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EFFECTS OF BIRD BLOWFLY PARASITISM ON EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS

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ABSTRACT.—Large numbers of bird blowfly (*Protocalliphora*) larvae in nests reportedly cause nestling morbidity and mortality in some host species, but other studies have failed to find significant effects. We conducted controlled blowfly removal and addition experiments to reveal the effects of blowfly infestations on nestling growth, development, and survival of Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Iridoprocne bicolor*). Blowflies were found in about 70% of the nests of both species. Intensity of blowfly parasitism averaged 95 blowflies/infested nest. Mean parasite burdens in infested bluebird nests were significantly greater than in swallow nests. The number of nests parasitized and the intensity of blowfly infestations increased significantly during the breeding season. There were no significant differences in nestling survival or fledging age among blowfly removal, addition, and control treatments for either species. Average bluebird nestling mass on day 14 was significantly lower in control nests than in blowfly removal nests, but the difference was small; for swallows, differences in nestling mass among treatments were not significant. Regressions of average nestling mass against mass of blowflies/nestling were significant for bluebirds on day 10 and for swallows on day 14 but explained only 14.5% and 5.5%, respectively, of variation in nestling mass. The effects of blowfly parasitism on reproductive success were minor and apparently exerted little selection pressure for nest dispersion in the two study species. *Received 9 Oct. 1991, accepted 18 April 1992.*

Larvae of the blowfly genus *Protocalliphora* (Diptera: Calliphoridae) are obligate hematophagous parasites on a wide variety of nestling birds (Sabrosky et al. 1989). Most species of bird blowflies are intermittent ectoparasites that live concealed in nest material, rarely are observed obtaining blood meals from nestlings, and obtain most blood meals at night (George and Mitchell 1948, Boyd 1951, Kenaga 1961). Pupation occurs either in the nest or on the ground under the nest. Species of birds that nest in cavities or in nests constructed of mud generally support higher infestations of blowfly larvae (Mason 1944, Pinkowski 1977, Gold and Dahlsten 1983). *Protocalliphora avium* specializes on parasitizing the nestlings of larger, open-nesting hawks, eagles, and owls (Hill and Work 1947, Bohm 1978, Crocoll and Parker 1981). The larvae of *P. avium* live continuously as ectoparasites on the head, neck, and especially in the aural cavities of nestlings (Bortolotti 1985). *Protocalliphora hirudo* is the only member of the genus confirmed to be an obligate subcutaneous

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parasite (George and Mitchell 1948, Bédard and McNeil 1979, Garrison et al. 1986), capable of remaining with the host after fledging (but see Halstead 1988).

Bird blowflies have received considerable attention from managers of bluebird nest box trails, whose goal is to maximize production of fledglings from nest boxes. Pupal cases of *Protocalliphora* frequently are encountered in nest boxes after nesting season and blamed for death of nestlings. Low nestling weights, slow development, anemia, and mortality in the nest have all been attributed to blowfly infestations (Henshaw 1908; Johnson 1929, 1930, 1931, 1932; Mason 1936; Kenaga 1961). Recent popular articles blame heavy infestations (>100 larvae) for nestling mortality and recommend treating infested nests with 1% rotenone powder (Zeleny 1986, Audubon Society of New York State 1986).

Despite these reports, several studies have been unable to detect significant nestling mortality as a consequence of *Protocalliphora* infestation, even in cases where the parasite loads were high (Mason 1944, Bennett 1957, Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1983). However, these were correlational investigations and none included controlled experiments designed to reveal the effects of blowfly infestations on nestlings. In the present study, we investigated the impact of bird blowflies on the growth, development, and survival of nestling Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Iridoprocne bicolor*) in artificial nest boxes. Our objective was to gain insight into the effects of blowfly infestations by taking an experimental approach and actively manipulating blowfly parasite burdens in nests. To our knowledge, the present study represents the first experimental attempt to test the hypothesis that bird blowflies have a negative effect on their hosts (Sabrosky et al. 1989).

