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Effects of the parasitic botfly *Philornis carinatus* on nestling house wrens, *Troglodytes aedon*, in Costa Rica

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Abstract. I studied the life cycle of a botfly (Diptera: Muscidae: *Philornis carinatus*) and examined the effects of botfly ectoparasitism on nestling house wrens (Passeriformes: Troglodytidae: *Troglodytes aedon*) during three years in Costa Rica. At three study sites, I found that nestlings were relatively unaffected by botflies, in contrast to all other studies of birds infected with philornid botflies. At Monteverde, the main study site, infected chicks grew slightly slower and had slightly shorter tarsi and wing chords than uninfected chicks, but both groups fledged at similar weights. Since weight at fledging is the only growth character associated with post-fledging survivorship, botfly infections likely cost wrens little in terms of fitness. At all sites, fledging success did not differ between infected and uninfected nests. Botfly infections were more prevalent at two lower elevation sites than at the high elevation Monteverde side. Infection prevalence increased during the nesting season at all study sites, which suggests a botfly life cycle in which adult population levels increase during the wren breeding season and then decline during a dormant period when wrens are not nesting. Finally, botflies may attack chicks throughout the period before fledging, but there is no indication they locate nests before hatching. In sum, botfly parasitism on wrens appears to be benign, perhaps because the study sites are at the edge of the botfly's range or because wrens are not a preferred host.

Key words: Ectoparasite – Host-parasite Interaction – House Wren – *Philornis* life cycle – Tropics

In the last decade, ecologists and evolutionary biologists have begun to appreciate the importance of parasites and diseases (here collectively referred to as parasites) on the biology of vertebrate hosts (Price 1980; Toft 1991). In birds, parasites can cause range contractions and extinctions (Warner 1968; van Riper et al. 1986), restrict colony size (Brown and Brown 1986), cause heavy nestling mortality (Smith 1968; Arendt 1985b; Delannoy and Cruz 1991), and play a role in the evolution of bright plumage coloration (Hamilton and Zuk 1982). Despite the potential importance of parasites in regulating populations (Anderson and May 1979, 1982), few studies quantify the effects of parasites on their avian hosts (Toft 1991), and fewer document geographical variation in the importance of a parasite to its host. Here I document the interactions between the botfly *Philornis carinatus* (Diptera: Muscidae) and the house wren *Troglodytes aedon* (Passeriformes: Troglodytidae) in three habitats in Costa Rica. In addition, I add to our knowledge of the annual cycle and natural history of the parasite.

Natural history of botflies and house wrens

As part of a related study on house wren breeding biology in Costa Rica, I examined botflies and their effects on nestling wrens. *Philornis* is a genus of fly that specializes on birds. It can infect both nestling and adult birds in tropical and subtropical areas (Dodge 1955, 1968; Hicks 1959; Dodge and Aitken 1968; Arendt 1985a, 1985b). The most recent review lists 21 species in the genus, and 75 species of birds that have been reported infected (Couri 1985).

In most botfly species, larvae live beneath the host skin between the dermis and body musculature (but see Dodge 1963 for a coprophagous example). The larvae feed on red blood cells and other cellular debris which build up in the lesions (Uhazy and Arendt 1986). The larvae breathe by means of spiracles oriented toward a hole in the host integument. After a rapid period of growth and development (approximately 4–6 days), the larvae drop out as third instars and pupate in the host nest (Uhazy and Arendt 1986). Adult flies emerge after a 1–3 week pupation period and fly off to mate and infect new hosts (Oniki 1983; this study). It is not certain whether female flies lay eggs or deposit newly-hatched larvae on nestlings or nest material, but chicks just a few days old can be infected by botfly larvae (Smith

1968; Uhazy and Arendt 1986; Delannoy and Cruz 1991; this study). Multiple infections by several cohorts of larvae are commonly reported. Adult birds may become infected, presumably when they brood nestlings.

House wrens are ubiquitous cavity-nesters in most human-disturbed areas from Canada to Tierra del Fuego. They are migratory at the northern and southern extremes of their range and sedentary in subtropical and tropical habitats. Both members of a pair defend a territory and both help in feeding chicks. Clutch size varies from 3–4 or rarely 5 in tropical regions (Skutch 1953; Alvarez-Lopez et al. 1984; Freed 1986) to 5–12 in temperate regions (Gross 1948). House wren nestlings have been reported with *Philornis* infections in Trinidad (Dodge and Aitken 1968), Panama (L Freed, *pers comm*), Colombia (G Kattan, *pers comm*) and Costa Rica (this study). In north temperate regions, house wrens can be parasitized by *Protocalliphora* blow flies (Diptera: Protocalliphoridae), an analogous blood-sucker (Sabrosky et al. 1989). No study, however, has documented the effect of a botfly infection on house wrens.

