Host, nest, and ecological relationships of species of *Protocalliphora* (Diptera: Calliphoridae)

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A total of 4781 nests of 110 species of birds was examined for the presence of *Protocalliphora* in several localities in Ontario, Canada, and the intermountain region of northern Utah. Twenty species belonging to this genus were found in 1621 (33.8%) nests of 73 avian species. Some species, such as *P. chrysorrhoea* and *P. halli*, showed strong host preferences, whereas others, such as *P. metallica* and *P. interrupta*, preferred specific nest environments. The nests of birds that live in colonies and (or) return to the same site annually were more frequently and heavily infested than those of other birds. In Utah, where 17 species of *Protocalliphora* occurred, most species showed a degree of host preference, whereas in Ontario, where there were only 9 species, most species preferred specific nest sites. Of the 20 species of *Protocalliphora* collected during this study, 3 were found exclusively in Ontario and 11 in Utah, with 6 species common to both study areas.

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Au total, 4781 nids de 110 espèces d'oiseaux ont été examinés au cours d'une étude du genre *Protocalliphora* en différentes localités de l'Ontario, Canada, et de la région inter-montagneuse du nord de l'Utah. Vingt espèces ont été trouvées, réparties dans 1621 (33,8%) nids de 73 espèces d'oiseaux. Certaines espèces, notamment *P. chrysorrhoea* et *P. halli*, ont de fortes préférences pour certains hôtes, alors que d'autres, *P. metallica* et *P. interrupta* par exemple, manifestent des préférences pour des conditions spécifiques reliées aux nids mêmes. Les nids des oiseaux coloniaux et (ou) des oiseaux qui retournent au même site pour nicher chaque année sont plus souvent et plus gravement infestés que les nids des autres oiseaux. En Utah, où habitent 17 espèces de *Protocalliphora*, la plupart des espèces ont une certaine préférence d'hôte, alors qu'en Ontario, où il n'y a que 9 espèces, la plupart des espèces préfèrent des sites particuliers de nidification. Des 20 espèces de *Protocalliphora* rencontrées au cours de cette étude, 3 n'ont été trouvées qu'en Ontario; 11 ont été trouvées exclusivement en Utah, et 6 étaient communes aux deux zones d'étude.

[Traduit par la rédaction]

Introduction

The existing literature on *Protocalliphora* has either concentrated almost entirely on the taxonomy of the group, or is solely a record of the avian species attacked and the harm inflicted by the various species of the genus. In both the North Amerian and European literature there has been little study on, or suggestion of, ecological relationships influencing nest selection by the female flies. Such literature that has referred to this concept in both continents has been ably summarized by Sabrosky et al. (1989).

The doctoral dissertations by Bennett (1957) and Whitworth (1976) explored the concept of the ecological relationships between host and parasite. These two studies, separated by both time and geography, are combined herein and presented as a data base of 4781 nests of 110 species of birds collected over a 40-year period (1950–1990), including 1622 infested nests of 73 avian species. This paper thus represents a broadly based ecological investigation of 20 of the 26 species of *Protocalliphora* that occur in North America, in which their relationships to both hosts and nest sites were studied in some detail. The relationship between nest structure and location and the presence of these dipterans was considered, and the results of experimental studies on the rate of spread and distribution of some *Protocalliphora* species are documented.

Materials and methods

The first study was conducted in the eastern portion of North America, the Great Lakes region of Ontario (Bennett), and the second in the Rocky Mountain region of Utah (Whitworth). Additional material from the area of Tacoma, Washington, is also included. In the context of this study, "eastern" and "western" are used as terms of convenience to identify Bennett's and Whitworth's material, respectively, and do not refer to the precise geographical distribution.

In Ontario the study was conducted in 1950–1956 at the Wildlife Research Station in Algonquin Park. Algonquin Park is in the southern portion of the Canadian Shield, where the boreal coniferous forest merges with the Carolinian deciduous climax forest. These two forest types, together with numerous lakes, streams, and marshes, provide a wide variety of habitats for a diversity of avian species. In 1954 and 1955, bird nests were examined from the rural district surrounding Caledon East, a village about 50 km northwest of Toronto, where areas of tilled land are separated by windbreaks and woodlots; marshes, ponds, and streams are relatively scarce. In 1954, a few nests were also collected in a farming community near Hawkesbury, Ontario, an area similar to that at Caledon East but situated some 500 km to the northeast on the Ottawa River. In 1955, a small sample of nests was also obtained from a mixed farm – woodlot area near Rice Lake, Ontario, about 110 km east of Toronto. Because all three regions are topographically and vegetationally similar (Carolinian forest climax) and support the same species of birds, the data are combined as "Caledon East."

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In the west, most nests were collected in 1969–1974 within a 120-km radius of Logan (Cache County), Utah. This area, at the northern end of the Wasatch Mountains, ranges from deserts at 1200 m elevation, with 225 mm annual rainfall, to conifer forests at 2100–2700 m, with 625–1000 mm annual rainfall. Nests collected in the area of Tacoma, Washington, from 1975 to 1990 are also included; Tacoma is near sea level, with average temperatures of 10–20°C and an annual rainfall of 1000 mm. Nests were collected in suburban Tacoma as well as in forest and grassland areas of nearby Fort Lewis.

Protocalliphora were collected most frequently from recently vacated bird nests. When nests were found, their height above ground and the nest-site location were recorded. Nests with young were usually left undisturbed until the young had fledged. Nests were placed in paper sacks and taken to the laboratory, where they were examined for larvae and puparia.