STUDY AREA AND METHODS

Field work was conducted during the 1987 and 1988 breeding seasons at Genesee Country Museum, Mumford, Monroe County, New York. The study area consisted of ca 480 ha of rolling terrain and varied habitat, including agricultural fields, fallow fields, thickets, second growth hardwood forest, and swampy bottomlands. Forty-seven nest boxes were erected in 1985, prior to initiation of the study. In 1987, a total of 205 nest boxes were in place prior to the onset of nesting, and in 1988 this number increased to 325. Most nest boxes (N = 273) were erected in meadows, fallow fields, and mowed areas at least 30 m from the nearest hedgerow, thicket, or wooded area, with the remainder erected in thickets (N = 24), at the edge of agricultural fields (N = 20), and around the perimeter of a 3-ha lake (N = 8). Nest boxes were erected at 30 m intervals.

Nest boxes were half-gallon paper milk cartons lined on the inside and outside with asphalt roofing felt. We drilled entrance holes (38 mm diameter) near the top edge of the milk carton. Milk cartons were placed in wooden holders consisting of a solid roof, back, and floor with vertical braces on each side. Copper wire stretched across the front of the braces held the milk carton insert in place. This design allowed us to take inserts containing intact nests to the lab and examine them carefully for parasites. Each nest box was mounted 2 m above the ground on 2.5 cm (1 inch) black steel pipe that was greased to prevent access by climbing predators.

All nest boxes were numbered and checked weekly for nesting activity throughout the breeding season (early April to mid-August). Active bluebird and swallow nests were checked daily during the hatching period to ascertain hatching date. Each bluebird nest that successfully hatched young was alternately assigned to either the control or removal (experimental) treatment. Each swallow nest with young was systematically assigned to either the control, removal, or addition treatment. At 6, 10, and 14 days post-hatching, each nestling was weighed in the field to the nearest 0.25 g using a Pesola spring scale (50 g capacity) and placed in a substitute nest insert lined with tissue paper. The substitute insert was then replaced in the wooden frame to allow the parents to continue caring for nestlings while the nest was searched for parasites. The insert containing the nest was taken indoors where nest materials were emptied into a large tray for examination. We attempted to remove all bird blowflies from nest material, using lepidopterist's tweezers, and placed them in a weighing pan. It proved very difficult to locate and remove all blowfly eggs and first instar larvae from nest material because of their small size (<1.5 mm). Larvae removed from nests were counted and weighed to the nearest 0.1 g on a triple beam balance. Average body mass of blowflies in each nest was estimated by dividing the total mass of blowflies by the number in the nest. When eggs and first instar larvae were detected, they were noted and the number present was estimated.

After removal of blowflies, all nest material was returned to the insert from which it came. Nests were reconstructed by layering the fine nest material on top of the coarse and shaping the material into a cup. Nestlings were sufficiently advanced by six days post-hatching that the minor reduction in insulative quality associated with nest reconstruction was considered inconsequential. For nests in the control group, all blowfly larvae were placed on top of the replaced nest material. These larvae quickly moved out of sight into the nest material. For nests in the removal group, no blowflies were returned to the nest. For nests in the addition group, all blowflies removed from the nest were returned and any blowflies found in a nest from the removal treatment were added. The number and mass of larvae added to nests in the addition group was recorded. Inserts containing the nests were returned to their original location, nestlings were replaced, and the insert replaced in its holder. Nestlings were back in their original nests within 1–2 h of removal.

After nest examination on day 14, each nest was checked daily to determine fledging date. In nests where fledging was asynchronous, the age at which each nestling fledged was used to calculate a mean fledging age. In a few instances it was evident that certain nestlings had fledged prematurely (i.e., disappeared from the nest several days before the other nestlings). Premature fledging can result from the disturbance associated with checking nests. These individuals were not included in the calculation of mean fledging age.

