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The ecology of *Protocalliphora* (Diptera: Calliphoridae) parasitism of two cavity nesting passerine birds in southwestern Québec.

by

©Matt Smar

A thesis submitted in partial fulfillment of the requirements for the degree of

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ABSTRACT

The ecology of *Protocalliphora* parasitism was studied for a two-year period in two species of cavity nesting passerine birds breeding in southwestern Québec, the eastern bluebird (*Sialia sialis* Linnaeus) and the tree swallow (*Tachycineta bicolor* Vieillot). Both species occupied nest boxes in open field habitats. Nests were parasitized primarily by *Protocalliphora sialia* Shannon and Dobroscky. In the first year of the study, 100% of bluebird nests (N=11) and 82% of tree swallow nests (N=22) were parasitized. The mean number of larvae per parasitized nest was 92.0 and 58.8, respectively. In the second year of the study, 100% of bluebird nests (N=7) and 95% of tree swallow nests (N=21) were parasitized. The mean number of larvae per parasitized nests (N=7) and 95% of tree swallow nests (N=21) were parasitized. The mean number of larvae per parasitized nests (N=7) and 95% of tree swallow nests (N=21) were parasitized. The mean number of larvae per parasitized nests (N=7) and 95% of tree swallow nests (N=21) were parasitized. The mean number of larvae per parasitized nests (N=7) and 95% of tree swallow nests (N=21) were parasitized.

The relationship between the number of *Protocalliphora* larvae per nest and selected nesting variables was examined for the two species. The variables included hatching date of the host young, nest material volume, number of fledglings, and percent canopy cover above the nest box. In bluebirds, the number of larvae per nest was significantly correlated with nest material volume in 1989 and number of fledglings in 1990. In tree swallows, the number of larvae per nest was significantly correlated with number of larvae per nest was significantly correlated with number of larvae per nest was significantly correlated with number of larvae per nest was significantly correlated with number of larvae per nest was significantly correlated with hatching date and number of fledglings in 1989.

Information on reproduction in *Protocalliphora* was obtained. Observations were made of possible mating and oviposition behaviour. Data on the timing of oviposition in relation to the host nesting cycle were obtained by trapping female flies as they visited host nests. Gravid flies were captured in active nests up to the end of the second week of the nestling period. *P. sialia* was determined to be at least bivoltine through mark, release, and recapture studies. The time between oviposition of a female fly and first oviposition of her female progeny was conservatively estimated to be 35 or 36 days under natural conditions. It was determined that nulliparous *P. sialia* can complete egg development within 9 or 10 days after eclosion. The practicality of a new *Protocalliphora* trapping technique and a mark, release, and recapture was demonstrated.

RÉSUMÉ

Au cours de deux ans, j'ai étudié la connexité écologique entre les mouches calliphoridés du genre *Protocalliphora*, parasites d'oisillons, et deux espèces d'oiseaux nicheurs au sud-ouest du Québec, le Merle bleu (*Sialia sialis* Linnaeus) et l'Hirondelle bicolore (*Tachycineta bicolor* Viellot). Les deux espèces d'oiseaux se nichaient en nichoirs situés en prés. *Protocalliphora sialia* a été trouvé le plus souvent dans les nids. Pendant la première année de l'étude, le taux de parasitisme a atteint 100% chez le Merle bleu (N=11) et 82% chez l'Hirondelle bicolore (N=22). Le nombre moyen de larves dans les nids parasitisés était de 92,0 chez le Merle bleu et de 58,8 chez l'Hirondelle bicolore. Pendant la deuxième année de l'étude, le taux de parasitisme a atteint 100% chez le Merle bleu (N=7) at 95% chez l'Hirondelle bicolore (N=21). Le nombre moyen de larves était de 115,6 et 60,3, respectivement.

Les corrélations entre le nombre de larves et quelques mesures du nid et de la saison de la ponte ont été calculées chez les deux espèces d'oiseaux. Les mesures ont inclus la date d'éclosion d'oisillons, le volume du matériaux du nid, le nombre d'oisillons, et la densité de la voûte au-dessus du nichoir. Chez le Merle bleu, le nombre de larves était en corrélation significative avec le volume du matériaux du nid en 1989 et le nombre d'oisillons en 1990. Chez l'Hirondelle bicolore, le nombre de larves était en corrélation significative avec la date d'éclosion d'oisillons et le nombre d'oisillons en 1989.

Des données sur la reproduction, la comportement nuptiale, et l'oviposition chez *Protocalliphora* ont été obtenues. Des données sur la coordination entre l'oviposition de mouches et la nidification d'oiseaux ont été obtenues en prennant les mouches au piège quand elles visitaient les nids. Des mouches capables d'ovipositer ont été prises au piège jusqu'à la fin de la deuxième semaine après la date d'éclosion. Des expériences avec des mouches marquées en laboratoire, puis relâchées et recapturées au piège, ont révélées que deux générations de *P. sialia* se reproduisent par saison. L'intervalle entre la date d'oviposition d'une mouche et la date de première oviposition de ses filles a été estimé à 35 ou 36 jours. Il a été déterminé que les femelles nullipares de *P. sialia* sont capables d'ovipositer 9 ou 10 jours après avoir sorties de la chrysalide. L'utilité d'une méthode pour marquer les mouches du genre *Protocalliphora* et pour les prendre au piège a été démontrée.

ACKNOWLEDGMENTS

This study was conducted and completed with the support of a large number of people. Family and friends helped indirectly by expressing interest in my research and giving encouragement. Others helped by providing employment when other forms of financial support were limited. Although these people are not mentioned here by name, their support, while indirect, was real and I am grateful to them.

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The oversight of my two supervisors, Dr. David J. Lewis and Dr. Rodger D. Titman of the Department of Natural Resource Sciences, McGill University, deserves special recognition. When advice was needed in steering the course through the sometimes uncharted waters of *Protocalliphora* ecology, Dr. Lewis and Dr. Titman provided guidance. Of equal importance, at times when other priorities interrupted the progress of my research, they remained patient. I am grateful for their help and understanding.

Finally, I wish to thank my boss, Mr. Joseph VanderMeulen of the Michigan Legislative Service Bureau. His tireless flow of alternately encouraging and chiding remarks kept the incentive to finish this thesis burning bright long after I had left McGill University to begin my career.

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INTRODUCTION

Larvae of the bird blow fly genus *Protocalliphora* (Diptera: Calliphoridae) are obligate blood feeding parasites of nestling birds. Twenty-six species of *Protocalliphora* are known in North America and 139 species of birds have been recorded as hosts (Sabrosky *et al.*, 1989). Some species of *Protocalliphora* are frequently found in birds' nests. However, little is known about the life history and general ecology of many members of the genus.

My objective in this study was to collect basic information on *Protocalliphora* parasitizing two species of cavity nesting passerines in southwestern Québec, the eastern bluebird (*Sialia sialis* Linnaeus) and the tree swallow (*Tachycineta bicolor* Vieillot). Both species commonly nest in man-made nest boxes in open field habitats.

The information I sought to collect fell into three broad categories. First, I wanted to identify the main species of *Protocalliphora* parasitizing eastern bluebirds and tree swallows in the study area. The literature indicated that, in eastern Canada, *P. sialia* Shannon and Dobroscky is commonly collected from cavity nests in open field habitats. Second, I wanted to investigate the influence of nest site characteristics and other variables upon the intensity of *Protocalliphora* infestations. For example, some published studies showed that the amount of nest material and the number of nestlings are positively correlated with the number of larvae in a nest. Third, I wanted to obtain basic information on reproduction in *Protocalliphora*, including information on timing of oviposition, voltinism, and parity. Some studies indicated that oviposition could occur at any time during the host nestling period. There was little information published on voltinism and parity.

To obtain the information on reproduction, I needed a means of trapping wild gravid flies. In addition, I needed a means of recapturing and identifying flies reared from hosts' nests in the laboratory and released in the field. The literature showed that, apart from manual trapping techniques such as the use of sweep nets, a trap for *Protocalliphora* had not been designed and tested. Further, mark, release, and recapture studies had not been attempted for the genus. Therefore, two additional objectives of the study were to develop a trap for *Protocalliphora* and to develop a means of marking flies in the laboratory for identification following release and recapture.



LITERATURE REVIEW

Part I. Protocalliphora Ecology

General Distribution

The bird blow fly genus *Protocalliphora* (Diptera: Calliphoridae) is Holarctic in distribution, with 26 known species in the Nearctic region. The genus is found in Alaska, throughout Canada, Greenland, most of the continental United States, and the Nearctic portion of Mexico. In the southernmost reaches of the range, the genus appears to be restricted to high altitudes. There are few records from the southeastern U.S., the southern Mississippi valley, the Great Plains states, and the Prairie provinces of Canada (Sabrosky *et al.*, 1989).

Sabrosky et al. (1989) reported that eight species of *Protocalliphora* have been recorded in southwestern Québec, including: *P. braueri* Hendel; *P. aenea* Shannon and Dobroscky; *P. avium* Shannon and Dobroscky; *P. chrysorrhea* Meigen; *P. hirundo* Shannon and Dobroscky; *P. metallica* Townsend; *P. shannoni* new species; and *P. sialia* Shannon and Dobroscky. A ninth species, *P. bicolor* Sabrosky, Bennett and Whitworth, has not been recorded in Québec but has been collected in southeastern Ontario and northern New England.

Life History of Protocalliphora

Apparently, *Protocalliphora* overwinter as adults, both males and females surviving to the following spring (Sabrosky *et al.*, 1989; Stiner, 1969). It is not known if mating occurs prior to hibernation or when the flies become active during the first warm days of late winter and early spring. Mating behaviour has not been observed in the wild, although there is some evidence that male *Protocalliphora* gather at mating sites in the manner of certain other Diptera (Sabrosky *et al.*, 1989).

Information on oviposition behaviour is limited. Once a gravid fly locates a nest containing nestlings, the fly oviposits either directly on the young or in the nest material. It is not known how many gonotrophic cycles female flies undergo, although Whitworth (1976) found evidence for multiparity in *P. asiovora* Shannon and Dobroscky and *P. chrysorrhea*. Gold and Dahlsten (1989) determined that *P. sialia* is at least biparous. There is no conclusive information for any species on the number of generations per breeding season.

The eggs of Protocalliphora appear to be adapted to the warm, dry conditions of

the nest environment. Erzinclioglu (1988) examined the eggs of the European P. *azurea* Fallen under a scanning electron microscope. The median area of the chorion differed from that of the eggs of many carrion breeding calliphorids. In other blow fly genera, the median area extends almost the entire length of the egg. Water and oxygen molecules traverse the median area, which serves as a physical gill when the egg is submerged. In *P. azurea*, the median area was found to extend less than half the length of the egg. The surface of the median area was also less porous than in related genera. Erzinclioglu hypothesized that the denser, less extensive median area of the chorion in *P. azurea* minimizes water loss.

The egg stage ranges from less than a day in *P. sialia* (Bennett, 1957) to 72 hours in *P. asiovora* Shannon and Dobroscky (Whitworth, 1976). The first and second larval instars are short in comparison to the third instar, which requires 2 or 3 blood meals for maturation. The total larval period ranges from 7 to 15 days, the prepupal period 1 to 4 days, and the pupal period from 9 to 36 days or more, depending on the species (Sabrosky *et al.*, 1989) and ambient temperature (Bennett and Whitworth, 1991). The duration of the egg and subsequent larval stages generally reflect the length of the host nestling period. Species parasitizing large birds with long nestling periods have longer egg and larval stages than species parasitizing small passerines.

