PHILORNIS ECTOPARASITISM OF PEARLY-EYED THRASHERS. II. EFFECTS ON ADULTS AND REPRODUCTION

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ABSTRACT.—A rain-forest population of the Pearly-eyed Thrasher (*Margarops fuscatus*) suffered heavy ectoparasitism from the larvae of a tropical fly recently identified as *Philornis deceptivus*. The impact of parasitic attack was of less consequence to adult thrashers than to nestlings. Nestling mortality was high and was caused mostly by philornid ectoparasitism, other factors being negligible (3%). The extent of larval infestations fluctuated seasonally and was related to monthly rainfall. Infestation did not have to be heavy to cause debilitation and death. Larval infestation sites varied with the nestling's ontogeny, especially pterylae development. Overall 4-yr fledging success was 53.3%, fairly high for a tropical passerine. However, observations of heavily parasitized nestlings that died during fledging attempts and the deaths of postfledging juvenile thrashers suggest that first-year mortality may be as high as 80% in nestlings that suffered heavy larval infestations (357 of 448 nestlings). Juveniles face keen intraspecific competition after leaving the nest. A combination of high nestling and juvenile mortality and little opportunity for juveniles to enter the breeding population could greatly reduce this host's numbers. There are signs, however, that the Pearly-eyed Thrasher is adjusting to heavy philornid ectoparasitism by lengthening the breeding season and reproducing while fly populations are seasonally low (December–March) and, thus, may remain in abundance in the rain forest. *Received 31 August 1983, accepted 10 June 1984.*

MYIASIS "is the infestation of live human and vertebrate animals with dipterous larvae, which, at least for a certain period, feed on the host's dead or living tissue . . ." (Zumpt 1965). In the Old World, 5 genera of bird-infesting diptera from 3 major families (Neottiophilidae, Calliphoridae, and Muscidae) are reported to infest adults and nestlings or inhabit nests of at least 9 avian orders, 28 families, and some 70 species of birds (Owen 1954, Zumpt 1965, Pont 1974, Bakkal 1980). In the New World, species of the common European bird parasite *Protocalliphora* spp. (Calliphoridae; Plath 1919a, b) and a unique genus *Philornis* (Muscidae; Dodge 1955, 1963, 1968; Pont 1972) have been reported. Some 30 *Philornis* species have been collected and described from birds south of the United States to the Neotropics (Pont 1972). On Trinidad alone 10 species of *Philornis* associated with 29 avian species from 17 families are recognized (Dodge and Aitken 1968).

In Puerto Rico the endangered Puerto Rican Parrot (*Amazona vittata*), a cavity-nesting bird, is parasitized by larval philornids, which have caused the death of parrot nestlings. As part of a large-scale restoration program to save the parrot, study was begun on the Pearly-eyed Thrasher (*Margarops fuscatus*), a more abundant cavity-nesting species with a similar ecology. Pearly-eyed Thrasher nestlings also are infested by and die from philornid larvae. The Pearly-eyed Thrasher is restricted to the West Indies and has a patchy distribution, ranging from St. Vincent in the Lesser Antilles to the Bahamas (Bond 1979). This rapacious passerine, well known for its predatory habits (Rolle 1965a, b; pers. obs.), is omnivorous, feeding on a variety of fruits, invertebrates, and vertebrates. In the Luquillo Mountains it is monogamous and a secondary cavity-nester, often nesting in crevices and tree hollows.

Because several *Philornis* species are polytypic (Dodge and Aitken 1968), the taxonomy of this group has always been extremely difficult (reviewed by Aldrich 1923). In Puerto Rico two *Philornis* species have been reported: *P. obscura* (Van der Wulp) from Ponce and *P. pici* (Macquart) from Mayaguez (Wolcott 1948). Recently, adult specimens that emerged from puparia that I collected from thrasher nests in the Luquillo Mountains were identified as *P. deceptivus* Dodge and Aitken, 1968, by M. S. Couri, of the National Museum of Rio de Janeiro, Brazil. *Philornis deceptivus* previously had been recorded only on Trinidad, its type locality (Dodge and Aitken 1968, Pont 1972).

Although many host records involving philornid flies have been cited (Pont 1972), few studies have concentrated on the deleterious effects that infesting fly larvae can have on an avian host over extended periods of time. With the exception of recent studies by Smith (1968, 1980), Bakkal (1980), Hector (1982), and Winterstein and Raitt (1983), most of the literature on avian ectoparasitism involving Old and New World dipterans has been limited to the taxonomy of the adult flies and to partial description of their life history stages (Nielsen 1911; Gilbert 1919; Dodge 1968; Ledger 1969; Pont 1972, 1974). Some reports are anecdotal accounts of larval impacts on host species (Plath 1919a, b; Hindwood 1930).

This study was designed to better understand the host-parasite relationship and to quantify the direct effects that dipteran ectoparasitism can have on an avian host and its reproduction. Specific objectives were to determine 1) the general prevalence (percentage of host individuals infested; terminology of Margolis et al. 1982) and intensity (mean number of larvae/infested host) of larval infestations, 2) seasonal changes and how they affect the host-parasite relationship, 3) at which of the host's anatomical sites larvae are most often found, 4) the overall effects on host reproductive success, and 5) possible responses by the host to counter *Philornis* ectoparasitism.

Study Area and Methods

This study took place within the 11,200-ha Luquillo Experimental Forest located in eastern Puerto Rico (18°19'N, 65°45'W) at an elevation of ca. 800 m within subtropical lower montane forest (Holdridge 1947, 1967; Ewel and Whitmore 1973). A detailed description of this forest can be found in Odum and Pigeon (1970).