Nestling mortality was recorded if a dead nestling was found in the nest after day 6 or if a nestling disappeared from the nest between day 6 and day 14. By day 10, dead nestlings were apparently too large for parent swallows or bluebirds to remove then from the nest; nestlings older than 10 days that died were invariably found in the nest. Some nestling mortality occurred prior to the day 6 nest examination, usually in the first or second day post-hatching. These losses could not be attributed to blowfly parasitism because of the absence or very small size of any *Protocalliphora* larvae at this stage.

Brood size varied considerably among nests of both study species. The parasite burden experienced by a nestling is dependent on both the total mass of parasites in the nest and the number of brood mates that share that burden. In order to adjust parasite burden for differences in brood size, the mass of blowflies infesting a nest was expressed on a per nestling basis. Pupae from several bluebird nests were collected after the nestlings had fledged and held until adults emerged. Adults were identified by C. W. Sabrosky and deposited in the insect collection at the Illinois Natural History Survey, Urbana.

Regression analysis and ANOVA were performed using Statworks version 1.0. All analyses involving percentages were performed on arcsine-transformed data. Test statistics were considered significant when $P \leq 0.05$.

RESULTS

Adult flies raised from pupae collected from nest boxes were identified as *Protocalliphora sialia* by C. W. Sabrosky. The limited number of blowfly adults identified to species raises the possibility of infestations of other *Protocalliphora* species or mixed infestations. However, *P. sialia* is a common species infesting Eastern Bluebird and Tree Swallow nests in the Northeast and it is likely that infestations were primarily, if not entirely, of this species (Sabrosky et al. 1989).

A total of 142 nests were included in the study—51 Eastern Bluebird nests and 91 Tree Swallow nests. Of these nests, 99 (69.7%) were infested with blowfly larvae. The prevalence of infestation was slightly higher in bluebird nests (76.5%) than in swallow nests (65.9%), but this difference was not significant ($\chi^2 = 1.719$, $P > 0.05$). Overall prevalence of infestation was somewhat greater in 1987 (84.0%) than in 1988 (62.0%), but this difference was not significant ($\chi^2 = 7.456$, $P > 0.05$) and data from the two years were combined for further analyses.

Parasite numbers in infested, control nests on day 10 post-hatching averaged 95 larvae/nest (SD = 78.8, N = 41). Mean parasite number in 21 infested, control bluebird nests (116 larvae/nest ± 78.9 [SD]) was significantly greater than that of 19 swallow nests (60 larvae/nest ± 47.7, $t = 2.77$, $P < 0.05$). The maximum number of blowfly larvae found in a nest was 284 for bluebird nests and 319 for swallow nests. For infested nests, per nestling parasite burden for bluebird nestlings on day 14 averaged 1.2 g ± 0.96 (N = 36) with a maximum of 3.2 g and for swallows averaged 1.0 g ± 0.74 (N = 52) with a maximum of 2.8 g. These per nestling parasite burdens are equivalent to 4.3% (maximum = 11.7%) and 4.7% (maximum = 12.6%) of average nestling body mass on day 14 for bluebirds and swallows, respectively.

The significantly lower average intensity of parasitism in swallow nests was apparently due to density-dependent factors that affected the size and number of blowflies in nests. In swallow nests, the average mass of blowflies on day 14 was negatively correlated with the number of blowflies in the nest ($r = -0.292$, $P = 0.007$) and positively correlated with swallow brood size ($r = 0.213$, $P = 0.029$). In a multiple regression model, number of blowflies and host brood size explained 15.4% of the variation in

