1976

Host and Habitat Preferences, Life History, Pathogenicity and Population Regulation in Species of Protocalliphora Hough (Diptera: Calliphoridae)

Terry Lee Whitworth
Utah State University

HOST AND HABITAT PREFERENCES, LIFE HISTORY, PATHOGENICITY AND POPULATION REGULATION IN SPECIES OF PROTOCALLIPHORA HOUGH (DIPTERA: CALLIPHORIDAE)

by

Terry Lee Whitworth

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

of

DOCTOR OF PHILOSOPHY

in

Biology

(Zoologv)

UTAH STATE UNIVERSITY
Logan, Utah

1976

ACKNOWLEDGMENTS

I would like to extend thanks to the following people who assisted me in this study: To Dr. Wilford J. Hanson, my major professor, for his continual guidance and advice; to Mr. Kenneth J. Capelle, Bear River Research Station, for initially interesting me in this project and aiding me throughout its completion; and to Mr. Curtis W. Sabrosky of the U. S. National Museum of Natural History for his assistance in identification of specimens.

I also wish to acknowledge the assistance of several ornithologists who aided me in the collection of bird nests. Thanks go to Dr. Keith L. Dixon, Utah State University, who provided me with considerable information on bird habits and life histories. I am especially indebted to Ms. Janet Young, for allowing me to examine a variety of bird nests in her study area. Others who assisted me in the collection of nests include, Mr. Scott Sawby, Mr. Richard Burr, Mr. Tim Burr, and Mr. Dennis Martin, and I gratefully acknowledge their aid.

I also received advice and assistance from several physiologists. I would especially like to thank Ms. Joyce Johnson, of the poisonous plants laboratory, for teaching me a variety of laboratory techniques, and providing me with access to her laboratory equipment. Thanks also go to Mr. Earl Johnson for his advice, and allowing Ms. Johnson to work with me. In addition, I would like to acknowledge the assistance of Drs. James Gessaman, and LeGrande Ellis for providing me with laboratory equipment, as well as helpful advice.

Also thanks to Drs. Clayton Gist and Donald Sisson, for advising me on statistical techniques.

Finally, special thanks to my wife, Faye, for assisting me both in the field and the preparation of this manuscript.

Terry Whitworth

Terry Lee Whitworth

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

LIST OF FIGURES

ABSTRACT

Host and Habitat Preferences, Life History, Pathogenicity and Population Regulation in Species of Protocalliphora Hough (Diptera: Calliphoridae)

by

Terry Lee Whitworth, Doctor of Philosophy

Utah State University, 1976

Major Professor: Dr. Wilford J. Hanson
Department: Biology

The host, habitat preferences, and life histories of species of Protocalliphora were investigated in northern Utah. The effect of species of Protocalliphora on blood levels (hematocrit and hemoglobin) and weight gains of nestling birds also was studied.

A total of 1,819 bird nests were examined, representing 68 bird species from 10 habitats. Forty-eight percent (869) of the nests of 51 bird species found were infested. Eighteen species of Protocalliphora, including 11 undescribed, were collected.

Birds experiencing a high rate of infestation included most colonial nesters (such as bank swallows and yellow-headed blackbirds), cavity nesters (such as starlings and tree swallows, excluding woodpeckers), and some solitary open nesters, such as magpies, warblers, and flycatchers. Many solitary open nesters (such as sparrows and robins) and one colonial nester (red-winged blackbirds) experienced lower rates of infestation.

Two species, P. chrysorrhoea and P. hirundo, appeared to be specific to their hosts, bank swallows and cliff swallows, respectively. Several undescribed species had narrow host or habitat preferences, including the dominant species infesting warblers and flycatchers, and a species infesting only marsh birds. One rare species (undescribed) was found primarily in the nests of Falconiformes. P. asiovora infested many bird species, but was the dominant species infesting Corvidae (magpies, ravens and crows). P. sialia occurred in the nests of many species, but favored cavities.

Multiple infestations, involving more than one species of Protocalliphora in a nest, were found in 7.1% of the infested nests examined. Brewer's blackbirds and five species of swallows commonly experienced mixed infestations, especially those nesting in peripheral habitats. Only P. hirudo was regularly involved in mixed infestations.

Life history studies were conducted and developmental periods were determined for larvae and pupae of five species of Protocalliphora. Behavioral observations were made on larvae and adults in the field and laboratory.

