Pathogenicity of larval *Protocalliphora* (Diptera: Calliphoridae) parasitizing nestling birds

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Controlled tests showed that feeding by larvae of several species of *Protocalliphora* lowered haematocrit and haemoglobin levels of nestling magpies and bank swallows. Subsequent studies showed that natural populations of nestling magpies and Bank Swallows infested by *P. asiovora* and *P. chrysorrhoea*, respectively, experienced significantly reduced blood levels at the $P_{0.05}$ and $P_{0.01}$ levels except in the youngest nestlings. Despite the presumed heavy blood loss, most nestlings are not killed by larvae of *Protocalliphora*. Studies of natural populations of *Protocalliphora* in 48 species of birds indicate that the larval populations are usually too small to kill or seriously injure most nestlings.

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Des expériences dans des conditions contrôlées ont démontré que des oisillons au nid de Pies bavardes et d'Hirondelles de rivage nourris de larves de plusieurs espèces de *Protocalliphora* subissaient une diminution de leur hématocrite et de leur hémoglobine. Des études ultérieures ont par ailleurs montré que des populations naturelles d'oisillons de pies et d'hirondelles infestés, les uns de *P. asiovora*, les autres de *P. chrysorrhoea*, enregistraient aussi une perte significative ($P_{0.05}$ et $P_{0.01}$) de leur sang, sauf les oisillons les plus jeunes. En dépit de la forte perte de sang apparente, la plupart des oisillons survivent aux infections de larves de *Protocalliphora*. L'étude de populations naturelles de *Protocalliphora* chez 48 espèces d'oiseaux a indiqué que les populations de larves sont généralement trop petites pour tuer ou affecter sérieusement la plupart des oisillons.

[Traduit par la rédaction]

Introduction

The potential for species of *Protocalliphora* to cause nestling mortality and (or) pathogenicity has been debated by a variety of authors since the early 1920s. A thorough review of the existing literature on this subject is provided by Sabrosky et al. (1989), but detailed studies are lacking and most conclusions regarding the impact of larval feeding have been based on observations of dead or apparently sick nestlings in nests.

In the present study, based primarily on the work of Whitworth (1976) in Utah, infested nests with young that appeared ill were observed regularly and dead nestlings were occasionally found. In heavily infested nests, nestlings characteristically lacked glossy plumage, the interior of the mouth was pale or white instead of red, and skin was shrunken, wrinkled, and covered with scabs. However, such qualitative criteria were inadequate to determine the impact of *Protocalliphora* on nestlings. The need for objective criteria to evaluate the effect of larval *Protocalliphora* on nestling birds prompted a search for quantifiable parameters to measure the impact of their feeding.

Two additional parameters considered were the rate of nestling weight gain and measurable blood levels. However, a series of experiments (Whitworth 1976) revealed that rates of weight gain, though of some value, were generally less sensitive than blood values for measuring the impact of larval feeding. A variety of blood values were considered and haemoglobin and haematocrit measurements were selected, as samples could easily be obtained in the field and required only small quantities of blood. Using these criteria the impact of larvae of *Protocalliphora* on nestling birds is discussed. In addition, some qualitative observations on the impact of *Protocalliphora* on nestlings from eastern North America are presented.

Materials and methods

Most of this study was conducted on nestling birds during the period 1969–1974 within a 120-km radius of Logan (Cache County), Utah at the northern end of the Wasatch mountain range. This area is considered to be in the "western" portion of North America for *Protocalliphora*, as defined by Bennett and Whitworth (1992). Generalized observations on fledging success for a variety of bird species (primarily Common Grackles and Barn Swallows) in the Algonquin Park region of "eastern" North America are also included.

The protocols used for locating and examining birds were as described by Bennett and Whitworth (1991). However, in most of those nests, the young were allowed to fledge before the nest was examined and larvae were removed. In the present study it was necessary to examine the nests while the nestlings were present. The candidate host species for such studies had to be readily accessible and available in large numbers with concurrent high levels of *Protocalliphora* infestation. In western North America, although the nests of both Cliff Swallows (*Hirundo pyrrhonota*) and Barn Swallows (*Hirundo rustica*) were common and had high infestation rates, they were difficult to enter and examine without causing total destruction. Black-billed Magpies (*Pica pica*) and Bank Swallows (*Riparia riparia*) were finally selected for intensive study, as their nests were both common and readily accessible, with high rates of infestation (Black-billed Magpies 88.7%; Bank Swallows 78.3%). Data were also gathered on Starlings (*Sturnus vulgaris*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), and American Kestrels (*Falco sparverius*).

