (single vs two: $P = 0.00$; single vs three: $P = 0.04$, single vs four: $P = 0.03$) (Fig. 20A). For all four brood categories combined, on average chicks received about

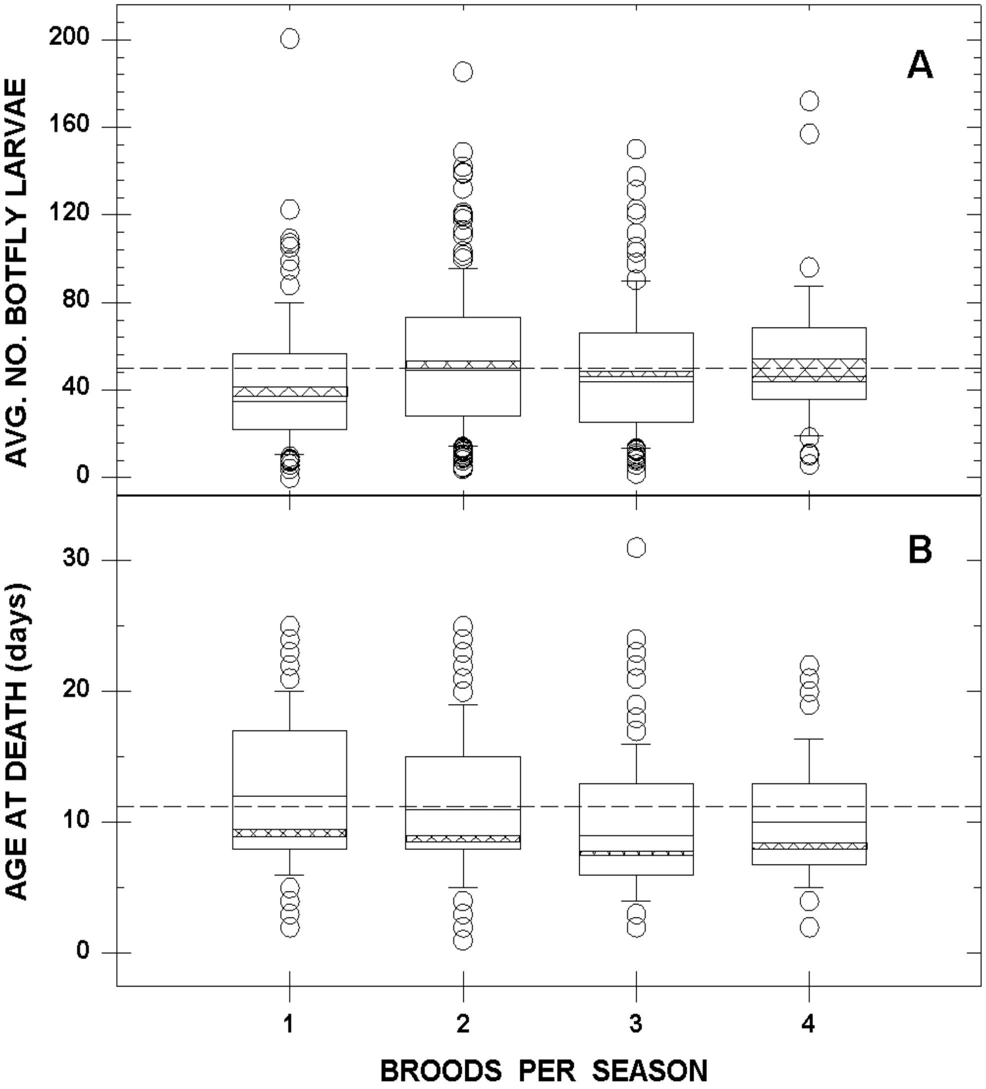

FIG. 20. Comparison of the intensity of botfly larval infestations (A) and age (days after hatching) at death (B) among chicks of multiple broods. With the exception of first broods, all subsequent broods suffer about the same intensity of philornid ectoparasitism. On average, chicks harbor about 40–50 larvae during the infestation period. Box-plot parameters and statistical inferences are described in Figure 8.

50 larvae while in the nest. No significant differences resulted in minimum, maximum, or average larval intensities per chick among multiple broods. Nor were there significant differences in larval intensities among any of six pre- and post-habitat disturbance comparisons (Table 6).

Effects of larval implantation sites on chick mortality. Nestling birds are known to succumb to

Table 8. Intensity of botfly ectoparasitism (total number of infesting larvae) by hatch order among chicks at a maximum of 42 Pearly-eyed Thrasher nest boxes (avg. = 34 per year) monitored between 1979 and 1995. Median number of larvae by hatch order (1st- to 4th-hatched) for nests in which chicks either died or fledged was, respectively, 63, 60.5, 49, and 28. For nests in which chicks died, the median number of larvae was, respectively, 49, 47, 37, and 26.5. As with age at death (Table 7), first- and second-hatched siblings suffered about the same number of infesting larvae, whereas their younger, and smaller, siblings suffered fewer. For nestlings that succumbed to their infestations, on average 13–14 fewer larvae were found on first- to third-hatched siblings, but only about two on fourth-hatched young, when compared to nestlings that either died or fledged (see Table 3 for explanation of statistical procedures and results).

Hatch orders	Died or fledged[1]		All died[1]	
	Q	$P < 0.05$	*Q*	$P < 0.05$
First vs second	0.65	No	0.82	No
First vs third	4.14	Yes	3.25	Yes
First vs fourth	3.73	Yess	4.82	Yes
Second vs third	3.60	Yess	2.95	Yes
Second vs fourth	3.47	Yes	4.66	Yes
Third vs fourth	1.91	No	3.21	Yes

[1] Chick fate.

Philornis ectoparasitism at different ages not only as a result of the intensity of larval infestations, but also as a consequence of the placement of the infesting larvae (see Smith 1968, Arendt 1985a). However, because larval implantation strategies of the ovipositing female botflies follow the ontogeny and pterylae development of each sibling within a brood throughout the breeding season (Arendt 1985a), the effects of larval placement will be similar within and among hatch orders and brood numbers. Therefore, analyses encompassed comparisons among brood number and hatch order.

Age at death of chicks varied significantly among the four brood categories. Half of the six between-brood comparisons were significant (Table 7, Fig. 20B), whereas there were no significant within-brood ages at death before vs after habitat disturbance.

Botfly larvae per chick among hatch orders. Quantifying larval loads per nest and for chicks among multiple broods reveals the intensity of the ectoparasitism at each nesting attempt, over the course of many breeding seasons, and in relation to pre- vs post-habitat disturbance conditions. However, it does not treat the more relevant question of individual sibling fitness. Because brood sizes are virtually equal (mean of 3 chicks) for parrots and thrashers, it is imperative to determine among hatch order (and at what ages) siblings may be more susceptible or resistant to infesting botfly larvae. Various analyses were performed under three broad categories: (1) by hatch order only (broods lumped); (2) by hatch order and brood number (1–4/season); and (3) by hatch order before and after habitat disturbance. Within each category, total numbers of infesting larvae per chick were compared.