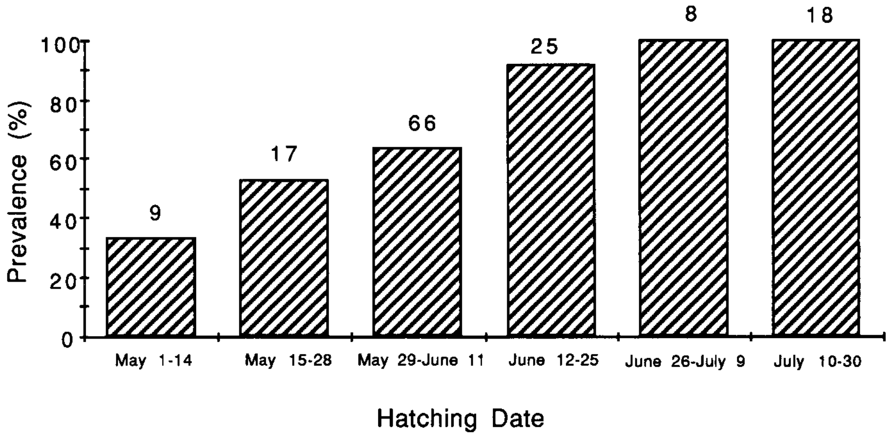

FIG. 1. Seasonal trend in blowfly parasitism in Eastern Bluebird and Tree Swallow nests.

average blowfly mass ($F_{2,61} = 5.53$, $P = 0.006$). Also, in heavily parasitized swallow nests the numbers of blowflies often declined substantially from day 10 to day 14. The change in number of blowflies in control nests from day 10 to day 14 was significantly dependent on the number of blowflies on day 10 ($F_{1,30} = 19.55$, $P < 0.0005$, $r^2 = 0.40$, $b = -0.47$). These results suggest that both the number and size of blowfly larvae in swallow nests were constrained by intraspecific competition for limiting resources.

The prevalence of parasitized nests increased as the breeding season progressed (Fig. 1). Less than half of nests that hatched in May were parasitized (N = 26), while all nests that hatched in July were parasitized (N = 22). Eastern Bluebirds normally raise two broods annually in western New York (D. D. Roby, unpubl. data) and first broods have a lower probability of being infested with blowflies than second broods. Among parasitized bluebird broods, parasite burden per nestling at day 6 increased significantly with Julian hatch date ($F_{1,36} = 6.055$, $P = 0.018$, $r^2 = 0.144$, Fig. 2). Tree Swallows normally raise a single brood in a breeding season. Swallow nests in which eggs hatched before the median hatching date had a significantly lower average parasite burden (49 larvae/nest ± 39.2, N = 31) than those that hatched after the median hatching date (86 larvae/nest ± 63.2, N = 32, $t = 2.802$, $P < 0.05$).

The mean mass of blowfly larvae/nestling on day 6 (before treatment) did not differ significantly among treatment groups for either bluebirds or swallows (Table 1), indicating that treatment groups had similar blowfly burdens up until experimental manipulation of blowflies was initiated on day 6. Removal treatments frequently did not eliminate infestation com-

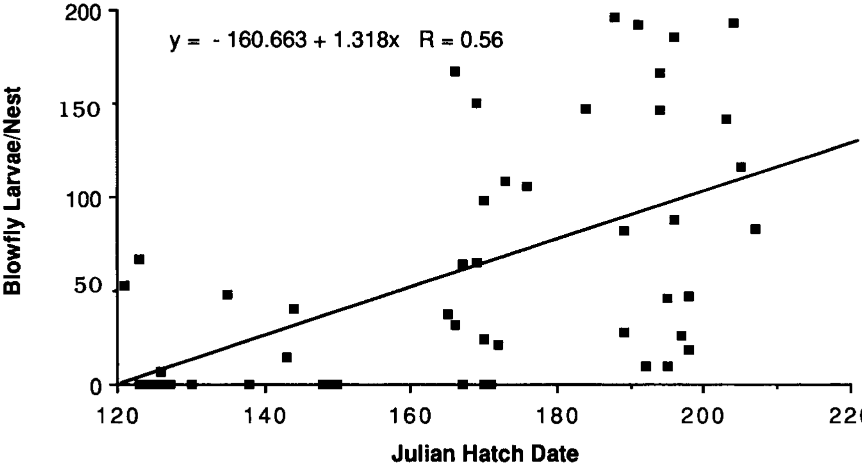

FIG. 2. Seasonal trend in intensity of blowfly parasitism in Eastern Bluebird nests at six days post-hatching.

pletely, as indicated by persistent blowfly burdens on days 10 and 14 (Table 1). This was partly because not all blowfly eggs and first instar larvae were detected and removed on day 6 and, in some cases, reinfestation occurred after removal on day 6. Nevertheless, the average mass of blowflies/nestling on days 10 and 14 in both bluebird and swallow

TABLE 1

AVERAGE MASS[a] (G) OF BIRD BLOWFLY LARVAE PER NESTLING IN EASTERN BLUEBIRD AND TREE SWALLOW NESTS AS A FUNCTION OF TREATMENT

	Age (days after hatching)		
	6	10	14
Eastern Bluebird			
Removal	0.15 (0.165, 25)	0.35 (0.392, 24)	0.32 (0.468, 24)
Control	0.17 (0.235, 26)	1.07 (0.750, 25)	1.44 (1.034, 25)
ANOVA	$F_{1,49} = 0.16$	$F_{1,48} = 8.73$	$F_{1,47} = 23.48$
	$P = 0.693$	$P = 0.005$	$P < 0.0005$
Tree Swallow			
Removal	0.02 (0.043, 29)	0.06 (0.094, 29)	0.15 (0.233, 29)
Control	0.02 (0.049, 32)	0.29 (0.420, 32)	0.76 (0.706, 32)
Addition	0.06 (0.125, 30)	0.50 (0.703, 30)	0.95 (0.878, 30)
ANOVA	$F_{2,88} = 1.843$	$F_{2,88} = 6.04$	$F_{2,88} = 11.44$
	$P = 0.162$	$P = 0.004$	$P < 0.0005$

[a] Mean (SD, N).

TABLE 2

SURVIVAL[a] OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Nestling survival (%)		
	Mean	SD	N
Eastern Bluebird			
Removal	77.5	35.6	25
Control	87.0	22.1	26
ANOVA	$F_{1,49} = 1.32$	$P = 0.255$	
Tree Swallow			
Removal	97.3	8.2	29
Control	94.3	18.6	32
Addition	89.8	25.6	30
ANOVA	$F_{2,88} = 1.19$	$P = 0.309$	

[a] Percent of nestlings alive on day 6 post-hatching that successfully fledged.

nests was significantly greater for control and addition treatments than for removals (Table 1).

Despite significantly lower parasite burdens in removal treatments, there was no significant difference in nestling survival between treatments for either bluebirds or swallows (Table 2). Also, nestling survival was not significantly dependent on the mass of blowflies/nestling on day 14 for either bluebirds ($F_{1,47} = 0.081$, $P = 0.774$) or swallows ($F_{1,89} = 2.513$, $P = 0.113$). Some bluebird and swallow nests with high per nestling blowfly burdens experienced 100% nestling survival. However, bluebird nestling survival was significantly dependent on the number of blowflies in the nest on day 10 ($F_{1,48} = 9.328$, $P = 0.004$, $r^2 = 0.163$). This significant regression resulted from two nests with the highest blowfly infestations found in bluebird nests. In one nest containing 284 blowfly larvae on day 10, one of four nestlings died on day 16 and the others fledged. In the other nest containing 265 larvae on day 10, three of four nestlings died by day 10 and the fourth was dead by day 14. One of the parents of this brood apparently abandoned the nest, but it is possible that high numbers of blowflies contributed to the death of the entire brood. In the Tree Swallow nest with the highest blowfly infestation (319 larvae on day 10), one of five nestlings was dead by day 10, but the other four fledged.

There were no significant differences in fledging age among treatments for either bluebirds or swallows (Table 3). The regression of fledging age against the mass of blowflies/nestling on day 14 was also not significant for either bluebirds ($F_{1,44} = 0.027$, $P = 0.864$) or swallows ($F_{1,86} = 0.569$, $P = 0.541$).