The effect of larval blood-sucking on nestling magpies and bank swallows was determined by comparing rates of weight gain (only in magpies) and blood levels (hemoglobin and hematocrit) between infested and uninfested nestlings. Although the number of fledged nestlings was not reduced substantially in heavily infested nestlings, they did experience significantly lower rates of weight gain and blood levels. Blood levels also were examined in infested and uninfested starlings,

kestrels, and yellow-headed blackbirds. Of these, only starlings experienced infestations large enough to cause significant reductions in blood levels.

Factors regulating larval populations of _P. asiovora_ in magpie nests also were investigated. The relative importance of predation and interspecific and intraspecific competition in regulating larval populations was considered. Although several factors appeared to be interacting, intraspecific competition appeared to be the most important regulatory factor.

(156 pages)

GENERAL INTRODUCTION

The larval stages of all known species of Protocalliphora (Diptera: Calliphoridae) are obligate, blood-sucking parasites of nestling birds. The larvae or puparia[1] of Protocalliphora may be found frequently in the nests of most nidicolous birds, although some bird species are more commonly infested than others.

Although species of Protocalliphora morphologically resemble other Calliphoridae, the larval habit of blood-sucking on nestling birds makes them unique members of the family. The African genus Auchmeromyia also is an intermittent blood-sucker in the larval stage, but it feeds only on mammals. Larval forms of two genera of Muscidae, Passeromyia in Africa and Asia and Philornis in South America and southern North America, suck the blood of birds, as does Neottiophillium (Neottiophillidae) in Europe (Zumpt, 1965).

The biology of Protocalliphora is poorly known, primarily because of the difficulty of obtaining specimens for study. Protocalliphora have not been colonized, because workers have been unable to induce them to reproduce under laboratory conditions. Bennett (1957) found that ovaries of females fed a variety of protein and carbohydrate diets did not develop although their spermathecae contained active sperm. Since an artificial diet has not been developed for rearing the larvae,

[1] According to Wigglesworth (1967, p. 28), the puparium is formed by sclerotization of the endocuticle of higher diptera larvae and contains the pupa.

it is necessary to use nestling birds, which are available for only a short period each year. Because of these difficulties, laboratory observations on Protocalliphora have been restricted to specimens taken from nests in the field.

The study of Protocalliphora is further complicated because the genus contains many undescribed species.[1] Adults have few reliable distinguishing characteristics and, according to Sabrosky and Bennett (1958), some adults cannot be identified to species without associated immature stages. Sabrosky and Bennett (1958) presently are revising the taxonomy of the genus which should aid future studies. Their work also will include data from Bennett (1957) and Whitworth's (1971) studies on the ecology and life history of eastern and western species of Protocalliphora. Except for Whitworth (1971) few biological studies have been conducted in the western United States and these consist only of scattered observations (Plath, 1919; Neff, 1945).

The impact of large populations of Protocalliphora upon nestling birds has not been determined. Whether or not Protocalliphora can cause nestling mortality has been debated by several authors. Plath (1919), Johnson (1929), Stoner (1936), Mason (1936), and Neff (1945), have written on the deleterious effects of larval feeding on nestling birds. In contrast, Coutant (1915), Jellison and Phillip (1933), and Bennett (1957), claimed that Protocalliphora did not affect nestling birds. Bennett (1957) rarely observed dead nestlings in nests. He found only two dead nestlings in 672 infested nests and 12 dead nestlings in 1,800

[1]Adult and immature stages of the 7 described and 11 undescribed species of Protocalliphora found in this study are stored in the Utah State University Insect Collection.

uninfested nests. In 1970, I observed many dead nestlings in nests, especially those of yellow-headed blackbirds[1] and cliff swallows. Cause of nestlings' death was not determined, but it seems likely that birds experiencing daily blood losses to Protocalliphora would be somewhat anemic and perhaps less able to withstand additional stresses. However, the cause of sickness and death in nestlings is very difficult to determine because of the many factors involved, such as: 1) adverse weather, 2) starvation, 3) poor adult care, 4) disease, and 5) parasites. In the field I frequently found heavily infested nestlings in apparent poor health. The birds characteristically lacked normal glossy plumage, the interior of the mouth was pale white, instead of red, and their skin was shrunken, wrinkled, and covered with scabs from larval feeding sites. However, qualitative criteria such as these alone are inadequate to determine the impact of Protocalliphora upon nestlings. Therefore, I initiated the present study to attempt to explain the relationships between the larval parasite and its nestling host.