To compare the intensity of botfly ectoparasitism among hatch orders (all broods combined), two analyses were done: one on all infested chicks (either died in the nest or

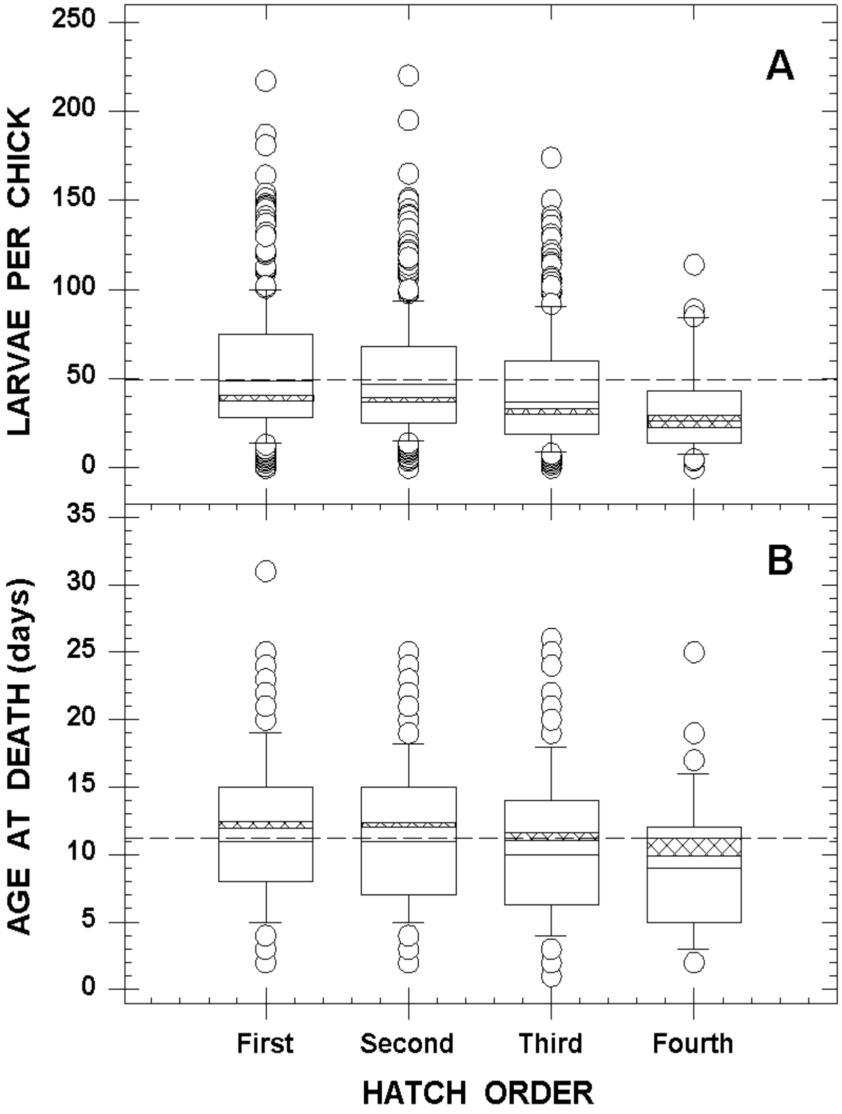

FIG. 21. Comparison of the number of infesting larvae (A) and age at death (B) by hatch order (broods combined) among chicks that died as a consequence of botfly ectoparasitism. Because of their larger size (owing to asynchronous hatching), the two oldest siblings live longer and harbor more infesting larvae than do their younger nest mates. As a result of brood reduction, fourth-hatched siblings, although receiving fewer infesting larvae, often succumb much earlier than even third-hatched young. Box-plot parameters and statistical inferences are described in Figure 8.

fledged), and the other on only chicks that died as nestlings as a result of the ectoparasitism. Results were similar for both comparisons. On average, the two oldest chicks in each nest (1st- and 2nd-hatched) received about the same number of larvae, which was

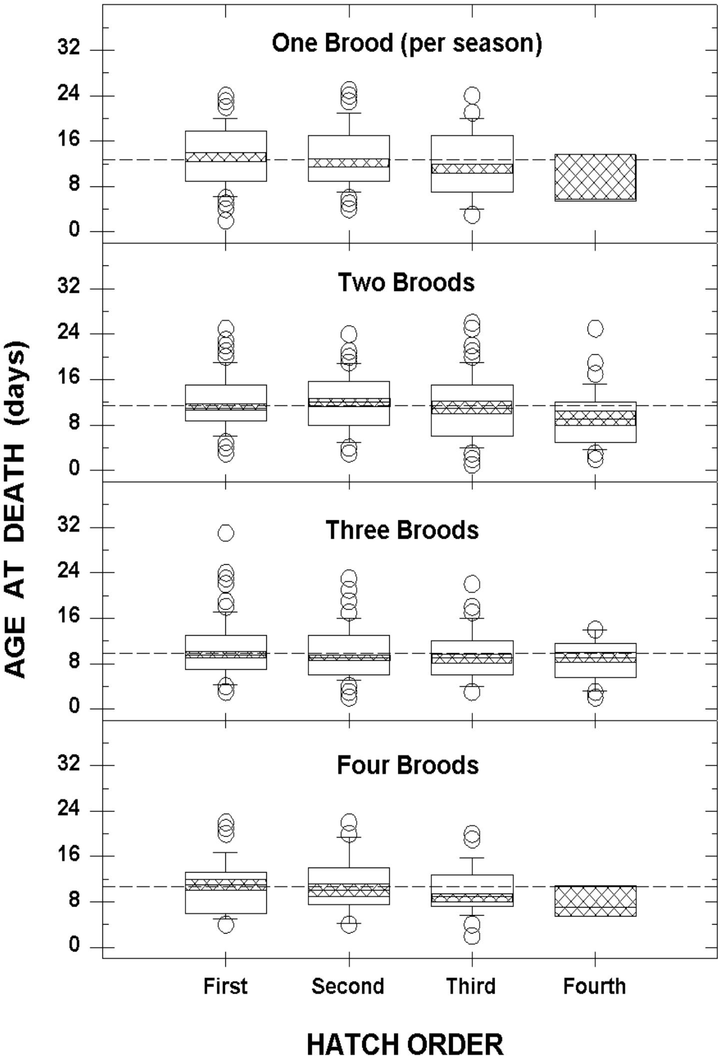

FIG. 22. Comparison of ages at death by hatch order among multiple broods at 42 thrasher nest boxes from 1979 to 1995. In general, The age (days old) at which siblings succumb to philornid ectoparasitism is comparable among hatch order and brood number, i.e., between 8 and 13 days of age. Box-plot parameters and statistical inferences are described in Figure 8.

significantly greater than larval intensities experienced by their two younger siblings (3rd- and 4th-hatched) (Table 8, Fig. 21A). The only difference between the two comparisons was that in nests in which all the chicks died from the effects of ectoparasitism, the youngest (4th-hatched) sibling received significantly fewer larvae than the third-hatched sibling (Table 8). Similar to larval intensities experienced, on average, the two oldest siblings in each nest lived longer than their younger nest mates before succumbing to the effects of

Table 9. Inter-brood comparisons among unparasitized and 100%-parasitized nestings throughout 14 thrasher breeding seasons from 1979 to 1995, excluding the 1983, 1984, and 1989 seasons. Proportions (*Z*-) tests were performed on the number of unparasitized or 100%-parasitized broods considered as proportions of all existing first or subsequent broods. Data used in this analysis are presented as percentages in Figure 23. Significantly more first broods escape ectoparasitism, whereas 100% parasitism is common in all broods throughout the breeding season.

Brood comparison	Unparasitized		100% parasitized	
	Z	P	Z	P
First vs second	3.17	0.00	0.74	0.45
First vs third	3.83	0.00	1.20	0.22
First vs fourth	2.07	0.03	1.39	0.16
First vs fifth	0.60	0.54	0.11	0.91
Second vs third	1.69	0.09	0.50	0.61
Second vs fourth	0.90	0.36	1.76	0.07
Second vs fifth	0.20	0.83	0.25	0.80
Third vs fourth	0.66	0.50	2.00	0.04
Third vs fifth	1.85	0.06	0.07	0.94
Fourth vs fifth	4.67	0.00	0.58	0.56

botfly ectoparasitism (Fig. 21B). The median age at death by hatch order (1^{st}- to 4th-hatched) was, respectively, 11, 11, 10, and 9 days, and age differences at death were significant in 4 of the 6 comparisons (Table 7). In comparisons of ages at death by hatch order among multiple broods, no significant age differences resulted except in two broods per season. In this category, 4^{th}-hatched chicks died at significantly earlier ages than either 1^{st}-hatched ($Q = 2.825$, $P < 0.05$) or 2^{nd}-hatched ($Q = 2.832$, $P < 0.05$) siblings (Fig. 22). In general, however, on average all siblings, regardless of hatch order or brood number, succumbed to philornid ectoparasitism at about the same age (mean = 10.6, minimum = 8, maximum = 13.2, days old).