In this study, I examine the details of the life cycle and natural history of *P. carinatus*, including: stage in the wren breeding season that infections occur, time of infection relative to chick age, number of botfly cohorts raised by a single chick, larval development time, and pupation time. I use these results to hypothesize a life cycle and search mode for hosts. I also examine the effect of *P. carinatus* infection on nestling weight gain and other growth measures, and nestling fledging success. To examine the generality of the interaction, I monitored two additional house wren populations for infection prevalence (defined in methods) and effects of botflies on fledging success.

Methods

Study sites

This study was conducted at three study sites centered near Monteverde, Puntarenas Province, Costa Rica (10°18′ N, 84°45′ W). Monteverde is located near the continental divide at 1500 m elevation in a mountainous region of the Cordillera de Tilarán. A pronounced rainy season occurs from May to December, but moisture in the form of mist borne by the trade winds bathes the area during the rest of the year. The study site is classified by Holdridge (1967) as Lower Montane Wet Forest. In Monteverde, the main site, I erected nest boxes on 60 house wren territories in September 1988. The boxes were attached to either remnant trees or metal posts in dairy pastures adjacent to cloud forest (described by Lawton and Dryer 1980). I monitored nesting activity here during the 1989–1991 nesting seasons which last from February or March to August each year. Here house wren pairs usually raise two broods per year (Winnett-Murray 1986). I checked boxes weekly for clutch initiation, daily when I expected hatching to occur, and every three days during the chick stage. The site was established for an ongoing study of factors influencing clutch size in house wrens. As a part of that study, 1–2 day old chicks were moved from one nest to another to create brood sizes from 1–6 instead of the normal range of 3–4. I measured growth rates of chicks in Monteverde only.

I also monitored botfly parasitism and effects on wren fledging success at two other sites with the help of local field assistants. The San Luis site is 3 km SW of Monteverde but at an elevation of 800 m in the Tropical Premontane Wet life zone (Holdridge 1967). San Luis is in the rain shadow of the Cordillera de Tilarán and consequently receives no precipitation between mid December and mid May. There is a normal rainy season in the intervening months. Wrens breed here between April and September (B Young, *unpub data*). I erected boxes at 21 territories scattered through dairy and coffee farms in March 1990. I monitored nesting activity including clutch initiations, clutch size, hatching success, fledging success and prevalence of botfly infection during weekly visits to the nest boxes throughout the 1990 and 1991 breeding seasons.

The third site was at La Lucha de La Tigra, San Carlos Province, located 24 km ENE of Monteverde at 200 m elevation in the Caribbean lowlands. Rainfall here is heavier and less seasonal than at the other sites and the forest is classified as Tropical Wet (Holdridge 1967). I set up nest boxes in 19 wren territories in June 1990. They were located in a 10 ha combination plantain, cassava, and dairy farm that is part of a larger matrix of farms surrounding a 10 ha fragment of primary forest. I began monitoring the boxes for nesting activity and parasite infection during weekly visits immediately after erecting the boxes. Since local farmers claimed that house wrens breed year round there, I made visits continuously through August 1991.

Definitions

I follow the definitions of parasitological terms recommended by Margolis et al. (1982) with one important modification. The host unit for botflies in this system is a nest of house wren chicks. Since I never found an unmanipulated nest in which fewer than all of the chicks were infected, I assume that botflies infect all chicks of the nests they find. Thus, a botfly searches for nests to infect, not individual chicks. Individual chicks could still be appropriate host units if the variance in growth measures was higher in infected chicks than in uninfected chicks. This is not the case, so I analyze the data based on nest means, not individual chicks.

Infection *prevalence* is the number of nests with chicks that have infections during some or all of the 18 day chick stage divided by the total number of nests with chicks in a given time interval. *Intensity* is the number of *Philornis* individuals per chick based on nest means. An *infected nest* is a nest in which chicks were found parasitized during some stage of their development.