Annual rainfall varies from 3,000 mm in the foothills to more than 5,000 mm on the highest peaks (Odum et al. 1970). Rainfall within the main study site averaged 4,660 mm from 1935 to 1943 (Wadsworth 1948). A more recent 12-yr summary of NOAA data (1970–1981) from the Pico del Este weather station located about 5 km from the study site shows a mean rainfall of 4,117 mm, which indicates that rainfall patterns remain similar over long periods. Photoperiod varies little, with 12–14 h of daylight throughout the year. For a 9-yr period, Wadsworth (1948) showed that the temperature within the study site averaged 21.1°C (range 11.1–32.2°C).

Over a 4-yr period (1979–1982), I took data on 272 nests, 681 nestlings, and 105 adults of the Pearly-eyed Thrasher. I used artificial nest boxes designed as part of the Puerto Rican Parrot restoration program (Snyder 1977, Snyder and Taapken 1977). Boxes were installed at 0.1-km intervals between kms 12 and 17 along Highway 191, 3–50 m from the roadway within the rain forest. Additional nest boxes were added until the number of available boxes increased from 26 the first year to 48 the fourth year. From January 1979 to August 1982 nest boxes were visited throughout the breeding season on an average of every two days, but often on a daily basis during critical periods (laying, hatching, and fledging). During the nonbreeding season (September–November) boxes were checked once a week or once every two weeks for signs of nesting, depending on the proximity of breeding activity. After eggs hatched, I checked the nestlings for fly larvae at every nest visit, noting numbers, positions, and infestation periods of the larvae. I trapped larvae in funnels below the nest cup and allowed them to pupate in small sawdust and woodchip vials covered with screens. I also collected puparia that adhered to nest twigs. During the 1979 and 1980 breeding seasons I removed larvae from some nestlings as soon as they were detected in order to determine thrasher fledging success in the absence of ectoparasitism.

To determine if ectoparasitism was dependent upon sibling hatch order, I randomly chose 90 parasitized nestlings (3/nest), separated them by hatch order, and performed a one-way analysis of variance test ($\alpha = 0.05$; Snedecor and Cochran 1980) on the mean number of infesting larvae/nestling (from the total number of infesting larvae found during the entire nestling period). Bartlett's test revealed heterogeneous variance among classes, so I used a square-root transformation to stabilize the variance.

I tested the significance of the difference between two proportions (Sokal and Rohlf 1969) to determine if adult female thrashers experienced significantly more fly larvae than adult males and to determine if site specificity of the infesting larvae on thrashers differed significantly between adults and nestlings. To test for a significant correlation between site specificity of the larvae on nestling thrashers (dorsal locations on young nestlings vs. ventral sites on older young), and to test for possible temporal variation (early vs. late season) in larval site specificity, I used a nonparametrics test for correlation (phi coefficient; Conover 1971).

Adult and nestling thrashers were individually marked with color bands and a metal USFWS band for field identification. Outside of the breeding season adult thrashers were captured in mist nets located in their territories. During the breeding season adults were captured by the use of pull-string trapdoors mounted on the nest boxes. Observations were made from burlap blinds with fiberglass roofs placed

TABLE 1. Monthly prevalence and mean intensity of *Philornis deceptivus* larvae on 105 adult Pearly-eyed Thrashers (1979-1982).

Month	Percent prevalence (n)[a]	Intensity (range)
January	0 (7)	0
February	0 (6)	0
March	15.0 (20)	3.3 (2-6)
April	21.1 (19)	1.7 (1-2)
May	25.9 (27)	4.0 (1-6)
June	64.3 (14)	3.5 (2-7)
July	91.7 (12)	3.2 (1-6)

[a] n = number of parasitized adult thrashers.

TABLE 2. Monthly prevalence and mean intensity of *Philornis deceptivus* larvae on 448 nestling Pearly-eyed Thrashers (1979-1982).

Month	Number of nestlings sampled	Prevalence (%)	Number of parasites	Intensity (range)
January	3	100	69	23.0 (19-26)
February	25	80.0	432	20.6 (0-49)
March	43	81.4	1,086	25.3 (0-73)
April	97	96.9	4,215	40.9 (0-220)
May	115	100	4,720	45.4 (6-131)
June	95	100	6,294	61.7 (3-169)
July	70	100	2,946	42.1 (5-135)

5-20 m from the nest boxes. Four nestlings were fitted with radio transmitters in a study of postfledging mortality. Three of these birds hatched in the same nest box, 1 young from the first brood (March) and 2 from the second (May). The fourth individual was selected from a distant nest box at the end of June. Each radio package consisted of a model 1220-LD transmitter with elastic harnesses. Each transmitter weighed 5.5 g, or ca. 5% of the nestling's body mass. A 3-element Yagi null-peak system antenna and model TRX 24 receiver were used to locate radio signals. Radiotelemetry equipment was supplied by Wildlife Materials, Carbondale, Illinois.