In comparisons of intensity of botfly ectoparasitism by hatch order "before*,*" "after*,*" and "before vs after" a major habitat disturbance, the intensity of larval loads per chick did not differ significantly in any of the three categories except for three broods per season. Before disturbance, median numbers of larvae per chick by descending hatch order (1–4) were, respectively, 75, 66.5, 50, 29. Post-disturbance median numbers were, respectively, 85, 79, 73, 23. Pre- vs post-disturbance differences in larval intensities were significant (Mann-Whitney rank sum test: $T = 15{,}705$, $P = 0.00$). Ages of chicks at death did not vary significantly among hatch order or brood number in any of the three habitat disturbance-related categories ("before*,*" "after*,*" and "before vs after"), except in two broods before disturbance. Within two broods per season, the two oldest siblings lived significantly longer than did their 4^{th}-hatched siblings ($Q = 2.676$, $P < 0.05$, $Q = 2.639$, $P < 0.05$, respectively). Median ages at death within double broods by descending hatch order were 15, 15, 12, and 6.5.

Ecological correlates of botfly ectoparasitism. The two extremes of ectoparasitism are unparasitized and 100%-parasitized broods (= nests). In the following analyses "unparasitized" always refers to unparasitized broods. Only 50 of 526 broods (less than 10%) produced in 22 boxes over the past 17 breeding seasons escaped ectoparasitism. Contrarily, the category "100% parasitism" refers to broods in boxes (n = 21 boxes) in which all nesting attempts (39%) experienced botfly ectoparasitism (n = 430 of 1112 broods).

The frequency of unparasitized nestings varied greatly among brood numbers (Fig. 23), but significantly so only between first and subsequent broods (Table 9). Most unparasitized nestings (38 of 50, or 76%)

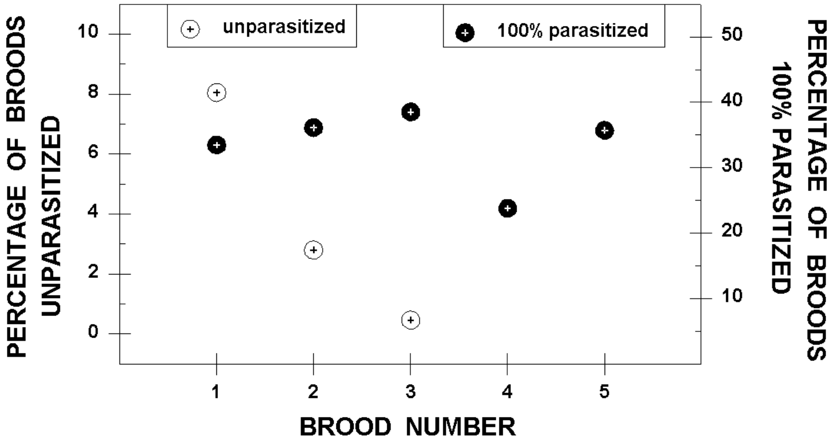

FIG. 23. Comparison of unparasitized nestings (n = 50) and nestings in which philornid ectoparasitism was evident during every nesting attempt (n = 430) among multiple broods at 42 thrasher nest boxes from 1979 to 1995. Not a single nest box remained unparasitized throughout the specified period, whereas half (n = 21) of the boxes experienced philornid ectoparasitism during every thrasher nesting attempt throughout the course of the study.

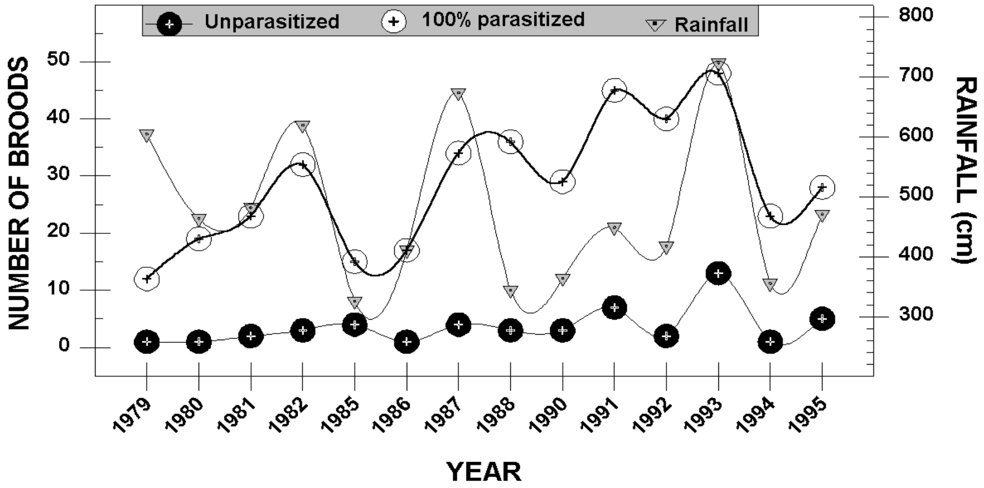

FIG. 24. Yearly comparisons between rainfall and instances of unparasitized and 100%-parasitized nestings. Correlations were not significant for either unparasitized or 100%-parasitized broods. However, there was a tendency for a direct correlation between years with heavy rainfall and 100%-parasitized broods.

occurred within first broods of the season, and no fourth or fifth broods escaped ectoparasitism. At the other extreme, within boxes in which every nesting attempt experienced ectoparasitism, 100%-parasitized nestings were more evenly distributed among all five

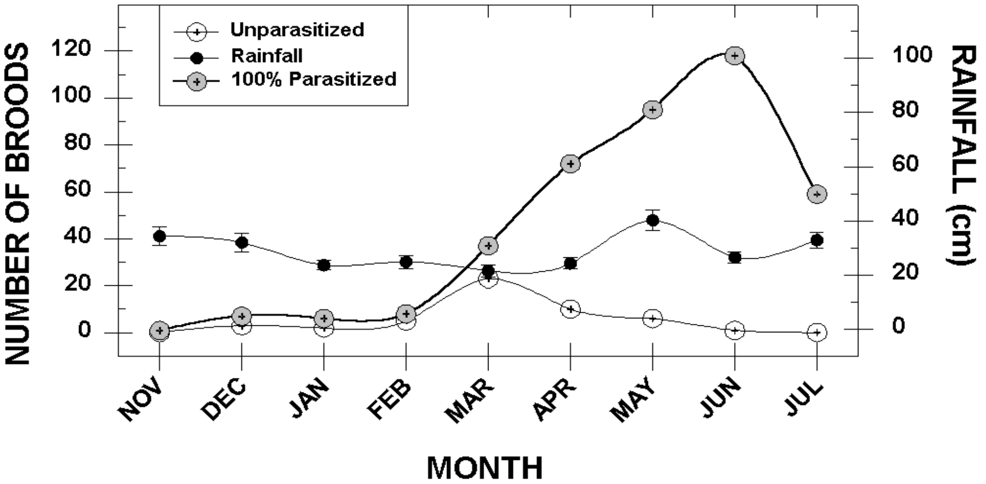

FIG. 25. Monthly comparisons between rainfall and instances of unparasitized and 100%-parasitized nestings. As among years, monthly comparisons were not significant for either unparasitized or 100%-parasitized broods, although unparasitized broods decreased and 100%-parasitized broods increased with a monthly increase in rainfall.

broods (Fig. 23, Table 9). However, although there was no significant difference in numbers of unparasitized broods before (median = 2.5) or after (median = 4) a major habitat disturbance (*T* = 55, *P* = 0.22, Mann-Whitney rank sum test), there were significantly more (*T* = 73.5, *P* = 0.04) 100%-parasitized broods following disturbance (median = 35.5) than prior to it (median = 21).