Life cycle of P. carinatus

In Monteverde, I visited nests with chicks every three days noting the chick age at which botfly larvae first appeared and counting the number of larvae per chick. In a fortuitous event, I moved two two-day-old chicks that happened to have been infected with botfly larvae to a new nest. Since the new nest contained additional chicks that were never parasitized, I was sure that the infected chicks raised just a single cohort of botfly larvae. Without the confounding influence of multiple cohorts, I could learn how long a single cohort of larvae remain in a chick.

To find out how many sequential cohorts are raised by a single brood of chicks, I collected nests (with pupae attached) after chick fledging, placed them in plastic bags, and counted the number of adult flies that emerged daily. When the pattern of emergence was multi-modal, I assumed the number of peaks corresponded with the number of cohorts reared by the chicks in a nest.

On several occasions when handling chicks with mature larvae, a few larvae dropped out. I placed these in vials with a bit of nesting material on which they could pupate. I then timed the

pupation period as the number of days between pupating and adult emergence.

I also examined two characteristics of wren breeding that could influence susceptibility to parasitism. To see how time of year affected infection prevalence, I calculated the fraction of nests parasitized in two month intervals throughout the breeding season for the three study sites. For a nest to be included in an interval, the clutch had to be initiated in that interval. Only nests that had chicks through day 12 were included in the analysis, since infections were not reliably detectable before this stage. Second, I examined the effects of brood size on infection prevalence at each study site.

Effects on house wrens

To study the possible negative effects of botflies on growth rates, I weighed chicks at ages 9, 12, and 15 days (fledging usually occurs on day 18). Hatching always occurred over a <24 h period, and I defined day 0 as the first day I found any hatched chicks. I used pesola scales accurate to ± 0.1 g to weigh chicks. On day 15, I also measured tarsus length (using dial calipers accurate to ± 0.1 mm) and wing chord (using a ruler accurate to ± 1 mm). To control for time of day, I made all measurements between 0500 and 0600 local time. To compare growth in infected an uninfected chicks, I matched each infected nest with the uninfected nest of the same brood size that hatched closest in time to the infected nest. I compared growth measures using one-tailed paired t-tests on nest means, pooling data from the three years of the study. A nest pair was added to the analysis beginning with the first observation day in which the infection was noticeable.

A complication of the analysis is that the weight of the botfly larvae can artificially inflate an infected chick's weight. Since I could not remove the larvae, weigh the chick, and then replace the larvae, I had to resort to another tactic. In a subset of infected chicks in both Monteverde and an additional site near San Luis, I removed all larvae and weighed them on an electronic scale (Fisher Scientific model 7301A) accurate to ± 0.001 g. These chicks were of ages that reflect the ages of chicks I weighed and therefore had infestations that were not biased to any developmental stage. I calculated a mean larval weight by taking an average of the average larval weight per chick. I then multiplied this mean larval weight by the number of visible larvae in each chick weighed in the Monteverde growth rate sample. Subtracting this product from the chick weight gave an estimated "botfly free weight" which I used in the analyses.

To look at the effect of botflies on fledging success, I compared fledging success in infected and uninfected nests at each site. I defined fledging success as the percent of nestlings alive on either day 3 (Monteverde) or the first nest visit after hatching (La Lucha and San Luis) that survived to fledge. In Monteverde, I compared the matched pairs of infected and uninfected nests. Only nests that did not suffer predation were included in the analysis. Since the less frequent nest checks in San Luis and La Lucha made it more difficult to distinguish predation from mortality due to botflies (adult wrens haul dead chicks out of the nest), predation is a possible confounding factor in these analyses. The data could not be normalized by transformation, so I used Mann-Whitney tests to make the comparisons.

Results

Life cycle of P. carinatus

P. carinatus infections could appear on chicks at any nestling age. I rarely noticed 3-day old chicks with botfly larvae, but this may have been because the larvae were too small to be detected in the dim early morning light when I weighed the chicks. On 15 June 1991 I moved two 2-day old chicks from one box to another. I failed to notice botfly larvae on the chicks on day 3, but on day 6, the two foster chicks had larvae and the two host chicks had none. I counted 12 larvae on these chicks on day 6, but just one large larva remained on day 9. There were no more larvae for the rest of the nestling period, nor were the nonfoster chicks ever infected. I therefore calculate that larvae remain on the chicks from 5–8 days.