TABLE 3

FLEDGING AGE OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Fledging age (days after hatching)		
	Mean	SD	N
Eastern Bluebird			
Removal	18.0	1.66	21
Control	18.0	1.65	25
ANOVA	$F_{1,44} = 0.01$	$P = 0.940$	
Tree Swallow			
Removal	19.4	1.25	29
Control	19.8	1.36	31
Addition	19.7	1.53	28
ANOVA	$F_{2,85} = 0.596$	$P = 0.558$	

The effect of blowfly parasitism on nestling body mass was investigated by calculating average nestling mass for each brood on day 10 and day 14. Average nestling mass on day 10 was not significantly different among treatments for either bluebirds or swallows (Table 4). However, average bluebird nestling mass on day 14 was significantly less for control broods compared with broods in the blowfly removal group (Table 4). Average

TABLE 4

AVERAGE MASS[a] (G) OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Age (days after hatching)		
	6	10	14
Eastern Bluebird			
Removal	16.3 (2.12, 24)	25.2 (3.03, 24)	28.2 (1.73, 23)
Control	16.0 (2.96, 25)	24.3 (3.51, 25)	27.0 (2.48, 25)
ANOVA	$F_{1,47} = 0.22$ $P = 0.647$	$F_{1,48} = 1.37$ $P = 0.246$	$F_{1,46} = 4.13$ $P = 0.045$
Tree Swallow			
Removal	13.2 (1.95, 29)	20.9 (1.86, 29)	22.5 (1.60, 29)
Control	13.0 (2.26, 32)	20.5 (2.21, 32)	22.1 (1.97, 32)
Addition	12.9 (2.12, 30)	19.9 (2.78, 30)	21.4 (2.29, 30)
ANOVA	$F_{2,88} = 0.11$ $P = 0.898$	$F_{2,88} = 1.58$ $P = 0.211$	$F_{2,88} = 2.71$ $P = 0.070$

[a] Mean (SD, N).

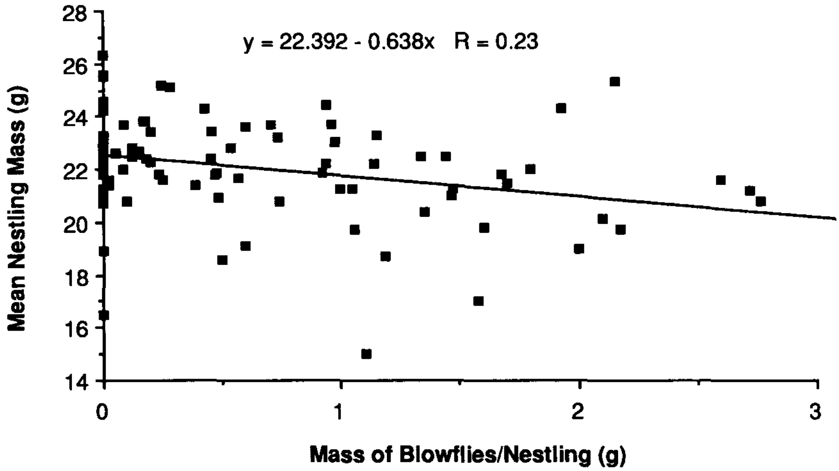

FIG. 3. Average mass of Tree Swallow nestlings at 14 days post-hatching as a function of per nestling burden of blowflies.

bluebird nestling mass on day 14 was 1.2 g (4.3%) lower in the control group compared with the removal group. Average swallow nestling mass on day 14 was lowest in the addition group and highest in the removal group, but differences were small and marginally nonsignificant (Table 4).