The primary objectives of my study were:

1. To determine specific hosts, habitats, and life histories of species of Protocalliphora
2. To study pathogenic effects of selected species of Protocaliphora on nestling birds
3. To study factors regulating larval populations of Protocaliphora in birds nests.

---

[1]Scientific names of all bird species are listed in the Appendix, Table 24.

PART I

STUDIES OF HOST AND HABITAT PREFERENCES AND LIFE HISTORIES OF SPECIES OF *PROTOCALLIPHORA*

REVIEW OF LITERATURE

Several studies have been conducted on the ecology and life history of species of Protocalliphora in the eastern United States. Early studies by Countant (1915), Dobrosky (1925), and Mason (1936) were reviewed by Hall (1948), Owen (1954), and Owen and Ash (1955). These works, however, are of limited value, because the taxonomy of the genus was confused and identification of species cited therein are questionable. More recently, a detailed study of the eastern species of Protocalliphora was conducted by Bennett (1957) in Ontario, Canada. He examined more than 2500 nests of 71 bird species and found 13 species of Protocalliphora in 672 infested nests. He studied the taxonomy of the immature stages, as well as the ecology of larval, puparial, and adult stages.

Until recently, in-depth studies of the western species of Protocalliphora were lacking. In the Seattle, Washington area, Plath (1919) examined 54 bird nests, of which 34 were infested by two species of Protocalliphora. Neff (1945) examined the nests of an unspecified number of birds and gathered some valuable ecological data on species of Protocalliphora in mourning dove nests. Other studies have been conducted by Jellison and Philip (1933) on P. avium (probably P. asiovora) in nests of magpies and crows in Montana. Protocalliphora species also have been studied in nests of sparrow hawks and golden eagles in California (Hill and Work, 1947).

In 1970 I examined 733 bird nests in the northern Wasatch Range and found 49% of these nests infested by 16 species of Protocalliphora (Whitworth, 1971). In preliminary studies for the present work, two additional species of Protocalliphora were found. Based on limited distributional data, Protocalliphora appears to be most diverse in the Intermountain Region. Studies on the ecology and life history of the species in this area, therefore, are of value. I will discuss herein the host and habitat preferences of species in this region, as well as the life histories of some of the more common species.

METHODS

Nest Collection Sites

The specimens obtained for this investigation were collected during the summers of 1969 through 1974. Most nests were collected within a 75-mile radius of Logan (Cache County), Utah, in the northern end of the Wasatch Mountain Range in northern Utah, southern Idaho, and southwestern Wyoming (Figure 1 and Table 1). Habitats examined ranged from the deserts at 4,200 feet elevation, with 9 inches annual rainfall, to the conifer forests at 7,000-9,000 feet, with 25-40 inches annual rainfall.

The study area was divided into 10 sub-divisions, following the general plan used by Bennett (1957). The Intermountain Region is quite diverse topographically, which results in a wide variety of flora and fauna. The existing habitat types are numerous, but present nest collections are inadequate to associate most Protocalliphora species with definite habitats. Therefore, general nest collection site categories were established to aid in characterizing species, but the construction of more definite divisions must await further collections. Some of the categories included here are quite heterogeneous, but in analyzing their subdivisions, differences did not seem sufficient to justify separation.