Parasite intensity increased to a peak at day 6 and declined thereafter (Fig. 1). In Monteverde, no chick harbored more than 17 visible larvae at a time. In San Luis, however, I observed chicks with up to 22 larvae. A brood of chicks could raise up to three or possibly four cohorts based on counts of emergence peaks (Fig. 2), although single cohorts predominated (five of the eight nests examined had unimodel emergence peaks). I collected ten large larvae from two nests that successfully pupated in vials. All ten hatched 19–20 days after pupating.

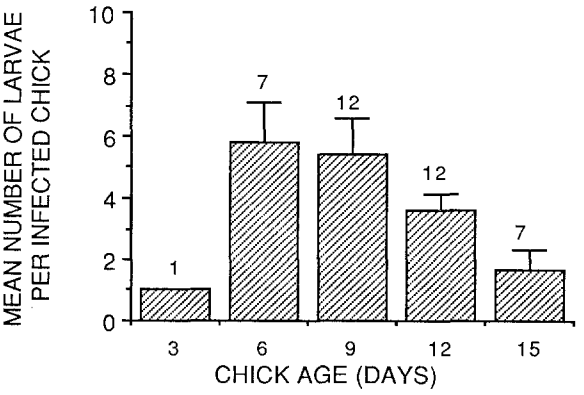

Fig. 1. Changes in intensity of botfly infection with age. Plotted are mean ($\pm$SE) number of larvae per chick of nest averages for nests with active infections at each chick age. Sample sizes of nests are listed above each bar

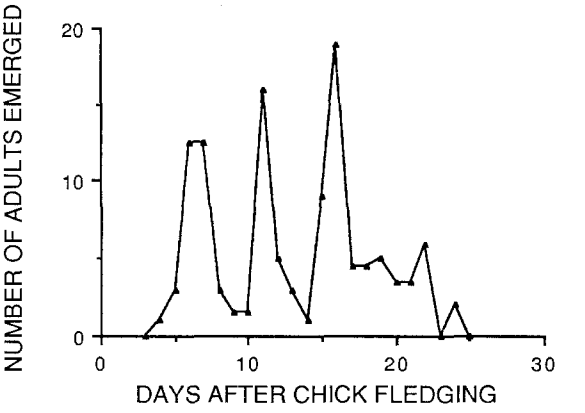

Fig. 2. Pattern of adult *Philornis* emerging from pupae collected from a single nest in July 1990. Peaks indicate cohorts that developed from separate infection bouts. When two days elapsed between counts of emerged flies, I assigned average values to each of the two days involved

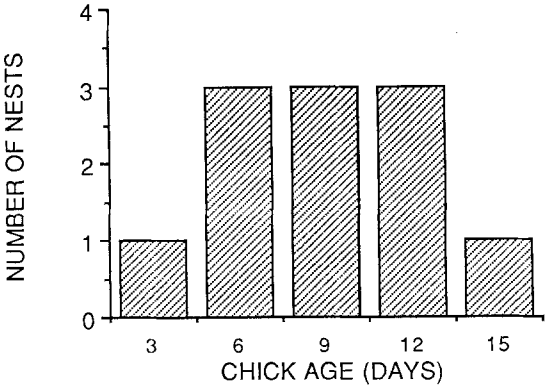

Fig. 3. Age of chicks when infections were first detected

Table 1. Seasonal prevalence of botfly parasitism in house wren nests at three study sites. Data from all years of study pooled. (Sample sizes in brackets)

Month	Monteverde	San Luis	La Lucha
Dec–Jan	– (0)	– (0)	0.00 (3)
Feb–Mar	0.02 (50)	0.00 (1)	0.11 (9)
Apr-May	0.04 (114)	0.13 (16)	0.14 (7)
Jun–July	0.27 (48)	0.33 (21)	0.57 (7)
Aug-Sept	0.00 (2)	0.67 (9)	0.50 (4)
Oct–Nov	– (0)	– (0)	1.00 (1)

Table 2. Effect of brood size on infection prevalence of philornid botflies. (Sample sizes in brackets)

Brood size	Monteverde	San Luis	La Lucha
1	0.00 (22)	0.33 (3)	0.00 (1)
2	0.03 (36)	0.00 (9)	0.00 (3)
3	0.07 (55)	0.35 (20)	0.26 (19)
4	0.13 (46)	0.47 (15)	0.20 (15)
5	0.03 (29)	0.00 (2)	– (0)
6	0.10 (21)	– (0)	– (0)

Newly infected nests were detected at all stages of the nestling period (Fig. 3). Since new infections were not skewed to the early nestling period, it appears that female botflies do not first locate nests, then wait until hatching to infect the nestlings. Instead, botflies seem to find nests randomly and infect them upon discovery, regardless of the age of the nestlings.