The larvae are obligate blood-feeders, using mouth hooks to cut through the skin of the host, then lodging in the wound with the aid of backward-directed prothoracic fringes. All species, including those which cause myiasis, appear to feed primarily on blood (Sabrosky *et al.*, 1989).

Effect of Protocalliphora Parasitism on Young Birds

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It has been shown that the feeding activities of *Protocalliphora* larvae can kill nestlings of certain passerine species in the laboratory (Whitworth and Bennett, 1992). However, it has not been clearly demonstrated whether *Protocalliphora* parasitism is lethal to nestlings under natural conditions. Various authors have attributed the death of nestlings to blow fly infestations, but these reports seem to have been cases of "guilt by association" (for example, see Johnson, 1929). Other authors, including Gold and Dahlsten (1983), studying mountain and chestnutbacked chickadees (*Parus gambeli* Ridgway and *Parus rufescens* Townsend, respectively), Johnson *et al.* (1991), studying house wrens (*Troglodytes aedon* Vieillot), Wittman and Beason (1991), studying eastern bluebirds (*Sialia sialis* Linnaeus), and Roby *et al.* (1992), studying eastern bluebirds and tree swallows (*Tachycineta bicolor* Vieillot), have concluded that the effect of blow fly parasitism on nestling survival is slight to negligible.

While *Protocalliphora* parasitism alone may not be lethal to the host, Whitworth and Bennett (1992) demonstrated that larval feeding can lower the haemoglobin and haematocrit values of nestling birds under natural conditions. Therefore, the anemia caused by larval feeding activity may be one of a number of factors that combine to result in nestling mortality. For example, Pinkowski (1977a) found that broods of the eastern bluebird experimentally deprived of food suffered heavier parasite loads than controls. Poorly fed bluebird nestlings were weaker and less active than controls, and this may have facilitated attachment and feeding of *Protocalliphora* larvae. Under natural conditions, nestlings may not receive sufficient food during spells of cold, wet weather when insect prey is less available. Mason (1944) observed that nestling mortality of tree swallows in his Massachusetts study was greatest under the combined conditions of *Protocalliphora* infestation, cold weather, and persistent rain.

Some studies have indicated that Protr calliphora parasitism has the potential to impair fledgling survival. Whitworth (1976), Gold and Dahlsten (1983), and Johnson et al. (1991) suggested that nestlings from heavily parasitized nests might suffer increased mortality after fledging. For example, nestling magpies (*Pica pica* Linnaeus) parasitized by P. asiovora larvae exhibited retarded weight gain and anemia, but still managed to fledge normally under natural conditions (Whitworth, 1976). Gold and Dahlsten (1983) estimated that parasite loads of more than 8 Protocalliphora larvae per nestling mountain or chestnut-backed chickadee would result in an average daily loss of 10% of the total blood volume. The authors believed that blood loss of this magnitude, while non-lethal, would have debilitating effects that might impact fledgling survival. The first-year mortality of mountain chickadees in their study area was calculated to be 85%. Johnson et al. (1991) found that house wren nestlings from nests infested with P. parorum weighed 8% more than control nestlings. They hypothesized that parasite feeding delayed the normal recession in weight that occurs prior to fledging. This weight recession is due to water loss from the tissues as the nestlings mature. Presumably, this could mean that parasitized young have a lesser muscle functional capacity when they leave the nest than their unparasitized cohorts.

Host Selection

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Sabrosky *et al.* (1989) list 139 species of North American birds that are recorded hosts of *Protocalliphora*. Most of these birds are from the order Passeriformes and all bear altricial young. Some *Protocalliphora* species seem to parasitize certain species of birds more frequently than others. Although this might suggest the operation of

some form of host preference, the general concensus is that the flies do not exhibit host specificity. Rather, it is thought that a given species of *Protocalliphora* prefers certain habitats and will oviposit in the nest of almost any species of bird found in that habitat (Sabrosky and Bennett, 1956; Bennett, 1957; Sabrosky *et al.*, 1989).

For example, *P. metallica* is most often found in nests close to the ground or at shrub level, particularly in open fields or marshes. Within these habitats it parasitizes a wide range of passerines. Other species have more narrowly defined habitat preferences. *P. chrysorrhea* has been recovered primarily from bank swallow (*Riparia riparia* Linnaeus) nests. However, there are a few records of this species parasitizing barn swallows (*Hirundo rustica* Linnaeus) and violet-green swallows (*Tachycineta thalassina* Swainson). The apparent host specificity of *P. chrysorrhea* is the consequence of there being, under usual circumstances, only one species of bird exploiting the bank swallow nesting niche (Sabrosky *et al.*, 1989).

Sabrosky et al. (1989) described the habitat preferences of the eight species of *Protocalliphora* found in southwestern Québec. Of the eight, *P. sialia* and *P. metallica* are the species most often found in open field habitats. However, *P. sialia* often parasitizes cavity nesting birds while *P. metallica* does so infrequently. In Bennett's (1957) southern Ontario study, *P. sialia* accounted for 36% (15 nests out of 42) of *Protocalliphora* infestations in open field habitats (Bennett's Habitat 4). All nests containing *P. sialia* larvae in open field habitats were taken from cavities. *P. metallica* accounted for 43% (18 nests out of 42) of the infestations in Bennett's open field habitats. However, none of these infestations were in cavity nests. In Bennett's study, 152 nests were infested by *P. metallica* (all habitats taken together), but only 7 of these nests (4.7%) were in cavities. Data presented by Whitworth (1976) also indicated that *P. sialia* is more likely to infest cavity nests than open nests. Of the 71 nests infested by this species in his study, 50 (70.4%) were in cavities.

Although the general concensus is that *Protocalliphora* exhibit habitat specificity rather than host specificity, the results of one study suggested that host preference may operate in some species. Gold and Dahlsten (1989) observed that gravid female *P. sialia* visited nests of mountain and chestnut-backed chickadees but did not oviposit after crawling over the nestlings. However, cavity nests of the western bluebird (*Sialia mexicana* Swainson) in the study plots were infested with *P. sialia* larvae. The bluebird nests were at the same height as the chickadee nests. Conversely, *P. parorum* (*Protocalliphora* n. sp. in their paper) consistently

parasitized nests of the two chickadee species but was never recovered from western bluebird nests in the same habitat. These observations led the authors to propose the existence of two sets of stimuli involved in host finding and acceptance. Long-range stimuli (*e.g.*, olfactory or visual cues) would attract gravid flies to active nests while other stimuli associated with the nest and/or nestlings would induce oviposition.

Protocalliphora Species Parasitizing Eastern Bluebirds and Tree Swallows

Of the Protocalliphora species found in southwestern Québec, P. bicolor and P. metallica have been collected from tree swallow nests and P. hirundo, P. shannoni, and P. sialia have been collected from both eastern bluebird and tree swallow nests. P. braueri is the only species of the genus that invariably causes true subcutaneous myiasis (P. avium and P. asiovora do so only occasionally). It has been collected from tree swallow nestlings, and there is a record from Montana in which it was collected from a nest of young bluebirds (species unspecified) (Sabrosky et al., 1989). Whitworth (personal communication) reported collecting P. braueri from western bluebirds in the northwestern U.S. P. aenea, P. avium, and P. chrysorrhea have not been recorded as parasites of the eastern bluebird nor the tree swallow (Sabrosky et al., 1989).

Nesting Variables Influencing the Intensity of Infestations

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Some studies have indicated that the substrate of the nest or the physical properties of the nest material may influence the number of *Protocalliphora* larvae it can hold. In Bennett's (1957) study, cavity nests had a higher rate of *Protocalliphora* infestation than nests supported by twigs or branches. This was probably due to the containing effect of the cavity. Woodpeckers (Picidae) seem to be an exception to this generality, apparently because these birds often have wet, messy nests (Whitworth, 1976; Sabrosky *et al.*, 1989). Open cup nests made of coarse, loosely-woven material, such as the twig nests of the mourning dove (*Zenaida macroura* Linnaeus), furnish few suitable resting or hiding places for blow fly larvae (Sabrosky *et al.*, 1989). Thus, a loose nest framework may limit the number of larvae the nest can hold.

The amount of nesting material used in cavity nests may also influence the intensity of a *Protocalliphora* infestation by determining the number of resting or hiding places for the larvae. Whitworth (1976), Pinkowski (1977a), and Gold and Dahlsten (1989) all found positive correlations between the amount of nesting material used and the number of *Protocalliphora* larvae in the nest. These authors suggested three hypotheses to explain the observed correlations. The authors proposed that larger nest material volumes allowed the larvae to avoid detection

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and predation by the adult birds (Pinkowski, 1977a; Gold and Dahlsten, 1989), avoid contact with toxic constituents of their own excrement (Whitworth, 1976), or avoid exposure to low temperatures (Whitworth, 1976).

Finally, Whitworth (1976) found that young *P. asiovora* larvae would attach themselves to the host for periods up to several days. Common sites of attachment were the rear edge of the wings and the base of the body feathers. The author hypothesized that such attachment might enhance larval survival. Since attachment sites on a single host are limited, large broods may support larger larval populations than smaller broods.

Reproduction in Protocalliphora

Some reproductive aspects of the life history are known for a few species of *Protocalliphora*. Bennett (1957), Whitworth (1976), and Gold and Dahlsten (1989) have made notable contributions in this area based on laboratory and field studies. However, complete information on mating, oviposition, voltinism, and parity is not available for any North American species of *Protocalliphora* (Sabrosky *et al.* 1989).

Mating Behaviour

The literature on North American species of *Protocalliphora* does not include observations of mating in the field. Bennett (1957) observed mating in several species of *Protocalliphora* held captive in glass tubes and screened cages in the laboratory. Mating would occur shortly after the flies emerged from the puparia and tanning was complete. Mating was observed intermittently throughout the remainder of the flies' lifespan (often on the order of several months). On some occasions, Bennett observed the flies performing a "mating dance" in which the male circled the female on stiffly held legs. A receptive female would raise and extend the middle leg on the side closest to the male. Copulation occurred within 15 to 30 seconds. However, copulation was not always preceded by this behaviour.

It is not known whether Bennett's observations represent typical mating behaviour of wild flies. Further, it is not known how the sexes come together for mating. Bennett's (1957) findings indicate that the nest might be the site where some mating occurs in nature. However, adults emerging while nestlings are still

present might flee the nest soon after tanning is complete to escape predation by the adult birds. In such circumstances, mating would take place at another location.

Thornhill and Alcock (1983) note that a male strategy common in many species of winged insects is to congregate at "landmarks," or distinctive topographical or physical features in the habitat. Apparently, receptive females visit these landmarks for mating. Sabrosky *et al.* (1989) have suggested that male *Protocalliphora* may congregate at landmarks for mating purposes. The authors based this conjecture on the fact that male specimens of *P. sialia*, *P. braueri*, and *P. spatulata* new species have been collected from mountaintops, which are often the site of mating congregations in other species of Diptera. For example, Dcdge and Seago (1954) captured 27 *Protocalliphora* of 2 species, including *P. sialia*, on the summit of a mountain in northeast Georgia over 1,400 m in altitude. The flies, most of which were males, were taken from a utility pole on the summit. The researchers observed other flies, which could not be captured, on the trunks and larger limbs of scrub oaks fringing the summit.