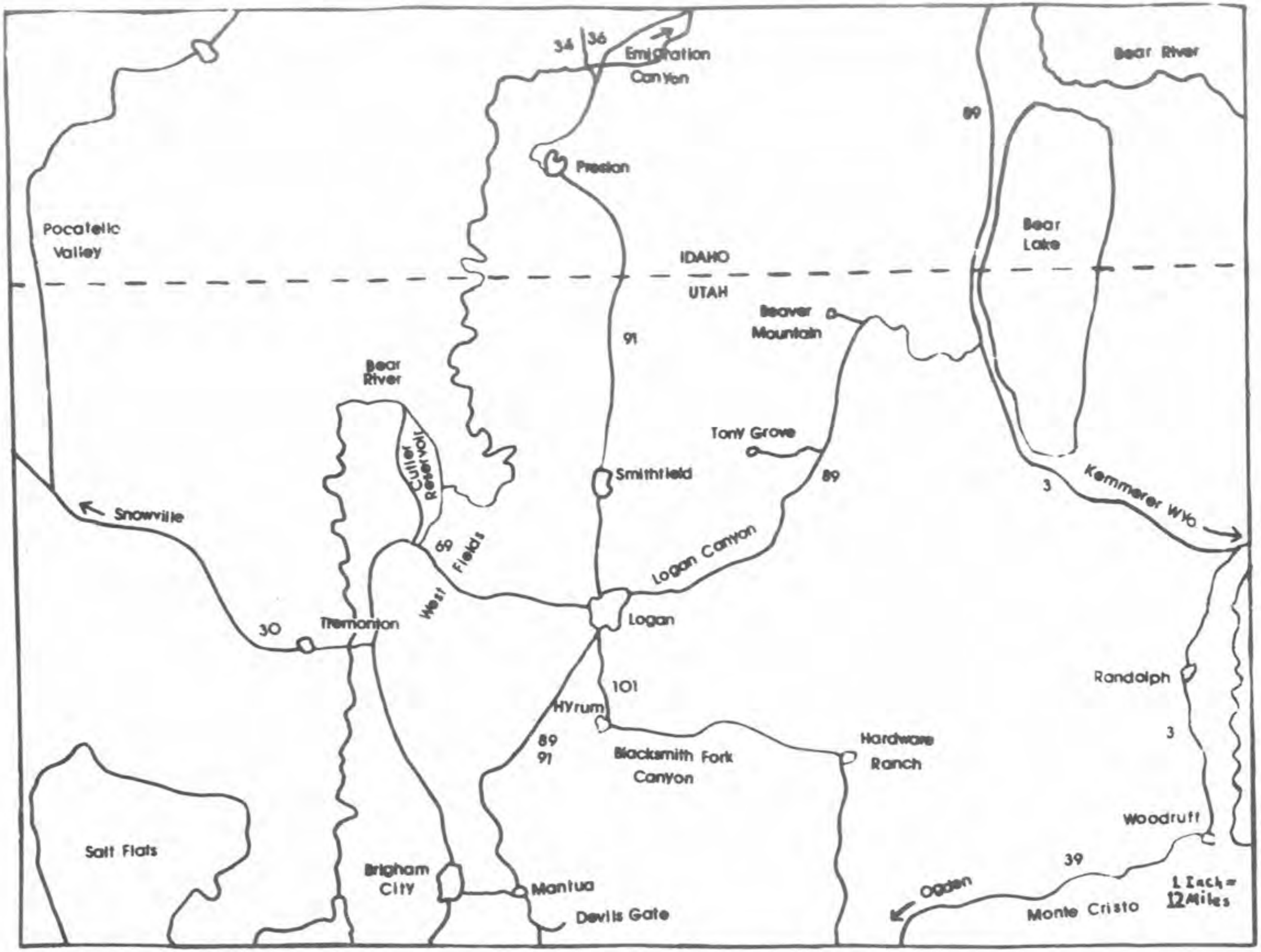
34
36
Emigration
Canyon
Bear River
89
Preston
Pocatello
Valley
Bear
Lake
IDAHO
UTAH
Beaver
Mountain
91
Bear
River
Cutler
Reservoir
Tony Grove
Smithfield
89
Snowville
3
Kemmerer WYo
69
Fields
West
Logan Canyon
30
Tremonton
Logan
101
Randolph
HYrum
89
91
Blacksmith Fork
Canyon
Hardware
Ranch
3
Woodruff
Salt Flats
39
Brigham
City
Mantua
Devils Gate
Ogden
Monte Cristo
1 Inch =
12 Miles

Table 1. Major areas in the northern Wasatch region where bird nests were collected[a]