Infection prevalence increased during the course of the breeding season, particularly after the rainy season began in late May (Table 1). The likelihood of botfly infection did not increase linearly with brood size. Instead, nests with three or four chicks seemed more likely to be infected than either smaller or larger broods (Table 2).

Effects on house wrens

Monteverde. In Monteverde, 18 of 214 possible nests (those that had chicks reaching at least 12 days of age) suffered botfly infections in the three years of the study. Prevalence increased from 3.3% in 1989 ($n=61$ nests) to 7.8% in 1990 ($n=77$) to 13.2% in 1991 ($n=76$).

I weighed 113 botfly larvae taken out of 14 chicks from five nests. The average larval weight per chick ranged from 0.040 g to 0.106 g. The mean larval weight was 0.075 ± 0.022 (SD) g. In paired comparisons between infected and uninfected chicks, I found no significant differences in weight at ages 9 or 15 days (Table 3). Infected chicks, however, weighed less on day 12 and fledged with significantly shorter wings than uninfected chicks (Table 3). In addition, there was a trend toward infected chicks fledging with shorter tarsi than uninfected chicks (Table 3).

Fledging success was not affected by infection in Monteverde. Fledging success averaged 92% in infected nests and 95% in uninfected nests.

San Luis and La Lucha. The 1990–1991 combined prevalence of infection was much higher in both San Luis (30.6%) and La Lucha (27.3%) than in Monteverde (8.4%). In San Luis, 15 of 49 nests were infected. In La Lucha, 9 of 33 possible nests were infected. The figures for San Luis and La Lucha are minimum estimates since minor, single-cohort infections could have been overlooked in the weekly nest visits. In contrast, I am certain I detected all Monteverde infections since I checked nests every three days.

In San Luis, botfly infection had a slight negative affect on fledging success. The average fledging success of nests with infected chicks was 81% ($n=13$) whereas fledging success in nests with uninfected chicks averaged 95% ($n=30$). However, the difference was not significant when I compared the percent of chicks fledging from infected versus uninfected nests (Mann-Whitney test, $z=1.15$, 1-tailed $P=0.13$). In La Lucha, there was no affect of botfly parasitism on fledging success. All

Table 3. Effects of botfly parasitism of house wren growth measures. *P*-values are for one-tailed paired *t*-tests

Growth measure	Infected mean (± 1 SE)	Uninfected mean (± 1 SE)	Paired *t* value	D.F.	*P*
Day 9 weight (g)	10.7 ± 0.2	10.8 ± 0.2	0.588	12	0.29
Day 12 weight (g)	12.4 ± 0.1	12.7 ± 0.1	1.895	14	0.04
Day 15 weight (g)	12.6 ± 0.2	12.6 ± 0.1	0.068	13	0.48
Day 15 tarsus (mm)	18.2 ± 0.2	18.6 ± 0.2	0.840	13	0.07
Day 15 wing (mm)	38.4 ± 0.4	39.9 ± 0.3	3.429	13	<0.01

28 infected chicks survived to fledge as did all 76 non-infected chicks.

Botfly infection appeared to be timed with rainy season in San Luis and La Lucha as well as in Monteverde (Table 1). In both sites, infections disproportionately occurred during the rainy months of June through November.

Discussion

Philornis life cycle and natural history

From the data gathered here, I hypothesize the following life cycle for *P. carinatus* attacking house wrens in Costa Rica. Based on the concordance of this model with notes on philornid life history described by other authors, this scheme also probably represents a generalized life cycle for the genus. A few adults survive the wren non-breeding season. These infect early wren nests. The population of adults then grows as the flies reared from the early nests mate and reproduce. By late in the wren nesting season, the adult botfly population has swollen and the prevalence of wren broods infected with botflies increases. As wrens stop breeding, the flies probably enter a resting phase. Since there appear to be few adult flies alive early in the wren nesting season, I infer that there is substantial fly mortality outside of the wren nesting season. The increase in prevalence of botfly infections in Monteverde during the course of the study suggest there may be longer term cycles in botfly abundance as well.