Rainfall in the LEF is highly correlated with elevation (Garcia *et al.* 1996). Therefore, to compare unparasitized with 100%-parasitized nestings, rainfall was again correlated with year and month, and elevation (its topographical equivalent) was compared with the location of each box.

Rainfall was correlated (but not significantly, r_s = 0.242, *P* = 0.39, Spearman rank order correlation) with inter-year occurrences of unparasitized nestings (Fig. 24), but not inversely as expected. Contrarily, 100%-parasitized nestings were directly correlated (but not significantly, r_s = 0.255, *P* = 0.36) with rainfall (Fig. 24). On a monthly basis, the frequency of unparasitized nestings was inversely correlated (but not significantly, r_s = -0.321, *P* = 0.43) to rainfall (Fig. 25). There was no correlation (r_s = 0.100, *P* = 0.78) between rainfall and 100%-parasitized nestings on a monthly basis (Fig. 25). The frequency of 100%-parasitized nestings continued to climb after February of each year, dropping slightly in July because of many fewer samples for that month.

In relation to elevation, unexpectedly, there was a strong direct correlation (r_s = 0.50, *P* = 0.017) between the frequency and percentage of unparasitized broods and an increase in elevation (Fig. 26A). There was also an unanticipated weak indirect correlation (r_s = 0.202, *P* = 0.376) between increasing elevation and the frequency of 100%-parasitized broods (Fig. 26A). Another evident and noteworthy trend was a cluster of boxes (nos. 21–31) at higher elevations in which the frequency of unparasitized nestings is at its greatest and, conversely, no 100%-parasitized nestings have occurred within this

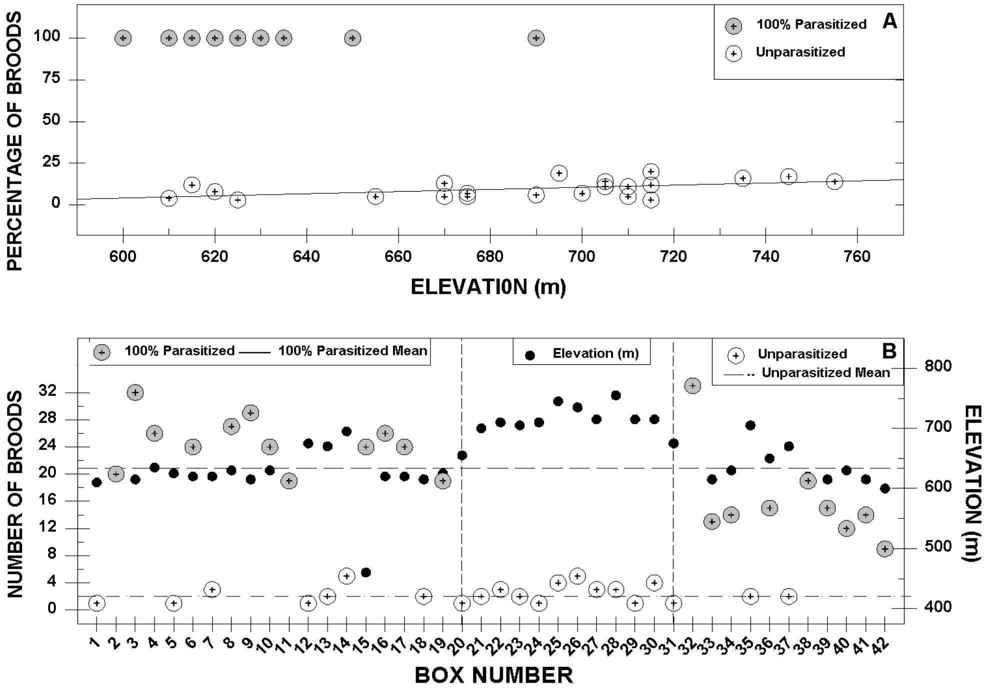

FIG. 26. Comparisons between elevation and instances of unparasitized and 100%-parasitized nestings. Contrary to the expected, the frequency and percentage of unparasitized nestings were higher at higher elevations, whereas most 100%-parasitized nestings occurred at lower elevations. Note the cluster of boxes (nos. 21 through 31— bordered by vertical dotted lines) in which about half (10 of 21) of the unparasitized nestings took place, but not a single box within the cluster experienced 100% ectoparasitism.

cluster of boxes during the past 17 breeding seasons (Fig. 26B).

DISCUSSION AND CONCLUSIONS

Populations of the Pearly-eyed Thrasher in Puerto Rico and other islands

Historical records show that in Puerto Rico, as among many other islands (Montserrat, Bonaire, and several northern Bahamian islands), populations of the Pearly-eyed Thrasher have undergone substantial intra-island population increases within the last 30–60 years (Arendt 1993, in press). Thrasher numbers have increased considerably in the Sierra de Luquillo within the last 40–50 years (Snyder *et al.* 1987). This documented influx of thrashers to these mountains closely followed the immigration of thousands of people to cities and subsequent urban sprawl during the 1950s and 1960s. Extensive urban development and planting of abundant fruit-bearing exotics as ornamentals during this period may well have augmented thrasher populations by creating more nesting and food resources in urban areas. Dispersing thrashers, capable of inter-island dispersal (Arendt 1993), might easily have immigrated to the nearby species-poor habitats of the Sierra de Luquillo. These, as well as other species-poor interior mountain ranges, could have served as ecological “sinks” for dispersing individuals. However, over the past half century, thrasher populations have leveled off or even decreased in many of these montane habitats, possibly due to saturation dispersal.

Effects of nest predation and bothflies: nest boxes vs natural cavities

Nest predation at thrasher nest boxes. Concern has been raised regarding the validity, or at least the equivalency, of nest predation and parasitism results obtained from studies of "nest-box" vs "natural" cavity populations of birds (Møller 1989, 1992; Purcell *et al.* 1997). Rates and results of nest predation on thrashers could be significantly different in nest boxes if they were placed so close as to significantly increase thrasher densities along the transect, thus increasing the probability of nest predation and, consequently, a reduced reproductive success.

Long-term life-history and population census data from the LEF and comparative population census data in similar habitat on other islands have shown that the 42 boxes used in this study are not numerous enough or spaced so close (every 0.1 km) as to increase thrasher numbers or densities (Arendt, in press). This reduces the possibility of artificially or significantly increasing nest predation. That nest predators and competitors accounted for less than 10% of egg and chick losses substantiates this premise. Furthermore, the 10% reduction in reproductive potential observed in this study is similar to percentages observed elsewhere in the insular Neotropics. Moreover, nest predation in insular species is often higher than that in continental breeders (Loiselle & Hoppes 1983, Gibbs 1991, Latta *et al.* 1995). Whereas nest predation at elevated nests is commonly 1–3 percent in tropical forests on the mainland (Costa Rica and Panama), it is 7–10 percent (or higher — see Loiselle & Hoppes 1983) in insular forests (Barro Colorado Island — Panama, and Puerto Rico). It is noteworthy that Latta *et al.* (1995), after having conducted an independent, short-term experimental study (29 April–26 May 1993) using elevated open-cup nests in the LEF, arrived at a similar rate of egg predation as found in the present study (6.5% and 9%, respectively). Thus, it is highly unlikely that nest predation results from this nest box study are sufficiently different to merit concern than if, for instance, they had been obtained from natural-cavity nests.

Ectoparasitism within thrasher nest boxes. Also expressed, has been a concern that old nest material left in boxes or natural cavities often harbors large populations of nest parasites, which may in turn affect the host's acceptance of the nest site and subsequent reproductive success (Møller, *et al.* 1990, 1993; Rendell & Verbeek 1996). Contrarily, in nest-box studies in which nest material from previous broods is removed, one may be biasing for increased nesting attempts and an artificially higher reproductive success. There is growing evidence that some species of birds are adapted to heavy parasitism and thus select clean (parasite-free) boxes, or at least parasite-free nests, over those boxes in which nesting material has been left or nests that contain large numbers of parasites (Møller 1990, Oppliger *et al.* 1994, Merino & Potti 1995, and references therein). In contrast, other avian species apparently do not prefer clean boxes (Thompson & Neill 1991, Davis *et al.* 1994, Johnson 1996, Pacejka & Thompson 1996). In the present study, the ecology of the ectoparasite and behavioral traits of its thrasher host act in unison to minimize these concerns.

In this study, 95% of 1170 thrasher nestings were parasitized. Half of the 42 nest boxes suffered 100% parasitism (every brood attempted within a given box throughout the study period suffered from parasitism), and more than half of the thrasher chicks succumbed to the effects of ectoparasitism over a period of 16 years (17 breeding seasons). Clearly, philornid botfly ectoparasitism is a major (if not the most important) biological factor lowering reproductive success in the forest's nest-box population of Pearly-eyed Thrashers. But, in light of the predation and ectoparasitism concerns outlined above, would these results have been similar for thrashers nesting in natural cavities or open-cup nests? I advocate that the answer is yes, although my conclusion is based on a much smaller sample size of natural nests.

In comparison with the results from the ongoing thrasher nest-box study, botfly ectoparasite loads were similar in natural-cavity nests of thrashers in parrot areas and from open stick-nests of thrashers found occasionally throughout the forest (Snyder *et al.* 1987, Arendt, unpubl. data). As yet, no evidence has been found suggesting that botfly ectoparasitism is higher (or lower) in nest boxes than in natural cavities or open-cup nests. To the contrary, when a "natural" (tree-cavity or open-cup) thrasher nest is found away from the nest-box area late in the breeding season (May and June), two heavily parasitized young of about the same size are usually present. Because third- and the occasional fourth-hatched chicks are noticeably smaller than their two oldest siblings, which are quite similar in size (Arendt 1985a), I have always surmised that the original brood size was the normal three (possibly four) chicks, and that the younger sibling(s) had died as a result of heavy philornid ectoparasitism, although other sources of mortality are possible (Arendt 1993). After May in any given year, in open-cup nests (many in bamboo thickets), I find parasitized thrasher young with more than 50 larvae (the average number in nest-box chicks during this period), thus substantiating the claim that thrasher chicks from natural cavities and open-cup nests do indeed receive comparable numbers of infesting botfly larvae.

Another reason that box- and cavity-nesting thrashers most likely experience similar rates of nest predation and ectoparasitism is that most of the concerns (e.g., biased densities of the host, predators, competitors, and ectoparasites) are not applicable to nesting thrashers. In my study, I do not discard old nest material from boxes before subsequent clutches, neither within nor between seasons, which could potentially lead to increased parasite loads and a lower reproductive success. However, within-season prevalence and intensities should be similar in both nest-box and natural cavities since females in both circumstances often use previous nests, only adding additional lining. More often however, in both cases, in response to heavy larval infestations, thrasher nestlings suffer from chronic diarrhea. Thus, at the time of fledging or death of the brood, the nest has "disappeared" into the matted and soiled substrate, necessitating construction of a subsequent (parasite-free) nest. Moreover, philornid pupae do not remain in nest boxes between breeding seasons. Instead, the adult flies emerge 2–3 weeks following pupation. Therefore, "old" nests left in boxes during the non-breeding season, and still present at the beginning of each subsequent breeding season, are free of viable philornid pupae. Furthermore, in thrasher boxes, it is common practice during nest building for the builder to toss (often hundreds) of twigs into the cavity, forming a platform over the old nest or substrate. In artificial nest structures built for parrots, thrashers have formed platforms towering more than two meters and composed of thousands of twigs. This behavior is no doubt an adaptation for (a) reducing the probability of inundation of nest contents in areas of high rainfall; (b) minimizing the effects of parasitism, (c) improving accessibility of the nest itself, and (d) facilitating the chicks' fledging and exit from within the confines of the box.

One final concern, that of the use of nest boxes and the scientific rigor of experimental studies (Møller 1992), is also not relevant to my thrasher research. Experimentation purposely has been kept to a minimum over the past twenty years with the objective of obtaining baseline data on the natural effects of predators, competitors, and ectoparasites on nesting thrashers, with additional observations on parrots. That having been accomplished, upcoming experimental studies will be more meaningful.

Nest predation, *Philornis* ectoparasitism, and habitat disturbance

Timing of nest predation and length of the parrot's breeding season. Results of the thrasher research show that each potential predator begins breeding in different months: thrashers (September–May); owls (March–April); and rats (April–May), and have variable-length nesting seasons: thrashers (8–11 months); owls (4–5 months); and rats (6–7 months). Not surprisingly, their monthly predation rates reflect both the onset and duration of their own breeding seasons. Rates of nest predation within the category "all predators combined" (= "missing from nest") are more or less evenly dispersed among all months, which reflects their combined wide temporal influence. Although thrashers depredate nest boxes of other thrashers early in the breeding season while searching for their own nest sites, much heavier losses of nest contents occurred in late May and June when more thrashers are searching for food for their own young, and recruits (first-time nesters) are pioneering for nest sites (Arendt, unpubl. data). Therefore, the potential for nest predation at parrot nests will remain high virtually throughout the entirety of its reproductive period, and will escalate at the same time that parrot chicks are most vulnerable.

Adaptations of nest predators and ectoparasites to prey availability. On average, nest predators prey upon thrasher chicks about three days before the average age at death (10 days) of chicks that succumb to botfly ectoparasitism. Predator-prey and host-parasite theories predict that predators and ectoparasites, respectively, will adapt strategies to "pluck the prey from the nest" or "exploit the host" before it fledges or dies. At the onset of this study, it was questioned why owls didn't postpone nest depredations until thrasher nestlings were much larger (almost fully-grown by the third week of the nestling stage), offering double the biomass (mean = 100.3 g at 21 days vs mean = 54.3 g at 7 days old) and thus greater nutritional value to both adult and dependent owls. Several years of data suggest that the thrasher's, and parrot's, major nest predators (owls, rats, and other thrashers) are depredating nests just before nestlings succumb to philornid ectoparasitism. It is not impractical to conclude that nest predators of avian species whose young frequently fall victim to ectoparasitism are capable of adapting a strategy of preying on chicks just prior to death, especially since the predators live and nest within close proximity of thrasher boxes and could easily monitor chick development almost on a daily basis. In the case of the thrasher, the most opportune time for the predator to take its prey is within the first 1–1.5 weeks of the nestling stage. In other species such as the parrot, there is probably a similar critical period just before the host's death. Most likely, the probability of finding prey after that critical time when most host young die from ectoparasitism may be so low as not to warrant the predator's efforts. It is imperative, then, that because the same predator-prey relationship holds true for the parrot, with its similar cohort of nest predators and ectoparasites, intense and constant nest guarding and other preventative measures must be undertaken during this critical period in the parrot chicks' development. Unfortunately, sample sizes of depredated and larval infested parrot chicks over the years has not been large enough to determine the critical period of growth and development as it relates to the timing of depredation and death resulting from ectoparasitism. Much more research is needed (see below).

Impact of Philornis *ectoparasitism on parrot and thrasher nesting.* Over a period spanning more than two decades, although the prevalence of philornid larvae among parrot nests and young was well below that of thrashers, larval intensities were quite comparable in the two species (see Snyder *et al.* 1987, Appendix 28). Furthermore, if nest monitoring and human intervention had not been enforced, it is likely that parrot nestling mortality and reproductive losses to *Philornis* ectoparasitism would have rivaled or surpassed (at least in percentage of losses) those of the thrasher.

In the thrasher, there are significantly fewer larvae in single-brood nests, often laid early in the season. One might logically assume that because the parrot is generally a single-brooded species, usually double clutching only after a previous nest failure, that the prevalence and intensity of *Philornis* ectoparasitism would be of less consequence to the parrot than it is to the thrasher. Past experience has shown us, however, that this is not the case. Historically, parrot chicks are known to suffer heavy larval infestations (Snyder *et al.* 1987, pers. exper.). This occurs because, even though the parrot may lay but a single clutch, it often lays 3–5 months later in the season than do thrashers laying their first clutches, and egg and chick development are slower in the parrot as well. Thus, chicks in the first broods of parrots are in the nest and exposed to heavy larval intensities at about the same time as second- and third-brood thrasher young (April–June). With a combined brood average of 50 infesting larvae per thrasher chick during this season, clearly parrot nestlings are also highly susceptible to heavy philornid botfly larval infestations.

First- and second-hatched thrasher siblings suffered heavier larval infestations than their younger nest mates. However, on average, third- and fourth-hatched chicks died at a younger age than the two oldest chicks as a result of ectoparasitism. Thus, the impact of botfly ectoparasitism is unquestionably more severe on younger thrasher nestlings, which often lose out to their older siblings in competition for food and parental care (brood reduction). Personal experience (and that of J. W. Wiley, pers. comm.) with infested parrot chicks from nests in the wild confirms that this is also the case in the Puerto Rican Parrot. Moreover, the relative vitality of infested parrot chicks is poorer than that of unparasitized young even when revived through management intervention (J. W. Wiley, pers. comm.). Knowing that younger siblings in a brood are more susceptible to the effects of philornid ectoparasitism, generally at an earlier age, will assist parrot managers in early detection and mitigation of the effects of infesting larvae.

One might intuitively predict that because numbers of infesting larvae continue to sharply increase with the passage of the breeding season, parrot chicks in broods hatched later in the season would succumb at earlier ages to botfly ectoparasitism, as was first thought to be the case in the thrasher. However, after separating age at death by hatch order, age at death did not decrease with the progression of the season, but was about the same among thrasher chicks from all broods. These results may also serve as a cue for parrot biologists. The overall average age at death among parrot nestlings may vary greatly to that of thrashers because of species differences in size, metabolism, other physiological processes, and especially exposure in the nest (length of the nestling period). However, ages at death of parrot chicks separated by hatch order may also reflect significantly disparate larval intensities. Older siblings may live longer before succumbing to ectoparasitism, and thus receive more larvae. Therefore, it may be unwise for parrot biologists to assume that just because a younger parrot chick harbors fewer larvae than its older sibling(s), it is in less danger of becoming incapacitated or succumbing to the ectoparasitism. However, more research is needed in this area (see below).

Parrot management following major habitat disturbances. Thrasher research has shown that following Hurricane Hugo, which caused extensive habitat destruction, owl and rat predation, as well as honeybee swarms, sharply increased. The roosting and predation rates of owls at thrasher nest boxes escalated sharply following major habitat destruction and probable resultant food shortages (see Lugo & Frangi 1993), from "before" vs "after" frequencies of, respectively, 20 to 40 and 20 to 30 instances. Similarly, rat predation on thrasher eggs and instances of honeybee swarming and cavity takeovers have also increased following habitat disturbance, and rat predation continues to increase. In the Pearly-eyed Thrasher, egg and chick losses to predation, competition, and philornid ectoparasitism were significantly higher following Hurricane Hugo, possibly owing to food shortages (Lugo and Frangi 1993), damage to, and successional regeneration of, forest vegetation (see Torres 1992) and destruction of traditionally proven (successful) nest sites. Following the passage of Hurricane Hugo, there was an obvious destruction of nest sites and a general opening of the forest canopy around nest boxes. Site surveys at thrasher nest boxes three days after the storm's passage showed that many boxes were exposed to direct sunlight as a result of defoliation and in some cases crown loss. In extreme cases, nest boxes and nest-box trees were felled as a result of the storm. Consequently, competition for thrasher boxes was keen within a few days after the storm (thrashers guard their nest boxes year-round) and lasted for weeks following disturbance, intensifying once again during the early weeks of the first post-disturbance (1990) breeding season. All of the post-disturbance events shown to affect thrashers also have been cited as impacting the Puerto Rican Parrot (Meyers *et al.* 1993, Meyers 1994, Vilella & Arnizaut 1994, Vilella & Garcia 1995). Thus, post-disturbance planning and management of the endangered Puerto Rican Parrot, as well as other cavity-nesting forest birds, must take into account these physical, biological, and ecological factors, making adjustments where necessary, such as initiating supplemental feeding, re-establishment of adequate nest sites, and reduction of exposure to predators, competitors, and ectoparasites.

Effects of rainfall, elevation, and botfly ectoparasitism on parrot nesting. Thrasher research has shown that botfly ectoparasitism varies significantly from month to month and year to year (significant in 81–97% of the 260 possible yearly combinations among three multiple-brood categories), and was generally correlated with rainfall. Thus, parrot stewards must be wary of especially wet years, seasons, and months, checking for larvae more frequently during wetter periods. That rainfall and elevation were not highly correlated with the prevalence and intensity of botfly ectoparasitism is most likely due to an artifact of the temporal scale used and the limited range of elevations involved in this study. In thrasher nest boxes during drier periods, nestlings remain unparasitized or are minimally parasitized by botflies. But, after especially rainy periods, heavy ectoparasite loads are found throughout the boxes. This cycle continues throughout the reproductive period. It is likely that monthly and yearly rainfall, even using only totals coinciding with the length of each thrasher breeding season, are too crude to show a tight correlation with larval intensities. Therefore, daily and weekly rainfall totals during each of the thrasher's breeding seasons over the course of the study are being analyzed to detect potential correlations between daily, weekly, and seasonal rainfall and the intensity of botfly ectoparasitism. With the exception of a single box located at an elevation of 460 m (up from Quebrada Juan Diego along Highway PR 191), the remaining boxes were located at heights ranging from 600 to 755 m (mean = 657, median = 630, mode = 615 m). Therefore, the limited elevational range has probably masked any biological relevance between elevation and severity of botfly ectoparasitism.

An additional ecological factor influencing the prevalence and intensity of botfly ectoparasitism may be the "openness" of the canopy surrounding the boxes. A closer look at nest boxes 21 through 31 located at higher elevations and, within which, more unparasitized broods were observed, revealed that most of the boxes were placed in "open," sparsely foliated areas. Surely, other physical, biological, and ecological factors (light, insolation, microhabitat humidity, and interspecifics — such as nearby arthropod communities), may be influencing nest-site selection and reproductive success, not only in thrashers and parrots, but also in other forest cavity-nesters. To adequately address these issues, nest boxes must be placed along a wide elevational gradient within the forest and among different forest types. In compliance, an expanded research study is under way (Arendt 1998). Ideally, boxes should be placed from sea level to mountain summit (1500 m). This, however, introduces other variables that must be taken into account. Additional confounding variables include: (1) a greater diversity, composition, and physiognomy of surrounding vegetation, (2) a much greater host of parasites, hyperparasites, and diseases, and (3) an increase in the constant threat to major habitat alterations in thrasher nest-box areas, including anthropogenic and natural stochastic events such as cutting, fires, and cyclonic disturbances.

Holistic approach to nest predation, nest-site competition, and ectoparasitism

In the early 1990s, a management decision was made to greatly reduce parrot nest guarding on the grounds that fledging success at minimally guarded nests is comparable to that in heavily guarded nests (Vilella & Arnizaut 1994, Vilella & Garcia 1995). This claim is now under evaluation because "fledging success" was often equated to empty nests at the estimated time of fledging (USFWS nest watchers, pers. comm.). Results from the thrasher research demonstrate that cavity-nesting birds such as the parrot and thrasher are vulnerable to a diverse host of biological agents that act in consort to reduce nesting success, and thus their lifetime reproductive success. Predation rates, nest-site competition, and the prevalence and intensity of botfly ectoparasitism vary significantly among years and months, increase with the progression of the breeding season, and escalate following major habitat disturbances. Moreover, the instances of predation, cavity takeovers, and the prevalence and intensity of botfly ectoparasitism are highly correlated with each predator's, competitor's, and ectoparasite's own breeding seasons which, altogether, virtually span the parrot's entire reproductive period.

Summary of threats to parrot nesting

The breadth and extent of the predatory and parasitic habits of the Puerto Rican Parrot's five main predators, competitors, and ectoparasites (i.e., thrashers, owls, rats, bees, and *Philornis* botflies) show that constant, intensive nest guarding, poisoning and trapping (rats), and repellents (against honeybees and botflies) in the vicinity of nesting parrots (cavities and cages) are necessary in our recovery efforts, especially during months of peak parrot egg (March–April) and chick (May–July) production. Nest guarding will be crucial at least until the parrot population increases to a point in which it can once again withstand these natural biological stresses. Unfortunately, nest predation, competition for nest sites, ectoparasitism, and related threats from a diverse group of organisms will continue to be a major threat to the reproductive vigor, and thus the very existence, of the Puerto Rican Parrot for many years to come.

RESEARCH AND MANAGEMENT GUIDELINES

Parrot research and management needs

1. Micro-habitat studies around parrot nest cavities to determine the relevance of selected site characteristics to the prevalence and intensity of botfly ectoparasitism, e.g., elevation, aspect (valley, hillside, ridgetop), canopy cover, penetrating light, moisture, humidity, heat, plant species diversity, composition, and physiognomy among other potential factors.

Many species of volant dipteran flies are known to "hilltop." They will select elevated topographical features to "stage" in preparation for mating, finding food, and host organisms. Another trait of dipteran flies is that they are also known to "trapline." They use regular flightways along which reliable food and host species occur in concentrations large enough as to warrant constant surveillance and energy expenditure. At the onset of the thrasher-botfly research, two immediate questions came to mind. How are botflies dispersed throughout the forest? Where are the heaviest concentrations, and how are the ovipositing philornid females cueing in on thrasher boxes? Because of the nature of the rugged montane terrain surrounding thrasher nest boxes (steep hillsides and deep valleys), "hilltoping" was not obvious and thus was thought to be irrelevant. However, well designed research, conducted over a longer period of time, in different forest types, and along an elevational gradient might prove fruitful (this behavioral trait of philornid botflies will be explored in cooperative research with J. E. Loye, Univ. California, Davis).

To learn how adult female flies were finding their thrasher hosts, an experiment was done to determine if botflies were attracted to light or dark surfaces. A light meter was used to compare light intensities at nest-box entrances, but no conclusive results were obtained. In a related experiment, white and black construction paper was coated with glue and placed on outer surfaces of nest boxes, but again without conclusive results. It is possible that with alternative study designs (heavy rains caused rapid deterioration of the construction paper), or possibly additional studies of longer duration, that the results of such studies may culminate in relevant management guidelines.

Ovipositing female botflies may be using chemoreceptors and olfaction to home in on hosts since it is known that botfly numbers increase after heavy rains, and odors such as chick excrement within boxes travel faster and over longer distances in moist air. The use of chemoreceptors and olfaction by botflies to find avian hosts may be a promising avenue of investigation (see below).

Because of its importance to nesting birds, the extent of "edge effects" on *Philornis* ectoparasitism is being addressed by Loye & Carroll (1995, and *in litt.*) and her colleagues in Belize. In her (and others') experience, dipteran ectoparasitism increases with edge. It is greater in open areas (Bennett & Whitworth 1991).

The question of "edge" and how it influences the prevalence and intensity of *Philornis* botfly ectoparasitism on nesting thrashers and parrots has always been a part of this research. Contrary to the above-cited studies, however, results obtained from this study suggest that thrasher boxes under closed canopy are receiving higher instances of botfly ectoparasitism. Why opposing results? It may be due to the dispersion of boxes in the present study. Because of the ruggedness of the mountainous terrain, most thrasher boxes are along road cuts. Although many are often recessed 10–30 from "edge" vegetation under closed canopy, there may not be enough true forest "interior" boxes to allow a forest "edge" vs. "interior" comparison. Other factors that could significantly affect my study results are the frequent high winds and periodic hurricanes constantly changing the physiognomy of the vegetation surrounding nest boxes, and sometimes the nest-box trees themselves, thus greatly influencing the effects of edge.

There is, however, one more alluring piece of evidence that suggests a reduced, rather than increased, rate of philornid ectoparasitism in "open" canopy and forest "edge" nest boxes. There is a noticeable absence of 100%-parasitized nests between boxes 20 and 31 in Figure 26B. Most of these boxes are placed along forest "edge" (trees bordering roads or in gaps) and many of them are distributed around the Puerto Rican Parrot (Luquillo) aviary near buildings and along driveways and footpaths. At the opposite extreme, most of the unparasitized broods resulted from nests within these same boxes (Fig. 26B). My expanded research, in cooperation with J. D. Loye, will address this enigma.

2. Test for plant species with natural compounds that would act as biocides and toxicants to repel adult botflies and their larvae, and inhibit or retard development.

The diversity and usage of secondary plant metabolites is well known. What is not so well known or understood is that birds, even passerines once thought not to possess the ability to smell their food, may be using olfaction, albeit seasonally, to discriminate among the volatile cues emitted by plants and thus line their nests with green vegetation containing these volatile compounds in an effort to deter nest ectoparasites (Clark 1991). Two species of European birds, long established in North America and both prone to nesting in cavities, the European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*) line their nests with plant species, such as wild carrot and fleabane (starling) and margosa (sparrow) containing ß-sitosterol which is effective as a repellent and oviposition inhibitor for mites, and is also used as a tick repellent by Indians (Clark 1991). In a separate study, McDonald *et al.* (1995) showed that leaf extracts from seven of eight tree species had significant repellent effects on houseflies.

Over the past 20 years, at least four commercially available pesticides have been used in experiments on the surrogate thrasher to test for suitability and use in parrot cavities to deter ectoparasites. Because of the high toxicity and long lasting toxic residuals of the chemicals used in commercial pesticides, they have never been used in parrot nest cavities. I propose that studies be done to find an alternative, and hopefully much safer and environmentally sound, natural biological control of nest ectoparasites. Ideally, plant species with volatile secondary compounds that could deter insects from parrot cavities should be used. Native forest species should be sought first, with additions of non-native or exotic species only as a last resort. A good place to start would be by examining and assaying green vegetation found in nests of other species of forest birds.

3. Determine which aspects of the ectoparasites' developmental stages are affected by the secondary metabolites in the identified and pre-selected green vegetation to be used in parrot nests.

Biocides and toxicants in green plants affect nest ectoparasites in many diverse ways, ranging from the inhibition of bacterial growth, hatching of the ectoparasite's eggs, retardation in its various developmental stages, emergence from the puparium, and the disruption of feeding and associated behaviors, to the stimulation of inhibitory sensory processes which in turn suppress appropriate orientation behavior (Clark 1991). To be fully effective, the mechanisms behind the observed effects of the secondary compounds found in the plant species identified for use in parrot nests must be recognized and understood. For example, if the volatile component in a pre-selected plant only inhibits the hatching of botfly eggs, it would be futile to assume success if the plant were placed in a parrot nest in which the larvae are already on the chicks.

4. Identify the sensory, behavioral, environmental, and ecological cues ovipositing female botfly are using to find their avian hosts.

As stated earlier, the use of chemoreceptors and olfaction, in relation to moisture-laden air, may be important in facilitating adult botflies in finding their hosts. But, there may be many other environmentally and ecologically related factors used by adult botflies to home in on their hosts. Identifying and understanding this multiplicity of factors is crucial in our attempts to ameliorate the effects of philornid ectoparasitism on the parrot. This research need becomes even more paramount with the recent discovery of ectoparasitism in captive parrots. Knowing how botflies find their host will help us micromanage the environments, especially surrounding vegetation, at both wild nests and parrot aviaries. The results from such studies could then be used by agriculturists and other animal husbandry entities whose livestock are infested by dipteran ectoparasites, especially the widespread species in the families Oestridae (bot and warble flies), Calliphoridae (blow flies), and Cuterebridae (robust botflies).

5. Keep and make available quantitative records of hatch order and ages of parrot siblings when they are infested and die as a result of *Philornis* ectoparasitism to determine the species' periods of greatest susceptibility.

Precise, quantitative records of *Philornis* ectoparasitism in the Puerto Rican Parrot must be kept and made available. Because psittacines are of a much older phylogenetic lineage than passerines such as the thrasher, such important physiological processes as growth and development, metabolism, core body temperature, and age at which homeothermy is attained, are much lower and slower in the parrot. All of these traits may influence the timing and development of botfly ectoparasitism. Whereas thrashers reach asymptotic growth in less than two weeks in at least five external characters (Arendt 1985a), parrots take more than a month (Snyder *et al.* 1987). Given comparable (to their size) numbers of infesting larvae, it is probable that parrot chicks can withstand larval infestations 2–3 weeks longer than thrashers before succumbing to the effects of ectoparasitism. But before meaningful management guidelines can be prescribed, more research is needed, perhaps by including studies with a more experimental approach involving surrogate psittacines.

Management recommendations

Pearly-eyed Thrashers. With the realization of the need for, and implementation of, deep nesting structures and the establishment of "sentry" thrashers (*sensu* Snyder *et al.* 1987), predation at parrot nests by the Pearly-eye has not been a major management concern over the past two decades. As an example, five of the last six parrot breeding seasons (1990–1995) have been free of thrasher predation. Only twice in 1993, at a single nest (SF1A), eggs and chicks were lost to thrashers in both the first and replacement clutches (USFWS, monthly reports). Overall, thrashers depredated only 2 of 34 nesting attempts (6%). Because thrasher predation is now minimal and generally involves a single offender, a "changing of the guard" (dispatching the culprit) may remedy the problem. However, the need for intensive and constant nest guarding, at least until the parrot population can withstand low predation rates, cannot be over emphasized.

Owls. Puerto Rican Screech-Owls roost and nest in tree cavities and thus pose at least a potential threat to nesting parrots because they are known predators of adults and nestlings of other cavity-nesting birds such as the Pearly-eyed Thrasher. Once again, close parrot nest guarding, with frequent nest checks for signs of owls roosting and nesting is imperative. Owls often leave a feather or two in the cavity and noticeably flatten the cavity substrate. Being able to recognize such signs early will greatly assist parrot stewards in identifying early roosting and pre-nesting behavior by the owl, which will give them an advantage in combating the situation and resolving the problem.

Rats. Rats are known to prey on nestling birds and are major predators of eggs. However, during the earlier years of the Puerto Rican Parrot restoration program (1972–1986), rats were a problem only at nests experiencing other problems, wherein the adult parrots were not displaying "normal" attendance behavior (Wiley 1980). Thus, nesting parrots, or at least those not suffering from abnormal parental behavior, apparently are effective in keeping rats away from their nest cavities. If this is generally the case in the wild, once parrot numbers increase substantially, rat predation may not be a major factor in lowering the parrot's reproductive success. However, because most nest predation at thrasher and parrot nests occurs during the rat's (April–June) breeding season (which largely overlaps with those of the thrasher and parrot), rat control should still be considered a high priority, especially in the early months (Feb. April) when most depredations of nesting parrots have been documented. Moreover, rat predation has increased sharply at thrasher nest boxes following a major habitat disturbance (Hurricane Hugo), a trend that may continue in light of the increase in frequency and intensity of violent windstorms in recent years.

Because rats are known to depredate nests unguarded by the adult parrots, nest guarding certainly would be a potential added benefit, especially during crepuscular hours when rats are just initiating or concluding their activities, and the time at which human sentinels could best intervene. In the past, nest guarding has helped to alleviate parrot losses to rats. However, nest guarding alone may not substantially lower the rate of predation owing mostly to the rat's ecology. Rats generally spend most of the daylight hours in the upper canopy, descending only at night to forage on the ground and in the mid-canopy, the location of most parrot nest cavities (Layton 1986, Snyder *et al.* 1987).

It would be more beneficial and ecologically sound to implement and maintain an effective trapping and baiting regime. However, the traditional baiting strategy (anticoagulant baits, namely warfarin and diphacinone, and occasionally a highly toxic zinc phosphide) used during the first two decades to control rats in and around parrot nest areas is undesirable owing to the potential of killing non-target organisms and the toxic residuals left in the environment for many years afterwards (see discussion in Snyder *et al.* 1987, p. 239). A more feasible alternative would be the use of non-toxic (to the environment and non-target organisms) rat poisons (e.g., Delmar Monitoring Pellets™ — composed of corn oil, cellulose, and molasses) around active parrot nests, and to install rat guards to minimize the potential of rat predation. Rat guards would need to be re-designed as they have been generally ineffective in the past (J. W. Wiley, pers. comm.). The intertwining of the branches of nest-trees with those of surrounding forest trees render conventional guards ineffective. Rat guards protecting (e.g., a shield surrounding) the nest cavity entrance would have to be designed separately for each cavity, owing to the disparate sizes and shapes of cavity entrances. This type of entrance-enveloping guard has been successful in the past (H. Abreu, pers. comm.; and pers. exper.).

Honeybee. The greatest threat by honeybees is the takeover of parrot nest cavities. This threat becomes crucial during the December-August breeding season, especially at active nests during critical stages of the reproductive cycle, namely, pairing and nest site tenacity, laying, hatching, and fledging. Instances of swarming and cavity takeovers in the LEF have increased over the years, especially after a major habitat disturbance and the arrival of the Africanized hybrid. Swarming and invading bees can injure or even kill adult parrots and their young. Swarm traps near cavities containing pheromone attractants to lure swarms away from nest cavities and repellent pheromones near the entrances of cavities should greatly reduce the threats that honeybees pose.

Philornis *botflies.* Removal of infesting larvae, although helpful, carries with it a high risk of injury, infection, impairment, and even death to the parrot host because of the species' thick integument and often sensitive locations of the infesting larvae (e.g., sensory organs, arteries, veins, and respiratory pathways). Alternative control measures must be sought. Moreover, control and management of botflies in and around parrot nest cavities will greatly depend on the outcome of the research proposed above in # 1 through # 4. Not until we better understand the ecology of philornid botflies, identify the sensory, environmental, and ecological cues used to find hosts, and identify suitable plants with natural volatile metabolites to repel or deter the ectoparasite's development, will we be able to prescribe effective management strategies to mitigate the impact of botflies on parrots or other forest birds.

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