Site	Location
1, 2, 3	Emigration Canyon (Idaho), Beaver Mountain, Tony Grove, Hardware Ranch, Monte Cristo, Devils Gate (Utah), and along the Green River, north of Kemmerer, Wyoming. Major bird species collected were house wrens, tree swallows, mountain bluebirds, chickadees, flycatchers, warblers, woodpeckers, red-tailed hawks, and goshawks
4	The canyon between Monte Cristo and Woodruff, Utah, and also the cliffs along the Green River north of Kemmerer, Wyoming. A primary source of cliff swallows, it also included some red-tailed hawks, and prairie falcons
5, 6, 7	Usually associated with the Bear River and its tributaries through Wyoming, Idaho, and Utah. Major bird species collected were magpies, starlings, sparrow hawks, sparrows, bank swallows, and herons
8	The large marsh west of Logan, and numerous other smaller marshes along the Bear River. A primary source of yellow-headed blackbirds, red-winged blackbirds, Brewer's blackbirds and long-billed marsh wrens
9	A heterogeneous category including two major divisions: 1) bridges along the Bear River and its tributaries for barn swallows, some cliff swallows, and house sparrows 2) abandoned houses and farms in Cache Valley and Pocatello Valley where nests of Brewer's Blackbirds, mourning doves, Brewer's sparrows, and Say's phoebe were found
10	The deserts west of Snowville. A source of ferruginous and red-tailed hawks, and horned lark nests

Specific collection sites: Four bank swallow colonies were located: 1) just east of Wellsville, 2) at Hyrum Dam, 3) at a quarry north of Logan (all in Utah), and 4) a quarry north of Weston, Idaho. Two great blue heron rookeries were found in Utah: 1) northeast of Mendon and 2) southeast of Newton. A snowy egret rookery was found near Mendon south of the heron rookery

[a]All areas named are shown on the map in Figure 1.

Mountain nest sites (1, 2, 3, 4)

From 5,000 to 10,000 feet, are characterized by interdigitation of vegetation, depending on the direction of slope and local soil conditions. This is a highly variable area including many vegetation types. Aspen (Populus tremuloides) is common at all elevations, with Douglas fir (Pseudotsuga menziesii) dominant on steep, north-facing slopes and at elevations above 8,000 feet. Bigtooth maple (Acer gradidentatum) and sage (Artemesia tridentata) are common shrubs occupying drier areas throughout this habitat.

Site 1. Mountain arboreal. Open nests 10 feet or higher in trees, exposure variable, usually partially protected from wind, rain, and sun.

Site 2. Mountain shrub. Open nests in forest understory, shrubs 10 feet or below and ground level, usually well-protected.

Site 3. Mountain cavities. Nests in cavities in trees, usually less than 15 feet above ground, exposure variable, highly exposed in areas with many dead trees, protected in areas of dense living forest.

Site 4. Mountain overhang. Nests on cliff overhangs, usually partially protected from wind, rain, and sun.

Valley nest sites (5, 6, 7, 8, 9, 10)

Essentially flat land, the vegetation type dependent on rainfall (determined by rain shadow), and available ground water. Some areas were along streams or irrigation having much green vegetation. Others were dry valleys with low rainfall and no irrigation such as those bordering the northern and western end of the Great Salt Lake, the dominant natural vegetation being sagebrush and juniper (Juniperus osteosperma).

Site 5. Valley arboreal. Open nests 10 feet or higher in trees, usually small groves along rivers, springs, or areas with high ground water, rarely dense forest.

Site 6. Valley shrub. Open nests in shrubs, and rarely forest understory 10 feet or less.

Site 7. Valley cavity. Nests in cavities in trees and banks, immediate external environment exposed.

Site 8. Valley marsh. Open nests in marsh, including cattails (*Typa latifolia*), reeds (*Scirpus acutus*), and willows (*Salix exigua*) over water. Quite moist, usually somewhat exposed.

Site 9. Valley structural. Nests in or on man-made structures such as bridges and buildings. A heterogeneous category, but present collections are inadequate for further subdivision.

Site 10. Valley desert. Nests in deserts, ranging from valleys with relatively high rainfall and sage to extremely arid regions with sparse vegetation.

Parasite Collections

Specimens of *Protocalliphora* were collected most frequently from active or recently vacated bird nests. The usual procedure for finding nests was to search an area when the eggs were being incubated. It was easiest to find nests at this time, since adults were flushed directly from them. Some nests were found after the young had hatched, but the evasive action of the nearby adults often made it difficult to determine nest locations. When nests were found, their height above the ground and habitat location were recorded. Nests with young birds usually were left undisturbed until the birds had fledged. The nests then were collected in paper sacks and taken to the laboratory, where they were carefully examined for larvae and puparia. Protocalliphora eggs were obtained by capturing gravid females around bird nests and either dissecting them or allowing them to oviposit. Adults were captured with an aerial net or aspirator. Eggs also were obtained from nest material by means of a series of nested sieves with 9, 14, 20, 35, 42, and 60 per inch mesh screens. Most eggs were stopped by 42 and 60 mest per inch sieves.

Preparation of Specimens

Some larval specimens of all three instars were placed in KAA (kerosene, alcohol, and acetic acid) to cause them to distend, and after a few hours they were transferred to 95% alcohol for storage, as recommended by Peterson (1959). In instances where only the first and second instars were present in the nest, some usually were reared to the third instar on young nestlings in the laboratory to ensure having representative adults from the nest. If third instar larvae were present some were preserved in alcohol, but most were allowed to pupate and emerge as adults. Before emergence, puparia were sorted into individual vials so that each adult could be pinned with its own puparial case. Empty puparia from the nests were preserved in dry, corked vials.

Laboratory Rearing

Rates of larval development were determined by rearing larvae on nestling Brewer's blackbirds or magpies in artificial nests in the laboratory. Larvae were aged by measuring their total length in millimeters. Efforts were made to follow larval development in the field, but it was difficult to keep a precise larval count, and multiple infestations confounded the data.

Rates of pupal development were determined by maintaining puparia in conditions of controlled temperature, humidity, and light. Temperature and humidity were monitored with a Weather Measure Corporation (Sacramento, California) hygrothermograph, Model H-311. Photoperiod was regulated with a Time-all electronic timer manufactured by the International Register Company (Chicago, Illinois).

Adults were reared from pupae and maintained in 18-inch square wooden frame oviposition cages, covered with nylon mesh on three sides and glass on a fourth. Adults were furnished a diet of honey, brewer's yeast, and water.

Taxonomy

Major characters used for adult identification were: (1) the shape of the male genitalia, (2) the color of male and female squamae, and (3) female body color. Puparial characters often were used in combination with those of adults to make species' determinations. Primary puparial characters were: (1) size and shape of circumstigmal folds, (2) size and distribution of spines, and (3) size and shape of ventral spine bands. Puparial slides were prepared by clearing puparia with 5 M. KOH, dehydrating in cresote, and mounting in Canada balsam, after techniques suggested by Bennett (1957).

RESULTS AND DISCUSSION

Factors Affecting *Protocalliphora* Infestation Rates in Bird Nests

During the summer of 1969 and the summer and fall of 1970-74 a total of 1,819 bird nests representing 68 different bird species (Tables 2 and 3) was examined. Of these, 869 nests, representing 51 bird species, were infested with *Protocalliphora*, for an overall infestation rate of 47.8%. From these infested nests 18 species of *Protocalliphora* were reared, including 11 undescribed species. The nests of colonial birds were most easily found and, therefore, represent the majority of those examined. These included cliff swallows, barn swallows, bank swallows, yellow-headed blackbirds, and Brewer's blackbirds. The solitary nests of robins and magpies also were frequently collected, since they were common and often conspicuous. Efforts were directed toward finding nests of many different bird species from a variety of habitats to increase the likelihood of finding different species of *Protocalliphora*.

Infestation in relation to bird species

A variety of factors probably influence a female *Protocalliphora* in the selection of nests for oviposition. Two interrelated factors which may be important are the location of the nests and its attractiveness (e.g. odor). The nests of most birds apparently attract some species of *Protocalliphora*, but the nests of a few species were never found with *Protocalliphora* (Table 2).

Table 2. Distribution by nest site of bird nests uninfested by <u>Protocalliphora</u>

Bird species	Total uninfested	Uninfested nests by site									
		1	2	3	4	5	6	7	8	9	10
catbird	2						2				
dove, rock	2									2	
egret, snowy	3					3					
falcon, prairie	1										1
grosbeak, blackheaded	7	3	1			2	1				
hawk, marsh	1						1				
hawk, sharp-shinned	2		2								
heron, great blue	5					5					
kingfisher, belted	1							1			
oriole, Bullock's	8					3			5		
sapsucker, yellow-bellied	5			5							
sapsucker, Williamson's	2			2							
sparrow, Brewer's	6		1								5
sparrow, savannah	1										1
sparrow, song	1		1								
sparrow, vesper	2										2
towhee, green-tailed	4		4								
woodpecker, hairy	3			3							
Total	56										

Some colonial birds had high infestation rates, probably because their nests were both attractive and easily found. Cliff swallow, bank swallow, and yellow-headed blackbird nests had respective infestation rates of 64.9%, 78.4% and 51.6% (Table 3). Other colonial bird nests had somewhat lower infestation rates including: Barn swallows, 30.9%; Brewer's blackbirds, 27.2%; and red-winged blackbirds, 20%. Red-winged blackbirds nest in peripheral marsh habitat (rather than central as do yellow-headed blackbirds), and were rarely infested by the common marsh species, species V,[1] which frequently infests yellow-headed

[1]Undescribed species are designated by Roman numerals.