RESULTS

General patterns of infestation.—Examination of 105 adult Pearly-eyed Thrashers during the reproductive period (January-July) in 1979-1982 showed that 31% were infested with larvae of *P. deceptivus* (Table 1). A mean intensity of 3.1 larvae/bird (range 1-7) was observed. Because sample sizes were small, between-year comparisions were not made. However, it was apparent that prevalence of infestation (percentage of host individuals infested) did change over the reproductive period. No adult thrasher was found infested during January or February, while prevalence of infestation increased from 15.0% in March to 91.7% in July. Mean intensity of infestation (mean number of larvae/infested host) ranged from 3.2 to 4.0 for all months except April, when 1.7 larvae/bird were observed. The presence of large cutaneous lesions (ca. 3-4 mm in diameter), left by vacating larvae about to pupate, indicated that successive larval infestations occurred. Incubating and brooding female thrashers were infested more frequently than males, which do not incubate or brood. Of 60 captured females, 28 (46.7%) were parasitized, while only 6 of 45 males (13.3%) were infested ($P < 0.0001$; Sokal and Rohlf 1969). Females constituted 80% (28 of 34 individuals) of adult thrashers found to be parasitized by philornid flies.

Ninety-six percent of 448 nestling Pearly-eyed Thrashers examined from 1979 to 1982 were infested with philornid larvae (Table 2). Prevalence of larval infestation over the reproductive season ranged from 80 to 100%. With few exceptions, all nestlings were parasitized each month. Overall mean intensity was 37 larvae/nestling (range 0-220). However, mean intensity increased from 20.6 larvae/nestling in February to 61.7 larvae/young in June. This increase corresponded with an increase in the number of nestling thrashers available for philornid infestation and the total number of fly larvae found on nestlings (range 69 in January to 6,294 in June). Wide monthly ranges in the number of larvae/nestling show the variability of larval infestations at different nest boxes each month.

Initial infestation by philornid larvae on nestling thrashers varied greatly over the reproductive period. Throughout the first two-thirds of the breeding season (February-May) adult flies did not parasitize a nest until the oldest nestling was about one week old (Table 3). Although the oldest nestling was not always the first sibling parasitized, I based the timing of initial parasitism on the vulnerability of the first available host (first-hatched nestling). Larvae remained in the hosts an average of 5.1 days (SD = 1.07, range 3-9, n = 500). Although successive infestations were common, larvae

TABLE 3. Mean age (days) of the oldest Pearly-eyed Thrasher nestling in a brood at initial infestation by *Philornis deceptivus* larvae (1979–1982).

Month	Mean age ± SD	n	Range[a]
February	6.90 ± 2.49	23	5–14
March	7.00 ± 4.02	30	2–14
April	7.26 ± 4.35	50	1–17
May	7.07 ± 3.32	50	3–14
June	4.32 ± 1.87	50	0–8
July	2.41 ± 1.17	50	0–4

[a] 0 = hatch day, i.e. less than 24 h old.

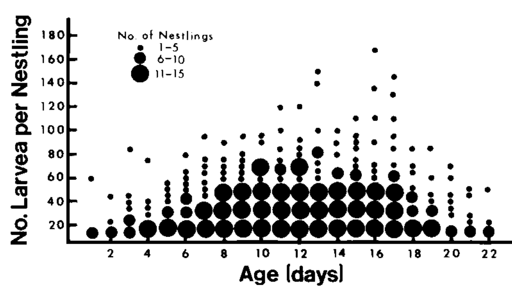

Fig. 1. Numbers of *Philornis deceptivus* larvae infesting Pearly-eyed Thrasher young during the nestling period. Outlying points, especially those at the beginning and end of the nestling period, represent late-season young.

tended to complete development during the middle portion of the nestlings' development period (Fig. 1). Late-season nestlings that hatched in June and July, however, were heavily parasitized within the first two days after hatching. Late-season young that lived to fledge often harbored 50 or more larvae during their last day in the nest (Fig. 1).

No significant difference was found in the total number of larvae/young and hatch order of the nestlings within individual nest boxes. All siblings within a brood received about the same numbers of infesting larvae ($\bar{x}$ = 30.8, 32.0, and 32.8 larvae/nestling, respective to hatch order; $F_{2,147} = 0.04$, $P > 0.250$).

Site specificity.—Although philornid larvae were observed on all body surfaces of the birds, significant differences in some specific sites of infestation were found between adult and nestling thrashers (Table 4). Almost 60% of the larvae found on adults were located on the ventral surface of the wings, with 30% in the patagial membranes, 17% in the axillaries, and the remaining larvae in brachial sites more or less evenly distributed among the humerus, ulna, and manus. A large larva (15 mm long × 5 mm wide) was found at the base of a recently replaced primary pinfeather on one adult thrasher. The second most common site of infestation on adult birds was the head region. Most larvae were found at the base of the bill, lores, and above the eye orbits. One larva was found developing in a lower eyelid, forcing the lid to close partially. Larvae also were found in the ventral tracts, humeral tracts, and interscapular regions of the capital tract.

Of the larvae infesting nestling thrashers, 54% were found on the trunk, with 38% on ventral surfaces in association with feather papillae at the base of the two ventral tracts (Tables 4, 5). It was not uncommon to find 50 or more larvae along the tracts, lying in clusters of 10 or more. Many larvae also were found on the wings of the nestlings throughout development (Tables 4, 5). Common sites included the rapidly developing manus and ulnas, future sites of the fast-growing brachial feather papillae (Table 5). Interestingly, in the tarsi, whose growth was greatly affected by philornid ectoparasitism (Arendt 1983), larvae aggregated in the region of the tibiotarsus and at the tibiotarsal joints throughout the nestling period (Table 5).

The distribution of infesting larvae varied with the nestling's ontogeny (Table 6). There was a positive correlation [$\alpha = 0.05$, phi coefficient = 0.4, critical level (P-value) < 0.001] showing that significantly more larvae infested dorsal areas in young nestlings (0–9 days old) and significantly more larvae infested ventral areas in older nestlings (10–19 days old) during the first half (early season) of the reproductive period. A positive correlation also was found for nestlings hatched during the second half

TABLE 4. Site specificity of *Philornis deceptivus* larvae on adult and nestling Pearly-eyed Thrashers (1979–1982).

Site of larval infestation	Larvae at each site (%) Adults (n = 34)	Nestlings (n = 432)	P
Wing	58.8	19.2	$P < 0.0001$
Head	14.7	17.2	NS
Trunk			
Ventral	11.8	30.4	$P < 0.02$
Dorsal	8.8	14.1	NS
Legs	5.9	19.1	$P < 0.05$

TABLE 5. Comparison of relative abundance of *Philornis deceptivus* larvae at specific anatomical sites on 205 nestling Pearly-eyed Thrashers (1982).

Early season (9 Feb. to 15 May)			Late season (16 May to 27 July)		
	Larvae			Larvae	
Site of infestation (n)[a]	n	%	Site of infestation (n)[a]	n	%
Ventral tracts (93)	1,690	34.2	Ventral tracts (82)	1,555	23.6
Tibiotarsus (91)	582	11.8	Tibiotarsus (97)	864	13.1
Ulna (84)	374	7.6	Crown, orbits (83)	580	8.8
Manus (83)	312	6.3	Ulna (84)	448	6.8
Crown, orbits (66)	283	5.7	Manus (74)	404	6.1
Tibiotarsal joint (70)	220	4.5	Tibiotarsal joint (72)	373	5.7
Humeral tract (66)	210	4.3	Humeral tract (80)	315	4.8
Throat and underneck (61)	182	3.7	Throat and underneck (71)	288	4.4
Dorsal region (62)	157	3.2	Dorsal region (87)	288	4.4
Flanges (76)	148	3.0	Pelvic region (77)	227	3.4
Cloaca (50)	146	3.0	Humerus (76)	222	3.4
Humerus (66)	136	2.8	Patagial membrane (69)	198	3.0
Pelvic region (66)	135	2.7	Flanges (88)	191	2.9
Patagial membrane (54)	123	2.5	Foot pads (65)	121	1.8
Base of culmen (37)	59	1.2	Upper neck (55)	118	1.8
Upper neck (34)	54	1.1	Cloaca (32)	114	1.7
Interscapular region (33)	51	1.0	Interscapular region (50)	113	1.7
Oil gland (20)	37	0.7	Oil gland (55)	91	1.4
Foot pads (25)	36	0.7	Base of culmen (47)	85	1.4
Total	4,935	100.0		6,595	100.0

[a] n = number of parasitized nestling thrashers.

(late season) of the reproductive period, but it was less obvious (phi coefficient = 0.28) because of the presence of more larvae in the ventral areas early in the nestling stage (Table 6). However, the critical level remained less than 0.001.

Nestling death and debilitation.—Nestling mortality was high and was caused almost exclusively by *Philornis* ectoparasitism. Of 448 thrasher nestlings infested with fly larvae in naturally parasitized nests over the 4-yr study period, 209 young died as a result of ectoparasitism (Fig. 2). Other causes of mortality were incidental (3%). Fifteen nestlings died from such causes as disease, death during hatching, rat and unknown predation, windstorms, and being trampled by siblings. During the 1979 and 1980 breeding seasons 73 of 74 (98.6%) unparasitized nestlings successfully fledged at nests in which all larvae were removed from nestlings. In contrast, during the 1981 and 1982 breeding seasons nestling mortality at naturally parasitized nests reached 55.8% in 1981 and 41.6% in 1982.

In nestlings that succumbed to philornid ectoparasitism, the pattern of larval infestation was similar to that found in parasitized nestlings in general (Fig. 1). The numbers of infesting larvae increased during the middle portion of nestling development and declined rapidly as the normal fledging period approached (Fig. 3). Among nestlings that succumbed to ectoparasitism, first- and second-hatched siblings withstood significantly greater numbers (Duncan's New Multiple Range Test)

TABLE 6. Distribution of infestation sites of *Philornis deceptivus* larvae on 205 nestling Pearly-eyed Thrashers during development and throughout the reproductive season (1982).[a]

	Early season (n = 88)[b]		Late season (n = 117)[b]	
	Age (days)		Age (days)	
Site	0–9	10–19	0–9	10–19
Dorsal	785	495	1,383	479
Ventral	767	2,888	1,951	2,782
	$\phi^c = 0.402$, $P < 0.0001$		$\phi^c = 0.282$, $P < 0.0001$	

[a] Presented as total numbers of larvae from each anatomical zone. Early season is 9 February to 15 May; late season is 16 May to 27 July.
[b] n = number of parasitized nestling thrashers.
[c] Phi coefficient of correlation (see Methods).

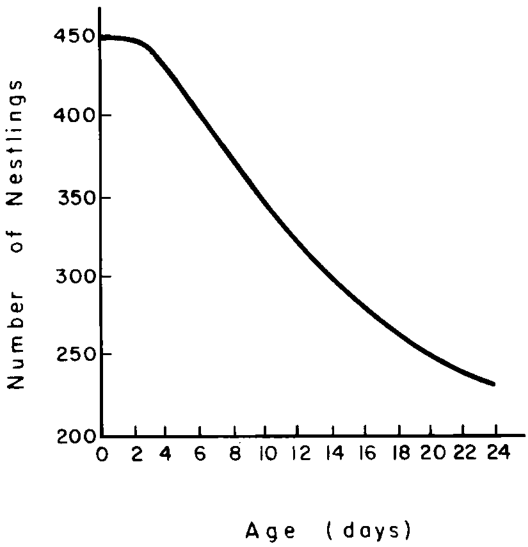

Fig. 2. Survivorship of 448 Pearly-eyed Thrasher young during the nestling period (1979-1982). Not all nestlings were parasitized by *Philornis deceptivus* larvae, nor did all infested nestlings die.

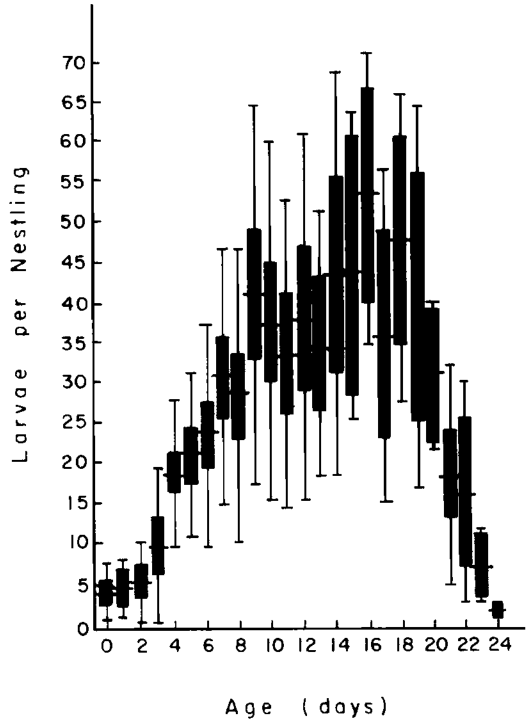

Fig. 3. Daily numbers of *Philornis deceptivus* larvae on Pearly-eyed Thrasher young that died from ectoparasitism during the nestling period. Vertical lines are ±1 SE, horizontal lines are mean numbers, and closed rectangles are 95% confidence intervals; width of rectangles was chosen arbitrarily.

of infesting larvae ($\bar{x} = 65.1$ and 59.6 larvae, respectively; $F_{2,87} = 4.13$, $P < 0.025$) and survived longer ($\bar{x} = 12.9$ and 12.1 days, respectively; $F_{2,87} = 3.12$, $P < 0.05$) than third-hatched nestlings ($\bar{x} = 41.0$ larvae and 9.1 days).

The extent of larval infestations on thrashers fluctuated seasonally, increasing each month (Fig. 4), and apparently was related to monthly rainfall. Increased rainfall was associated with higher mortality (Fig. 5). Nestling mortality was higher in the wetter 1979 (50.0%) and 1981 (55.8%) breeding seasons than in the drier 1980 (35.6%) and 1982 (41.6%) seasons. Similarly, nestling mortality from February to May averaged 60% in the wetter years, as compared to only 20% in the drier years. Post-May mortality increased in all years as host and parasite populations increased.

The age at which thrasher nestlings succumbed to philornid ectoparasitism was dependent upon their initial age and size at the onset of larval infestation, the total numbers of infesting larvae, and the season. I arbitrarily designated larval infestation as light (1-30 larvae/individual), moderate (31-60), and heavy (>60). In recently hatched nestlings as few as 5 larvae caused death. Therefore, lethal infestations (no matter how few infesting larvae) were considered heavy. Of those nestlings that succumbed to philornid ectoparasitism, the average age at death was 11.1 days (SD = 5.19; range 2–31) from February to June. It dropped to 7.4 days for July of each year, when fly populations had greatly increased. Nestlings hatched in late June and July were often parasitized within a day after hatching, suffered higher larval infestations, and died within a week.

If larval infestation occurred at or just after hatching, even light larval loads caused death up to the fifth day (Table 7). Heavy larval infestations suffered by nestlings in June and July raised the average number of larvae at death greatly, as shown by the wide ranges in Table 7.

A single or a few infesting larvae caused debilitation when they occurred in sensitive areas of the nestling's body. In a nestling infested with 3 larvae, scar tissue remaining after the evacuation of single larvae from the left and right auditory meatus caused them to close

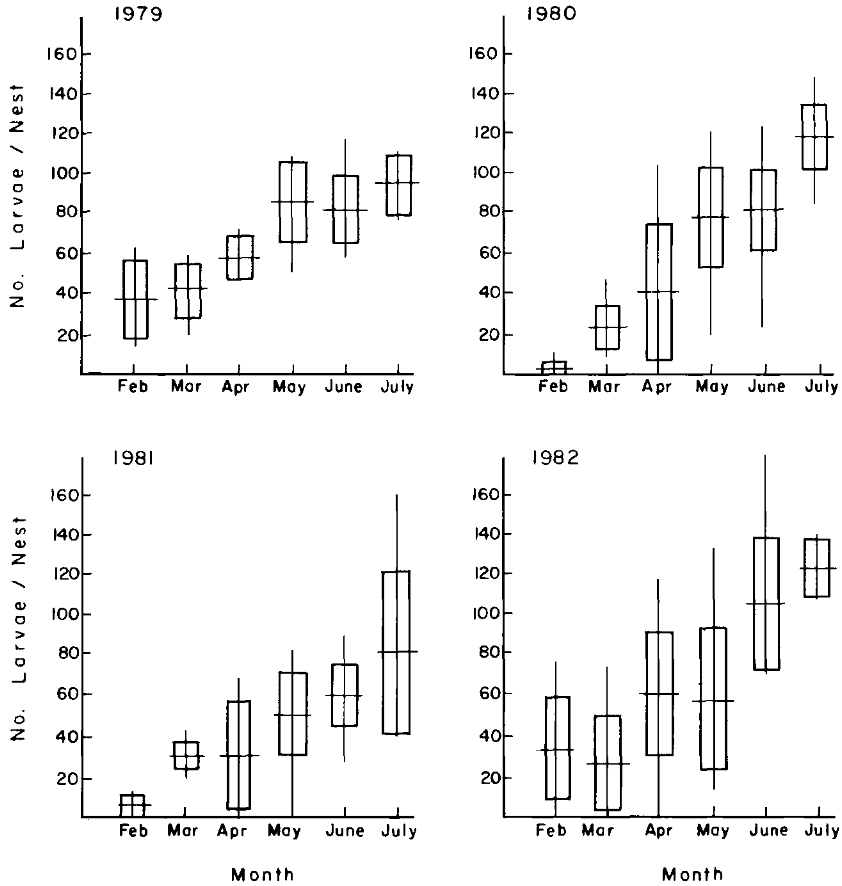

Fig. 4. Numbers of *Philornis deceptivus* larvae on Pearly-eyed Thrasher nestlings each month in the Luquillo Mountains, Puerto Rico (1979–1982). Vertical lines are ranges (minimum and maximum numbers of infesting larvae/nest), horizontal lines are means, and height of each rectangle is ±1 SD; width of rectangles was chosen arbitrarily.

completely. Even if the developing larvae did not destroy auditory tissues during development, loss of hearing was certain simply by the blockage of the external orifices. Similarly, in other young, larvae evacuating from orbital sites and even eyelids left eyes completely covered with scar tissue. Clusters of larvae found on the ventral surfaces of the throat and neck physically blocked the passage of food and caused audible interference with normal respiration. Some nestlings with infesting larvae in the region of the esophagus starved to death.

Host fledging success.—Although philornid ectoparasitism was high, with an average of 95.8% of all nests and 96.4% of all nestlings being parasitized each year, the average 4-yr fledging success was 53.3% (range 44.2–64.4%; Table 8). An average of 1.47 nestlings fledged/nesting attempt, and except for 1.16 young in 1981, an average of 1.50 nestlings fledged/nesting attempt each year. With the exception of a small sample in 1979, when 5 of 8 females lost all broods attempted to ectoparasitism, slightly more than 20% (22.2, 24.0, and 22.2%) of the nesting females lost all broods attempted in one season to philornid larvae. The percentage of females that succeeded in fledging at least 1 young/nesting attempt each year varied greatly (25.0, 44.0, 12.0, and 30.6%, respectively). However, a much higher fledging success was observed in the two drier years (1980 and 1982).

Juvenile thrasher mortality.—To study the effects of philornid ectoparasitism on postfledging thrashers, I radiotagged 4 individuals. The

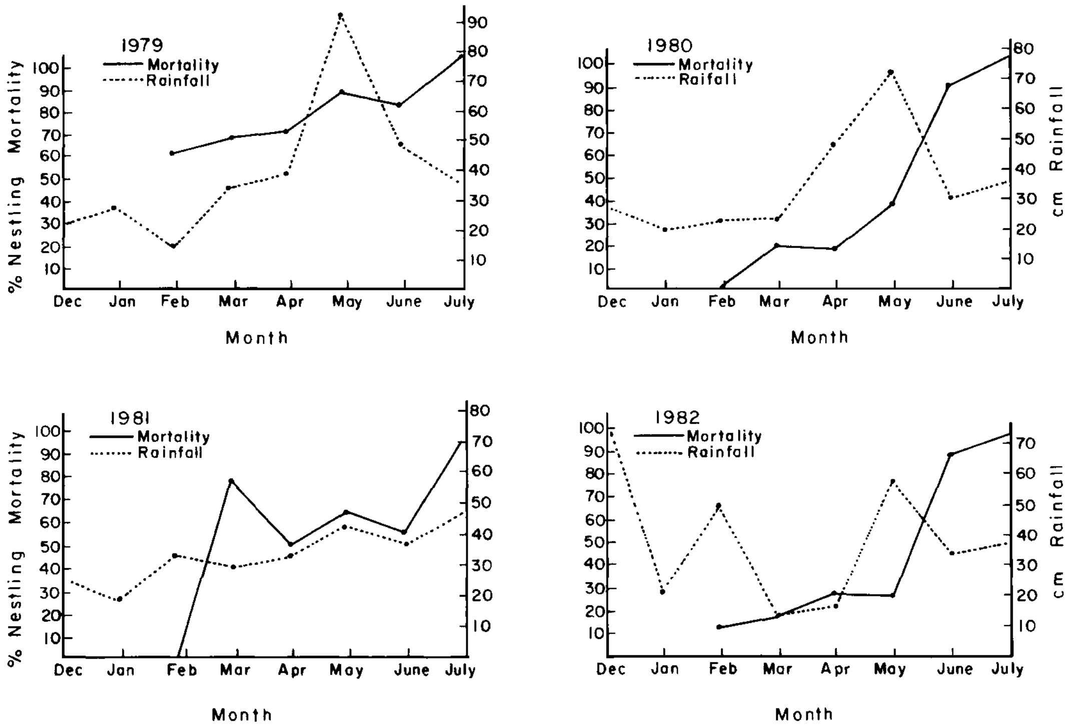

Fig. 5. Relationship between mortality of Pearly-eyed Thrasher young and rainfall each month in the Luquillo Mountains, Puerto Rico (1979–1982).

first juvenile fledged in March and was 1 of 7 unparasitized March nestlings. I was able to follow this bird successfully for 73 days before the transmitter failed. This thrasher had emigrated about 2 km from the nest area and appeared healthy at the last sighting. Unfortunately, the 3 remaining fledglings were heavily parasitized before leaving the nest, and all 3 died after fledging. Two May nestlings fledged from the same nest box as the March fledgling. Each suffered more than 60 infesting larvae as nestlings, but all infesting larvae had evacuated by the time of fledging and both chicks weighed as much as the first radio-tagged individual (97 g). I watched them make short flights of 5–10 m in the canopy surrounding the next box. However, one sibling died 9 days after fledging, while the other died 15 days after leaving the nest. They had remained within 10 m and 30 m, respectively, of the nest box. The fourth radio-tagged thrasher left the nest in June. It had received more than 90 larvae as a nestling, and all but 4 larvae had evacuated. This nestling weighed 95 g at fledging. I watched it from a blind on the day that it fledged. It weakly fluttered to the understory but managed to hop up to safety. Both parents fed it. I never saw it fly, nor did it move more than 10 m from the nest box tree. It died within a few days and I retrieved the transmitter about 10 m from the tree. If I had not observed the March and May fledglings flying normally with their transmitter packs, I would have suspected that the transmitter weighed too much for the latter 3 nestlings, inhibited normal activity, and contributed to their deaths.

DISCUSSION

The reproductive cycle of *Philornis deceptivus* is highly adapted to that of the Pearly-eyed Thrasher. Ninety-six percent of all nestling thrashers examined over a 4-yr period were parasitized by philornid larvae. Nestling thrashers were more vulnerable to philornid ectoparasitism than adults. Although the percentage of adult thrashers parasitized increased to more than 90% by the end of the thrasher's

TABLE 7. Mean number of *Philornis deceptivus* larvae infesting 81 Pearly-eyed Thrasher nestlings that died early in the nestling stage (1979–1982).

Age at death (days)	Mean number of larvae	Number of nestlings	Larval ranges
2	5.3	5	5–6
3	9.8	6	6–16
4	18.8	16	7–52
5	21.0	14	5–46
6	23.4	12	9–58
7	30.8	15	7–66
8	28.4	13	8–63

breeding season, when fly populations were high, numbers of larvae/adult did not increase. In contrast, the percentage of nestling thrashers parasitized and numbers of infesting larvae/nestling were high throughout the reproductive season. Larval numbers/nestling increased until late in the season, when fewer thrashers were breeding and more nestlings were dying at a younger age from the effects of increased parasitism.

For most of the thrasher's reproductive season, philornid larvae did not appear on nestlings until they were about one week old. Most thrasher nestling growth occurs within the first week or so of life (Arendt 1983). It is during this period of development that nestlings are most susceptible to the effects of philornid ectoparasitism. Therefore, it is advantageous for the parasite to delay infestation until the host is better able to withstand the effects of parasitism. With a larval stage of about 5 days for the parasite and a nestling period of about 21 days for the host, successive larval infestations are possible and were commonly observed. However, most larvae were shown to complete development within the middle portions of the thrasher's nestling stage. This decreases the possibility of killing young hosts prematurely, while increasing the chances of larval survival. Once a nestling has fledged, the chances for a successful larval evacuation and pupation are greatly reduced.

Larval infestation sites.—On adult Pearly-eyed Thrashers, all infesting larvae were found in areas inaccessible, for the most part, to a preening bird. Almost 15% of the larvae were found in regions of the head. Most larvae, however, were found in the patagial membranes, whose fleshy surfaces may facilitate larval entry. Interestingly, larvae found in brachial areas were always on ventral sides of the wings. Adult philornids must avoid detection and possible capture by adult birds.

In thrasher nestlings, the appearance of philornid larvae was associated with the young's ontogeny, especially pterylae development. The general sequence of larval infestations was as follows. Until midseason (May), larvae appeared in dorsoanterior regions of young nestlings; the most common sites included the crown and nape, orbits, auditory meatus, flanges, and the spinal column from the interscapular to the pelvic regions. Young nestlings were more or less immobile, with heads and gaping mouths more accessible to adult philornids. Older nestlings were more active and readily moved about in the nest. This probably allowed for easier access to ventral areas by adult philornids. The ventral tract, one of the last major feather tracts to develop, appeared at about two weeks after hatching. At that time larvae began to appear along the ventrolateral feather tracts from the vent to their apex on

TABLE 8. Pearly-eyed Thrasher fledging success in response to heavy ectoparasitism by *Philornis deceptivus* larvae.

	1979		1980		1981		1982	
	n	(%)	*n*	(%)	*n*	(%)	*n*	(%)
Females	7		14		27		38	
Nestings attempted[a]	8		18		63		78	
Nests parasitized	8	(100)	16	(88.9)	61	(96.8)	75	(96.2)
Nestlings hatched	24		45		165		214	
Nestlings parasitized	22	(91.7)	43	(95.6)	162	(98.2)	205	(95.8)
Nestlings fledged	12	(50.0)	29	(64.4)	73	(44.2)	125	(58.4)
Nestlings fledged/nest	1.52		1.61		1.16		1.6	

[a] At least 1 egg hatched/nest.

the upper breast. Other regions of the nestling used less frequently were the dorsal and ventral bases of the somewhat "stubby" tail feathers (in early development just prior to fledging), the oil gland, and the sphincter muscle around the cloaca. The chin and throat regions occasionally were parasitized in young nestlings, but larvae appeared in those areas more frequently when other ventral sites were parasitized. When host and parasite populations were higher (June and July), site specificity disappeared and larvae appeared anywhere that space was still available.