To standardize the eastern and western results, the nest sites were categorized into six types, according to their environment:

1. Nests inside occupied or unoccupied buildings, such as barns and sheds, or under highway bridges, under verandas, porches, and eaves, in ruined and derelict buildings, and on cliffs and under rock ledges; in all cases, nests were sheltered to some degree from wind, sun, and rain, and were usually extremely dry.
2. Nests on the ground, in clumps of grass or shrubs in open fields; nest sites 125 cm or less above ground, with direct exposure to rain and sunlight; nests normally damp.
3. Nests in clumps of cattails, sedges, reeds, and *Chamaedaphne calyculata*; usually 50 cm or less above the surface of the water; fully exposed to sun, rain, and wind; usually damp.
4. Cavity nests in stubs and dead trees, sand and gravel banks, or nest boxes; nest sites usually fully exposed to sun and rain, but the nest itself usually well sheltered; bank nests usually damp, but cavity nests in trees and nesting boxes usually extremely dry.
5. Nests in the canopy and intermediate stratum of forested areas (including orchards, windbreaks, roadside hedgerows), 3 m or more above ground (top of understorey to forest canopy); usually exposed to the elements.
6. Nests in the understorey and ground stratum of forested areas (ground level to 3 m); nest sites usually partially sheltered from the elements, but ground nests tend to be damp.

The common names of birds used throughout the text and in the tables are those used in *The A.O.U. Check-list of North American Birds* (American Ornithologists' Union 1983).

Results and discussion

Table 1 summarizes the distribution of 4668 nests of 73 avian species by nest site, and the prevalence of *Protocalliphora* in them. In the east, 2806 nests were examined, of which 667 (23.7%) were infested, whereas in the west, 964 of the 1862 (51.8%) nests examined contained *Protocalliphora*. Twenty species of *Protocalliphora* were found in the nests of 73 species of birds: 9 in the east and 17 in the west. Only 3 eastern species (*P. avium*, *P. bicolor*, and *P. fallisi*) were not recorded in the west, whereas 11 of the western species were not seen in the east. Two eastern species (*P. deceptor*, *P. tundrae*) and four western species (*P. beameri*, *P. hesperioides*, *P. sapphira*, *P. spatulata*) recorded in North America by Sabrosky et al. (1989) were not encountered in this study.

Factors affecting infestation rates in bird nests

In both studies, a few species of birds represented the majority examined, owing to their abundance and ease of collection. In the east, the common nests were those of Bank Swallows, Barn Swallows, Common Grackles, Red-winged Blackbirds, American Robins, American Goldfinches, phoebes, and "vireos." In the west they were the nests of Brewer's Blackbirds, Yellow-headed Blackbirds, Black-billed Magpies, American Robins, starlings, and Bank, Barn, Cliff, and Tree swallows. The data (Table 1) indicate that almost any species of altricial bird, particularly passeriforms, are susceptible to attack by *Protocalliphora*, as Hall (1948), Owen (1954), and Owen and Ash (1955) also reported. However, 113 nests of 37 species examined in this study were not infested with *Protocalliphora*, though the number of nests for each species was so small that further conclusions are unwarranted.

The nests of six Chimney Swifts were located in abandoned cabins in Algonquin Park within a metre of Barn Swallow nests heavily infested with both *P. aenea* and *P. sialia*, but none contained *Protocalliphora*. Their absence might be explained by the structure of the swift's nest, which is an open lacework of small twigs cemented together by salivary secretions of the swift. Small first- and second-stage larvae of *Protocalliphora* could readily fall through the interstices of such a nest. Nest structure may also explain the absence of *Protocalliphora* in the flimsy nests of Brewer's Sparrows, grosbeaks, orioles, some thrushes, and towhees, and the paucity of *Protocalliphora* infestations in the nests of Blue Jays and Chipping Sparrows (Table 1). The presence of *Protocalliphora* larvae in the meagre stick nests of Mourning Doves (Neff 1945) could be explained by the solid substrate provided by the large branches on which the nests were supported.

The nests of Cedar Waxwings, American Goldfinches (in the east), and various species of vireos were rarely infested (Table 1), although the construction of the nests was suitable for *Protocalliphora*. Possibly adult *Protocalliphora*, for unknown reasons, rarely oviposit in the nests of birds such as these, although once in the nest, the larvae can develop normally. The low rate of infestation of the nests of Western Bluebirds (Table 1) is also difficult to explain. The nests were in nest boxes and seemed to be ideal for *Protocalliphora*. They were also near Tree Swallow and House Wren nest boxes heavily infested with *P. braueri* and *P. sialia*, and it seems unlikely that they were unattractive to *Protocalliphora*.

Protocalliphora were rarely found in the nests of woodpeckers (Table 1) but were common in the nests of starlings and Tree Swallows, which subsequently built nests in the woodpecker cavities. The nests of woodpeckers, particularly flickers, are exceptionally foul, as the adult birds make no apparent effort to remove the faeces of the nestlings. Consequently, by the time the young are fledging, a layer of 5–7 cm of faecal matter covers the bottom of the nest cavity. Two flicker nests were observed containing first- and second-instar larvae of *Protocalliphora*. One nest was observed periodically from hatching of the eggs in late June until the nestlings fledged a month later. In the first 2 weeks, when the nest was reasonably clean, larvae were observed on four occasions, but no third-instar larvae or puparia were observed. As the nestlings matured and the nest became increasingly saturated with faeces, only dead larvae were found. The wet environment typical of both flicker and sapsucker nests appeared inimical to *Protocalliphora* larvae and prevented their maturation.