Table 3. Species of Protocalliphora infesting different bird species, by nest site

Bird species Protocalliphora sp.	Total[a] infestation	Infestation by site[b]									
		1	2	3	4	5	6	7	8	9	10
blackbird, Brewer's											
asiovora	16						1		3		12
hirudo	3								1		2
sialia	1										1
III	8						2				6
V	11								11		
X	3										3
XII	15								15		
Total	43/158=27.2%					0/2	3/19		30/61		24/76
blackbird, red-winged											
III	2						1		1		
V	9								9		
VII	1						1				
XII	5						1		4		
Total	17/85=20%						3/37		14/48		
blackbird, yellow-headed											
hirudo	1								1		
V	110								110		
XII	2								2		
Total	110/213=51.6%								113/213		
bluebird, mountain											
sialia	4			1				3			
	4/9=44.4%			1/4				3/5			
bunting, lazuli											
III	1						1				
Total	1/5=20%		0/1				1/4				
chickadee, black-capped											
VI	5			5							
Total	5/5=100%			5/5							
chickadee, mountain											
VI	5			5							
Total	5/8=62.5%			5/8							
crow, common											
asiovora	2					2					
Total	2/2=100%					2/2					

Table 3. Continued

Bird species Protocalliphora sp.	Total[a] infes- tation	Infestation by site[b] 1	2	3	4	5	6	7	8	9	10
dipper											
aenea	2		2								
Total	2/3=66.7%		2/3								
dove, mourning											
asiovora	1					1					
Total	1/5=20%		0/1			1/1	0/1				0/2
eagle, golden											
asiovora	2						1				1
Total	2/3=66.7%						1/1				1/2
finch, Cassin's											
hesperia	1	1									
Total	1/2=50%	1/2									
flicker, red-shafted											
"gigantia"	1			1							
undet.	1			1							
Total	2/4=50%			2/2				0/2			
Empidonax flycatcher											
II	6		4						2		
Total	6/8=75%	0/1	4/5						2/2		
goldfinch, American											
II	2		2								
Total	2/5=40%		2/3				0/2				
hawk, Cooper's											
asiovora	1	1									
undet.	1	1									
Total	1/6=16.6%	2/7									
hawk, ferruginous											
asiovora	14					1					13
Total	14/17=82.4%					1/1					13/16
goshawk											
asiovora	3	3									
"gigantia"	1	1									
Total	3/7=42.9%	4/7									

Table 3. Continued

Bird species *Protocalliphora* sp.	Total[a] infes- tation	Infestation by site[b]									
		1	2	3	4	5	6	7	8	9	10
hawk, red-tailed											
asiovora	7	1	1		1	2					2
"gigantia "	2	1			1						
	7/8=87.5%	2/2	1/1		2/2	2/2					2/3
hawk, sparrow											
"gigantia "	2							2			
sialia	7							7			
Total	9/24=37.5%							9/22		0/1	0/1
hawk, Swainson's											
asiovora	2					2					
Total	2/2=100%					2/2					
junco, Oregon											
VI	1		1								
unknown	1		1								
Total	2/4=50%		2/4								
kingbird, eastern											
II	2						2				
Total	2/6=33.3%					0/1	2/4		0/1		
kingbird, western											
sialia	1					1					
II	1					1					
Total	1/2=50%					2/3					
magpie, black-billed											
asiovora	128		11			110	1		4		2
hirudo	2					2					
Total	128/141=90.8%		11/11			112/122	1/1		4/5		2/2
martin, purple											
VIII	6			6							
Total	6/6=100%			6/6							
owl, flammulated											
sialia	1			1							
Total	1/1=100%			1/1							
owl, great horned											
sialia	1					1					
Total	1/5=]0%	0/2				1/2					0/1