Increasing philornid abundance later in the nesting season is common to other forms of botflies that have been studied. Arendt (1985b) showed that prevalence of *P. deceptivus* infection of pearly-eyed thrashers (*Margarops fuscatus*) in Puerto Rico also increased during the nesting season. Similarly, the one aplomado falcon (*Falco femoralis*) nest infected with botflies was the latest initiated of 17 nests studied in eastern Mexico (Hector 1982). Winterstein and Raitt (1983) also found the season's last beechey jay (*Cyanocorax beecheii*) nest to be infected with what was probably *Philornis*. Other studies investigating *Philornis* infections of birds have not presented seasonal data (Smith 1968, 1978; Delannoy and Cruz 1991).

Could the botflies be using alternative avian hosts? *Philornis* has been reported to infect a wide range of species (Dodge and Aitken 1968; Delannoy and Cruz 1991; Couri 1985) and may persist in alternative hosts when wren chicks are not available. This is unlikely in Monteverde since the vast majority of bird species nest when wrens do at the dry/rainy season transition (Stiles and Skutch 1989; B Young, *pers obs*). The few birds that may nest when wrens do not, namely hummingbirds (Trochilidae) and quail (Phaisianidae), are of different sizes, of different taxonomic affinities, and have different nesting habits such that it would be unusual for them to be infected by the same stage of the same parasite species. Besides house wrens, *P. carinatus* has only been recorded infecting an unidentified *Myiarchus* flycatcher in Brazil (Couri 1991). Despite examinations of dozens of nests of other birds in Monteverde, no nestling has ever been discovered infected by *P. carinatus* or any other philornid botfly (B Young, *pers obs*; S Sargent, *pers comm*).

How do flies find nests? Figure 3 suggests that flies do not find a suitable wren nest site and then wait there until the eggs hatch to infect the chicks. Instead, it appears that botflies find their hosts randomly with respect to host age. There is also no indication that botflies show philopatry to particular nest sites. In Monteverde, no box had more than one infected nest per year and only one box was the site of infection in more than one year of the study. Infections, then, represent independent events of botflies finding nests.

Litte is known about the cues *Philornis* uses to locate the nests that it parasitizes. Smith (1968:691) wrote that *Philornis* flies are "conspicuous" and "noisy" around oropendula (*Zarhynchus wagleri, Psarocolius decumanus*, and *Gymnostinops montezuma*) and cacique (*Cacicus cela*) colonies. Yet, to my knowledge, no other study has reported sightings of free-ranging adults. Specimens for taxonomic studies of the genus are usually reared from larvae found in infected birds (Aldrich 1923; Aitken et al. 1958; Dodge 1963; Dodge and Aitken 1968), or collected at fly traps (Dodge 1955, 1963) or lights (Dodge 1963).

Effects on house wrens

Philornis carinatus infections had slight adverse effects on growth in house wren chicks. Growth in mass was retarded somewhat at age 12 days, but infected chicks weighed the same as uninfected chicks by day 15 (Table 3). Apparently growth in infected chicks was slowed by the botflies enough to cause the chicks to reach asymptotic weight later than uninfected chicks. The asymptotic weight was the same in both groups, however, indicating that there were no differences in fledging weights.

Tarsus length at fledging tended to be shorter in infected chicks and wing chord at fledging was significantly shorter in infected chicks (Table 3). Thus the ill effects of philornid ectoparasitism on nestling growth do not manifest themselves evenly on all growth characters. Arendt (1985a) also found that a combination of body mass, feather lengths, and long bone lengths should be used when comparing between parasitized and non-parasitized nestling birds.

The net effect of ectoparasitism on wren fitness was small. Fledging success was not significantly affected by ectoparasitism at any site. In San Luis, however, there were several severely-parasitized nests in which the entire clutch died. I suspect that heavy parasite loads either killed the chicks or weakened them such that they succumbed to another disease. Uhazy and Arendt (1986) suggested that mortality in pearly-eyed thrashers infected with *Philornis* was due mostly to tissue loss. In the vast majority of nests in this study however, all chicks survived to fledge.

Could post-fledging survivorship have been affected by past philornid ectoparasitism? Arendt (1985b) speculated that a large fraction of infected pearly-eyed thrashers that survived to fledge probably died soon after fledging due to their weakened condition. These birds fledged in much worse shape than did the house wrens in this study. In a separate study of survivorship to two weeks after fledging in Monteverde house wrens, I found that survivors were significantly heavier at fledging (day 15) than non-survivors. Weight at day 12, wing length, and tarsus length were all unrelated to survivorship (B Young, *unpub data*). Since there was no difference in day 15 weight between infected and uninfected chicks, there probably also was no difference in post-fledging survivorship.

This study is the first to report that philornid ectoparasitism did not affect nestling survivorship. Arendt (1985b) found that 47 percent of all infected thrasher nestlings died before fledging. Nestling oropendulas and caciques that were infected by *Philornis* "suffered high mortality" (Smith 1968:692), although details are not given. Similarly, nestling mortality was four times greater in infected than in uninfected Puerto Rican sharp-shinned hawks, *Accipiter striatus venator* (Delannoy and Cruz 1991). Winterstein and Raitt (1983:263) also found that one of the three infected beechey jay chicks died and that the other two were so weak they "could no longer support their heads or stand." The study ended before the investigators could determine whether these latter chicks survived.

Given that the above interpretation is based on the nonsignificance of the paired t-tests in Table 3, it is worthwhile to ask what is the confidence interval around the difference I measured. For day 15 weight, the most critical measure due to its importance in predicting fledgling survivorship, uninfected chicks weighed an average of 0.014 g more than paired, uninfected chicks. The 95% confidence interval for the comparison is ± 0.371 g. However, even if uninfected chicks weighed the extreme 0.385 g more than infected chicks, there would be at most a 5% difference in survival based on the relationship between fledging weight and fledgling survivorship (B Young, *unpub data*). Also, the fact that I made several comparisons of growth measures increased the likelihood of finding statistically significant differences by chance. However, this bias would lead me to conclude that botflies have an important affect, the opposite of what I have in fact concluded.

Between-site comparisons

Monteverde house wrens had a much lower prevalence of infection than either San Luis or La Lucha wrens. An obvious factor may be that Monteverde has a climate that is harsher for flies. Mean monthly temperatures in Monteverde varied between 17.4° C in February and 19.6° C in June. By contrast, mean monthly temperature in San Luis was 23.2° C in February and 23.0° C in June. In La Lucha, these temperatures were 28.5° C and 28.0° C respectively (B Young and J Campbell, *unpub data*). In addition, Monteverde's position perched atop the continental divide exposes it to strong northeast trade winds throughout much of the year. San Luis is protected from these winds and La Lucha is too low to be affected.

A second possibility, host density, seems unlikely to account for the between-site differences in infection prevalence. A high prey density can allow predators to hunt more efficiently (Martin 1988; Picman 1988). Similarly, parasites may be more efficient at finding their hosts when their hosts occur at high density as host-parasite models assume (Anderson and May 1979). This hypothesis predicts that sites with similar host densities should have similar infection rates. Although I do not have exact measures, the nest boxes in both Monteverde and La Lucha were spaced approximately 50–60 m apart while the boxes in San Luis were all spaced >100 m apart. Since I originally placed the boxes where there were singing territorial males, these spacing differences accurately reflect wren densities in the three sites. Also, all natural nests (those not built in boxes) occurred on territories with boxes that were temporarily vacant. Monteverde and La Lucha had similar wren densities but had different infection prevalences. La Lucha and San Luis had different wren densities but had similar infection prevalences. Thus, I conclude that host density is unimportant in determining infection prevalence, at least at the range of densities that I examined.

Whatever the cause of between-site differences in prevalence, *P. carinatus* would be a poor candidate for an agent regulating house wren populations at any study site. Since they are not much of a hindrance to reproduction, botflies probably do not play a large role in population regulation. Interestingly, theory predicts that parasites such as botflies that do not depend on their hosts for vectors should be selected to be highly virulent, since there is no cost to the parasite of killing the host (Ewald 1983). While all species of *Philornis* that have so far been studied fit Ewald's prediction, the *P. carinatus* × house wren interaction described here does not. Possible explanations might be (1) that house wrens are not actually the botfly's preferred host or (2) that my study areas are at the edge of the parasite's range. Further study focusing on geographical and host ranges of *P. carinatus* could be illuminating.

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