Distribution of Protocalliphora *in relation to host behaviour and nest site*

Protocalliphora occur more frequently in the nests of some birds than others (Table 1). Birds with the highest infestation rates were those that renest in a specific area year after year (including colonial nesters and noncolonial cavity nesters) and those that build large nests, such as crows, magpies, and

TABLE 1. Prevalence and distribution of *Protocalliphora* infestations in nests of birds from six nest-site environments

Avian species	Overall		Prevalence by nest site environment					
	Prevalence	% infested	1	2	3	4	5	6
Blackbirds								
Brewer's (W)	47/194	24.2		25/131	22/61		0/2	
Red-winged								
E	37/132	28.0			37/132			
W	17/88	19.3		3/40	14/44			
Yellow-headed (W)	110/213	51.6			110/213			
Bluebirds								
Eastern (E)	2/4	50.0				2/4		
Mountain (W)	4/9	44.4				4/9		
Western (W)	5/69	~~1.9~~ 7.3				5/69		
Lazuli Bunting (W)	1/5	20.0		1/4				0/1
Gray Catbird								
E	5/55	9.1		0/8	0/8		3/25	2/14
W	0/2	0						
Chickadees								
Black-capped								
E	0/3	0				0/3		
W	5/7	71.4				5/7		
Mountain (W)	5/8	62.5				5/8		
American crow								
E	17/20	85.0						17/20
W	2/2	100.0						2/2
Black-billed Cuckoo (E)	1/2	50.0					1/2	
American Dipper (W)	2/3	66.7	2/3					
Mourning Dove (W)	1/5	20.0		0/2			1/2	0/1
Golden Eagle (W)	1/2	50.0					1/2	
Cassin's Finch (W)	1/2	50.0					1/2	
Northern Flicker								
E	2/4	50.0				2/4		
W	2/4	50.0				2/4		
Flycatcher (*Empidonax*)								
E	2/16	12.5		0/3			0/5	2/8
W	6/8	75.0			2/2		0/1	4/5
American Goldfinch								
E	2/63	3.2		0/7	0/6		2/45	0/5
W	2/5	40.0		0/2				2/3
Northern Goshawk								
E	1/2	50.0					1/2	
W	3/7	42.9					3/7	
Common Grackle (E)	131/351	37.3	50/128		41/116	35/83	5/23	0/1
Hawks								
Broad-winged (W)	1/3	33.3					1/3	
Cooper's (W)	1/6	16.6					1/6	
Ferruginous (W)	14/17	82.4		13/16			1/1	
Red-tailed (W)	7/8	87.5	2/2	2/3			2/2	1/1
Swainson's (W)	2/2	100.0					2/2	
Jays								
Blue (E)	1/17	5.9					1/17	
Gray (E)	2/3	66.7					2/3	
Dark-eyed Junco								
E	2/8	25.0						2/8
W	3/7	42.9						3/7
American Kestrel								
E	0/1	0					0/1	
W	8/24	33.3				8/24		

TABLE 1 (*continued*)

Avian species	Overall		Prevalence by nest site environment					
	Prevalence	% infested	1	2	3	4	5	6
Kingbirds								
Eastern								
E	10/19	56.6	1/1		2/6		7/12	
W	3/7	42.9		3/5			0/2	
Western (W)	1/1	100.0						1/1
Black-billed Magpie (W)	125/141	88.7		3/3	4/5		107/122	11/11
Purple Martin (W)	8/8	100.0				8/8		
Ovenbird (E)	1/14	7.1						1/14
Owls								
Flammulated (W)	1/1	100.0				1/1		
Great-horned (W)	1/5	20.0					1/5	
Long-eared (W)	1/1	100.0					1/1	
Screech (E)	1/3	33.3					1/3	
Western Wood-Pewee (W)	5/7	71.4					5/6	0/1
Phoebes								
Eastern (E)	16/61	26.2	16/61					
Say's (W)	3/5	60.0	3/5					
Common Raven (W)	6/7	85.7	3/3	1/2			2/2	
American Robin								
E	73/373	19.5	10/65	0/5	0/3	0/8	60/279	3/13
W	27/109	24.8		2/18			11/49	14/42
Sparrows								
Chipping								
E	4/26	15.4		1/3			2/9	1/14
W	1/3	33.3		1/3				
Fox (W)	2/2	100.0		2/2				
House								
E	1/17	5.9	1/17					
W	10/43	23.2	10/43					
Savannah (E)	3/6	50.0		3/6				
Song								
E	10/33	30.3		1/13	1/1		1/2	7/17
W	0/2	0	0/2					
Swamp (E)	9/23	39.1		9/19				0/4
Vesper								
E	4/11	36.3		4/11				
W	0/2	0		0/2				
White-throated (E)	16/33	48.5		7/14	2/4		0/1	7/14
White-crowned (W)	1/6	16.7						1/6
Unknown species (E)	3/9	33.3		1/1				2/8
Common Starling								
E	11/16	68.7	6/9			5/7		
W	24/34	70.6				24/34		
Swallows								
Bank								
E	21/94	22.3				21/94		
W	101/129	78.3				101/129		
Barn								
E	239/578	41.4	239/578					
W	140/413	33.9	140/413					
Cliff (W)	139/212	65.6	139/212					
Rough-winged (E)	3/9	33.3				3/9		
Tree								
E	8/13	61.5				8/13		
W	50/92	54.3				50/92		
Violet-green (W)	2/4	50.0				2/4		
Brown Thrasher (E)	2/11	18.2		1/2				1/9

TABLE 1 (*concluded*)

Avian species	Overall		Prevalence by nest site environment					
	Prevalence	% infested	1	2	3	4	5	6
Thrushes								
Hermit (E)	1/12	8.3					0/2	1/10
Wood (E)	1/10	10.0					1/10	
Vireos								
Warbling (W)	1/11	9.1					0/2	1/9
Unknown species (E)	1/119	0.8		0/2			1/112	0/5
Warblers								
Nashville (E)	1/2	50.0					1/2	
Yellow								
E	1/3	33.3		0/1	1/1	0/1		
W	5/9	55.6					5/8	0/1
Yellow-rumped								
E	1/5	20.0			0/1		1/3	0/1
W	1/1	100.0					1/1	
Yellow-throated (E)	1/9	11.1		0/2	1/6			0/1
Unknown species (E)	2/3	66.7					2/3	
Northern Waterthrush (E)	1/1	100.0						1/1
Cedar Waxwing (E)	1/48	2.1		0/2			1/40	0/6
Downy Woodpecker (E)	2/11	18.2				2/11		
Wrens								
House								
E	7/12	58.3	6/10			1/2		
W	36/55	66.5				36/55		
Long-billed Marsh (W)	5/6	88.3			5/6			
Unknown species (E)	12/391	3.1	0/1	0/47	1/13		9/276	2/54
Total	1621/4668		628/1553	83/379	243/628	330/683	248/1105	89/320
Percentage	34.9		45.9	21.9	38.5	48.3	22.5	28.1

NOTE: Prevalence is expressed as the number of infested nests/number of nests examined. Nest-site environments are as follows: 1, in a structure; 2, a low nest; 3, in a marsh; 4, in a cavity; 5, in the canopy; 6, in the understorey. W, west; E, east.

hawks (which also remain in the nest for long periods and use the same nest in successive years). Colonial nesting is defined herein as nesting by colonial birds that habitually nest gregariously. In a few habitats, such as nest site 1, birds may nest close together because the nature of the environment causes them to crowd together. Thus, a robin or phoebe in this nest site may build a nest closely adjacent to that of a Barn Swallow, effectively creating a colonial situation, although ornithologically, neither species could be considered colonial.

Of the colonial birds studied, Bank and Cliff swallows in the west had the highest prevalence of infestation: 78 and 65%, respectively. Each occupied limited nest environments (Bank Swallows in dirt and sand banks, Cliff Swallows on rock cliffs), and each was infested by a single species (*P. chrysorrhoea* and *P. hirundo*, respectively). Conversely, Bank Swallows in the east had a much lower prevalence of infestation (22%) and were regularly infested with both *P. metallica* and *P. sialia*. The Yellow-headed Blackbirds, which nest in marshes, also had high rates of infestation (51%), primarily with *P. interrupta*. The colonial Brewer's Blackbirds (western only) and Red-winged Blackbirds (east and west) had much lower rates of infestation (24, 28, and 19%, respectively) and were infested with several species of *Protocalliphora*. Brewer's Blackbirds were observed nesting in many different environments, from deserts to the edge of marshes. Red-winged Blackbirds tend to nest on the periphery of marshes and rarely in the concentrations observed with Yellow-headed Blackbirds (in the areas studied).

The colonial-nesting Barn Swallow in the west was infested almost exclusively by *P. halli*; most nests were collected from under highway bridges. Rates of infestation were highly variable; some colonies showed 50% infestation, whereas in others it was much lower (4.6% in one case). The latter colony was a long-established one from which nests had never previously been collected. In the east, the colonial-nesting Barn Swallows in buildings and under highway bridges had about the same rate of infestation (Table 1) as noted in the west. However, the nests were infested regularly by *P. aenea*, *P. hirundo*, and *P. sialia*, and on occasion by *P. metallica*, a marked departure from the situation observed in the west.

High rates of infestation were also observed in both the east and west in a variety of noncolonial cavity nesters (Table 1), including Tree Swallows, House Wrens, and starlings. Most cavity nesters were infested with a single species of *Protocalliphora* and tended to return to the same nest annually, and the nest site appeared to provide an excellent environment for the development of larvae and pupariae.

High rates and intensities of infestations were also noted in some large, solitary-nesting birds, especially crows (85% prevalence in the east, 100% in the west); other large western birds with high infestation rates were magpies (89%) and Ferruginous (82%) and Red-tailed (87.5%) hawks. These birds

build large, bulky nests, and their population density is quite high in some areas. These birds were infested by *P. avium* in the east and *P. asiovora* in the west. Many owls also build large bulky nests, but their rates of infestation (Table 1) were inexplicably much lower.

Three interrelated factors are conducive to high rates of infestation with *Protocalliphora*: (*i*) Birds renesting in the same area and (or) nesting each year; this includes most colonial and noncolonial cavity nesters. This nesting habit allows large, stable populations of *Protocalliphora* to develop. (*ii*) Infestation by only a single species of *Protocalliphora*. Species of *Protocalliphora* that are specialized for a few species of bird hosts become more efficient at finding and infesting them at a time when nestling development maximizes their chances of survival. Many birds to which category *i* applies can also be included here, together with crows, magpies, warblers, and flycatchers, which tend to be infested by a single species of parasite. (*iii*) The structure of the nest is of a type that retains the larvae, and the nest is sufficiently free of moisture and faeces to permit the larvae to survive.

The highest prevalence of infestation would thus be expected to occur in the nests of colonial- and cavity-nesting species that are attacked by a single species of *Protocalliphora* with strong host preferences. Conversely, the lowest rates of infestation would be expected in the nest of noncolonial-, noncavity-nesting species that are not particularly favoured by any species of these flies.

Dispersal and population density of Protocalliphora

The possibility that colonial nesting provides the opportunity for the development of a large and stable population of *Protocalliphora* was tested in the field in Algonquin Park, utilizing a series of dilapidated but still relatively watertight cabins that once formed the bunkhouses and stables of a logging camp. These cabins, which represent a typical nest site 1 environment, were about 25 m apart, and each was populated with 10–15 nests (Barn Swallow, robin, phoebe, and Common Grackle, for the most part) over the course of a single summer (two broods). In 1952, all nests (approximately 75) were removed from seven cabins before any adult *Protocalliphora* emerged; 80–90% of the nests were infested. In 1953, only 5–10% of the first brood (approximately 50 nests) in these cabins were infested, the prevalence increasing to about 50% for the second brood (25 nests). Again all nests were removed prior to the emergence of any adults, and in the late fall of 1953, two cabins were seeded with adult *P. aenea*, two with *P. sialia*, and one each with *P. avium* and *P. metallica*; the latter two species never, or rarely, occur in this environment. Each cabin was seeded with 25–30 adult females of each species that had mated in captivity and were 50–60 days of age when released. In 1954, all nests in cabins seeded with *P. aenea* (12 nests) and *P. sialia* (10 nests) were infested with the species with which the cabin had been seeded; no infestations occurred in nests in cabins in which *P. avium* and *P. metallica* had been released during the rearing of the first brood, but about 50% of the second-brood nests contained *P. aenea* and (or) *P. sialia* infestations. In 1954, all nests were again removed before adult *Protocalliphora* could emerge, and in 1955, no first-brood nests were infested and only about 20% of the second-brood nests contained *P. aenea*, *P. hirundo*, and *P. sialia*. These nests were not removed prior to emergence of adult flies, and in 1956, 80–90% of the nests were again infested with these three species. During the period of this experiment, infestations of *P. metallica* and *P. shannoni* were frequently recorded in nests in the outdoor environment 10–15 m from the cabins. A nest containing *P. avium* was located about 50 m away. After the first year, the seventh cabin, was used as a control, and nests were not removed until after the adults had emerged. Throughout the experiment, 80–90% of the nests in this cabin were infested with *P. aenea*, *P. hirundo*, and *P. sialia*.

Similar evidence was obtained by removing all nests containing *P. aenea*, *P. hirundo*, and *P. sialia* from under five highway bridges and one other small cabin. The nests under two highway bridges remained uninfested for 2 years, after which a few *P. aenea* (3 nests) infestations were recorded. No infestation by *P. aenea* was recorded in 14 nests under two other highway bridges and four nests in the cabin during the first year after all infested nests had been removed before any flies had emerged. Nests under the remaining highway bridge remained uninfested for 4 years, after which *P. aenea* infestations were recorded. Other species such as *P. fallisi* and *P. metallica*, which occurred in nests less than 10 m from the bridges, did not invade the nests in this habitat. Similar results were obtained from a naturally infested building some 3 km from the nearest source of *P. aenea* infestation, where in 1950, Barn Swallows nested for the first time. Nests containing both *P. metallica* and *P. sialia* were obtained within a few metres of the building. No infestation by *Protocalliphora* occurred until 1954, when two nests with *P. aenea* were recovered.

The results of these experiments essentially confirmed that (*i*) these species of *Protocalliphora* have a slow dispersal rate and (*ii*) colonial or gregarious nesting leads to high and stable populations of the flies, which may serve as a nidus of infestation. The results also suggest that removal of immature stages of *Protocalliphora* prior to adult emergence decreases the rate of nest infestation the following year. Thus, prompt clearing of nest boxes of the old nests they contain may serve as an efficient biocontrol mechanism, rather than using chemical pesticides, as discussed by Sabrosky et al. (1989). Such a control technique, however, may well also remove the hyperparasites of *Protocalliphora*.

Host specificity

The occurrence of certain species of *Protocalliphora* primarily or exclusively in the nests of specific avian hosts (Table 2) raised the question as to whether the larvae of these species were truly host specific and could only mature on the blood of an appropriate host. In Ontario, *P. avium* occurred only in the nests of hawks and crows (Table 2). Attempts were made to rear larvae of *P. avium* on a variety of atypical hosts, and about 40 small second-instar larvae were reared to the adult stage by allowing them to feed on young Common Grackles, 50 larvae were similarly raised on domestic ducklings, and 20 larvae were reared on young mice. In addition, five larvae were reared from the second instar to adult stage following repeated feedings on one of the authors. In a second experiment, approximately 10 larvae each of *P. aenea* and *P. sialia* were successfully reared on mice, and 20 *P. sialia* larvae were reared on domestic ducklings. Again, this experiment showed that these three species of *Protocalliphora* can mature when fed on blood from totally atypical sources. If the other species of *Protocalliphora* can as readily mature on blood from atypical sources, then any apparent "host specific-

TABLE 2. Distribution of 20 species of *Protocalliphora*, by nest site

	No. of infested nests	No. of bird species	No. of nests as a percentage of total nests, by nest-site environment						Remarks
			1	2	3	4	5	6	
aenea									
E	165	7	100.0						Site specific
W	2	1	100.0						
asivora (W)	194	13	1.6	19.1	3.6		62.6	13.1	Nests in open
avium (E)	18	3					100.0		Large birds
bicolor (E)	8	6			12.5		87.5		Small birds
braueri									
E	7	4	14.3	28.6	28.6		14.3	14.3	Widespread
W	70	11	5.7	7.1	4.3	81.4	1.4		Widespread
brunneisquama (W)	1	1					100.0		
chrysorrhoea (W)	98	2	1.0			99.0			Bank nests
cuprina (W)	26	9	3.0	8.0	8.0		46.0	35.0	Small birds
fallisi (E)	11	5		9.1	63.6	18.2		9.1	Marsh nests
halli (W)	132	2	100.0						Host specific
hesperia (W)	14	2		7.1			50.0	42.9	Robins' nests
hirundo									
E	67	7	88.5	6.4				5.1	Site specific
W	174	6	91.4			8.6			Swallows
interrupta (W)	138	5		1.5	98.5				Marshes
lata (W)	6	4	16.7		50.0		33.3		Large birds
metallica									
E	149	21	3.4	11.8	45.5	4.7	11.8	19.7	Ubiquitous
W	15	5		86.6	6.7	6.7			
parorum (W)	27	4				96.3		3.7	Cavity nests
seminuda (W)	4	2	25.0	75.0					
shannoni									
E	104	12	16.0		5.0	1.0		78.0	Ubiquitous
W	8	2		12.5				87.5	Robins' nests
sialia									
E	212	15	58.0	7.5	11.0	20.1	2.4	1.0	Cavity nests
W	71	18	18.3	5.6		70.4	5.6		
spenceri (W)	1	1						100.0	

NOTE: For explanation of classification of nest-site environments see Table 1.

ity'' is a behavioural adaptation of the flies, possibly an aspect of resource partitioning.

Mixed infestations

Two or more species of *Protocalliphora* were found in 12.5% of the infested nests in the east and 6.5% of those in the west, as follows (number of infested nests is given in parentheses). In the east, *P. aenea* (38) and *P. sialia* (48) were the two species most commonly involved in mixed infestations. However, most of the species of *Protocalliphora* encountered in the east occurred to some extent in mixed infestations: *P. braueri* (5), *P. bicolor* (1), *P. hirundo* (16), *P. metallica* (20), and *P. shannoni* (11). In the west, *P. braueri* (15), *P. hirundo* (14), and *P. sialia* (19) were the species most frequently involved in mixed infestations. Other species occurring as mixed infestations were *P. asiovora* (4), *P. hesperia* (1), *P. lata* (3), *P. metallica* (3), and *P. seminuda* (3). Although it is quite clear that two species of *Protocalliphora* can develop together in a single nest, the small number of mixed infestations suggests that once a nest is infested by one species, other species tend to avoid ovipositing in the same nest. Detailed studies on *P. asiovora* and *P. chrysorrhoea* showed that these two species regularly reinfest the nests of favoured hosts, so the same species is apparently not discouraged from reinfesting a nest.

Host and nest-site preferences of species of Protocalliphora

The occurrence and distribution of species of *Protocalliphora* according to nest site are presented in Table 2. Mixed infestations occur in this analysis, and each species of the mixed infestation is recorded as a separate infestation, resulting in a higher total of infested nests than that cited in Table 1. Adult *Protocalliphora* are rarely caught or seen in the wild, and habitat and (or) host selection must be inferred from nests containing the immature stages of these flies, indicating that the females were present in the environment, at least to oviposit. The data (Table 2) indicate that the females of some species have either a ''nest site preference'' or a ''host preference,'' or possibly an interaction of the two, at the time of oviposition.

Protocalliphora aenea

This species occurred only in structures (nest site 1), primarily in the nests of birds such as Barn Swallows, Eastern Phoebes, House Wrens, and Common Grackles (Table 1). It was not recovered from nest site 1 in Caledon East, and was not taken in any cavity nest, which may seem to be at variance with its ''preference'' for nests in dark buildings. All records of *P. aenea* are from birds that were nesting in man-made structures in mountainous regions, although in the west it was found only in dipper nests under bridges. This association of

P. aenea with human structures is intriguing because in the Algonquin Park region, buildings have been present for less than 200 years and in Virginia for somewhat less than 300 years. This avian blow fly is not known from nests of cave-dwelling birds such as swifts. Its distribution and host preferences prior to the most recent arrival of Europeans is unknown, but whatever these were, this species appears to have converted to its new habitat and new range of avian hosts most recently. The eastern form of this species may have a different ethology from the western forms, which have been recovered only from dippers.

Protocalliphora asiovora

This western species was one of the most commonly found; it was collected in all nest-site environments, most frequently in nests in the intermediate stratum of the forest canopy (nest site 5). It was the dominant species in the nests of large birds such as magpies, crows, ravens, and hawks; it also occurred in the nests of a variety of bird species, but never in cavity nests. Sabrosky et al. (1989) cite a single record of this species in a starling nest in a cavity. The species shows broad host and nest-site preferences and is taxonomically close to *P. avium*, which has similar but narrower host preferences and appears to fill the same niche in the west as *P. avium* fills in the east.

Protocalliphora avium

This species was found only in the canopy or intermediate stratum in forested areas (nest site 5), and was recovered only from the nests of crows and hawks (Table 1). The records of this species (Sabrosky et al. 1989) refer to these hosts, as well as owls. *Protocalliphora avium* seems to be restricted to the nests of large birds, and it is also true that large birds usually nest in forest canopies, on cliffs, etc. This avian blow fly was not found in the nests of small birds in the same habitat, which suggests that its distribution is also governed by the host species and that there is a degree of "host preference." Whether this host preference or the nest-site preference is the controlling factor is unknown.

Protocallipora bicolor

This uncommon species was taken only eight times from nest sites 3, 5, and 6 (Table 2). One infestation occurred in a kingbird nest 12 m above ground in a dead elm in a small beaver pond; all other infestations were in nest sites 5 and 6 in deciduous forests, 4 m or more above ground. Specimens of *P. bicolor* were recorded by Johnson (1927) from the nests of the "blue-headed" vireo (i.e., the Solitary Vireo) in New Hampshire. All the hosts of *P. bicolor* listed by Sabrosky et al. (1989) are birds that nest in the intermediate or canopy level of deciduous or mixed deciduous–coniferous forests. All records are from east of the Great Plains, and the species can be considered uncommon, infesting the nests of birds utilizing Carolinian climax forest.

Protocalliphora braueri

This species occurred rarely in the east, and was found in Utah as a single or mixed infestation in a wide variety of nests in a variety of sites (Table 2). In eastern North America, with the exception of a single infestation in nest site 1, all infestations were in nests in low shrubs or on the ground, and two cavity nests near the water in a marsh were also infested. In Tacoma, Washington, this was the dominant species collected in both cavity and noncavity nests of a wide variety of bird species; of 90 infested nests examined, 63 (70%) nests of seven bird species were infested by this parasite. This species was commonly involved in mixed infestations and, though more common in cavity nests, seemed to have few nest-site or host preferences.

Protocalliphora brunnisquama

This western species was recorded on a single occasion from the nest of a Chipping Sparrow. It was collected regularly in Malaise traps in Utah and Washington and may occur in the nests of small shrub- and ground-nesting species whose nests are difficult to find.

Protocalliphora chrysorrhoea

This western species was recorded from only three host species, almost exclusively from the cavity nests of Bank Swallows in nest site 4. The Palaearctic forms also primarily attack Bank Swallows (= Sand Martins). Few other avian species nest in bank cavities. It is difficult to determine if infestations by this species are regulated by nest-site or host preferences or a combination of both.

Protocalliphora cuprina

This purely western species occurs primarily in the nests of birds utilizing nest sites 5 and 6 and may be the niche counterpart of *P. bicolor* in the east. It was the only species found in 8 of 12 warbler nests and 14 of 23 flycatcher nests examined (Table 1), but it was found in only 1 of 28 infested robin nests, which were common in the same environment. It was never found in a cavity nest. This species appears to prefer warblers and flycatchers but has been recorded in Barn Swallow and House Finch nests (Sabrosky et al. 1989). The species shows both nest-site and host preferences, but neither are marked.

Protocalliphora fallisi

This eastern species was recorded rarely in a few nests in sites 2, 3, 4, and 6 in both cavity and noncavity nests in Algonquin Park, Ontario. All infestations occurred in nests in marshes or ponds and were in nests 1 m or less from the water surface. Two single infestations were found, but this species normally occurred in association with *P. metallica* and *P. sialia*. The species is known only from Ontario, possibly represents a truly boreal species of this genus, and is present in low numbers in the intergrading Boreal–Carolinian zone of Algonquin Park.

Protocalliphora halli

This western species occurred exclusively in nest site 1, and infested only the nests of Barn Swallows and phoebes. This species, which is to some extent the niche equivalent of *P. aenea* in the east, shows evidence of strong host and nest-site specificity. It never infested the nests of House Sparrows, Cliff Swallows, or starlings that occurred in the same nest site, often in close proximity to nests infested with *P. halli*.

Protocalliphora hesperia

This western species was recorded most frequently in the forest environment (nest sites 5 and 6), with a limited host range. The primary host, the American Robin, nests ubiquitously, but *P. hesperia* was limited to nest sites 5 and 6. This species also occurred in a number of other hosts and appears to have a strong nest-site specificity rather than a host preference. *Protocalliphora hesperia* may well occupy the same niche in the western portion of the continent as *P. shannoni* in the east, although the two species compete for the same resources in the west.

Protocalliphora hirundo

This species was recovered as single (rarely mixed) infestations in nest sites 1, 2, 4, and 6 (Table 2). It occurred most frequently in the noncavity nests of site 1 and the cavity nests of site 4. Sabrosky et al. (1989) indicate that it is a broadly distributed species across the continent, usually in the nests of the Hirundinidae, many of which are colonial nesting and many closely associated with man-made structures, including the colonial nest boxes of Purple Martins. This species also occurs in nests of birds such as Common Grackles that will nest in association with man-made environments. In the west, this was the dominant species infesting the nests of Cliff Swallows (135 of 208 nests). Both eastern and western forms behaved similarly.

Protocalliphora interrupta

This western species occurs almost exclusively in the marsh environment (nest site 3) and was found in the nests of three species of blackbirds and of Marsh Wrens, but not in those of marsh-nesting warblers or magpies. The species is influenced by nest-site preferences and can be considered ethologically the western counterpart of the eastern *P. fallisi*.

Protocalliphora lata

This rare species occurred in nest site 4 in two kestrel nest boxes and a flicker nest. It was also found in three hawk nests in forest canopy (nest site 5). It resembles *P. sialia* in its ability to cross between cavity and noncavity nests, and favoured large birds as hosts, as do *P. asiovora* and *P. avium*, and like the two latter species, showed a broad ecological tolerance with some degree of host preference.

Protocalliphora metallica

This species was recorded in all six nest environments (Table 2) across the continent, most frequently in nest sites 2 and 3, in nests 2 m or less from the ground. A total of 164 nests infested with *P. metallica* were found; 134 of these were 1.5 m or less from the ground, 19 were 2−2.5 m from the ground, and 11 were 2.5−8 m from the ground. Nolan (1955) reported an infestation of this species in the nest of a Prairie Warbler 8 m above the ground.

This species was seldom taken in cavity nests and, when present, was usually associated with another species. A few *P. metallica* infestations were recorded in Bank Swallow and Common Grackle nests in tree cavities in Algonquin Park. *Protocalliphora metallica* in Bank Swallow nests situated 1 m or less from either the top or the base of a bank always occurred as mixed infestations with either *P. hirundo* or *P. sialia*; nests more than 1 m from the top or base of a bank contained infestations involving only *P. hirundo* or *P. sialia*. Similarly, grackle nests in tree stubs in nest site 4 containing *P. metallica* as well as *P. sialia* were only 1−1.5 m above the surface of the water; infested grackle nests in the same marsh that were 3 m or more above the water were infested with *P. sialia* only. Fewer infestations with *P. metallica* were found in the forest (nest sites 5 and 6, Table 2) than in sites that lacked canopy cover. Even in forest environments, however, most infested nests were on or near the ground. The host records for this species (Sabrosky et al. 1989) indicate that it occurs primarily in nests of a broad range of passeriforms that nest on or close to the ground, it occurs with great frequency in nests in marsh habitats, and its distribution is not markedly influenced by host preferences. This species was common in the east but rarely encountered in the west.

Protocalliphora parorum

This western species occurred primarily in cavity nests (nest site 4) of chickadees and House Wrens, and was never seen in nearby Mountain Bluebird or Tree Swallow nests. Gold and Dahlsten (1989) also observed narrow host preferences, recording it from the nests of Brown Creepers and nuthatches, with an unusual record from a Barn Swallow. The species is also strongly site specific (cavity nests, bird houses), and its behaviour is reminiscent of that of *P. chrysorrhoea*. The two species are found over the same geographical range, and their host specificity may indicate a degree of resource sharing.

Protocalliphora seminuda

This seldom-encountered western species (2 bird species, 4 nests, Table 2) occurred exclusively in nest site 2. The small sample size precludes the drawing of inferences regarding site or host specificity.

Protocalliphora shannoni

This species was distributed in five of the six nest environments (Table 2) across the continent, but was rare in the west. In the east, it occurred most frequently in nest site 5, where it was the major species; it was found in only a single cavity nest. *Protocalliphora shannoni* was recovered from the nests of a variety of small and medium-sized passeriform birds, approximately half of which were robins. The large number of robin nests involved, and the absence of this species from the nests of crows and hawks in the same habitat, suggest that it shows a degree of host preference. This species was also found infrequently in the nests of colonial birds, but this may be due to the fact that few such birds nest in forest habitats. This species is normally found in nests in the intermediate stratum and forest canopy, where the majority of the trees are deciduous, suggesting an association with and adaptation to the Carolinian climax forest. Eastern and western forms showed similar behaviour. In the west, this species appears to compete directly with *P. hesperia*.

Protocalliphora sialia

This species was the most frequently collected throughout Ontario, and was common in the west as well. It is also the species most frequently reported in the literature, although many of the citations refer to other species (Sabrosky et al. 1989). Distribution by nest site varied considerably between east and west. In the east, it occurred regularly in nest site 1 (58.5% cavity nests), whereas in the west it was found primarily in nest site 4 (70.4% cavity nests). It was one of the few species that infested both cavity and noncavity nests. The species has been found in the nests of a wide variety of bird species and appears to have few host or nest-site preferences, although Gold and Dahlsten (1989) recorded it entering but not ovipositing in nests of Mountain Chickadees. In the west, its absence from the common and widespread magpie nests and 13 chickadee nests (although it was present in nearby Mountain Bluebird and Tree Swallow nests) suggests that some host preference may have been in operation. *Protocalliphora sialia* occurs in two types of environment. The first is nest site 1, essentially a series of man-made environments, and the second is cavity nests; both habitats foster colonial nesting, and this undoubtedly fosters the development of a large, stable population of this species in these nest-site environments.

Protocalliphora spenceri

This species was only recorded on a single occasion, and no conclusions can be drawn.

Host and nest-site preferences

Twenty species of *Protocalliphora* are considered in this study, but only 15 species were collected in sufficient numbers to allow host or nest-site preferences to be characterized. In the east, where only nine species of *Protocalliphora* were found, nest-site preferences seemed to be the primary factor determining infestation; only *P. avium* showed evidence of host preferences. In the west, where 17 species of *Protocalliphora* occurred, only 4 species (*P. hesperia*, *P. interrupta*, *P. metallica*, and *P. shannoni*) seemed to be strongly influenced by nest site. Three transcontinental species, *P. braueri*, *P. hirundo*, and *P. sialia*, behaved in a similar fashion across the continent. *Protocalliphora braueri* and *P. sialia* showed little evidence of host or nest-site preferences. Both species occurred in every nest site, often as mixed infestations with other protocallophorids. *Protocalliphora hirundo* occurred primarily in nest site 1 and was usually limited to the Hirundinidae. The eastern *P. avium* and western *P. asiovora* are taxonomically and behaviourally close. Both species favour large bird hosts, and neither has been recorded from cavity nests (nest site 4). *Protocalliphora asiovora* might be considered to have a broader host range (it is found in 13 species, compared with 3 species for *P. avium*), but this probably only reflects the fact that few large birds were examined from nest site 5 in the eastern study. *Protocalliphora cuprina*, another western species, occurred mainly in the nests of warblers and flycatchers in nest sites 4 and 5 and rarely in nests of other avian species in these sites, although exceptions were noted. This species appears to have narrow, but not rigid, host preferences.

Three western species, *P. chrysorrhoea*, *P. halli*, and *P. parorum*, had narrow host preferences bordering on host specificity. In particular, the Holarctic *P. chrysorrhoea* was mostly restricted to the nests of Bank Swallows, the same host restriction as seen in its Palaearctic range. This may also be interpreted as nest-site specificity, as few avian species use bank burrows for nesting. The few species that utilize such a nest site, like kingfishers and Rough-winged Swallows, have not been recorded as hosts for this species. *Protocalliphora halli* in Barn Swallows and *P. parorum* in chickadees show a narrow host range; both species had frequent opportunities to infest nearby nests of other than the favoured species, but did not.

The evidence (Tables 1, 2) shows that infestation of bird nests by species of *Protocalliphora* is a combination of both ecological and host factors; the two factors have variable weight in determining the behaviour of each species of fly. At present, we can only speculate about the factors that regulate host and nest-site preferences. In areas with few species of *Protocalliphora* and more discrete nest-site environments (as in the eastern study area), species may infest any nest they encounter within a specific nest-site environment without competing with other protocalliphorid species. On the other hand, if a species such as *P. avium*, with a long developmental period (13–16 days), oviposited in the nest of a bird such as the Chipping Sparrow, which nests in the same type of habitat (nest site 5) but has a short nestling period (9 days), the nestlings would fledge before the larvae matured (Bennett and Whitworth 1991). This may explain why *P. avium* favours hosts with long nestling periods.

In the area of Logan, Utah, where most of the western study was conducted, at least 17 species of *Protocalliphora* coexisted. The nest-site environments were often in close proximity to one another, resulting in the potential for competition between many protocalliphorid species. It is not surprising, therefore, that among the western species of *Protocalliphora* studied, host preference appears to be of more importance as a mechanism for resource sharing.

Although the evidence suggests that there may be a certain degree of host preference, particularly among the western *Protocalliphora*, this conclusion should be tempered with caution. Birds with a narrow range of nesting environments (Table 1) will be infested with only a few species of *Protocalliphora*. For example, Barn Swallows nest exclusively in nest site 1, and in the east, such nests are infested primarily by *P. aenea*, *P. hirundo*, and *P. sialia*, and in the west by *P. halli*. Nests of Vesper and Savannah sparrows occur only in the open field (nest site 5) and are usually infested by *P. metallica* and, more rarely, *P. braueri*. Bank Swallows, which nest only in nest site 4, are infested by *P. metallica* or *P. sialia* in the east and by *P. chrysorrhoea* in the west. This apparent host specificity or preference is possibly only an indication of the narrow range of environments utilized by certain species of birds for nesting. With the exception of *P. chrysorrhoea* and *P. halli*, all the above species of *Protocalliphora* actually occur in the nests of a wide range of unrelated avian hosts. If one looks at the American Robin and Common Grackle, which breed in every one of the nest-site environments described (Table 1), one finds that each bird is the host for nine species of *Protocalliphora*. We suspect that the host and nest-site preferences of *Protocalliphora* may be somewhat fluid and may depend on the particular mix of bird and *Protocalliphora* species and the environments available in a specific area. It is hoped that more information on the relationships of hosts and parasites from different geographical areas will clarify the dynamics of this complex interaction.

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