Individual nestlings were distinguished by coloured bands affixed

to their legs. Initially, thread and rubber bands were used, but these caused severe constriction of the growing nestlings' legs. Finally, pipe cleaners were cut to size and used, the fluffy material keeping the band tight without causing constriction. Birds were aged by measuring the length of the second primary feather on the left wing and comparing this measurement with that of nestlings of known ages; only the feather sheath was measurable in very young birds. In older birds, when the rachis began to develop, only the exposed portion of the primary feather was measured (Pettingill 1970).

Blood for analysis was collected from the brachial vein–artery, following the protocols of Bennett (1970). The blood vessel was pricked with a No. 1 insect pin mounted in a cork stored in alcohol when not in use. Wings were alternated for blood sampling, as consistent use of the same region resulted in scarification and poor blood flow; on occasion blood was also obtained from one of the metatarsal vessels. Between 80 and 90 λ of blood were drawn into a Dade 100-λ heparinized microhaematocrit tube kept on ice in the field to limit haemolysis. Severe haemolysis resulted after 3–4 h at field temperatures of 26–38°C; samples could be kept up to 2 days under refrigeration, with minimal haemolysis, but best results were obtained when the samples were processed as soon as possible after the blood was drawn. Haematocrits were determined in the laboratory by heat-sealing one end of the tube and spinning it at 10 500 rpm in an International Microhaematocrit centrifuge for 5 min. Haematocrits were determined by comparing the packed erythrocyte and leucocyte portion (in mm) of the sample to the total sample and expressing the result as a percentage. Blood samples for haemoglobin analysis were taken directly from the haematocrit tube as soon as the sample was drawn. A Spencer Hemoglobinometer (American Optical, Model 1010D) was used to measure haemoglobin levels, and the haemoglobin level was read by comparing the light absorption of the blood with a standard scale. Readings could be made to the 0.10 level of accuracy if done in subdued light.

Results and discussion

The observations in this study span a period of 40 years (1950–1990), although most were made during the period 1969–1974, primarily in the Utah area. During this period, sick, dying, or dead nestlings were observed regularly, and when such birds were found in nests heavily infested with *Protocalliphora*, it seemed logical to assume that the feeding larvae were responsible. However, many other factors may affect nestling health and survival, such as other parasites, predation, and reduced food supply due to poor climatic conditions. Myiasis by species such as *Protocalliphora braueri* is sometimes clearly the cause of nestling mortality, but these cases are relatively rare. The overall impact of intermittent feeding by these and other species of *Protocalliphora* was much more difficult to evaluate.

In the Utah area, 1819 nests were examined during the period 1969–1974, and dead nestlings were observed in 21 nests. (1.0%). In the area of Tacoma, Washington, 232 nests were examined between 1975 and 1990, 11 of which (4.75%) contained dead nestlings, for a total of 32 nests (1.6%) containing dead nestlings in the western North American sample. The Tacoma observations were based primarily on cavity nests, where adults may be less prone to remove dead nestlings. However, the western Washington climate seemed harsher during the nesting season than in Utah, and the higher nestling mortality may reflect problems with food supply, especially with the insectivorous birds. In contrast, in eastern North America, only 14 of 2571 (0.6%) nests contained dead fledglings, a figure nearly three times lower than in the overall western American sample and eight times less than the Tacoma area; 2 of 671 (0.3%) infested nests contained dead birds, whereas 12 nests (0.7%) with no *Protocalliphora* (twice as many) contained dead nestlings. *Protocalliphora braueri* was responsible for the death of the nestlings in both nests infested with *Protocalliphora*; one of these nestlings was a Vesper Sparrow lying outside its nest, and the second was a young Ovenbird that was lying outside its nest, which had obviously been devastated by a mammalian predator; the bird may well have been killed by this predator rather than by the *Protocalliphora*. In two other cases, myiasis by *Protocalliphora avium* in young crows was noted, but all birds fledged.