Table 3. Continued

Bird species Protocalliphora sp.	Total[a] infes- tation	Infestation by site[b]									
		1	2	3	4	5	6	7	8	9	10
owl, long-eared											
asiovora	1		1								
Total	1/1=100%		1/1								
pewee, wood											
II	5	5									
Total	5/7=71.4%	5/6	0/1								
pheobe, Say's											
sialia	1										1
IV	2										2
Total	3/5=60%									0/1	3/4
raven, common											
asiovora	5									2	3
sialia	1										1
Total	6/7=85.7%									2/2	4/5
robin											
asiovora	11		4			6					1
hesperia	11	5	4			1	1				
sialia	2		1			1					
II	1		1								
VII	6		6								
Total	28/109=25.7%	5/29	16/42			8/20	1/14				1/4
sparrow, chipping											
hesperia	1		1								
Total	1/3=33.3%		1/3								
sparrow, fox											
	2		2								
Total	2/5=40%		2/5								
sparrow, house											
chrysorrhoea	2									2	
sialia	4									4	
Total	5/18=27.8%					0/3				6/15	
sparrow species											
III	1		1								
VII	1		1								
XII	1						1				
Total	3/9=33.3%		2/8				1/1				

Table 3. Continued

Bird species Protocalliphora sp.	Total[a] infes-tation	Infestation by site[b] 1	2	3	4	5	6	7	8	9	10
sparrow, white-crowned											
undet.	1		1								
Total	1/6=16.7%		1/6								
starling											
hirudo	3		1					2			
sialia	20							20			
Total	23/33=69.7%		1/2					22/31			
swallow, bank											
chrysorrhoea	95							95			
hirundo	10							10			
sialia	2							2			
undet.	2							2			
Total	98/125=78.4%							109/125			
swallow, barn											
chrysorrhoea	1									1	
hirundo	2									2	
sialia	7									6	1
II	1									1	
IV	114									114	
VIII	1									1	
X	1									1	
Total	121/392=30.9%									126/391	1/1
swallow, cliff											
hirundo	118				96					22	
sialia	4				4						
VIII	4				4						
Total	135/208=64.9				104/145					22/63	
swallow, tree											
sialia	9			9							
VIII	10			10							
Total	17/22=77.3%			19/22							
swallow, violet-green											
sialia	1						1				
VIII	1				1						
Total	2/3=66.7%				1/1		1/2				
vireo, warbling											
XV	1		1								
Total	1/11=9.1%	0/1	1/9			0/1					

Table 3. Continued

Bird species Protocalliphora sp.	Total[a] infes-tation	Infestation by site[b] 1	2	3	4	5	6	7	8	9	10
warbler, Audubon's											
II	1	1									
Total	1/2=50%	1/2									
warbler, yellow											
II	5	1				4					
Total	7/10=55.6%	1/2	0/1			4/6					
warbler sp.											
undet.	2		2								
Total	2/2=100%		2/2								
wren, house											
hirudo	4			4							
sialia	3			3							
VI	16			16							
undet.	1			1							
Total	21/33=63.6%			24/31				0/2			
wren, long-billed marsh											
hirudo	1								1		
VI	5								5		
Total	5/7=85.7%								6/7		
unknown											
hesperia	1		1								
Total	1/1=100%		1/1								

Total $\frac{\text{infested}}{\text{nests examined}} = \frac{869}{1763}$

[a]The sum of the numbers will exceed total nests examined where mixed infestations occurred.

[b]1. mountain arboreal
2. mountain shrub
3. mountain cavities
4. mountain overhang
5. valley arboreal
6. valley shrub
7. valley cavity
8. valley marsh
9. valley structural
10. valley desert

blackbirds. Since other Protocalliphora species were uncommon in the marsh, this would account for a lower infestation rate in red-wing nests.

Infestation rates in Brewer's blackbird and barn swallow colonies varied considerably from one area to another. In some areas, nests of both of these birds had infestation rates approaching 100%, but in other areas rates were near zero. Brewer's blackbirds nested in several different sites (5, valley arboreal; 6, valley shrub; 8, marsh; 10, desert), where they were infested by seven species of Protocalliphora (Table 3). In site 8, infestation approached 50%, whereas in 10 it was only 33%. Actually, most of the colonies in site 10 had more than 50% of their nests infested, but in one area a colony of 17 nests was uninfested. