

# PHILORNIS ECTOPARASITISM OF PEARLY-EYED THRASHERS. I. IMPACT ON GROWTH AND DEVELOPMENT OF NESTLINGS

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**ABSTRACT.**—Growth rates varied little among unparasitized (normally developing) Pearly-eyed Thrasher nestlings. Botfly ectoparasitism, however, significantly retarded growth and development in parasitized young. Parasitized nestlings showed different growth patterns at various ages, depending on the timing of the initial parasitic attack and the extent of larval infestation. Nestling growth was most affected within the first 1.5 weeks after hatching, the period of maximum growth rate in 4 of 5 sampled growth characters (body mass, culmen, ulna, tarsus). The ninth primary feather showed accelerated growth as fledging approached. Body mass and tarsus were most affected by ectoparasitism. Nestling body mass fluctuated markedly in response to the biomass of the infesting larvae. Tarsus length was retarded in parasitized young throughout the nestling period. A combination of inherent and environmental factors showed the need to consider morphological characters in addition to body mass as possible determinants of avian growth. Received 6 February 1984, accepted 10 June 1984.

DIPTERAN ectoparasitism has been shown to contribute to the mortality of some nestling birds. Plath (1919) was one of the first to document this in nestling passerines in California that died from parasitic attack by the blood-sucking larvae of *Protocalliphora azurea* (Fallen). Bakkal (1980) reviewed published accounts of nestling mortality believed to be caused, at least in part, by calliphorid flies in Central Europe, Norway, and the USSR. He also cited personal observations of nestling weight loss and death due to parasitism by *Calliphora* spp. in Finland. In Panama, Smith (1968, 1980) found significant nestling mortality in colonies of Chestnut-headed Oropendolas (*Psarocolius wagleri*) and Yellow-rumped Caciques (*Cacicus cela*) caused by larvae of a tropical botfly of the complex genus *Philornis* (Meinert). Recently, Winterstein and Raitt (1983) reported ectoparasitism by larvae of an unidentified (probably Muscoidea) botfly on nestlings of the Purplish-backed Jay (*Cyanocorax beecheii*) in western Mexico. The biomass of the infesting larvae about a week before fledging caused the young to weigh significantly more than uninfested young. Remex and rectrix growth also were significantly retarded in parasitized young. Botfly ectoparasitism was believed to be the cause of one nestling's death. In a study of the Pearly-eyed Thrasher (*Margarops fuscatus*), Arendt (1983) reported that *Philornis* ectoparasitism, 1 of 7 caus-

es of nestling mortality over a 4-yr period, was responsible for the deaths of 93% of the 224 young that died in the nest.

It has been established that young birds die as a result of dipteran ectoparasitism, but many questions remain unanswered regarding the impact that ectoparasitism has on the growth and development of nestlings. For example, what constitutes a serious larval infestation? How many (or how few) larvae are necessary to cause death or impede development? At what stage in the nestling's development are larvae most likely to cause death or physical retardation? Do infesting larvae have a varying impact on the development of different morphological characters, depending upon their particular implantation sites? And which characters should be selected to test for possible deleterious effects of parasitism? This study was designed to address these questions for a population of the Pearly-eyed Thrasher in Puerto Rico.

## 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). This forest has been described in detail in Odum and Pigeon (1970; also see Arendt 1985).

Within a 4-yr period (1979–1982), 681 thrasher nestlings were examined to assess the impact of bot-

TABLE 1. Mean weights and long bone lengths of 50<sup>a</sup> Pearly-eyed Thrasher nestlings at hatching (day 0) by hatch order.

	Hatch order			
	1	2	3	4
Weight (g)				
$\bar{x}$	7.28	7.71	7.18	6.85
SD	0.914	0.876	0.929	0.443
Culmen (mm)				
$\bar{x}$	3.41	3.34	3.44	3.43
SD	0.254	0.265	0.271	0.171
Ulna (mm)				
$\bar{x}$	8.48	8.46	8.30	8.20
SD	0.347	0.506	0.573	0.141
Tarsus (mm)				
$\bar{x}$	8.93	8.79	8.73	8.78
SD	0.487	0.541	0.728	0.275

<sup>a</sup>  $n = 50$  for hatch orders 1-3;  $n = 23$  for hatch order 4.

fly ectoparasitism on their growth and development. A total of 18,441 measurements was taken on 5 growth characters (body mass, culmen, ulna, tarsus, and ninth primary) throughout the normal 21-day development period. Each nestling was individually marked at hatching by nail clipping and was measured every 2 days throughout the nestling period. Young were weighed to within 0.1 g with a Pesola scale and measured with dial calipers accurate to 0.01 mm. The culmen was measured from the anterior portion of the nares to its tip. The ulna was measured by bending the wing against the body and folding the manus. The tarsus was measured from the intertarsal joint to the last complete scute. The pinfeathers and exposed shafts of the ninth primary were measured separately. Adult measurements were compared to those of the nestlings.

I visited nest boxes every 1-2 days and recorded larvae as they appeared, noting total larval numbers, their positions on nestlings, larval mass, and length of infestation. Life history information of both the parasite and host has been presented previously (Arendt 1983).

*Statistical analyses.*—Care was taken to assure that lay and hatch order were represented equally among sampled nestlings and among years. To determine if growth in the selected morphological characters varied significantly among unparasitized and parasitized nestlings, I separated nestlings by hatch order (1 vs. 2, 1 vs. 3, 1 vs. 4, etc.), by season (early-, middle-, and late-season hatchlings), and by year.

Growth and development in thrasher nestlings were affected by many factors such as the numbers of infesting larvae, larval size, specific infestation sites, and host age during multiple infestations. I therefore structured the data analysis following a split-plot (hi-

TABLE 2. Mean weights, long bone, and feather lengths of 50<sup>a</sup> Pearly-eyed Thrasher nestlings at age 20 days by hatch order.

	Hatch order			
	1	2	3	4
Weight (g)				
$\bar{x}$	97.0	97.4	96.3	95.7
SD	5.020	3.863	5.406	— <sup>b</sup>
Culmen (mm)				
$\bar{x}$	11.9	11.8	11.8	11.7
SD	0.721	0.713	0.576	— <sup>b</sup>
Ulna (mm)				
$\bar{x}$	43.3	42.8	42.6	41.3
SD	0.977	0.982	1.064	— <sup>b</sup>
Tarsus (mm)				
$\bar{x}$	38.9	38.7	38.2	38.0
SD	0.994	1.023	0.832	— <sup>b</sup>
Ninth primary pin (mm)				
$\bar{x}$	11.7	11.2	11.3	11.9
SD	1.102	1.592	1.396	— <sup>b</sup>
Ninth primary shaft (mm)				
$\bar{x}$	45.1	45.4	44.5	42.0
SD	2.181	5.265	3.157	— <sup>b</sup>

<sup>a</sup>  $n = 50$  for hatch orders 1-3;  $n = 8$  for hatch order 4.

<sup>b</sup> Insufficient sample size.

erarchical) analysis-of-variance experimental design using a factorial effects model (all possible combinations) for independent variables (Snedecor and Cochran 1980, Gill and Hafs 1971).

I defined adjusted body weight as the total body mass of the nestling minus the average weight of the infesting larvae (0.3 g for third-instar larvae, or the maximum weight that an infesting larva could contribute to the total body mass of the nestling).

Variation extremes in growth patterns of normal and parasitized nestlings were determined by stepwise multiple regression with a forward inclusion of the partial regression coefficients to obtain least squares estimators of the growth parameters in third-order (cubic) polynomial response surface curves. Although data pooling (unparasitized and parasitized nestlings) masked much of the variation, the resulting three-dimensional response surface curves aided in showing when and where parasitism was affecting growth.

Response surface curves indicated possible variation in growth patterns of parasitized nestlings. However, they could not be used to compare growth patterns among nestlings suffering from varying intensities of larval infestation because data were pooled. Therefore, I divided all nestlings into 4 general categories of infestation: 1) unparasitized, 2) light (1-30 larvae/individual), 3) moderate (31-60 larvae), and 4) heavy (>60 larvae). Then, to fit a curve to the growth data, I compared various examples of linear

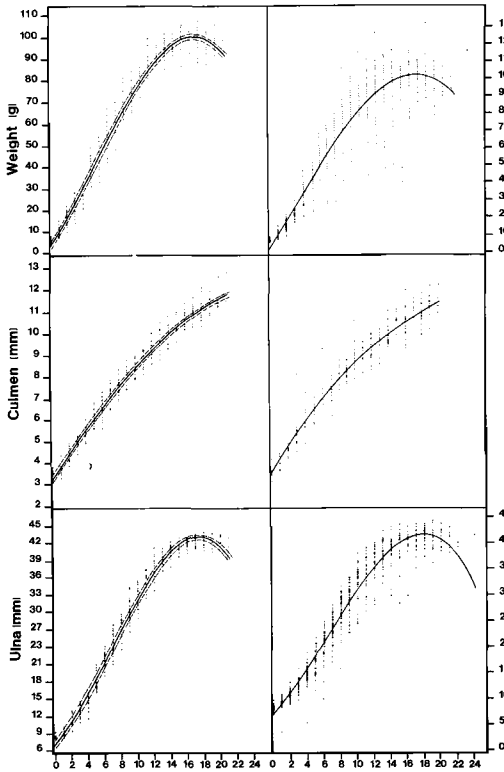


Fig. 1. Growth patterns for the body weight, culmen, and ulna of 200 unparasitized (left) and 200 heavily parasitized (right) Pearly-eyed Thrasher nestlings. Solid lines are regression curves fitted by least-squares procedures. Dashed lines are 95% confidence intervals.