Detailed studies of the impact of larval feeding by *Protocalliphora* upon nestling Black-billed Magpies and Bank Swallows were conducted during the summers of 1973–1974. A primary objective was to determine if high, natural populations of larvae contributed to a reduction in survival rates of nestlings. In addition, the haematocrit and haemoglobin levels of infested and uninfested nestlings were measured to determine the sublethal impact of larval feeding. Initially, the amount of blood consumed in a single meal by eight third-instar larvae of *Protocalliphora asiovora* and five third-stage larvae of *Protocalliphora chrysorrhoea* were measured. Blood samples were dissected from the larval crop in a coagulated clump, and only the bright red blood from the most recent meal was used. The blood samples were weighed on a Mettler (S5 semimicrobalance) readable to 0.00005 g. Samples probably contained some digestive fluids, which are included in the blood weights. The amount of fresh blood in *P. asiovora* averaged 0.0165 g (range 0.0064–0.0344 g), whereas the average in *P. chrysorrhoea* was 0.0809 g (range 0.0156–0.2010 g); the difference in content for the two species is due to the fact that *P. chrysorrhoea* is substantially larger than *P. asiovora*. The range within species resulted from some larvae being more fully engorged than others.

According to Altman and Dittmer (1961), blood constitutes about 10% of the body weight of a number of bird species. Assuming a similar percentage for both the Black-billed Magpie and the Bank Swallow, their total blood capacity can be crudely estimated. Twenty 13-day-old magpies (half-grown) weighed an average of 123.1 g and would contain about 12.3 g of blood. Assuming that only large larvae of *P. asiovora* were feeding and consumed the maximum observed (0.0344 g), then 360 larvae of *P. asiovora* could exsanguinate a nestling in 1 day. Six 18-day-old Bank Swallows (nearly fledged) weighed an average of 11.3 g, therefore each contained about 1.1 g of blood. Assuming that only large *P. chrysorrhoea* with a capacity of 0.201 g fed, then 5 or 6 large larvae could exsanguinate a single nestling in a day. Since Bank Swallows are small birds and their nests are infested by large *Protocalliphora* larvae, it would be expected that either the nests would contain relatively few larvae or high nestling mortality rates would be encountered. Conversely, since *P. asiovora* occurs in nests of larger birds, it would be expected that larger larval populations would be supported and tolerated. Both of these expectations are borne out when the average numbers of larvae occurring in the two species are compared (Table 1). In the 126 infested nests of the Black-billed Magpie examined, the average number of larvae was 55 per nest, 38 nests harbouring 100–600 larvae; in 101 infested Bank Swallow nests there was an average of 38 larvae per nest, with only 8 nests harbouring 100–199 larvae.

The larval populations of *Protocalliphora* occurring in the nests of 48 species of birds (Table 1) showed that *P. asiovora* occurred in the largest numbers in the nests of Black-billed

TABLE 1. Numbers of larvae of species of *Protocalliphora* in nests of various species of birds

Bird species	Total nests: Examined	Infested	No. of larvae per nest in infested nests of each bird species: 1–25	26–50	51–75	76–100	101–199	200–299	300–399	400–499
Blackbird										
Brewer's	158	41	36	4	1					
Red-winged	85	17	15	1	1					
Yellow-headed	213	111	93	9	6	1	1	1		
Bluebird, Mountain	9	4	4							
Bunting, Lazuli	5	1	1							
Chickadee										
Black-capped	5	5	3		1	1				
Mountain	8	5	1	1	3					
Crow, American	2	2				1			1	
Dipper, American	3	2	2							
Dove, Mourning	5	1	1							
Eagle, Golden	3	2	2							
Finch, Cassin's	2	1	1							
Flicker, Common	4	2	1	1						
Flycatcher (*Empidonax*)	8	6	2	4						
Goldfinch, American	5	2	1	1						
Goshawk, Northern	7	3	3							
Hawk										
Cooper's	6	1	1							
Ferruginous	17	14	12	2						
Red-tailed	8	7	7							
Swainson's	2	2	2							
Junco, Dark-eyed	4	2	2							
Kestrel, American	24	8	7	1						
Kingbird										
Eastern	6	2	1				1			
Western	2	1	1							
Magpie, Black-billed	141	126	45	18	13	12	24	6	6	2
Martin, Purple	6	6	3	3						
Owl										
Flammulated	1	1	1							
Great Horned	5	1	1							
Long-eared	1	1	1							
Phoebe, Say's	5	3	1	2						
Raven, Common	7	6	2	1			1		1	1
Robin, American	109	27	23	2	2					
Sparrow										
Chipping	3	1	1							
Fox	5	2	2							
House	18	5	5							
White-crowned	6	1	1							
Starling, European	33	22	6	10	1	2	2			1
Swallow										
Bank	125	101	44	29	15	5	8			
Barn	392	125	85	22	6	4	6	1	1	
Cliff	208	78	65	10	2					
Tree	22	17	13	2		2				
Violet-green	3	2	2							
Vireo, Warbling	11	1		1						
Warbler										
Yellow	9	5	4		1					
Yellow-rumped	2	1	1							
Wood-Pewee, Western	7	5	4	1						
Wren										
House	33	20	16	3		1				
Marsh	7	5	1	1		2	1			

NOTE: Common names are given according to the American Ornithologist's Union *Check-list of North American Birds*, 1983 edition.

Magpies, Common Ravens, and American Crows; 42 of 131 nests belonging to these species had infestations in excess of 100 larvae. One raven nest in Idaho had in excess of 1000 larvae of *P. asiovora*. This nest contained six nearly grown nestlings, all of which appeared reasonably healthy. Three crow nests in Algonquin Park had infestations of 800–1000 larvae

TABLE 2. Effect of actively feeding third-instar larvae of *Protocalliphora* on blood levels of nestling Bank Swallows

Age (days)	Avg. no. of third-instar larvae per nestling	Average haemoglobin level (g/100 mL)			Average haematocrit level (%)		
		Uninfested nestlings	Infested nestlings	Deviation below uninfested	Uninfested nestlings	Infested nestlings	Deviation below uninfested
5	35	11.25	9.50	1.75	—	—	—
		11.25	11.50	+0.25	—	—	—
6	30	11.00	6.80	4.20	49	35	14
		11.00	8.75	2.25	49	47	2
8	45	12.00	9.50	2.50	51	39	12
		12.00	8.75	3.25	51	44	7
9	45	12.40	8.30	4.10	51	47	4
		12.40	11.00	1.40	51	60	+9
11	35	12.60	9.50	3.10	52	53	+1
		12.60	10.00	2.60	52	50	2
13	30	13.20	6.25	6.95	52	31	19
		13.20	8.00	5.20	52	38	14
14	40	14.40	7.40	7.00	56	29	27
		14.40	9.10	5.00	56	49	7
16	25	16.10	10.50	5.60	59	49	10
		16.10	8.75	7.35	59	46	13

NOTE: Average blood levels are based on one infested nest with two nestlings and one uninfested nest with four nestlings.

of *P. avium*; only two of the nine nestling crows involved appeared to be stunted in growth, but as both birds had concurrent heavy infections of both *Haemoproteus* and *Leucocytozoon*, the stunted growth may have resulted from interaction of the three parasites or from the action of the blood parasites alone. Eight of 101 nests of Bank Swallows were infested with over 100 *P. chrysorrhoea* each, and of Barn Swallows nests infested with *Protocalliphora halli*, 8 of 125 had over 100 larvae. Over 100 *Protocalliphora interrupta* larvae occurred in 1 of 5 infested nests of Marsh Wrens and 2 of 111 nests of Yellow-headed Blackbirds, while infestations of 100 or more *Protocalliphora sialia* larvae occurred in 3 of 22 infested starling nests, and 1 of 2 infested Eastern Kingbird nests had over 100 *Protocalliphora cuprina* larvae. Based on these data, it appears that natural populations of *Protocalliphora* rarely occur in sufficient numbers to kill nestlings outright, although the species of host birds are frequently quite small and the biomass of larvae (at least in some nests) in the nest must closely approximate the weight of the nestlings. Generally, however, the larger numbers of larvae occurred in the nests of larger birds, which are presumably better able to survive heavy larval feeding.

Effect of high larval populations on nestling blood levels

A series of experiments was conducted in which the larval populations of *Protocalliphora* were artificially manipulated to determine the impact of larval feeding on nestling blood levels. In one study, four healthy 17-day-old magpies were brought into the laboratory and haematocrit levels were measured. Two birds were placed in an artificial nest with an average of 100 actively feeding third-instar *P. asiovora*, while the other two were controls in an uninfested nest. The haematocrit levels of both groups declined (Fig. 1), but those of the infested nestlings continued to decline more sharply until the 5th experimental day, when the haematocrit of one bird measured only 10.3%, which was 25% of the normal level for its age; it died shortly after the sample was taken. The other infested nestling had a haematocrit of 18.6% when all larvae were removed. It eventually recovered fully, but recovery was slow, with haematocrit readings of only 30.5% after 3 days and 38% after 6 days (the normal level was 40–45% at this age).