We further investigated the relationship between nestling mass and parasite burden by regressing average nestling mass against the mass of blowflies/nestling. For bluebirds, this regression was significant on day 10 ($F_{1,47} = 8.001$, $P = 0.007$, $r^2 = 0.145$), but not significant on day 14 ($F_{1,46} = 0.91$, $P = 0.652$). The significant regression on day 10 was due to a single nest where three of four nestlings had died, leaving the lone survivor in a nest containing 265 blowflies with a combined mass of 8.4 g. For swallows, the regression of nestling mass against per nestling mass of blowflies was not significant on day 10 ($F_{1,89} = 2.38$, $P = 0.123$), but was significant on day 14 ($F_{1,89} = 5.20$, $P = 0.023$, b = −0.64, SE = 0.28). However, per nestling blowfly burden explained only 5.5% of the variation in swallow nestling mass, and other factors were responsible for most of the variation in nestling mass (Fig. 3).

DISCUSSION

Differences in nestling growth, development, and survival between blowfly treatments were either nonsignificant or only marginally significant. Even in cases where parasite burdens were unusually high, effects of blowfly parasitism on nestling survival and mass (Fig. 3) were not pronounced. The few nests where blowfly parasitism may have caused nestling mortality were late nests, when the prevalence and intensity of blowfly parasitism were greatest. Also, brood sizes for late nests were generally lower, contributing to higher per nestling parasite burdens late in the breeding season.

These experimental results are consistent with previous correlational studies that failed to detect higher nestling mortality associated with blowfly parasitism (Bennett 1957, Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1983). It is possible that small reductions in nestling mass, such as those found in this study, may have a significant effect on fledging mass and post-fledging survival. But loss of blood to blowfly larvae normally declines prior to fledging, as larvae enter a prepupation stage, and ceases abruptly when fledglings leave the nest. Consequently, nestling recovery from the effects of blowfly parasitism may occur prior to or shortly after fledging.

Several investigators have speculated that, even in the absence of overt signs of impact on nestlings, blowfly infestations would be expected to contribute to nestling mortality during periods of food stress or adverse weather (Whitworth 1976, Gold and Dahlsten 1983). In the present study, the incidence of nestling starvation and brood reduction was relatively high in Eastern Bluebird nests, compared with Tree Swallow nests (Table 2). Most mortality of bluebird nestlings was associated with periods of cool, rainy weather, and mortality occurred in unparasitized as well as parasitized nests. While the survival of swallow nestlings was not significantly different among treatments, there was a trend toward lower means and higher variances in nestling survival with increasing parasite burden (Table 2). Consequently, a larger sample of swallow nests might reveal a significant effect of blowfly parasitism on nestling survival. This was not expected because mean intensity of blowfly infestations was considerably lower for swallow nests than for bluebird nests (Table 1).

Ectoparasites that live in nests have recently received attention from avian ecologists seeking to understand the relationship between nest dispersion and fitness (Hoogland and Sherman 1976, Brown and Brown 1986, Shields and Crook 1987). Using controlled experiments, Brown and Brown (1986) demonstrated that infestations of the swallow bug (*Oeciacus vicarius*) significantly lowered nestling body mass and nestling survival in the highly colonial Cliff Swallow (*Hirundo pyrrhonota*). Because the number of swallow bugs per nest was positively correlated with colony size, these parasites represent a cost to coloniality in Cliff Swallows. Similarly, Shields and Crook (1987) found parasitism by the bird blowfly *Protocalliphora hirundo* to be a major source of mortality for nestling Barn Swallows (*H. rustica*), a facultatively colonial species. Parasite numbers were positively correlated with colony size and negatively correlated with reproductive success, again suggesting a substantial cost to coloniality. Our results indicate that the effects of blowfly parasitism on reproductive success of Eastern Bluebirds and Tree Swallows are small and do not constitute an appreciable selection pressure for nest dispersion beyond current spacing. Unfortunately, nearest neighbor distances for active swallow and bluebird nests were not recorded in the present study, so it is not possible to test the hypothesis that proximity to an infested nest increased the probability of infestation in new nests. However, Tree Swallows nested semi-colonially in some fields within the study area, whereas active bluebird nests were more dispersed. Despite the greater dispersion of bluebird nests, prevalence of parasitism was not significantly different in nests of the two species, and intensity of parasitism was higher in bluebird nests than in swallow nests. These results suggest that nest dispersion had little effect on parasite burdens.

The small magnitude or complete absence of treatment effects on nestling survival, fledging age, or body mass raises the question of how blowfly parasitism can incur such minor costs for hosts. One factor contributing to the low pathogenicity of bird blowfly parasitism for Tree Swallow nestlings was the presence of density-dependent feedback on the size and number of larvae in nests, limitations that apparently mitigate the impact of blowflies on hosts. Although density-dependent feedback on the size and number of larvae was not as evident in bluebird nests, there was some evidence that the number of larvae in nests was constrained. For two bluebird nests in the blowfly removal treatment, a total of 471 and 467 blowfly larvae, respectively, were removed over the course of the nestling period. These numbers far exceeded the maximum number of larvae found in control nests at any one time (284 larvae), indicating that considerable mortality of larvae can occur at high densities. The results suggest that density-dependent constraints on blowflies would limit parasite burdens below the level where nestling mortality occurs, even if the two study species nested colonially.

Another potential explanation for the small effect of bird blowflies on their hosts is that the quantity of blood lost may be small relative to nestlings' tolerance for blood loss and hematopoietic capacity. If host nestlings mount little or no immune response to blowfly parasitism, the costs to hosts would be limited to replacing lost blood. No measurements of blood consumption rates are available for *Protocalliphora,* but some simple calculations will reveal the magnitude of potential blood loss. Bird blowfly larvae progress through three instars, totaling 11–13 days, prior to the prepupation stage, and the first two instar stages are relatively short (Sabrosky et al. 1989). The nestling period from day 6 to day 14 generally coincided with the third instar stage, when most larval growth takes place.

During this period, the mean mass of individual blowflies increased from 10 mg to 75 mg, or a growth increment of 65 mg. If we assume that blowfly larvae are 40% efficient at converting blood meals to biomass (Gold and Dahlsten 1983), then each larva consumed ca 160 mg of blood, or ca 20 mg of blood/day. Consequently, a 10-day-old swallow nestling in a nest of average brood size (4.4 nestlings) and with an average parasite burden (60 larvae) lost ca 270 mg of blood/day, or 1.3% of average body mass. A 10-day-old bluebird nestling in a nest of average brood size (3.4 nestlings) and with an average parasite burden (116 larvae) lost ca 680 mg of blood/day or 2.8% of average body mass. Blood volume in nestling passerines is ca 10% of body mass (Sturkie 1986:106), so these daily blood loss estimates are equivalent to 13% and 28% of total blood volume, respectively. These estimates of blood loss for average broods with average parasite burdens are not trivial, particularly for bluebird hosts, but estimates of blood loss for heavily parasitized broods are substantially higher. In the case of the swallow nest with the heaviest infestation of blowflies (319 larvae), the estimate of daily blood loss was 1.5 g/nestling, or ca 75% of total blood volume/day. In the case of the bluebird nest with the heaviest infestation of blowflies (284 larvae), the estimate of daily blood loss was 1.3 g/nestling, ca 50% of total blood volume/day.

It is difficult to conceive of how nestlings can tolerate blood loss of this magnitude for long. Birds, unlike mammals, can survive the loss of most of their blood volume (e.g., 70% of blood volume during prolonged hemorrhage in pigeons, Jones and Johansen 1972). Nevertheless, it is clear that blowfly parasitism can result in the loss of significant quantities of blood by nestlings of the two study species. The small effect of bird blowflies on their hosts is not adequately explained as a consequence of the quantity of blood lost to these parasites. The remarkable tolerance of nestling bluebirds and swallows to chronic blood loss warrants further investigation.

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