Ectoparasitism's effects on the host.—In birds, mortality caused by nest predation forms a latitudinal gradient ranging from often negligible in the Arctic to as high as 86% in the Neotropics (Ricklefs 1969). Most continental nest predation is caused by vertebrate predators, including a variety of ground and arboreal mammals and reptiles. With few exceptions (i.e. Smith 1968, 1980; Bakkal 1980; Hector 1982; Winterstein and Raitt 1983), dipteran ectoparasites have not been considered a major factor affecting bird populations. Ricklefs (1969) stated that "The effects of other bird parasites, such as fly larvae . . . are poorly known, but it is not likely that these constitute a major mortality factor for many species. It has been shown, however, that botflies exert a significant influence on the nesting success of oropend[o]las in Panama (Smith 1968)." On oceanic islands, native vertebrate predators are often absent and nest predation may be greatly reduced. Under such circumstances it is not unreasonable to assume that avian ectoparasitism may serve as a regulating factor or as an additional reproductive stress on insular bird populations.

In the Luquillo Mountains, prevalence of philornid ectoparasitism was low in adults, and no adult is known to have died as a direct result of larval infestation. The average 4-yr return rate was over 80% for adults of both sexes. Extended observations (sunrise to sunset on consecutive days) did not reveal any overt behavioral changes in either sex when harboring philornid larvae. However, infesting larvae significantly affected body mass and the growth and development of certain long bones and feathers in thrasher nestlings (Arendt 1983).

Survival of young Pearly-eyed Thrashers, both as nestlings and as postfledging juveniles, was reduced by philornid ectoparasitism. Thirty-two observations of nestlings with moderate to heavy larval infestations falling to the ground (two immediately falling prey to mongooses) when they fledged (jumped) from their nest boxes show that the 4-yr overall fledging success rate of 53.3% is questionably high. If all nestlings that died and/or received more than 30 larvae during the 1979-1982 seasons are considered lost to ectoparasitism, the 4-yr fledging success would drop to 20.3% (357 of 448 nestlings may have perished).

Juvenile thrashers face keen intraspecific competition after leaving the nest. Play-back experiments using various thrasher vocalizations showed that resident adults remain paired from year to year and that both sexes guard the nest box and territory throughout the year (Arendt unpubl. data). Because thrasher densities are high and adequate nest cavities are scarce (Snyder and Taapken 1977), less energy may be expended maintaining year-round territories and nest sites than would be spent trying to obtain new ones prior to each reproductive bout. Within their territories resident adults have been observed guarding food sources (e.g. fruits of the sierra palm, *Miconia* spp., and *Margravia*) from other thrashers and such species as the Black-throated Blue Warbler (*Dendroica caerulescens*), Scaly-naped Pigeon (*Columba squamosa*), Puerto Rican Tanager (*Nesospingus speculiferus*), Stripe-headed Tanager (*Spindalis zena*), and Puerto Rican Bullfinch (*Loxigilla portoricensis*). The radio-tagged juvenile that emigrated some 2 km from its birthplace was attacked vigorously as it moved from territory to territory and when it approached fruiting trees guarded by resident pairs. It was forced to remain in areas of few visible fruits. If interloping juveniles suffer heavy parasite loads as nestlings, their chances of survival may be greatly reduced in such a competitive environment. This also was suggested by the postfledging deaths of the other three radio-tagged juveniles. They died even though they were still receiving additional food from both adults.

Longevity in adult thrashers further lowers the probability of success for juvenile recruits into the breeding population. Observations of marked thrashers, including an 8-yr-old (minimum) female, yielded an 80-90% yearly return rate of nesting adults and showed that few young birds enter the breeding population. Of 452 young that fledged between 1979 and 1982 from naturally parasitized nests and from nests in which larvae were removed from nestlings, only 7 individuals (ca. 2%) have subsequently been recorded replacing older nesters in my sampled population. The longevity and sustained productivity of adults, while hindering juvenile recruitment, is helping to maintain thrasher numbers in the face of high juvenile mortality.

Snyder and Taapken (1977) summarized the status of the Pearly-eyed Thrasher in Puerto Rico. Thrashers were unknown in the Luquillo Mountains before the 1950's. Their numbers greatly increased for the first 20 yr or so and then began to level off, possibly in response to habitat saturation. Thrashers have remained abundant in recent years and have shown signs of adjusting to philornid ectoparasitism. While lowland populations breed mainly from April to July, a period of heavy rainfall and increased fruit and insect crops, highland populations have pushed back the initiation of the reproductive cycle, possibly to increase fledging success in the seasonal absence of heavy philornid ectoparasitism. In the sampled rain-forest population older females began nesting in late November and early December, and many were able to lay 3 and 4 clutches/year. Because of this, one might expect this prolific passerine always to remain in abundance in the Luquillo Mountains, despite continuing ill effects from philornid ectoparasitism.

ACKNOWLEDGMENTS

The field assistance and continued encouragement from my wife, Angela, is gratefully acknowledged. I sincerely thank my major advisor, Dr. John Faaborg, and my thesis committee members, Drs. Susan B. Chaplin, Terry Finger, and Leslie Uhazy, for their continued support and encouragement throughout my studies at the University of Missouri-Columbia. I thank S. Chaplin, J. Faaborg, T. Finger, P. Price, N. G. Smith, L. Uhazy, and two anonymous reviewers for helpful comments on the manuscript. L. Uhazy offered much assistance and insight into host-parasite relations. Mrs. Marcia Kelly-Nelson kindly helped with the illustrations. The study was supported by the U.S. Forest Service.

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