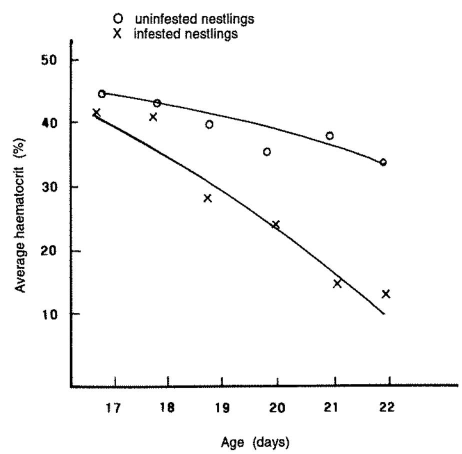

FIG. 1. Comparison of haematocrit levels of nestling magpies from experimentally heavily infested nests and uninfested nests. Note that as there were only two birds in each group, standard deviations are not given for the mean values. Note: For all figures, smooth curves were drawn by eye with the assistance of a French rule.

In an experiment with Bank Swallows, larvae of *P. chrysorrhoea* were added to a wild nest (with two nestlings) over a 14-day period. Larvae were added every 2–3 days in an effort to maintain 30–45 actively feeding third-instar larvae at all times. In another wild nest (with four nestlings of the same age as those mentioned above), larvae were removed regularly to keep the nest uninfested. Haematocrit and haemoglobin levels were measured periodically in both nests (Table 2). During the sampling period both haematocrit and haemoglobin levels tended to be lower in the birds in the infested nest than in those in the uninfested one. Despite the apparent stress, the infested nestlings successfully fledged at 26 days of age, about the same age as uninfested nestlings. This experiment demonstrated that nestling Bank Swallows are exceptionally resilient and able to survive continuous blood loss, and indicates that their haemopoetic tissues are capable of replacing blood cells in a short time. As there were only two nestlings in the nest (the average was about four), they possibly received abundant food and thus were able to regenerate blood more rapidly than nestlings in nests with more young.

Several factors interact to affect the impact of larval feeding on nestling birds. The total numbers of larvae found in the nests do not always reflect their pathogenicity to nestlings. Other factors to be considered are the number of nestlings per nest and the body size of the host species. Nestlings produce new blood more or less continuously, whereas larval feeding is intermittent. First- and second-instar larvae are so small that they probably have little impact except on very young birds. Third-instar larvae are much larger and feed actively for about 1–3 days (depending on species) before entering the nonfeeding prepupal stage. If many third-instar larvae reach this active feeding stage simultaneously, blood loss may be significant. Nestlings whose blood is sampled at this point may show below normal blood levels, the levels usually returning to normal a few days later. When studying the impact of *Protocalliphora* on nestlings, it is important to be certain that blood samples are taken when this critical point of heavy larval feeding is reached.

A number of variables may affect haemoglobin and haematocrit values in birds, including age, sex, season, time of day, parasites, and disease. These factors have been studied much more extensively on domestic than wild birds, and on adults rather than nestlings. Age affects blood values, and in altricial species the haematocrit and haemoglobin are lowest at hatching, rising to adult values as the birds mature. In the House Sparrow, Bush and Townsend (1971) found that the haemoglobin and haematocrit levels rose steadily from 4 g/100 mL and 20% at hatching to 14 g/100 mL and 40% at 50–80 days. The Red-winged Blackbird shows a similar steady rise, but blood values approached the adult level at 10 days of age, when the young fledged (Ronald et al. 1968). It is of considerable importance to determine the age of the nestlings under study if there are any conclusions to be drawn regarding deviations from normal blood levels and patterns.

Surprisingly little information is available on the effects of disease or parasites on the blood values of birds. Riddle and Braucher (1934) noted that "diseased" pigeons had substantially lower haemoglobin and red blood cell levels. Barlow (1927) found that pigeons with beri-beri had haemoglobin and red blood cell counts 25% below normal. Fallis et al. (1951) noted that *Leucocytozoon simondi* markedly lowered the haemoglobin and haematocrit and other blood values of domestic ducks. Clark (1966) noted the presence of a variety of blood parasites in the Yellow-billed Magpie, but their pathogenicity appeared to be low. Bennett et al. (1988) could not demonstrate any differences in weights of birds infected or not infected with protozoal blood parasites. Sato (1960) observed the haematocrits of chickens with a variety of diseases. Those with visceral lymphomatosis, pullorum, blackhead, and coccidiosis had haematocrits above normal, whereas those heavily infected with ascarids and cestodes had substantially lowered values.

The impact of blood-sucking arthropods on their mammalian hosts has been studied by numerous authors and there is a wealth of literature available on the subject, well summarized for North America by Laird et al. (1982) for biting flies and by Gregson (1956) for ticks. However, there are virtually no analogous studies of the impact of blood-feeding arthropods on birds. Chapman (1973) conducted a detailed study on the effect of swallow bugs (*Oeciacus vicarius*) on nestling Cliff Swallows. He found that feeding by this ectoparasite affected fledging success, mortality, and overall productivity among the swallows. He also observed significant reduction of haemoglobin and haematocrit levels in infested nestlings. Clearly, many factors may affect the health, and thus the blood values, of nestling birds and make it difficult to assign specific pathogenic effects to a single factor without taking into consideration the multifactorial approach.

The effect of P. asiovora *on the survival of nestling magpies*

During 1973–1974, 74 Black-billed Magpie nests were studied from egg hatching to fledging of the nestlings, and all but two of these nests were infested with *P. asiovora*, with an average of 170.6 larvae per nest in 1973 and 85.5 in 1974. A total of 414 eggs hatched and 283 (68.4%) of the nestlings fledged. A *T*-test comparing success of fledging between nests with less than 50 larvae and those with more than 50 larvae revealed no significant difference at the $P_{0.05}$ level. This finding contrasts sharply with Chapman's (1973) study of swallow bugs (*O. vicarius*) in Cliff Swallows, in which he found that the bugs caused significant nestling mortality before fledging. Although *P. asiovora* apparently did not kill a significant number of nestling magpies, studies were conducted on the effect of the larvae on the individual nestlings, especially since large numbers of larvae of this species were frequently observed in the nests.

During 1974, haematocrit and haemoglobin levels were measured regularly in 151 infested and 33 uninfested (including some infested nests that had 10 or less total larvae) nestling magpies 12–28 days of age; infested nests had an average of 116 larvae per nest. The mean blood levels of infested nestlings (Figs. 2, 3) tended to be lower than those of uninfested nestlings. Haematocrit (Fig. 2) and haemoglobin (Fig. 3) levels of both infested and uninfested nestlings rose steadily with age, but infested nestlings demonstrated more extreme fluctuations in blood values. Although the standard deviations of both haematocrit and haemoglobin levels overlapped at many ages (Figs. 2, 3), the trend clearly indicated that the blood values of the infested magpies were usually lower. The overlap in the standard deviations of the blood values (Figs. 2, 3) possibly resulted from the small sample size at some ages. To increase the sample size, data for ages were grouped for comparing blood values between nestlings from infested and uninfested nests. Data for haemoglobin were divided into two age groups (5–14 and 15–28 days), and those for haematocrits into three groups (5–12, 13–16, and 17–28 days). *T*-tests indicated that differences were not significant in the youngest group for either haemoglobin or haematocrit values. However, they were significant at the $P_{0.01}$ and $P_{0.05}$ levels in the older age groups.

Several interactive factors may contribute to variation in blood levels between nestlings within nests. Most magpie nests with several individuals had at least one nestling that was a "runt," a bird that was less healthy (possibly the last to hatch) than the others and who often got shoved down into the centre of the nest where it was not as competitive for food from the adults and could have been subjected to more intense larval feeding than the others. As the nestlings got older, some began perching on the edge of the nest where they no longer contacted larvae, and this would result in increased feeding on the "runt" nestlings that remained in the nest cup. Another factor that confounded the blood data was the presence of the blood-sucking dipteran *Carnus hemapterus* in 22 of 37 magpie nests also infested with *Protocalliphora*. *Carnus hemapterus* is a small blood-sucking fly whose larvae are believed to be saprophagous in bird nests (Capelle and Whitworth 1973), while

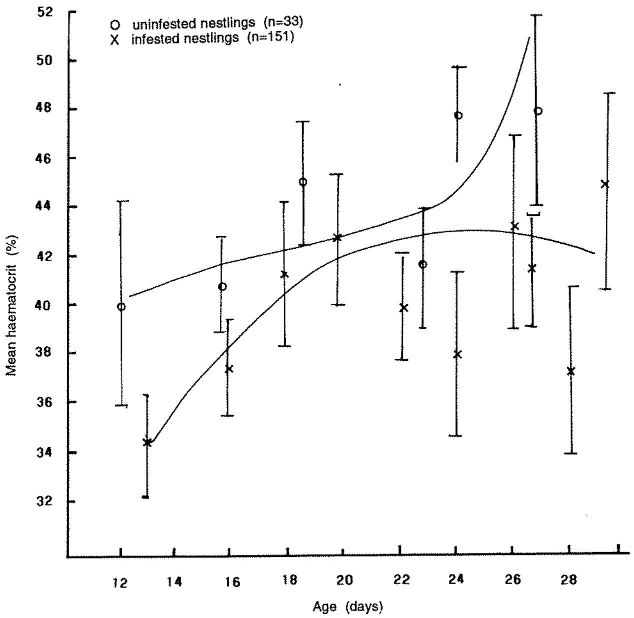

FIG. 2. Comparison by age of haematocrit levels of magpies from nests infested with *Protocalliphora asiovora* with those of nestlings from uninfested nests.

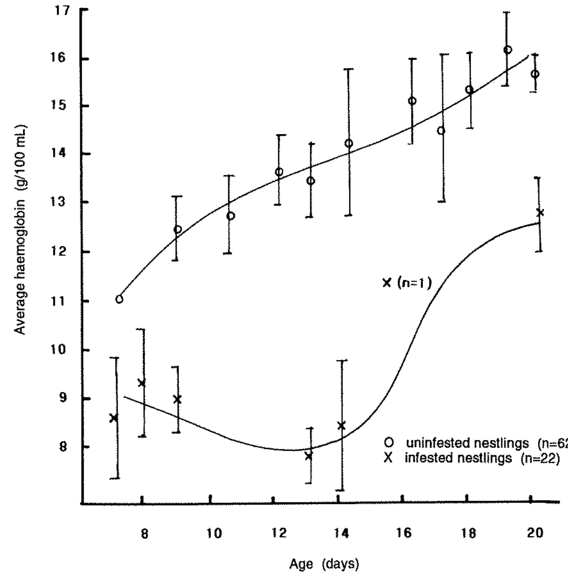

FIG. 4. Comparison by age of haemoglobin levels of Bank Swallows from nests infested with *Protocalliphora chrysorrhoea* with those of nestlings from uninfested nests.

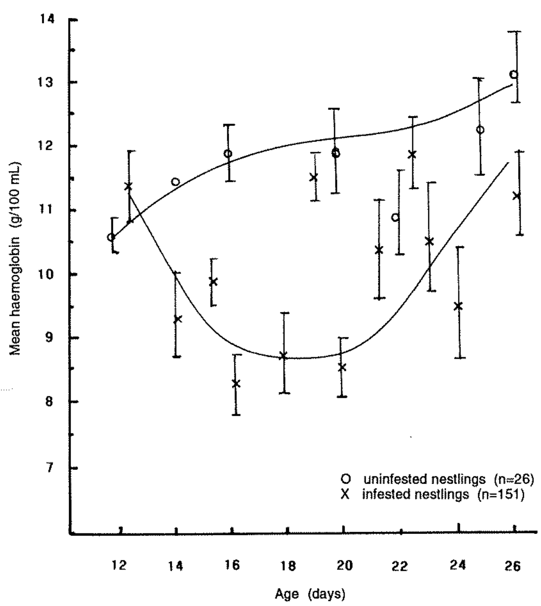

FIG. 3. Comparison by age of haemoglobin levels of magpies from nests infested with *Protocalliphora asiovora* with those from nestlings from uninfested nests.

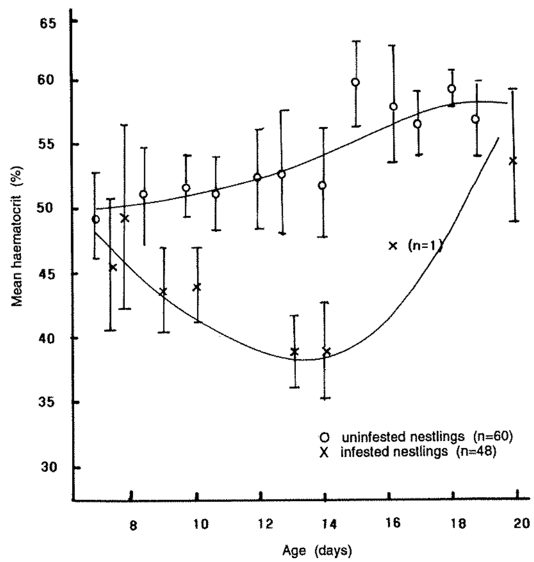

FIG. 5. Comparison by age of haematocrit levels of Bank Swallows from nests infested with *Protocalliphora chrysorrhoea* with those of nestlings from uninfested nests.

the adults create bloody, scabbed areas under the wings and on the stomachs of nestlings following their blood feeding. Heavy infestations of *C. hemapterus* also caused reduced haematocrit and haemoglobin levels. Under natural conditions, *P. asiovora* does not appear to cause substantial mortality in nestling Black-billed Magpies, as nestlings from infested nests usually overcome the blood loss caused by the larvae and fledge at about the same time as those from uninfested nests.

The effect of P. chrysorrhoea *on blood levels of nestling Bank Swallows*

The effect of *P. chrysorrhoea* on its primary host, the Bank Swallow, was studied in 25 nests. Haematocrit levels were determined in nestlings from 12 uninfested and 13 infested nests (Figs. 4, 5). Haemoglobin values were also obtained for 7 infested and all 12 uninfested nests. Infested nests contained 4–25 actively feeding third-instar larvae per nestling. The means of both haematocrit and haemoglobin values were lower in nestlings from infested nests. The standard deviations for haematocrit values overlapped for both the oldest and youngest of the nestlings, and the haemoglobin levels of nestlings from infested nests were significantly lower at all ages. *T*-test comparisons on haemoglobin levels in birds of 4–9, 10–14, and 15–20 days old and haematocrit values of birds 4–15 and 16–20 days old were performed; all blood values were significantly different between the uninfested and infested groups at the $P_{0.05}$ level. Obviously, larve of *P. chrysorrhoea* caused a significant reduction in blood values, but it appears that the impact was rarely, if ever, lethal.

Nestling survival rates and larval populations of *P. chrysorrhoea* were studied in 21 Bank Swallow nests. The number of nestlings surviving from 7 days to fledging (26+ days) was compared in six uninfested and 15 infested nests; the *T*-statistic was only 0.09. Based on this limited sample, *P. chrysorrhoea* did not reduce the number of nestlings surviving to fledge. However, nothing is known of the postfledging survival rate of Bank Swallows with low blood values. However, Pearly-eyed Thrashers infested with *Philornis* experienced 80% mortality after fledging (Arendt 1985).

The effect of Protocalliphora *on other nestling birds*

Haematocrit and haemoglobin levels were taken from starlings in 11 nests; 7 of these nests were infested with 39–441 *P. sialia* and 4 were uninfested. Dead nestlings were found in 2 of the 7 infested nests; 1 nest with six dead 10-day-old nestlings contained 215 third-instar larvae, and in another nest with 88 third-instar larvae, three of four 8-day-old nestlings were dead and the fourth was near death, with a haemoglobin level of only 4.5 g/100 mL and a haematocrit of 22%. The most heavily infested starling nest observed had four nestlings near fledging (20 days old) and contained 381 larvae and 60 puparia; three of the four birds had low blood values, but all were surprisingly healthy.

Although these data from western North America suggest that larvae of *Protocalliphora* can have a severe impact on nestlings of a variety of avian species, the evidence from eastern North America is quite contradictory. However, no blood values were measured and the comparison can only be qualitative on the basis of observed mortality and delay in time of nestling development. In the east, nestling Barn Swallows in 21 nests containing 400–900+ *Protocalliphora aenea* (averaging 150–300 larvae per nestling) fledged in the same time (23 ± 2 days) as those in 20 uninfested nests. The intensity of the infestations in these nests, on average, was nearly double that noted in Barn Swallows in the Utah sample, but no dead nestlings were encountered. Similarly, Common Grackles in 17 nests averaging 300 *P. sialia* – *Protocalliphora hirundo* per nest were neither killed nor delayed in fledging (11–13 days) compared with birds in uninfested nests. Three nestling crows in each of 3 nests containing an average of 960 *P. avium* per nest (320 larvae per nestling) fledged in 28–35 days, which is normal for the Common Crow (Bent 1946). This limited evidence suggests that in eastern North America, larvae of *Protocalliphora* have little impact on fledging success, a situation comparable to that seen in Utah. The major difference appears to lie in the lack of nestling mortality, which is more pronounced in Utah, with larval loads that are considerably lower than those experienced in eastern North America. The reasons for this difference are presently unknown, but possibly environmental conditions in Utah are more stressful on young birds than those in eastern North America.

In conclusion, this study has demonstrated that feeding by larvae of various species of *Protocalliphora* lowers both the haemoglobin and haematocrit values of nestling birds. This impact cannot be considered beneficial to the host species. On the other hand, this study has not unequivocally demonstrated that larvae of *Protocalliphora* are primary pathogenic agents or exert any significant control of the avian population. Much more detailed studies, involving manipulative techniques with a specific host species, are required to determine to what extent *Protocalliphora* species have a pathogenic effect on nestling birds. While some level of adverse effect can be anticipated, it is also true (in an evolutionary sense) that it is a poor parasite that kills its host, for this represents the parasite's suicide. The data suggest that although in some situations, larvae of *Protocalliphora* can be lethal, in most cases a state of equilibrium has evolved between the avian host and the *Protocalliphora* parasites, which ensures the survival of both.

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