Mating might occur in contexts other than mating congregations. Gold and Dahlsten (1989) observed both male and female *P. sialia* at active chestnut-backed chickadee nests in California. Males were not seen to enter the nest cavity. Copulation was not recorded at nest cavities nor at any other site in their study. However, the authors hypothesized that stimuli from chickadee nests during incubation triggered mating behaviour in the flies.

Oviposition Behaviour

Published information on oviposition behaviour is limited. Once a gravid fly locates a nest containing nestlings, the fly oviposits either directly on the young or in the nest material. The site of oviposition may depend on the species of *Protocalliphora*. Gold and Dahlsten (1989) obtained indirect evidence that some species oviposit in nest material. In their California study, *Protocalliphora* eggs, probably of *P. parorum*, were commonly found in material collected from mountain and chestnut-backed chickadee nests containing nestlings. According to these authors, this indicated direct oviposition in the nest material rather than on the nestlings. They also observed female *P. sialia*, apparently preparing to

oviposit, entering nest boxes and investigating nest material while ignoring the nestlings. Finally, Eshuis-van der Voet and Kluyver (1971) reported that the European *P. azurea* lays its eggs in the material of great tit (*Parus major* Linnaeus) nests "close to the nestlings."

In other cases, *Protocalliphora* have been recorded laying eggs directly on nestling birds. Whitworth (1976) observed a female *P. chrysorrhoea* oviposit directly on bank swallow nestlings. Eggs were grouped in small clumps and were attached to the feathers. Egg laying was accompanied by a dipping motion of the abdomen. No eggs were recovered from the nest material. Tirrell (1978) reported that *P. avium* oviposited directly on red-tailed hawk (*Buteo jamaicensis* Gmelin) nestlings. Female flies would settle on the nestling's head and crawl to the ear cavity. The flies would investigate the cavity and touch the tip of their abdomens to the edge. Tirrell interpreted this as egg laying behaviour although no eggs were observed at the time. However, scattered clumps of eggs were occasionally found near the axillary areas of the nestlings.

Timing of Oviposition in Relation to Host Nesting Cycle

Bennett (1957) noted that *Protocalliphora* species with the longest larval stages parasitized the nestlings of large birds such as corvids and birds of prey. These birds have relatively long nestling periods. In contrast, *Protocalliphora* with shorter larval stages parasitized birds with rapid rates of nestling development, such as certain ground nesting passerines. Bennett concluded that the length of the larval stage was adapted to the nestling period of the host birds in the species' preferred habitat.

For such an adaptation to be most effective, gravid females should be able to determine when oviposition would allow for complete larval development. Presumably, they would do so based on chemical, physical, or other cues associated with the nest or nestlings. Although a number of researchers have speculated about the nature of these cues, the cues have not been conclusively identified. Bennett (1957) made limited observations on the timing of oviposition in relation to the host's nesting cycle in barn swallows, grackles (*Quiscalus quiscula* Linnaeus), house wrens, and American robins (*Turdus migratorius* Linnaeus). His observations led him to suggest that infestations were initiated when nestlings

of these species were 5 to 7 days old. He noted that, at this age, the newly erupted feathers were associated with a "distinct odor peculiar to young birds." However, in a later paper coauthored with Whitworth (Bennett and Whitworth, 1991), the authors recognized that *Protocalliphora* parasitizing ground nesting warblers and sparrows, which undergo rapid nestling development, would have to oviposit soon after the young hatched for the larvae to complete development.

Some researchers have shown that oviposition can occur over a large portion of the host nestling period and result in complete larval development. For example, Gold and Dahlsten (1989) found that *P. parorum* larvae can complete their development within one week, or approximately one-third of the chickadee host's 21-day nestling period.

Voltinism and Parity

Published information on voltinism is based on indirect evidence. By comparing the lifespan of certain species of *Protocalliphora* in the laboratory to the length of the host nesting season, Bennett and Whitworth (1991) hypothesized that, in *P. avium* and perhaps *P. fallisi* Sabrosky, Bennett and Whitworth, one or possibly two generations of flies oviposit in the hosts' nests of a given year. This is because the hosts of these two species (mainly crows and large raptors, and red-winged blackbirds, respectively) nest only once per year in May and early June. Similarly, Gold and Dahlsten (1989) hypothesized that only one generation of *P. parorum* oviposited in nests of a given year. The hosts of this species, mountain and chestnutbacked chickadees, were single-brooded in the authors' study area.

Protocalliphora parasitizing hosts with lengthy or overlapping breeding seasons may have 2 generations ovipositing in a given year. Bennett and Whitworth (1991) noted that some species of passerines often raise 2 or more broods per year. This would allow overwintering female *Protocalliphora* to oviposit in the first and subsequent nests. Flies produced from the first brood might mature in time to oviposit in later nests and would overwinter to parasitize host nests the following year. However, the authors believed that no more than 2 generations reproduced in a single nesting season.

The literature includes information on parity for three North American species of *Protocalliphora*. Gold and Dahlsten (1989) dissected 10 female *P. sialia* captured at cavity nests and determined that this species is at least biparous.

Whitworth (1976) found evidence for multiparity in *P. asiovora* and *P. chrysorrhea*. Female specimens caught in the field had up to 3 immature follicles attached to each mature ovariole.

Part II. Breeding Ecology of the Eastern Bluebird (Sialia sialis)

The Nearctic thrush genus *Sialia* (Passeriformes: Muscicapidae) contains three species, the eastern bluebird, mountain bluebird (*Sialia currucoides* Bechstein), and western bluebird. The three bluebird species have diverged significantly from the other thrushes in the subfamily Turdinae. Sibley and Ahlquist (1990) suggest that the bluebirds should be accorded subfamily status of their own, based on evidence derived from DNA-hybridization studies. Further evidence for this divergence is the fact that the bluebirds are cavity nesters in a generally open nesting family. However, the genus *Sialia* seems to have acquired the cavity nesting habit more recently in its evolutionary history than cavity nesters of family rank (von Haartman, 1957).

The eastern bluebird is the only member of the genus that occurs east of Manitoba (Bull and Farrand, 1977). It breeds east of the Rocky Mountains from southern Canada to the Gulf Coast of the U.S., and south into the mountains of central Mexico. It vacates the northern parts of its range in winter, but occurs year-round in the southeastern U.S. It is an obligate cavity nester, although one case of open-site nesting has been documented (Bent, 1949). The shortage of natural cavities, together with competition for nest holes with the European starling, has made many populations of the eastern bluebird dependent on man-made nest boxes (Gowaty, 1985).

Bluebirds return to the northern parts of their range early in the spring, often arriving on their breeding grounds while there is some snow cover. Experienced males arrive a few days ahead of females and first-year males and claim the choicest territories. In southeastern Michigan, experienced males were present in their breeding locales before 20 April (Pinkowski, 1977b). Apparently, early arrival allows experienced males to claim territories with abundant perches. Bluebirds capture most of their prey after a short drop to the ground from an elevated perch (Pinkowski, 1977b, c).

Early arrival also allows for early nesting, which is advantageous in two respects. First, birds with early nests may raise more young than birds that start their first nests later in the season (Pinkowski, 1979). Second, early nesting bluebirds may avoid nest site competition from conspecifics and other cavity nesting species, particularly house wrens and tree swallows (Musselman, 1939; Pinkowski, 1977b). The nesting cycle starts once the male and female establish a territory. The female chooses a nest cavity and builds the nest, largely unaided by the male. The nest is completed in 6 days or less, depending on whether egg laying is imminent (Zeleny, 1976). The nest is a loosely built cup of dry grasses, weed stems, and fine twigs lined with finer grasses and sometimes hair or feathers (Harrison, 1984). One egg is laid per day, starting once the nest is complete. Schultz (1987) found that the average clutch size in her southwestern Québec study site was 4.5 eggs (n=34), which was slightly greater than the average of 4.2 (n=51) calculated by Peakall (1970) for birds in Ontario and Québec.

According to various sources, the incubation period ranges from 12 to 14 days (Zeleny, 1976; Gowaty, 1983; Harrison, 1984). The female alone incubates the eggs (Gowaty, 1983). Both sexes defend the nest against inter- and intraspecific nest site competitors and predators (Gowaty, 1985).

Both parents feed the young. At first, the parents give the nestlings mainly spiders and lepidopteran larvae, gradually expanding the diet to include orthopterans as well. Among these major prey groups, Pinkowski (1978) found that ground dwelling invertebrates were commonly captured in the spring, while species associated with vegetation accounted for an increasing proportion of the diet as the season progressed.

Schultz (1987) found that most young bluebirds in her Hudson-Rigaud study area (approximately the locale of the present study) fledged between 16 and 18 days of age. The parents continue to feed the fledglings until they are about 5 weeks old. Fledglings may remain in the parents' territory beyond that age, and have been observed helping to rear subsequent broods (Zeleny, 1976). Schultz (1987) found that the percentage of nests fledging at least 1 young averaged 47.1%. House wren interference and raccoon (*Procyon lotor* Linnaeus) predation were the main reasons for nest failure. Cold, wet weather may have caused the loss of 2 broods.

Bluebirds in different parts of North America may raise 1, 2, or 3 broods, depending on the geographic location. After examining data from 8,108 nest records, Peakall (1970) found that eastern bluebirds raised 2 broods throughout most of the range, but tended toward single broods in Canada and New England. Schultz (1987) found that eastern bluebirds in the Hudson-Rigaud area raised a single brood each season.



Part III. Breeding Ecology of the Tree Swallow (Tachycineta bicolor)

There are eight species in New World swallow genus *Tachycineta* (Passeriformes: Hirundinidae). The tree swallow is one of four Nearctic species in the genus (Turner, 1989). It is widely distributed in North America and is a common summer breeding bird, ranging from the tree line in Alaska and northern Manitoba across to Newfoundland at its northern limit, and south to the mid-Atlantic states, Nebraska, Colorado, and California. It winters in Central America and along the southern U.S. coastline, as far north as southern California in the West and occasionally as far north as Long Island and Massachusetts in the East (Bull and Farrand, 1977; Udvardy, 1977).

The tree swallow is the first swallow to arrive on its breeding grounds in the spring. In the study area the first birds arrive in early April (Robbins *et al.*, 1966). First-year birds are usually last to arrive on the breeding grounds and start their nesting attempts later than older birds (Turner, 1989; Stutchbury and Robertson, 1988).

Tree swallows construct their nests in natural cavities or nest boxes. Where natural cavities are scarce, tree swallows are dependent on nest boxes (Holroyd, 1975). Erskine (1979) estimated that, in Canada, roughly one-fifth of all pairs use nest boxes, while the remainder use natural cavities. The pair defends an area of approximately 15 m radius around the nest cavity (Robertson and Gibbs, 1982). Tree swallows will nest in large, loose groups if enough cavities are available. Adults tend to return to the same nest cavity, or one nearby, if they bred there successfully the previous year, and first-year birds often return to a site close to where they were hatched (Turner, 1989).

Nest construction takes from a few days to a few weeks, depending on the weather. The female arranges dead grass stems or pine needles into a loosely constructed pad at the bottom of the cavity. Whitworth (1976) reported that tree swallow nests in his study area (the northern Wasatch mountain range of northern Utah, southern Idaho, and southwestern Wyoming) were built of twigs. The nest cup is lined with feathers which the male helps to collect. White feathers seem to be preferred. Females continue to add feathers during incubation (Turner, 1989).

Tree swallows do not start a clutch once they obtain a nest site. Rather, they wait until favorable weather brings an increase in aerial insect populations. Once such conditions develop, pairs in an area synchronize egg laying (Stutchbury and Robertson, 1987). The eggs are laid at daily intervals, although poor weather conditions can impose a gap of a few days between eggs. The most common clutch size is 5 or 6 eggs, although clutches laid after the peak laying date are usually smaller. First-year females tend to start their nesting attempts later in the breeding season and have smaller clutches (Stutchbury and Robertson, 1988; Turner, 1989). Clutch size also seems to be influenced by the food supply available during the laying period, with greater levels of food resulting in larger clutches (Quinney *et al.*, 1986).

Incubation starts with the laying of the next-to-last egg and lasts 13 to 16 days (Harrison, 1984), 14 days being the norm (Turner, 1989). The female alone incubates the eggs, remaining on the nest for periods of about 20 minutes and leaving for shorter periods to feed. In cold weather she stays on the eggs for longer intervals, but in very bad weather she may desert them temporarily. If there is much inclement weather during the incubation period, the eggs may hatch asynchronously over a couple of days. This leads to a staggered size range among the nestlings (Turner, 1989).

The nestling period lasts about 19 or 20 days (Hussell, 1983). The female broods the young, but both male and female feed the nestlings (Turner, 1989). Adults forage aerially within a few kilometers of the nest, often over water. In one study, 95% of the prey items were from the insect orders Diptera and Homoptera (Quinney and Ankney, 1985).

The main cause of nestling mortality seems to be starvation following prolonged periods of cold, wet weather when the parents find it difficult to supply sufficient food (Turner, 1989). In one Ontario study the youngest (and therefore smallest) nestlings of broods represented 36% of all nestling mortality. The authors concluded that adults may sacrifice the youngest nestlings in times of food shortage (Quinney *et al.*, 1986).

Once the young fledge they do not usually return to the nest cavity. Tree swallows are normally single-brooded (Hussell, 1983).

DESCRIPTION OF STUDY AREA

The study area was located in the southwestern corner of Québec in the municipalities of Hudson, Ste-Anne-de-Bellevue, and St-Lazare (roughly 45° 20'N, 74° 00'W). Nest boxes were monitored at three sites: Mount Victoria (Town of Hudson); Ecomuseum (Ville de Ste-Anne-de-Bellevue); and St-Lazare (Ville de St-Lazare). The St-Lazare site was divided into two sub-sites separated by less than two kilometers, which will be referred to as Mubarak's farm and Dunn's stable. Each site was within a 20 km radius of the other two.

The soil at the Mount Victoria study site was classified as excessively draining upland sand (Lajoie and Stobbe, 1951). The land was used mainly as cattle pasture or hayfield. Hayfields were mowed two or three times per summer. The vegetation consisted of grasses (Poaceae) mixed with clover (*Trifolium* spp.), vetch (*Vicia cracca* Linnaeus), and alfalfa (*Medicago sativa* Linnaeus). Hawkweed (*Hieracicum* spp.) grew in the drier areas. Shrubs in the field edge included raspberries (*Rubus* spp.), buckthorn (*Rhamnus cathartica* Linnaeus), hawthorn (*Craetagus* spp.), and staghorn sumac (*Rhus typhina* Linnaeus). The northeastern border of the study site was adjacent to a residential area, and a portion of the eastern border abutted an abandoned apple orchard. The remainder of the site was bordered by a mature forest of beech (*Fagus grandifolia* Ehrhart), red oak (*Quercus rubra* Linnaeus), maple (*Acer* spp.), and white pine (*Pinus strobus* Linnaeus), with some hemlock (*Tsuga canadensis* Carrière) and birch (*Betula* spp.).

The soil at the Ecomuseum study site was a mixture of moderately well to imperfectly draining Rideau clay plus somewhat poorly draining Ste-Rosalie clay (Lajoie and Baril, 1954). The site was maintained as a wildlife area for the former Department of Renewable Resources (now the Department of Natural Resource Sciences) of McGill University, Macdonald Campus, and included a small pond. The predominant ground cover was grasses mixed with a variety of herbaceous plants such as vetch, goldenrod (*Solidago* spp.), asters (*Aster* spp.), clover, groundcherry (*Physalis* spp.), and milkweed (*Asclepias syriaca* Linnaeus). The site was neither grazed nor cut during the growing season. Shrubby vegetation included buckthorn, honeysuckle (*Lonicera* spp.), grapes (*Vitis* spp.), staghorn sumac, and hawthorn. Butternut (*Juglans cinerea* Linnaeus), elm (*Ulmus americana* Linnaeus), and sugar maple (*Acer saccharum* Marshall) were the most common trees in this study site.

The soil at Mubarak's farm was a mix of well draining Ste-Sophie loamy fine sand and imperfectly draining Baudette clay loam (Lajoie and Stobbe, 1951). The general habitat of the site was similar to that of Mount Victoria. Sugar maple was the

dominant tree species in the woods surrounding the fields. In the fields, white daisy (*Chrysanthemum leucanthemum* Linnaeus) was common, while alfalfa was absent.

The soil at Dunn's stable was Ste-Sophie loamy fine sand (Lajoie and Stobbe, 1951). Dunn's stable was a horse boarding facility and much of the pastureland was closely cropped grass. Between paddocks were strips of moist, overgrown pasture with ferns (Pteridophyta), horsetails (*Equisetum* spp.), sedges (Cyperaceae), goldenrod, asters, yarrow (*Achillea millefolium* Linnaeus), and shrubs such as meadowsweet (*Spirea latifolia* Borkhausen), raspberries, and buffaloberry (*Amelanchier* spp.). Trees included balsam poplar (*Populus balsaminifera* Linnaeus), quaking aspen (*Populus tremuloides* Michaux), black cherry (*Prunus serotina* Ehrhart), gray birch (*Betula populifolia* Marshall), and sugar maple. A small stream ran through one corner of the site.

MATERIALS AND METHODS

Design and Placement of Nest Boxes

Nest boxes (Figure 1) were constructed of 2 cm thick pine planking and had floor dimensions of 10 cm x 11.5 cm. The diameter of the entrance hole was 3.8 cm, the maximum diameter recommended to exclude starlings (Zeleny, 1976 and 1977). In most boxes, the distance between the floor and the bottom of the entrance hole was approximately 16 cm, although in a few boxes at Mount Victoria this distance was about 20 cm. Sixty-two nest boxes were monitored in 1989, including 32 at Mount Victoria, 14 at the Ecomuseum, 6 at Mubarak's farm, and 10 at Dunn's stable. Sixty-five nest boxes were monitored in 1990, including 33 at Mount Victoria, 15 at the Ecomuseum, 6 at Mubarak's farm, and 11 at Dunn's stable.

Some boxes were equipped with fly traps (Figure 2). Fly traps consisted of a 10 cm x 11.5 cm rectangle of waxed perforated cardboard coated on one side with an adhesive compound. The traps were mounted in a wire-floored compartment in the upper portion of the nest box, which was accessible only to the flies. Cardboard rectangles were placed in the compartments shortly before or after the eggs hatched. In 1989, 9 of the 62 boxes monitored were equipped with fly traps, including 7 at Mount Victoria and 2 at the Ecomuseum. In 1990, 15 of the 65 boxes monitored were equipped with fly traps, including 13 at Mount Victoria, 1 at the Ecomuseum, and 1 at Dunn's stable.

Boxes were mounted on tree trunks or wooden fence posts at heights ranging from 1.5 to 1.9 m above ground. Most boxes were located in open situations, as previous experience showed that the birds rarely used boxes placed in shrubbery.

Nest Box Monitoring and Data Collection

All nest boxes were inspected on an average interval of once per week from mid-April to the end of August. In general, a box was inspected every 4 to 7 days if it was in use. Boxes containing active nests and equipped with fly traps were checked every 2 to 4 days. If the box did not appear to be in use, the interval between inspections ranged from 7 to 11 days.

During an inspection, observations were made on the type of nest material, number of eggs and/or young present, and the presence of blow fly larvae and other arthropods. When adult *Protocalliphora* were encountered in the field, observations were made on their behaviour. Attempts were made to catch wild flies by hand. Flies





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Figure 1. A nest box equipped with a fly trap: exterior view. Birds (and flies) enter the nest compartment through the large front entrance hole (3.8 cm in diameter). The smaller diameter (2.5 cm) of the side entrance holes allows flies to access the upper compartment (the "trap") while preventing the entry of birds. A strand of wire across each side hole provides an additional impediment to birds.



Figure 2. A nest box equipped with a fly trap: interior view. A rectangle of hardware cloth divides the upper compartment from the nest compartment. A rectangle of waxed cardboard, coated on its upper surface with a sticky compound, is placed on the hardware cloth. Slits in the cardboard rectangle permit air from the nest compartment to diffuse into the upper compartment. Flies entering the upper compartment through the side holes adhere to the coated cardboard as they try to enter the nest compartment to oviposit. The side panel of the nest box can be swung open to retrieve the trapped flies.

caught by hand or captured in the fly traps were preserved in alcohol. Capture of gravid *Protocalliphora* by hand and in fly traps may have influenced the number of blow fly eggs deposited in the nest and, thus, the number of larvae. For this reason, nests in which female *Protocalliphora* had been caught were excluded from certain statistical analyses.

Measurements of the nest dimensions were also taken. The dimensions of a given nest were found to change very little over the incubation period. Nevertheless, to maintain consistency, measurements used in the study were taken during the incubation period within a few days of hatching. Nest measurements were not taken after the eggs hatched since it was thought that the active, growing nestlings would have compacted the nest material. The measurements were used to calculate the nest material volume as described in Appendix 1.

In some cases, the hatching date was known with certainty. In other cases, the hatching date could be estimated with reasonable accuracy by estimating the age of the nestlings. It was found that the hatching date for clutches of bluebird eggs could be calculated by counting 14 days from the date the last egg was laid (Pettingill, 1985). This method could not be used reliably with tree swallows because of this species' variable incubation period.

At the end of the breeding season, the percentage of canopy cover above the nest box was determined using a spherical densiometer (Lemmon, 1956).

Nest Collection

Nest boxes were examined and nests collected once the young had fledged. At this time, the presence of any dead nestlings was noted and the age at the time of death was estimated. The number of fledglings was assumed to be the number of live nestlings present at the previous inspection minus the number of dead young found at the time of nest collection. However, if dead nestlings were of fledging age, they were counted as fledglings.

The contents of the nest box, minus any dead nestlings, were collected in a Zip-Loc bag. Nests were teased apart in the laboratory using a pair of forceps and a dissecting probe to recover *Protocalliphora* larvae and pupae. *Protocalliphora* larvae were adept at hiding in the nest material and other nest debris, and diligent searching was necessary to account for all the larvae. Larvae, puparia, and emerged puparia were counted to determine the number of larvae per nest. The nest material was picked clean of nestling feces and sifted in a #30 sieve (Hubbard Scientific Co., Northbrook, Illinois) to remove fine debris. The material was then dried overnight at 110°C and weighed on a Mettler 2000 balance.

Protocalliphora Rearing, Marking and Release

Puparia and large larvae recovered from a nest were placed in a glass jar with a 1 cm layer of dry peatmoss. In the 1990 field season a sugar cube was placed in each jar to provide a carbohydrate source. The mouth of each jar was covered with perforated paper and secured with an elastic band. Jars were kept in a dark cupboard at room temperature and checked every 1 to 3 days for emerged adults. Jars containing tanned adults were placed in a cool room (8°C) for a period of a few hours to overnight to make the flies torpid and easy to manipulate. Several hundred adult *Protocalliphora* reared in preliminary studies conducted in 1988 were preserved in 70% ethanol or isopropyl alcohol. A smaller number of flies was similarly preserved in 1989 and 1990. Preserved flies were identified based on species descriptions provided in Sabrosky *et al.* (1989).

Most of the adult flies reared were marked on the mesonotum with minute dots of light-fast acrylic paint ("Plaka," manufactured by Pelikan AG, Hannover, Germany) using a fine brush, as described by MacLeod and Donnelly (1957) for mark and release studies. In most cases, flies from a given nest were marked with a pattern of coloured dots, or a "code," unique to that nest. However, flies from nests collected at the Ecomuseum site were marked with a code unique to the site. Once marked, the flies were transported back to the box where the nest was collected, and released. This procedure was repeated with each rearing jar until all normally developed adults had been set free.

Flies captured in the fly traps were freed of adhesive residue by rinsing briefly with gasoline. They were then kept in alcohol until their ovaries were dissected out for examination.

Statistical Analyses

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Data from the three sites was pooled for each year. I pooled the data because I considered the bluebirds, tree swallows, and blow flies at the three sites to be from the same populations, given the proximity of the sites, the migratory nature of the bird species, and the demonstrated dispersal abilities of other calliphorids (MacLeod and Donnelly, 1958; Norris, 1965). Mean values and coefficients of variability were calculated for the number of *Protocalliphora* larvae per nest and additional nesting

variables, including hatch date, nest material volume, number of fledglings, and percent canopy cover. Means were calculated using data from both parasitized and unparasitized nests. With the exception of percent canopy cover, variable means were compared between species within a given year using the t-test as outlined in Bahn (1974). Prior to comparing means, homogeneity of sample variances was tested using the F-test as described in Wine (1964). In some instances, the sample variances were significantly different. In those cases, means were compared using the weighted t-test as described in Snedecor and Cochran (1967). Pearson correlation coefficients between the number of *Protocalliphora* larvae per nest and selected nesting variables were calculated using SAS (SAS Institute, Cary, North Carolina).

RESULTS AND DISCUSSION

Part I. Protocalliphora Trapping and Mark, Release and Recapture Techniques

Two practical developments that resulted from my experiments may prove useful to future researchers studying *Protocalliphora* ecology. The first development was the fly trap used to capture wild female *Protocalliphora* coming to a nest to oviposit. This trap used the host's nest itself as an attractant without interfering with the activities of the parent birds and their young. The trap was developed because a review of the literature showed that techniques used by previous researchers involved the use of aspirators or sweep nets (see Whitworth, 1976, and Dodge and Seago, 1954). Such techniques are time consuming and labor intensive since the researcher must actively pursue the flies. Another drawback to the use of these manual techniques is that the researcher must wait in the vicinity of the host's nest to capture gravid flies. The presence of the researcher may disturb the parent birds or inhibit them from attending to their young.

The use of fly traps tested in this study avoided these drawbacks, since gravid flies attracted to a nest were caught on a sticky card in a chamber isolated from the nest cavity. Field tests showed that parent birds and their young were not disturbed by the presence of the traps. Further, flies caught in a trap could be removed within a few minutes, thereby minimizing disturbance to the birds.

However, there were three limitations associated with the use of the fly traps. First, no male flies were captured in the traps. Second, flies captured could not be examined alive, either because they died after being coated with the sticky substance or because they had to be cleaned of the substance by washing in gasoline. Third, the trap could be used to collect qualitative data only since some, possibly most, female flies avoided capture by entering the nest cavity through the birds' entrance hole. Nevertheless, use of this trap allowed collection of data on timing of female fly visits in relation to the host nesting cycle, reproductive status of flies visiting the nests, and, in conjunction with mark, release, and recapture techniques, data on age at first oviposition and voltinism. Additional applications for the traps may be discovered in the future.

The second development that resulted from my study was the demonstration that mark, release, and recapture techniques could be applied to *Protocalliphora*. Success of this technique was contingent upon the use of the fly traps, which provided a reliable means of recapturing the marked flies. Despite the demonstration that the technique produced the desired result, the efficiency of the technique could be improved. Approximately 1,680 flies of both sexes were marked and released during the two year study. However, only 4 marked flies were recovered, all female. Although valuable information was gained from the flies recaptured, this is slightly more than a 0.2% recovery rate. Use of additional fly traps might have addressed this problem.

Of the 4 marked flies recovered, 2 were captured in the fly traps, 1 was caught by hand, and the remaining fly recovered in a spider web. The 2 marked flies recovered in the fly traps represented 5.1% of the 39 female flies captured in the traps. Although methods are available for estimating the size of insect populations based on mark, release, and recapture techniques, my data were unable to satisfy several assumptions required for these methods. For example, the assumption of "equal catchability" could not be met. Equal catchability assumes that "the population is sampled randomly with respect to its mark status, age, and sex" (Southwood, 1978). Since the trapping technique I developed was useful for capturing female flies only, the data could not meet the equal catchability assumption. An additional assumption is that "Sampling must be at discrete time intervals and the actual time involved in taking the samples must be small in relation to the total time" (Southwood, 1978). However, I marked, released, and trapped flies concurrently throughout the hosts' nesting season. The failure to meet these and other assumptions precluded the calculation of a population size estimate for P. sialia. Nevertheless, use of the fly traps and the mark, release, and recapture technique may assist future researchers in studying *Protocalliphora* population parameters.

Part II. Protocalliphora Identified in Study Nests

Identification of adult *Protocalliphora* is sometimes difficult since many species have similar or overlapping characteristics. Some species possess readily identifiable external diagnostic features, although these features may be limited to only one of the sexes. This is true for *P. metallica* and *P. sialia*, the two species most commonly found in open field habitats in eastern Canada. In *P. metallica*, females have a shining coppery-green 5th abdominal tergite that contrasts with the blue or bluish-purple 2nd, 3rd, and 4th tergites. In eastern Canada, the only other species possessing this feature is *P. bicolor*, which has been collected mainly from birds nesting just below the canopy in deciduous forests. In *P. sialia*, females possess a polished black preocellar area. This feature sets female *P. sialia* apart from females of almost all other eastern Canadian *Protocalliphora*, except certain females of *P. shannoni*, a species that parasitizes birds nesting just below or in the canopy of deciduous forests

(Sabrosky et al., 1989).

Since the features of female *P. metallica* and *P. sialia* described above would be virtually diagnostic for flies collected from the study nests, I decided to focus my species identification efforts on females. A total of 262 female flies were examined. The flies were reared from 44 nests collected at the three study sites in 1988, 1989, and 1990 (Table 1). Two hundred and forty-four flies (93.1%) were identified as *P. sialia*. Of the remaining 18 flies, 7 (2.7%) were tentatively identified as other species of *Protocalliphora*, 10 (3.8%) were deformed and/or untanned and could not be used for identification purposes, and 1 (0.4%) could not be identified.

The predominance of P. sialia in the study nests is consistent with information in the literature. Studies conducted by Bennett (1957) and Whitworth (1976) suggested that, of the two species of *Protocalliphora* infesting nests in open field habitats, P. sialia commonly infests cavity nests. In contrast, the other species, P. *metallica*, preferentially oviposits in open nests such as those of ground nesting birds and rarely parasitizes cavity nesting birds. The remainder of this discussion is organized by study site.

Mount Victoria

One hundred and ninety-three of the flies examined came from 12 bluebird and 17 tree swallow nests at the Mount Victoria study site. One hundred and seventyseven flies were identified as *P. sialia*. The 10 deformed and/or untanned flies and the 1 fly that could not be identified came from the Mount Victoria site. The fly that could not be identified was reared from a bluebird nest collected in 1988 that was also parasitized by *P. sialia* and, possibly, by *P. metallica*. It did not match the species descriptions provided in Sabrosky *et al.* (1989), having a dull black thorax and a uniform'y coppery-green abdomen.

The remaining 5 flies were tentatively identified as *P. braueri*, *P. metallica*, and *P. shannoni*. The 2 *P. braueri* females were reared from a tree swallow nest collected in 1990. This nest was also parasitized by *P. sialia*. *P. braueri* has been recorded as a parasite of a large number of host species, including tree swallows, that nest in a wide variety of habitats. Sabrosky *et al.*, (1989) suggested that this species may be more common in the nests of birds at ground or shrub level. These authors noted that *P. braueri* larvae commonly cause true myiasis, burrowing beneath the skin of the host and remaining on the bird until after fledging. I did not observe larvae on any nestlings in the study nests, although live nestlings were never removed from the nests for examination. It is noteworthy that only 2 flies of the 262 examined in

Table 1. Female Protocalliphora reared from bluebirdand tree swallow nests. 1988-1990.

A. bluebird nests.

	<u>Mount_Victoria</u> (12 nests)	<u>Ecomuseum</u> (1 nest)	<u>St-Lazare</u> (7 nests)
P. sialia	108	1	50
P. metallica	1	0	0

B. tree swallow nests.

	<u>Mount Victoria</u> (17 nests)	<u>Ecomuseum</u> (5 nests)	<u>St-Lazare</u> (2 nests)
P. sialia	69	13	2
P. shannoni	2	0	2
P. braueri	2	0	0

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the study were identified as *P. braueri*, considering the apparent ubiquitous nature of the species. However, larvae remaining on the young after fledging would not have been recovered in the nest material.

A single female *P. metallica* was reared from a bluebird nest collected in 1988. This nest was also parasitized by *P. sialia*. Since female *P. bicolor* also possess a coppery-green 5th tergite and may be confused with female *P. metallica*, I also examined the male flies reared from this nest. Male *P. bicolor* possess a coppery-green 5th tergite, while male *P. metallica* do not. No male *Protocalliphora* from this nest had this distinctive feature, thus suggesting that the female was *P. metallica*. According to the list of hosts compiled by Sabrosky *et al.* (1989), this would be the first record of *P. metallica* parasitizing a nest of eastern bluebirds. Finally, 2 female flies reared from a tree swallow nest in 1988 were tentatively identified as *P. shannoni*. This nest was also parasitized by *P. sialia* and was on the edge of a woodlot containing red oak, maple, and black cherry trees. Female *P. shannoni* are very sir.ilar to *P. sialia* but have subshining preocellar areas and narrower parafacials.

Ecomuseum

Fifteen of the flies examined came from 1 bluebird, 4 tree swallow, and 1 blackcapped chickadee (*Parus atricapillus* Linnaeus) nests at the Ecomuseum site. All of the flies were identified as *P. sialia*. According to the list of hosts compiled by Sabrosky *et al.* (1989), the single female fly reared from the black-capped chickadee nest collected in 1988 would be the first record of *P. sialia* parasitizing this species.

St-Lazare

Fifty-four of the flies examined came from 6 bluebird and 2 tree swallow nests at the Dunn's stable study site and from one bluebird nest at the Mubarak's farm site. Fifty-two flies were identified as *P. sialia*. The remaining 2 flies, reared from a tree swallow nest collected in 1988 at Dunn's stable, were tentatively identified as *P. shannoni*.

Part III. Influence of Selected Nesting Variables on Intensity of Protocalliphora Infestations

The percentage of nests parasitized (prevalence of infestations) and the number of larvae per nest (intensity of infestation) differed between bluebirds and tree swallows. In 1989, 100% of bluebird nests (N=11) and 82% of tree swallow nests

(N=22) were infested (Table 2). The mean number of larvae per bluebird and tree swallow nest was 92.0 and 48.1, respectively. The difference between means was significant at the 0.02 level. In 1990, 100% of bluebird nests (N=7) and 95% of tree swallow nests (N=21) were parasitized (Table 3). The mean number of larvae per nest was 115.6 and 57.4, respectively. This difference was significant at the 0.01 level.

In part, the difference between the intensity of infestations in bluebird and tree swallow nests was significant because of the difference in the percentage of nests parasitized. For example, if the mean number of larvae in only *parasitized* nests was considered, the 1989 mean for bluebird nests would remain at 92.0 (range 11-161) but the mean for tree swallow nests would rise to 58.8 (range 13-149). These means are not significantly different at the 0.05 level.

However, prevalence does not explain all of the difference in intensity of infestations between the two host species. For example, the 1990 means for parasitized bluebird and tree swallow nests were 115.6 (range 33-173) and 60.3 (range 9-127), respectively. This difference was significant at the 0.01 level. Further, other researchers studying *P. sialia* parasitism in eastern bluebirds and tree swallows, including Roby *et al.* (1992), have found the intensity of infestations to be significantly greater in bluebirds where the two species nest in the same sites.

The observed differences in prevalence and intensity of infestations cannot be explained in terms of host preference. Field observations indicated that female *Protocalliphora* did not discriminate between bluebird and tree swallow nests as oviposition sites. Further, adult flies reared from nests of either species appeared equally viable. Therefore, the differences may be attributable to a difference in the length of the nesting season or differences in other variables related to nesting.

Comparison of Bluebird and Tree Swallow Nesting Variables

Hatching Date

There was no significant difference in mean hatching dates between bluebirds and tree swallows in 1989 or 1990 (Tables 2 and 3). In addition, there was no

Table 2. Means and coefficients of variability of selected nesting variablesfor bluebird and tree swallow nests, 1989.

	bluebird nests				tree swallow nests			
Variable	<u>Mean</u>	N	<u>CV</u>	<u>Mean</u>	N	<u>CV</u>		
Number of larvae *	92.0	11	0.55	48.1	22	0.88		
Hatching date *	172.8	11	0.15	160.3	22	0.03		
Nest material volume (cm ³) **	798.8	11	0.30	550.8	22	0.26		
Number of fledglings	4.0	11	0.15	4.6	22	0.20		
Percent canopy cover ^a	21.3	11	1.08	19.4	22	1.69		

* Indicates a significant difference between means at the 0.05 level.

** Indicates a significant difference between means at the 0.01 level.

^a Means not tested for statistical difference. See text for details.

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Table 3. Means and coefficients of variability of selected nesting variablesfor bluebird and tree swallow nests, 1990.

	bluebird nests			tre	tree swallow nests			
Variable	<u>Mean</u>	<u>N</u>	<u>CV</u>	<u>Mean</u>	<u>N</u>	<u>CV</u>		
Number of larvae **	115.6	7	0.42	57.4	21	0.72		
Hatching date	160.1	11	0.15	163.6	21	0.04		
Nest material volume (cm ³) *	732.2	11	0.19	588.2	19	0.31		
Number of fledglings	4.4	9	0.20	4.8	21	0.21		
Percent canopy cover ^a	27.5	11	1.01	14.5	21	1.79		

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* Indicates a significant difference between means at the 0.05 level.

** Indicates a significant difference between means at the 0.01 level.

^a Means not tested for statistical difference. See text for details.

significant correlation between hatching date and number of blow fly larvae for bluebirds in 1989 nor for bluebirds and tree swallows in 1990 (Tables 4A and 4B). The positive correlation for tree swallows in 1989 was largely due to a single nest at the Mount Victoria study site. This brood hatched 16 days after the mean hatching date and was the latest tree swallow hatching date in the 1989 season. Further, this nest contained the largest number of *Protocalliphora* larvae (149) of all tree swallow nests in both years of the study. Apparently, the combination of latest hatching date and largest number of larvae made this nest an outlying point in the data set with a disproportionate influence on the correlation coefficient.

However, the length of each species' nesting season may have influenced the pattern of *Protocalliphora* parasitism. The nesting season of the multi-brooded bluebird started earlier and ended later than that of the single-brooded tree swallow. I found that hatching dates for bluebird broods spanned from 16 May to 6 August over the two-year study, whereas hatching dates for tree swallow broods ranged from 3 June to 2 July. Further, tree swallows nesting in the study sites showed a high degree of nesting synchrony. Seventy-three percent of the tree swallow broods in 1989 (16 of 22) hatched within a 7-day period centered on the mean hatching date, 9 June (Figure 3). In 1990, 62% of the broods (13 of 21) hatched within a seven-day period centered on 13 June (Figure 4). The difference in length of the nesting seasons and degree of nesting synchrony was reflected in the coefficients of variability (CV) for hatching dates of the study. In contrast, the CV's for tree swallows were 0.03 and 0.04 in 1989 and 1990, respectively.

The early nesting habit of the eastern bluebird appears to have made early broods subject to heavy blow fly infestations. Figures 3 and 4 show that the first bluebird nests of the season harboured some of the largest infestations. Female *Protocalliphora* may have converged at early bluebird nests because there were few other passerine species with nestlings available. Of all passerine species occurring in or near the study sites, only the horned lark (*Eremophila alpestris* Linnaeus), common crow (*Corvus brachyrhynchos* Brehm), American robin, European starling (*Sturnus vulgaris* Linnaeus), and house sparrow (*Passer domesticus* Linnaeus) nest as early as the eastern bluebird (Aubry and Lambert, 1985).

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A. bluebird nests, 1989 and 1990.

	1989		1990		
<u>Variable</u>	r	N	r	N	
Hatching date	-0.2262	11	0.3846	7	
Nest material volume	0.8904**	11	0.2425	7	
Number of fledglings	-0.2477	11	0.7859*	7	
Percent canopy cover	0.5004	11	0.0298	7	

* Significant at the 0.05 level.

** Significant at the 0.01 level.

B. tree swallow nests, 1989 and 1990.

	198	9	1990		
<u>Variable</u>	r	N	r	N	
Hatching date	0.4910*	22	0.0921	21	
Nest material volume	-0.0596	22	0.2329	19	
Number of fledglings	0.4676*	22	0.2635	21	

* Significant at the 0.05 level.

Figure 3. Hatching date vs. number of *Protocalliphora* larvae for bluebirds (solid circles) and tree swallows (open circles), 1989. Gray line indicates mean hatching date for tree swallows.



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Figure 4. Hatching date vs. number of *Protocalliphora* larvae for bluebirds (solid circles) and tree swallows (open circles), 1990. Gray line indicates mean hatching date for tree swallows.



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Figures 3 and 4 show that the intensity of infestations in bluebird nests decreased during the first part of the nesting season. This decrease might also be explained in terms of availability of alternative hosts, since the number of host species feeding young increases as the season progresses (Aubry and Lambert, 1985). Thus, a larger selection of alternative hosts may have relieved parasite pressure on bluebird broods hatched in early June.

The availability of tree swallow nests appeared to influence the pattern of blow fly parasitism in bluebird nests. As discussed previously, tree swallows tended to nest synchronously. In addition, tree swallow pairs defended smaller territories than bluebirds. Synchronized nesting and small territories resulted in a high density of active tree swallow nests in the study sites during a 3 or 4 week period in late spring and early summer. As shown in Figures 3 and 4, the intensity of *Protocalliphora* infestations in bluebird nests reached a low at a point in the breeding season that coincided with the mean hatching date of tree swallow broods. Since tree swallow nests with nestlings were most abundant in the study sites at this time, bluebird broods may have been under less parasite pressure than at other times during their breeding season. This is supported by the observation that the intensity of infestations increased in bluebird broods hatched after the mean tree swallow hatching date. This increase reached a small and poorly defined peak in July.

The pattern of *Protocalliphora* parasitism described here for the eastern bluebird was not observed by Roby *et al.* (1992) in western New York state nor by Pinkowski (1977a) in southeastern Michigan. Roby *et al.*, who also included tree swallows in their study, found an increase in the number of *P. sialia* larvae per bluebird nest as the nesting season progressed. However, in their analysis these authors used counts of larval numbers that were taken when the nestlings were 6 days old, rather than after fledging as in my study. Pinkowski (1977a) found that the mean number of *Protocalliphora* larvae per nest was significantly greater in clutches begun in the "summer" period (7 June to 23 July) rather than in either the "spring" period (6 April to 14 May) or "intermediate" period (15 May to 6 June). The average number of larvae per nest did not differ significantly between the spring and intermediate periods. However, Pinkowski's investigation did not encompass the nesting dynamics of other passerine species at his study sites. Neither did he specify the species of *Protocalliphora* infesting his nests. Therefore, his results may reflect the population dynamics of a different suite of hosts and parasites.

Hori and Iwasa (1988) studied the population dynamics of two species of *Protocalliphora*, *P. azurea* and *P. maruyamensis* Kano and Shinonaga in Hokkaido, Japan. The most abundant hosts examined in their two-year study were two species of cavity nesting passerines, the great tit and the russet sparrow (*Passer rutilans* Temminck), which shared the same habitat. The authors did not describe the breeding dynamics of the two hosts, such as whether peak hatching dates were observed. However, their findings indicated that the host with the shorter nesting season, the russet sparrow, had a lower prevalence and intensity of infestations. This finding is similar to the results of my study.

If short nesting seasons are associated with low levels of parasitism, then synchronized breeding may be a response, at least in part, to parasite pressure. Various hypotheses have been advanced to explain the benefits of synchronized breeding in colonial species (see Emlen and Demong, 1975). My data suggest that an additional benefit of synchronized breeding may be to limit *Protocalliphora* parasitism.

Nest Material Mass and Volume

Measurements of nest material mass and volume were taken to provide estimates of the quantity of material in bluebird and tree swallow nests. Since mass and volume are both measures of quantity, they were highly and positively correlated for both species in both years. Pearson correlation coefficients for bluebird nests were 0.94 (P<0.0001) in 1989 and 0.68 (P<0.05) in 1990. Correlation coefficients for tree swallow nests were 0.77 (P<0.0001) in 1989 and 0.81 (P<0.0001) in 1990. These high correlations indicated that only one of the parameters should be used as a measure of quantity, while the other measure was redundant and could be dropped from the analysis (Tabachnick and Fidell, 1989).

I decided that nest material volume was the parameter that should be used in the analysis because, on an intuitive level, it had greater biological significance than nest material mass. The literature indicated that the quantity of nest material influenced the number of *Protocalliphora* larvae by determining the space available for resting and/or hiding (Gold and Dahlsten, 1989; Whitworth, 1976). Since space was seen to be the limiting factor, I concluded that nest material volume would be a better predictor of larval numbers than mass.

The mean volume of nest material differed significantly between bluebird and tree swallow nests in 1989 and 1990. In both years, bluebird nests contained greater volumes of material than tree swallow nests, the mean volume being greater by 248 cm³ in 1989 and 144 cm³ in 1990 (Tables 2 and 3).

In bluebird nests, the volume of material present was significantly correlated with the number of *Protocalliphora* larvae for the 1989 nesting season (Table 4A). In this instance, the correlation was strongly positive (correlation coefficient 0.89; P < 0.0002). A significant correlation was not observed in 1990, which might be attributable to the smaller sample size available in that year. Additionally, there was less variation in 1990 bluebird nest material volumes. The combination of these factors may have "hidden" a significant correlation.

Nest material volume did not appear to influence the number of *Protocalliphora* larvae in tree swallow nests (Table 4B). Tree swallows generally used less plant material in their nests and also incorporated substantial amounts of feathers in the nest lining. It is not known what effect, if any, this had on the number of blow fly larvae in the nests.

Other researchers have found positive correlations between nest material volume and intensity of blow fly infestations. Gold and Dahlsten (1989) found a strong correlation between the volume of material and the number of *Protocalliphora* larvae in chickadee nests. Pinkowski (1977a) found significantly fewer larvae in bluebird nests taken from natural nest cavities than in nests in boxes. He attributed this difference to the smaller amounts of nest material used in natural cavities. In both studies, the authors hypothesized that the number of larvae might be limited by the availability of resting or hiding places, which is determined by the amount of nest material present.

Whitworth (1976) offered two hypotheses to explain the relationship between the amount of nest material and the number of larvae. The first hypothesis was based on the response of the larvae to larval excrement. The author found that P.

asiovora larvae kept in close contact with their own excrement were less likely to pupate than control larvae or larvae kept in very wet soil. In addition, pupae kept in close contact with larval excrement were less likely to produce adults. Whitworth suggested that the apparent toxicity of the excrement at high concentrations indicated that larvae were sensitive to their waste at lower concentrations and might actively avoid it. Nest material absorbs wastes and provides resting places where the larvae can avoid contaminated areas of the nest. This might explain why larger volumes of nesting material often harbour larger larval populations.

Supporting Whitworth's first hypothesis is a study by Zvereva (1989), who found that ammonium ion (NH₄⁺), a metabolic waste excreted by fly larvae, was toxic to housefly larvae (*Musca domestica* Linnaeus). First instar larvae were most susceptible. Concentrations of 0.5% ammonium in food caused 100% mortality. Third instar larvae were least susceptible and 100% mortality was observed only at ammonium concentrations of 8%. In addition, larvae avoided food containing toxic levels of ammonium. If *Protocalliphora* larvae respond similarly to ammonium in their environment, then survival of first instar larvae may be contingent on availability of resting places where they can avoid larval excrement.

Whitworth's (1976) second hypothesis was based on the larval response to temperature. Whitworth found that artificially high infestations of *P. chrysorrhea* could be maintained in bank swallow nests only when the nesting material was augmented with additional feathers. Since larval excrement was absorbed into the sand beneath the nests, Whitworth did not believe that the larvae came in contact with their wastes. The author suggested that the larvae responded to the increased volume of feathers because of their heat-holding capacity. He suggested that, by increasing the volume of nest material, greater numbers of larvae could avoid contact with the cool sand. While this hypothesis might be applicable to groundnesting birds, it may not be pertinent to birds nesting in wooden nest boxes or tree cavities.

Gold and Dahlsten (1989) put forward a third hypothesis to explain the correlation between the volume of nest material and number of *Protocalliphora* larvae. These authors suggested that nest material provides cover for the larvae to escape detection by the adult birds. Although nestlings may be unable to capture

and consume larvae on their own, adult birds could consume any larvae found in the nest. The authors noted that *Protocalliphora* larvae were always absent from chickadee nests with less than 100 cm^3 of material. In addition, larvae in their study were often found at the bottom of the cavity underneath the bulk of the nest. These two observations lend indirect support to their hypothesis. This hypothesis might apply to birds that forage by picking their prey off a substrate, such as bluebirds. However, aerial feeders, such as swallows, usually do not pick their prey off a substrate and might not search through the nest material for insects.

Number of Fledglings

No significant difference in the mean number of fledglings was observed between bluebird and tree swallow nests in either 1989 or 1990 (Tables 2 and 3). The number of *Protocalliphora* larvae per nest was positively correlated with the number of young fledged for both bluebirds in 1990 and tree swallows in 1989 (Tables 4A and 4B). The absence of a significant correlation in 1989 bluebird nests may be attributable to one nest at the Mubarak's farm site which fledged 5 young but contained only 11 *Protocalliphora* larvae, an unusually low number for bluebird broods. The hatching date for this brood was 9 June, the mean hatching date for tree swallow broods in that year. No reason could be identified for the absence of a significant correlation in 1990 tree swallow broods.

Roby et al. (1992) found the mass of P. sialia larvae in tree swallow nests to be positively correlated with brood size. Pinkowski (1977a) noted a slight positive correlation between brood size and the number of larvae per nest in his eastern bluebird study. Whitworth (1976) also recorded weakly positive correlations between brood size and number of larvae per nest in magpies and bank swallows. Whitworth suggested that first instar larvae compete for feeding spaces on the bodies of the nestlings and that availability of these spaces may limit larval populations. In Whitworth's study, first instar P. asiovora larvae were observed to secure themselves to the nestling's body and remain there for several days. Although nestlings were not removed from the nest for physical inspection, such larval behaviour was not noted in my study.

Whitworth (1976) also suggested that competition for feeding spaces may affect older larvae when nestlings gain the ability to perch in the nest. At this time the nestling's feet and lower abdomen are often the only body parts contacting the nest material. This limits opportunities for the larvae to attach themselves to the skin. Therefore, the greater the number of nestlings in the nest, the more feeding opportunities for the larvae and the more likely they are to survive.

Percent Canopy Cover

Tree swallows in my study frequently nested in open situations. This resulted in a large number of nests with 0% canopy cover in both years. In contrast, the number of bluebird nests with 0% canopy cover was small in comparison to the total number of nests. Since percent canopy cover values appeared to be normally distributed in bluebirds, Pearson correlation coefficients were calculated for the bluebird data. However, there was no significant correlation between the number of blow fly larvae and percent canopy cover for bluebird nests in either 1989 or 1990 (Table 4A). Since the percent canopy cover values were not normally distributed for tree swallow nests, the variable was analyzed differently for this species.

Tree swallow nests were divided into two groups of approximately equal size. The first group included nests with 0% canopy cover. Nests in the second group had more than 0% cover. After testing for homogeneity of variances, the mean number of *Protocalliphora* larvae per nest was compared between the two groups in each year. In both years of the study, there was no significant difference between the mean number of larvae in nests with 0% canopy cover and nests with more than 0% cover (Table 5).

Gold and Dahlsten (1989) also did not find a significant correlation between number of larvae per nest and canopy cover. Further, their results did not indicate a relationship between size of infestations and any other site or tree stand parameter. This led them to propose that the flies' strong dispersal ability makes habitat features secondary in importance to nest cues.



Table 5. Mean numbers and coefficients of variability of *Protocalliphora* in tree swallow nests with and without canopy cover. 1989 and 1990.^a

Year		0% Canopy			>0% Canopy	
	<u>Mean</u>	<u>(N)</u>	<u>cv</u>	<u>Mean</u>	<u>(N)</u>	<u>cv</u>
1989	62.7	(10)	0.67	52.6	(11)	0.72
1990	56.6	(12)	0.77	37.9	(10)	0.94

^a No significant difference between means was found in either year.



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Part IV. Reproduction in Protocalliphora

Mating Behaviour

Field observations suggested that male *Protocalliphora* may congregate at specific sites in the habitat for mating purposes. At 12:45 on 29 May, 1990, several male *Protocalliphora* were observed on wooden posts of a fenceline at the Mount Victoria study site. The fenceline was located in an open field several metres distant from the nearest woody vegetation. Boxes containing active nests were mounted on several of the posts. The flies were positioned on the posts so that they were exposed to the sun but sheltered from the wind. There was no more than 1 fly on each post. One male was observed to make darting forays in pursuit of insects flying by and to return to the same post afterward. On another occasion, 13:00 on 7 July, 1990, a single male *Protocalliphora* was observed on a post in the same fenceline. It was also on the leeward side of the post exposed to the sun. No other males were found on neighboring posts on that date.

Observations made by other researchers indicate that *Protocalliphora* and other flies gather at specific sites for mating purposes (Thornhill and Alcock, 1983; Dodge and Seago, 1954). One particular feature that supports this interpretation is that one fly was seen to pursue insects passing in flight. Adult *Protocalliphora* are not known to be predatory and do not have mouthparts adapted for feeding on other insects. Therefore, it is unlikely that this behaviour was associated with capture of prey and feeding. It is more likely that this fly was seeking female *Protocalliphora* for copulation. Dodge and Seago (1954) reported similar aerial pursuits in males of other muscoid Diptera which they interpreted as probable courtship behaviour.

Oviposition

Oviposition Behaviour

Possible oviposition behaviour was noted on two occasions. On the first occasion, a female *Protocalliphora* was observed crawling among a brood of tree swallow nestlings about 4 days old. The fly moved about on the young, mainly on their ventral and lateral surfaces, touching her mouthparts to their skin. The nestlings did not appear to be disturbed by the movement of the fly over their bodies. The fly was captured, dissected, and found to contain well-developed eggs. On a second occasion, a female fly was observed in a recently abandoned bluebird nest containing one egg. This egg was all that remained of a clutch of 4 that had been completed 3 days previously. Apparently, the 3 other eggs had been removed by a predator. The nest itself appeared clean and undisturbed. The fly did not crawl on the egg but, rather, moved rapidly over the floor and sides of the nest cup. This fly was also captured, dissected, and found to contain well-developed eggs.

The two female flies observed were not seen to lay eggs or to dip the tip of their abdomen in the manner described by Whitworth (1976) and Tirrell (1978). However, their interest in the nest material and the nestlings, combined with their gravid condition, suggest that the purpose of the visits was oviposition. It is noteworthy that, in the second instance, the female fly visited the nest before nestlings were present.

Timing of Oviposition in Relation to Host Nesting Cycle

Data obtained by collecting larvae from nests and from fly trapping experiments yielded information on timing of oviposition in relation to the host nesting cycle. I found that small *Protocalliphora* larvae were sometimes present in nests collected after the nestlings had fledged. In some cases, the larvae were not sufficiently developed to pupate successfully. In other cases, the small larvae pupated but resulted in abnormally small adults. The presence of these small larvae suggested that female flies occasionally laid eggs in nests containing nestlings that were within a few days of fledging. This finding supports Gold and Dahlsten's (1989) results. By collecting material from nests of mountain and chestnut-backed chickadees and western bluebirds throughout the nesting cycle, the authors determined that *P. parorum* and *P. sialia* would oviposit at any time between hatching and fledging.

In contrast, the results of my fly trapping experiments suggested that female flies did not visit the nests after the nestlings reached a certain age. Gravid *Protocalliphora* visited bluebird and tree swallow nests during the incubation and nestling periods. Gravid females were captured in traps until the nestlings had reached approximately 13 days of age. No *Protocalliphora* were caught in the fly traps after the second week of the nestling period. I also collected data that show oviposition can occur over a large portion of the host's nestling period and can result in complete larval development. On one occasion, several well-developed *Protocalliphora* larvae were found in a nest containing tree swallow nestlings that had died 2 or 3 days previously. The nestlings were approximately 11 days old at the time of death. Many *Protocalliphora* larvae collected from this nest pupated, and 2 normally sized adult flies emerged from the puparia. On another occasion, 4 large larvae were collected from a tree swallow nest in which the young had died the previous day at 13 days of age. All 4 larvae pupated and resulted in normally sized adult flies.

Other researchers have shown that oviposition can occur over a large portion of the nestling period and can result in complete larval development. Gold and Dahlsten (1989) found *P. parorum* pupae in nests where the chickadee nestlings had been taken by a predator at 6 or 7 days of age. This indicated that larvae of this species can complete their development within one week. Therefore, oviposition could result in fully mature larvae into the last week of the chickadee's 21-day nestling period. *P. sialia* may also oviposit over a large portion of the period when bluebird and tree swallow nestlings are confined to the nest. Bennett (1957) reported that the period during which larvae actively fed ranged from 8 to 9 days. Since the reported nestling periods of eastern bluebirds and tree swallows range from 16 to 18 days and 19 to 20 days, respectively, there appears to be a "window" of several days during which oviposition may result in fully developed larvae.

Further, I made observations of possible carrion feeding in *Protocalliphora*. On two occasions, *Protocalliphora* larvae were found attached to dead nestlings, apparently feeding. On one occasion several larvae were observed attached by their mouthparts to the skin near the cloaca of a dead tree swallow nestling. This nestling had been dead approximately 2 days. On the other occasion a single larva was found attached to the flank of a bluebird nestling that had died earlier that day. On both occasions the larvae dropped off seconds after the nestlings were lifted off the nest material. I did not find published accounts of carrion feeding in *Protocalliphora*. However, Whitworth (personal communication) reported P. asiovora larvae feeding on the body tissues of a dead magpie nestling under experimental conditions. Sabrosky *et al.* (1989) note that the genus likely evolved from carrion feeding calliphoria larvae derive nutrition from dead nestlings,

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then carrion feeding may allow larvae to complete development after live nestlings have fledged. This behaviour would extend the "oviposition window."

An interesting finding was that gravid flies were captured in nests during the incubation period, in one case 8 days before the eggs hatched. Oviposition at this point would have resulted in larvae hatching several days before they could obtain a blood meal from the nestlings. This observation supports Gold and Dahlsten's (1989) hypothesis that long-range stimuli attract gravid flies to nests while other stimuli associated with the nest and/or nestlings induce oviposition. Apparently, the gravid flies I observed had been drawn to the nests by long-range stimuli and were examining the nest box contents for cues that would stimulate oviposition. I did not observe flies in nests during nest construction, although fly traps were not placed in the nest boxes before the hosts' eggs were laid.

Voltinism and Parity

I obtained data on voltinism through mark, release, and recapture studies. In 1989, 77 adult flies reared from a single bluebird nest collected on 3 June were marked and released on 17, 18, 19, and 21 June. All flies were marked and released within 48 hours of eclosion. The flies did not have access to food in the laboratory, and mating was not observed. Two of the marked females were recaptured in tree swallow nests with nestlings on 25 June. Both flies contained well-developed eggs.

These results indicate that *P. sialia* is at least bivoltine, since flies resulting from eggs laid earlier in the season were ready to oviposit later in the same season. However, the data indicate that additional reproducing generations are possible within a season. I used the mark, release, and recapture data to estimate the generation time, or the interval between oviposition by the parent to first oviposition by the progeny, for *P. sialia*. The 2 flies recaptured in a gravid condition on 25 June had been reared from a nest in which the nestlings hatched on 20 May. If one assumes that the flies resulted from eggs laid on 20 May, a conservative estimate of the generation time would be 36 days, or the interval between 20 May and 25 June. Using the same conservative assumptions, it was estimated that a female *P. sialia* reared from a bluebird nest in the 1990 nesting season and marked, released, and recaptured in a tree swallow nest had a generation time of 35 days.

I used the estimate of the generation time to estimate the number of generations of *P. sialia* per breeding season. The nest of bluebirds that hatched on 20 May, 1989

was one of the first passerine cavity nests at the study site. It is likely that the flies that oviposited in this nest, the "first" generation, had survived from the previous year. Therefore, flies reared from this nest, including the 2 gravid females recaptured on 25 June, were the first adults of the second generation. If these 2 gravid females had oviposited on 25 June, their female progeny (*i.e.*, the third generation) would be ready to oviposit 36 days later on 31 July. Hatching date records show that the last bluebird eggs laid in the study sites in 1989 hatched on 6 August. These nestlings were parasitized by *P. sialia*. Therefore, a third generation of *P. sialia* could have completed ovariole development in sufficient time to oviposit in this last nest.

My calculations showing that 3 generations of *P. sialia* are possible within a nesting season are based solely on bluebird and tree swallow data. The likelihood of a third reproducing generation becomes greater when other hosts of *P. sialia* are taken into account. For example, nestlings of the American robin may be encountered in southwestern Québec from the first week of May to the third week of August. House wren nestlings can be found even later in the summer, until the fourth week of August (Aubry and Lambert, 1985). My results show that *P. sialia* females are not host-specific. Therefore, by parasitizing a variety of hosts, populations of *P. sialia* in southwestern Québec could produce three breeding generations in a single nesting season.

I also used the data from the mark, release, and recapture studies to derive information on parity. The 2 gravid flies recaptured on 25 June, 1989 had been released no more than 9 days previously. If it is assumed that egg development did not occur under captive conditions, as reported by Bennett and Whitworth (1991), my results suggest that wild, nulliparous *P. sialia* can complete egg development in 9 days or less. Using the same conservative assumptions, the gravid fly marked, released, and recaptured in the 1990 nesting season completed egg development within 10 days. I estimated the parity of *P. sialia* by comparing these results to published information on longevity. Bennett and Whitworth (1991) reported that female *P. sialia* maintained outdoors survived for 40 to 50 days. When these flies were then brought indoors, their average total longevity was 76 days. Therefore, wild female *P. sialia* could potentially oviposit several times over the course of their reproductive lives. This hypothesis does not conflict with the findings of Gold and Dahlsten (1989), who reported that *P. sialia* is at least biparous.

CONCLUSIONS

My broad goal in this study was to obtain basic information on *Protocalliphora* parasitizing nestling bluebirds and tree swallows in the study area. Specifically, I had three primary objectives. As stated in the "Introduction," the first objective was to identify the main species of *Protocalliphora* infesting bluebird and tree swallow nests in open field habitats. The most common species reared from infested nests was *P. sialia*. I found that 100% of the bluebird nests in the study were infested, and the prevalence of infestations for tree swallow nests ranged from 82% to 95%. Studies conducted by previous researchers indicated that this species is a frequent parasite of cavity nesting birds in open field habitats.

Other studies have demonstrated that *Protocalliphora*, including *P. sialia*, are common parasites of bluebird and tree swallow broods. The importance of such findings appears to have been lost on at least some researchers studying the breeding ecology of bluebirds and tree swallows. For example, Quinney *et al.* (1986) studied sources of variation in the growth of tree swallow nestlings in colonies in southern Ontario. These authors examined a number of variables, including food abundance and location of the colony. However, they did not address the effect of parasite burdens on nestling growth, including parasitism by *Protocalliphora* larvae. Given the apparent frequency with which *Protocalliphora* parasitize tree swallows, the authors may have overlooked a significant factor influencing nestling growth.

My second objective was to investigate the influence of nest site characteristics and other variables on the intensity of *Protocalliphora* infestations. The variables examined included hatching date, nest material volume, number of fledglings, and percent canopy cover above the nest box. I found positive correlations between three variables (hatching date, nest material volume, and number of fledglings) and the number of larvae per nest, although none of the three variables was correlated with the intensity of infestations in both host species in both years of the study. These results suggest that each of the three variables has the potential to influence the intensity of *Protocalliphora* infestations. However, the actual influence of a single variable may depend on its interaction with the other two and, probably, with other unidentified variables. The fourth variable, percent canopy cover, did not appear to influence the intensity of infestations in either host species.

The positive correlation between nest material volume and number of larvae may have implications for management of cavity nesting birds. For example, Pitts (1988) found that eastern bluebirds nesting in boxes with small interior volumes used less nest material than birds nesting in larger boxes. Experiments conducted by Lumsden (1986) indicated that this species prefers to nest in boxes with smaller floor areas. Therefore, nest boxes with small interior volumes may limit the amount of nest material used by bluebirds and, thus, limit the intensity of *Protocalliphora* infestations.

A notable finding that emerged was that a number of host species nesting in the same habitat may influence the intensity of *Protocalliphora* infestations in each other's nests. In my study, the presence of synchronously-nesting tree swallows seemed to reduce the intensity of infestations in contemporaneous bluebird nests. To my knowledge, the effect of other species nesting in the habitat has not been reported before, and may merit consideration in future studies of host-*Protocalliphora* ecology.

My third objective was to obtain basic information on reproduction in *Protocalliphora*, including information on timing of oviposition, voltinism, and parity. Previously published information on reproduction was particularly sparse. I made observations of probable mating behaviour in *Protocalliphora*, which indicated that males gather at specific sites in the habitat for mating purposes. These observations bolstered evidence for mating aggregations obtained by previous researchers. I also obtained data on the timing of oviposition in relation to the host nesting cycle.

However, probably the most significant results of this study relate to the data on parity and voltinism and, in particular, the methods by which the data were obtained. I determined that *P. sialia* was at least bivoltine and that the generation time for female flies was, at a maximum, 35 or 36 days under wild conditions. In addition, I found that wild nulliparous *P. sialia* can complete egg development within 9 or 10 days following eclosion. Previous researchers, relying largely on observations of laboratory reared *Protocalliphora*, had not been able to obtain information on successive generations of flies. Further, no practical method had been developed for marking *Protocalliphora* and recapturing them after they were released in the wild. My results represent progress in addressing these limitations. The fly traps developed in this study, in conjunction with the mark, release, and recapture techniques I tested, allow information on parity and voltinism in wild *Protocalliphora* to be obtained more readily. Other applications of these methods may be tested by future researchers studying, for example, *Protocalliphora* dispersal or bionomics.

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APPENDIX 1. Calculation of Nest Material Volume.

For each nest that contained eggs or newly-hatched young, the following dimensions were measured to the nearest 0.5 cm using a centimeter ruler:

•The top diameter of the nest cup.

•The bottom diameter of the nest cup (the area occupied by the clutch of eggs).

•The depth of the nest cup.

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•The height of the nest *i.e.*, the distance between the floor of the box and the rim of the nest.

The volume of the nest cup was calculated using the top cup diameter, bottom cup diameter, and cup depth (Figure 5). The nest cup was approximated by a stack of n discs of radius x_i , each 0.5 cm thick, where n=cup depth/0.5 cm. The volume of the nest cup, V_{cup} , is then given by the formula:

$$V_{cup} = (0.5 \text{ cm})(\pi)\Sigma(x_i)^2 \text{ where } i=1, 2, ... n [1]$$

The total volume of the nest *i.e.*, the volume of the nest box taken up by the nest, V_{total} , is equal to the floor area of the box (in all cases 115 cm²) multiplied by the nest height. The volume of nest material used is thus equal to V_{total} - V_{cup} .



Figure 5. Schematic diagram of the nest cup used to calculate cup volume. A. Top diameter of nest cup. B. Bottom diameter of nest cup. C. Cup depth. D. Indicates 0.5 cm. x_1, x_2, x_3, x_i . Radii of discs.

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