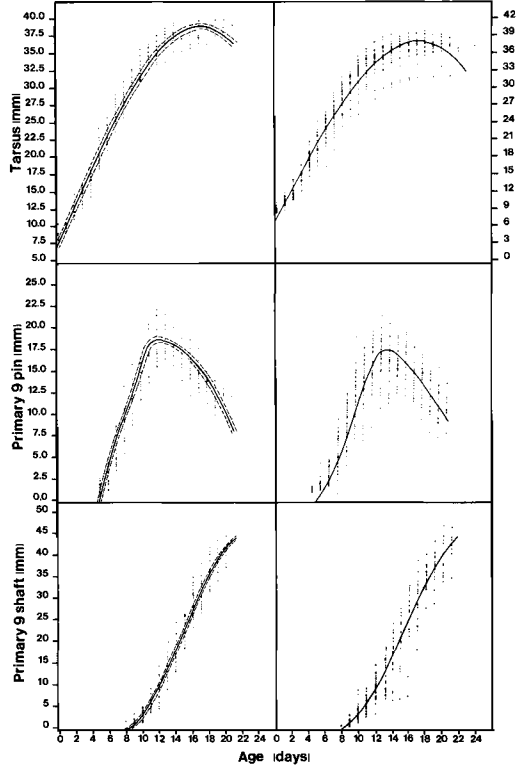


Fig. 2. Growth patterns for the tarsus and ninth primary pin and exposed shaft of 200 unparasitized (left) and 200 parasitized (right) Pearly-eyed Thrasher nestlings (solid and dashed lines as in Fig. 1).

## RESULTS

and nonlinear (second- and third-degree polynomials, exponential, and logistic) regression functions (Helwig and Council 1982). A second-order quadratic function fit the growth data well for each of the morphological characters (see Table 1). One-way classification analysis-of-variance tests were used to compare mean weights, long bones, and feather lengths on each day of the nestling period among the 4 infestation categories.

To determine the extent of natural variability in normally growing unparasitized nestlings, 95% confidence limits (Statistical Analysis System, Release 82.3) were constructed for representative growth curves of the 5 sampled characters. Scatter diagrams were used to show the variation in growth patterns among the 4 infestation categories.

Because nestling sample size was quite large in 1982, I used an additional 200 nestlings and conducted a separate set of growth analyses on the independent sample.

Analysis-of-variance tests did not reveal significant differences ( $\alpha = 0.05$ ) at hatching or by day 20 among unparasitized nestlings in different hatch orders, seasons, or years for any growth character (Tables 1, 2). For conciseness, only hatch order treatments are shown.

Figures 1 and 2 show that growth among unparasitized nestlings is quite uniform. Growth patterns among parasitized nestlings, however, were more varied in all growth characters. Scatter diagrams in the right-hand columns represent growth patterns of nestlings in infestation category 4 (>60 larvae/young), which were most variable. Growth patterns of nestlings included in categories 2 and 3 (not shown) were intermediate to those of categories 1 and 4.

Parasitized nestlings showed different growth patterns at various ages, depending on the extent of infestation and timing of initial para-

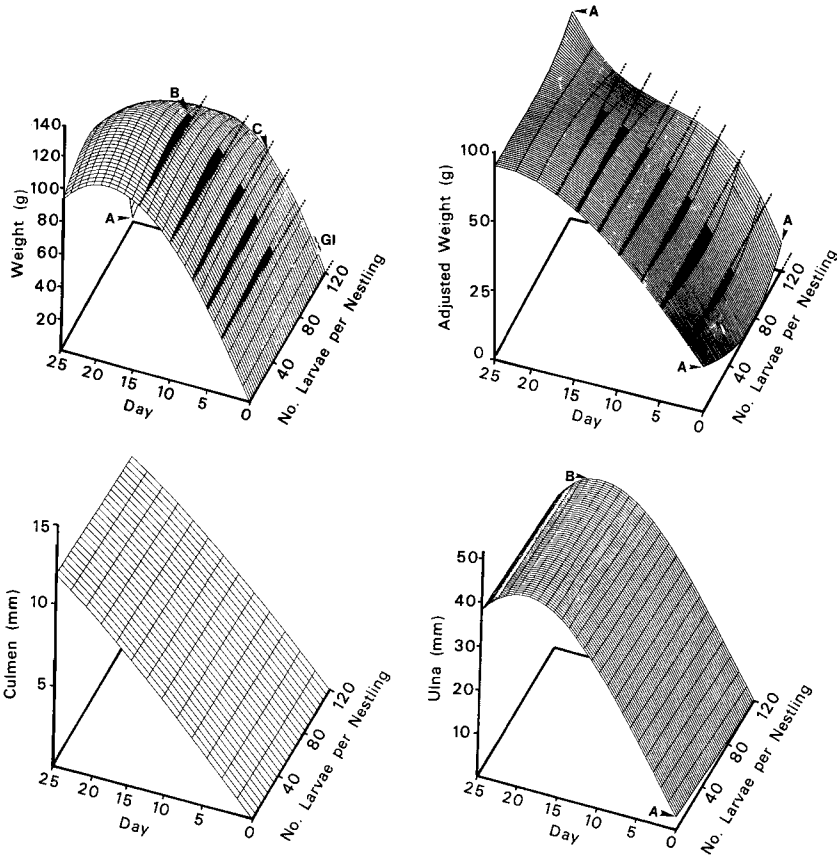


Fig. 3. Varied growth patterns in body weight, adjusted body weight, culmen, and ulna of 200 unparasitized and parasitized Pearly-eyed Thrasher nestlings (ca. 50 young in each of 4 infestation categories). See text for definitions of adjusted body weight and symbols and Appendix A for equations defining the response surface curves.

sitic attack. Patterns also varied among growth characters. Therefore, each character will be treated separately, with sections on response surface curves and second-order regression analysis.

It is difficult to interpret response surface curves, especially the warping effects at the extremities of the surfaces (point A in Figs. 3, 4). These effects are caused by extreme variations of growth among young, heavily parasitized nestlings and by prediction bias, or the forecast values, beyond the scope of the model (Neter and Wasserman 1974: 233-234, Schultz 1930). Such values and attempted interpretations of the resulting response surface configurations at their extremities are meaningless. I have superimposed dashed lines running parallel to the z-axis (number of larvae/nestling) in Figs.

3 and 4 to facilitate interpretation. If growth were equal among all nestlings, irrespective of the extent of parasitism, the horizontal lines in the response surfaces (delineating daily or alternate-day growth periods) would parallel that of the z-axis. Deviations from such a parallelism indicate variable growth patterns, but caution must be used, as noted above, in interpretation from areas of the extremities. Blackened areas show normal growth plus (or minus) actual growth represented by the regression curves. The vertical lines (y-axis) between days or alternate days denote growth increments (point GI in Figs. 3, 4), with shorter lines indicating less growth. They are also susceptible to prediction bias in the extremities or wherever warping occurs.

*Body mass.*—As a result of the added biomass

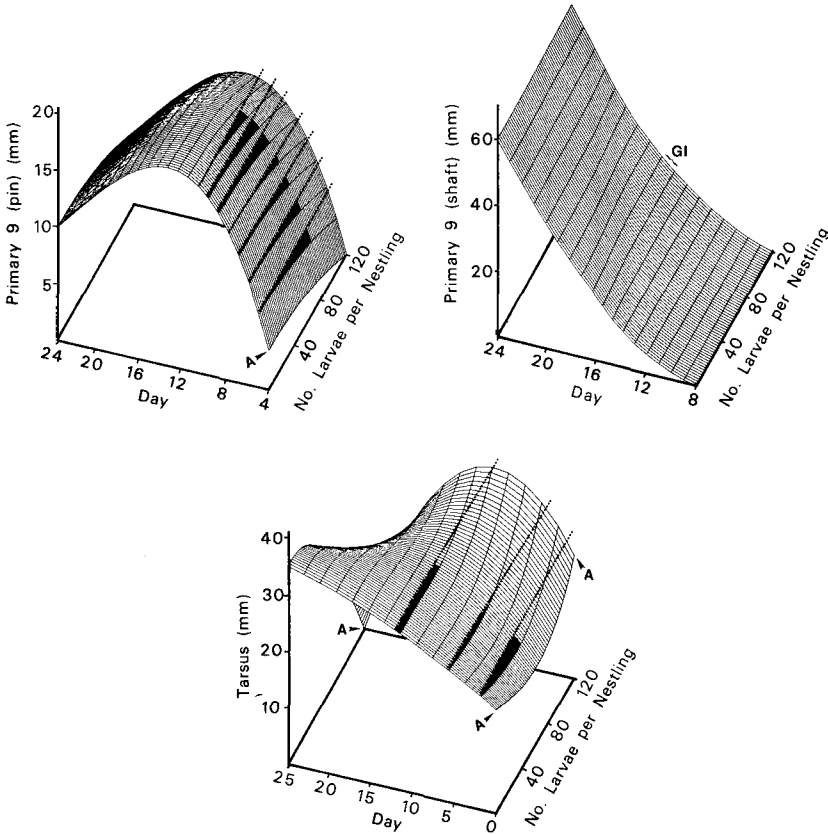


Fig. 4. Varied growth patterns in the ninth primary (pin and exposed shaft) and tarsus. See text for definition of symbols and Appendix A for equations defining the response surface curves.

of infesting larvae, nestling body mass (mean body weight at day  $D$ ) is greater in more heavily parasitized nestlings throughout the nestling stage, reaching 131 g in a heavily parasitized nestling (Fig. 3). A comparison of the solid horizontal lines along the  $z$ -axis of the response surface (actual growth) with the dashed lines (uniform growth) shows that the heaviest infested nestlings weighed more than unparasitized and lightly infested nestlings up to the end of the first week. After the first week, the upper-right corner of the response surface begins to warp downward (point C), suggesting that the most heavily parasitized young weighed less than even unparasitized nestlings during the last half of the nestling period and at fledging (contrary to field observations). Infestations of 120 larvae were rare. Very few nestlings harbored more than 80 larvae at any one time, but for infestations up to this intensity (point B) more heavily parasitized nest-

lings continued to weigh more than nestlings with fewer larvae. Thus the bowing downward of the horizontal lines near the right extremity of the surface response (beginning at point C) and the exaggerated downward warping of the surface's upper-right corner (point A) are results of prediction bias.

To include measurements of young that remained in the nest longer than the normal 21 days, I lengthened the nestling period to 25 days in the growth model ( $x$ -axis in Fig. 3). Note that even in unparasitized and lightly parasitized nestlings body mass dropped after about 21 days. Young that remained in the nest boxes after the normal nestling period were underweight and underdeveloped in response to botfly ectoparasitism (often single, heavily parasitized nestlings) or as a result of sibling competition (third- and fourth-hatched nestlings with no or few larvae).

Body mass varied most among categories

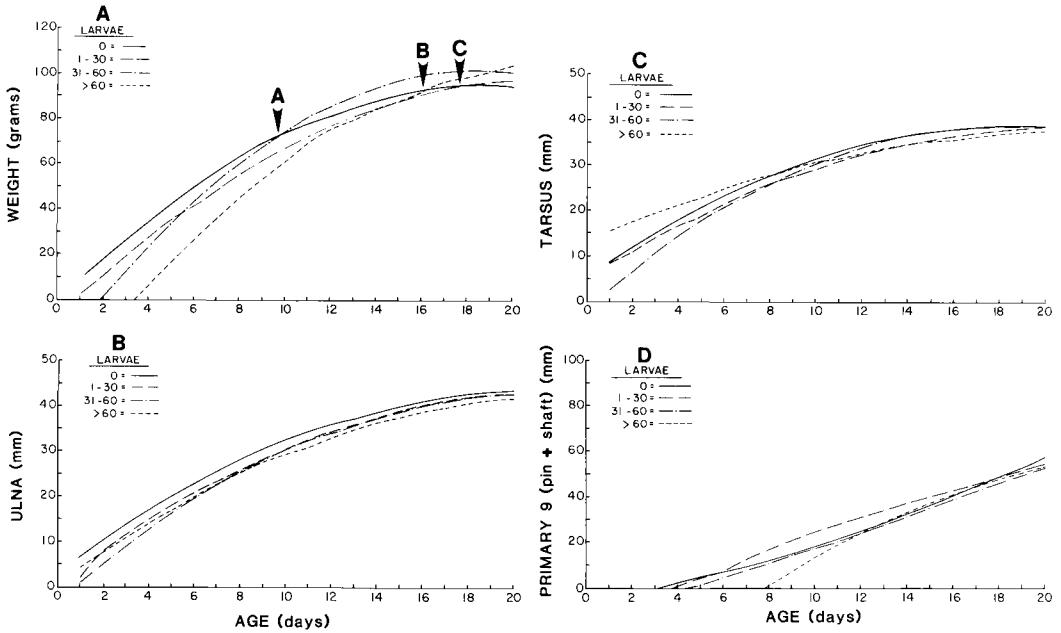


Fig. 5. Varied growth patterns in 200 unparasitized and parasitized Pearly-eyed Thrasher nestlings (ca. 50 young in each of 4 infestation categories). See Appendix B for equations defining the second-order regression curves.

within the first week and just prior to fledging. A regression of daily mean body weight is shown by infestation category in Fig. 5A. Parasitized young weighed significantly less than unparasitized young for about the first 1.5 weeks of the nestling period (Table 3). Heavily parasitized nestlings died during that time. Subsequently, the body mass of parasitized young surpassed that of unparasitized young at different stages of the nestling period, dependent upon the extent of the infestation. Body mass in the most heavily infested young lagged behind that observed in uninfested young until the third (final) week of the nestling period (point B in Fig. 5A). Adding the increased biomass of the larvae to nestling weight resulted in a sharp increase in total body mass of the heavily infested nestlings. This then surpassed the total body weight observed in unparasitized nestlings, resulting in heavier weights for parasitized nestlings at fledging. As an example, the heaviest nestling recorded in the study (June 1982) weighed 131 g at age 19 days and had 172 infesting larvae, that is, 137.3% of the average (95 g) uninfested nestling's weight at this age. Larval infestation and the accompanying increase in body mass oc-

curred early in this nestling's development. At 1 week old, it weighed 73 g (130% of the average nestling's weight) and harbored more than 50 larvae. At 2 weeks old it had more than 80 larvae and weighed 126 g, or 148.2% of the average 13-day-old nestling. Although numerous young endured well over 100 larvae (some over 200), their weights never reflected it because of successive infestations (the larvae have a 5-7 day development cycle).

Body mass in moderately infested nestlings surpassed that of uninfested young at about day 10 (point A in Fig. 5A) and then roughly paralleled it until fledging, again being influenced, although to a lesser extent, by the biomass of the infesting larvae. In nestlings exposed to light larval infestations, body mass lagged behind that of unparasitized young for most of the nestling period, surpassing it just before fledging (point C in Fig. 5A). In some cases where larval infestations caused nestling mortality, especially those involving heavily parasitized nestlings, death was preceded by a drop in body mass.

*Adjusted weight.*—Because the added biomass of the infesting larvae greatly biased the resulting body weights of heavily parasitized

TABLE 3. Significant  $t$ -values ( $\alpha = 0.05$ ;  $t_c = 1.96$ ) resulting from an analysis-of-variance test ( $F$ ) comparing the observed mean body weight, and ulnar and ninth primary feather lengths of 200 unparasitized and parasitized Pearly-eyed Thrasher nestlings.

Growth character	0 larvae vs.:					
	1-30		31-60		>60	
	$t$ -values	Days	$t$ -values	Days	$t$ -values	Days
Body weight	9.49-7.55	1-10	2.40-1.96	1-4	2.05-2.85	19-21
	6.94-2.96	11-16	2.06-2.80	17-21		
	2.22-2.97	20-21				
Ulna	3.74	1				
	2.04-2.97	3-16				
Ninth primary	6.69-1.97	1-4				
	2.38-7.24	6-17				
	3.15-4.61	20-21				

nestlings, a response surface curve was plotted after subtracting the average maximum weight that an infesting larva could obtain (Fig. 3). Extreme variation in the weight of young, heavily parasitized nestlings plus prediction bias caused exaggerations at the extremities (points A). However, the blackened areas in Fig. 3 show that nestlings with up to 80 infesting larvae had lower actual body weights than uninfested young, which is what was observed in the field.

*Culmen.*—The growth of the culmen appeared unaffected by botfly ectoparasitism (Fig. 3) and thus was not represented in Fig. 5. It is representative of how normal growth would appear if parasitism had no effect. Although growth diminished as fledging approached, culmen length averaged 11.0 mm, or about 7 mm shorter than its average length (18.0 mm) in adults. Thus, some culmen growth occurs after fledging in this species.

*Ulna.*—The overall growth of the ulna also appeared little affected by parasitism (Fig. 3). The lower-left corner (point A) of the response surface is raised slightly off the axis, indicating that ulna length was longer in young unparasitized nestlings. Growth decreased as fledging approached, the ulna obtaining more than 90% of adult length during the nestling stage. The warping effect at the surface's upper edge (point B) is caused by predicted values beyond the observed data. The ulnas of young nestlings were affected by increasing larval loads, but the overall growth pattern in older young was similar in all infestation categories (Fig. 3).

A regression of the average ulna length

showed little variation among parasitized young after day 4 (Fig. 5B). Ulna length was significantly shorter in lightly parasitized young (Table 3), and growth lagged behind that observed in unparasitized young throughout the nestling period (Fig. 5B). Ulna length was shortest in heavily parasitized young in the second half of the nestling period.

*Tarsus.*—The tarsus was the most affected of the long bones (Fig. 4). The length of the tarsus varied greatly in younger nestlings, growing more slowly as larval loads increased. Although the warping at the upper right edge (point A) of the response surface is exaggerated at day 25 due to forecast values, it is apparent that as larval loads increase, tarsus length decreases for infestations of less than 80 larvae/young (blackened areas). Tarsal growth diminished as fledging approached. More than 90% of adult tarsal length is obtained during the nestling stage.

A regression of the daily average tarsal length showed that its growth was extremely variable in heavily parasitized young, especially within the first week of development (Fig. 5C). The fit of the regression curve is poor for the first few days in heavily parasitized young, showing fictitious tarsal lengths twice as long as normal. Afterwards, growth more closely approximated that of tarsi in other categories. Analyses of the regression curves (Fig. 5C) did not reveal the variable growth among categories as well as the response curve because of the extreme variability among infestation categories and the resulting poor fit of the regression curve.

*Ninth primary pinfeather.*—There was a marked difference in the length of the ninth primary

pin in young nestlings caused by a delay in its emergence. This is represented by the raised lower-left corner of the response surface curve (point A in Fig. 4). Growth slowed until about day 12, when the pin began to recede. It was only a remnant at fledging, which was characteristic of pinfeathers of all the major feather tracts.

*Ninth primary exposed shaft.*—Daily growth increments (point GI in Fig. 4) in the ninth primary showed a marked increase beginning in the third week of development, a trend that continued up to the time of fledging. This was in contrast to the growth patterns shown in the other five growth characters, all of which exhibited slower growth as fledging approached. Growth patterns in the exposed shaft appeared similar among all infestation categories.

A second-order regression of the daily average increase in the length of the ninth primary (combined pinfeather and exposed shaft) in parasitized nestlings showed that growth was most affected during the first 1.5 weeks of development (Fig. 5D), as was the case in the other five growth characters. In unparasitized nestlings the ninth primary pinfeather emerged on day 3. Among parasitized nestlings it often did not appear for another 3-5 days, depending on the extent of infestation. No significant differences in the daily mean lengths of ninth primary among moderately and heavily parasitized young were detected (Table 3). When compared to unparasitized nestlings, the apparent greater length of the ninth primary throughout most of the nestling stage in nestlings with 1-30 larvae is the result of a poor fit of the regression curve during the first 1.5 weeks of development. Rapid growth following emergence of the ninth primary in heavily parasitized nestlings resulted in overall feather lengths that were similar (although somewhat shorter) to those in the unparasitized and moderately parasitized groups during the latter half of the nestling period (Fig. 5D).

Second-order regression analyses showed significant differences ( $\alpha = 0.05$ ) between the growth rates of unparasitized and lightly parasitized nestlings more frequently than between unparasitized vs. moderately and heavily parasitized young. This is contrary to what was expected. However, growth in moderately and heavily infested nestlings varied greatly (notably within the first 1.5 weeks), making it much more difficult to fit a representative curve

TABLE 4. Variances of predicted values given by quadratic equations fitted to the growth data.

Day	Number of larvae/nestling			
	0	1-30	31-60	>60
1	0.816	0.680	86.267	542.096
2	0.567	0.498	59.241	433.079
3	0.410	0.371	45.217	341.680
4	0.323	0.288	26.798	265.879
5	0.286	0.239	18.607	203.781
6	0.281	0.215	14.146	153.614
7	0.295	0.209	12.368	113.732
8	0.316	0.214	12.361	82.612
9	0.336	0.228	13.348	58.855
10	0.348	0.233	14.689	41.186
11	0.350	0.239	15.880	28.456
12	0.341	0.240	16.550	19.638
13	0.325	0.233	16.468	13.830
14	0.305	0.218	15.534	10.255
15	0.291	0.196	13.787	8.259
16	0.293	0.168	11.401	7.313
17	0.325	0.137	8.684	7.012
18	0.405	0.106	6.084	7.073
19	0.550	0.081	4.179	7.342
20	0.784	0.067	3.687	7.785
21	0.930	0.071	5.460	8.493

to the data (Table 4). Student's *t*-tests showed that even light larval loads affected normal growth patterns in most of the characters assessed. High variance in the moderately and heavily parasitized young resulted in an apparent statistical nonsignificance because it contributed to the standard error term in the denominator of the *t*-statistic (as the variance increased the *t*-value decreased).

#### DISCUSSION

Many factors in addition to parasitism influence the growth of an organism. These include inherent characteristics such as size, age, and even tissue growth (O'Connor 1975, Ricklefs 1979). Environmental factors include sibling competition, food supply, diet, temperature, and photoperiod, all of which may vary annually and geographically (Lack 1968, Hussell 1972, Ricklefs 1976). However, three different analyses (response surface curves, quadratic regression functions, and analysis-of-variance tests) showed uniform growth among unparasitized thrasher nestlings.

*Effects of ectoparasitism.*—Botfly ectoparasitism, although highly variable depending on the onset and intensity of larval infestation, was found to significantly retard growth and de-



velopment in thrasher nestlings. Although moderately and heavily parasitized young were affected the most, even light parasite loads often resulted in developmental retardation in nestlings less than one week old. However, light parasite loads did not appear to substantially jeopardize a nestling's chances of survival if infestation occurred after the first 1.5 weeks of life. Of 7 fledged young that eventually joined the sampled breeding population, 4 individuals had endured light (<30) larval infestations as nestlings, while 3 young had not been parasitized. More data are needed, however, to determine the long-range effects of light infestations on fledgling survival.

Growth increments were shorter in more heavily parasitized nestlings during the first week or so of life in three of the growth characters. The fit of the second-order regression curves was poorer during the first 1.5 weeks because of the great variability in the mean weights and lengths of the sampled growth characters among the more heavily parasitized nestlings. With the exception of the ninth primary, which grows faster as fledging nears, growth rate in the sampled morphological characters was highest during the first 1.5 weeks. Therefore, infesting larvae most affected growth during the most crucial period in a nestling's development.

Growth of the ulna and ninth primary appeared little affected by botfly ectoparasitism. Because a fledgling thrasher must be able to fly, it should channel a major portion of its energy supply to the development of its wing bones and flight feathers during the nestling period. As an apparent result, larvae concentrated on the wings throughout nestling development. Although they undoubtedly usurped many of the nutrients needed for bone deposition, the supply apparently was adequate enough to assure almost normal growth in the ulna and ninth primary even in heavily infested young. Feather growth has been shown to be little affected in the European Robin (*Erithacus rubecula*) even in times of starvation (Lees 1949a, b). Apparently, sufficient energy is supplied to the flight components even when the developing bird is under stress. However, a delay in the emergence of the ninth primary pin in the moderately and heavily parasitized nestlings probably accounted for its shorter length at fledging in the more heavily parasitized young. Except early in development, its pattern of

growth (daily increase in length) approximated normal growth among all larval infestation categories. Thirty-two observations of heavily infested young falling to the ground, with 2 young immediately falling prey to mongooses, show that retardation of pteryllae development can have substantial effects on flight and predator avoidance.

The tarsus was more affected by parasitism than the ulna or the ninth primary. The tarsus is more developed than the vestigial ulna at hatching because the tarsi support the neonate in the nest during feeding. Although the tarsus grows quickly to support the rapidly increasing body mass, it is not directly involved in flight, and the ulna surpasses it after the first 1.5 weeks of development. Slower growth of the tarsus may have been caused in part by the large concentrations of feeding larvae found at the constricted intertarsal joints, where blood flow is close to the skin's surface. The large numbers of larvae aggregating at these joints and elsewhere on the legs and feet for most of the nestling period may have usurped enough blood and body fluids to stunt growth. An alternative hypothesis is that infesting larvae may have a synergistic effect on growth and development simply because the nestling must reallocate growth energy into tissue repair and other physiological responses to parasitism.

*Selection of morphometric criteria in growth studies.*—In the past, comparative growth studies often have been based solely on body mass (Ricklefs 1967). However, body mass alone is not always an accurate determinant of body growth. In the present study, for example, the added biomass of the parasitic larvae resulted in apparent optimum growth (heaviest nestlings) in the most heavily parasitized nestlings. Fluid content constitutes the major portion of total body mass and varies significantly, depending upon a variety of inherent and environmental factors such as the organism's physiological processes (i.e. metabolic rates), diseases and parasites, competition, and physical factors such as temperature, humidity, and sunlight. In this study nestling body mass was greatly affected by infesting larvae, which caused induced dehydration of body fluids and (often masked) reduced body weights. For example, the two heaviest nestlings (one weighing 124 g at 19 days and the other 131 g at 21 days) harbored 145 and 172 larvae, respectively, at the time of their heaviest weighings. Using 0.3

g as the average weight of a mature third-instar larva and considering that the average normally developed thrasher nestling weighs 95–100 g between days 18 and 22, if the biomass of the larvae is subtracted, the resulting weights of both nestlings would be 80 g and 79.4 g, respectively. Considering also that a percentage of this final weight is connective and scar tissues, these nestlings would be markedly underweight.

Other factors make weight a questionable measure. In the study area nestling thrashers were fed a variety of large-seeded fruits from which they dissolved the pulpy pericarp and eventually regurgitated the naked seed pit. Nestlings were weighed early in the morning before much feeding had occurred, but the adults began feeding nestlings before dawn. Often a suspected heavy nestling would discard one or two tabonuco (*Dacryodes excelsa*) seeds, each the size of a small walnut, while others might produce 2–3 sierra palm (*Prestoea montana*) seeds the size of small marbles. Besides the large-seeded fruits, during handling nestlings would regurgitate pellets containing skeletal fragments of tree frogs and lizards. All of these food items affected total body weight.

From this study it is evident that body mass may not always be an accurate measurement of growth. Therefore, comparative growth studies, especially those concerned with the influence of environmental factors, should include a combination of body mass, long bones, and feathers from the major feather tracts as possible determinants of growth.

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APPENDIX A. Equations defining response surface curves illustrated in Figs. 3 and 4.<sup>a</sup>

Growth character	Equation
Body weight (g)	$Y = 0.974 + 8.256D - 0.621D^2 - 5 \cdot 10^{-3}D^3 + 1.7 \cdot 10^{-2}DL - 2 \cdot 10^{-7}D^2L^3$
Adjusted body weight (g)	$Y = 1.595 + 8.174D - 6.4 \cdot 10^{-2}D^2 - 5 \cdot 10^{-3}D^3 - 0.885L + 1.115 \cdot 10^{-4}L^3 + 0.127DL - 3.1 \cdot 10^{-4}D(L^2) - 4 \cdot 10^{-3}D^2L - 1.9 \cdot 10^{-6}D^2L^3$
Culmen (mm)	$Y = 3.182 + 0.549D - 3 \cdot 10^{-4}D^3 - 6 \cdot 10^{-4}DL$
Ulna (mm)	$Y = 5.132 + 2.719D + 0.027D^2 - 3 \cdot 10^{-3}D^3 - 0.023L$
Ninth primary pinfeather (mm)	$Y = -26.953 + 7.323D - 0.376D^2 + 0.005D^3$
Ninth primary exposed shaft (mm)	$Y = 16.195 - 7.066D + 0.728D^2 - 0.015L$
Tarsus (mm)	$Y = 6.076 + 3.138D - 0.059D^2 - 8 \cdot 10^{-4}D^3 - 0.196L + 2 \cdot 10^{-5}L^3 + 0.047DL - 0.002D^2L - 4 \cdot 10^{-5}D^2L^2 - 2 \cdot 10^{-6}D^3$

<sup>a</sup>  $Y$  = growth character,  $D$  = day,  $L$  = larval infestation.

APPENDIX B. Equations defining second-order regression curves illustrated in Fig. 5<sup>a</sup>

Growth character	Number of larvae	Equation
Body weight (g)	0	$Y = 1.732 + 10.102D - 0.263D^2$
	1-30	$Y = -7.472 + 9.71D - 0.224D^2$
	31-60	$Y = -23.75 + 13.293D - 0.352D^2$
	>60	$Y = -42.352 + 13.359D - 0.305D^2$
Tarsus (mm)	0	$Y = 5.165 + 3.552D - 0.095D^2$
	1-30	$Y = 5.114 + 3.106D - 0.072D^2$
	31-60	$Y = -1.661 + 4.441D - 0.124D^2$
	>60	$Y = 13.344 + 2.198D - 0.498D^2$
Ulna (mm)	0	$Y = 3.149 + 3.788D - 0.089D^2$
	1-30	$Y = 1.33 + 3.678D - 0.08D^2$
	31-60	$Y = -3.216 + 4.391D - 0.106D^2$
	>60	$Y = 0.449 + 3.74D - 0.084D^2$
Ninth primary (pin and shaft) (mm)	0	$Y = -5.154 + 1.694D - 0.071D^2$
	1-30	$Y = -16.042 + 4.515D - 0.049D^2$
	31-60	$Y = -13.165 + 2.894D - 0.021D^2$
	>60	$Y = -57.634 + 8.64D - 0.156D^2$

<sup>a</sup>  $Y$  = growth character,  $D$  = day.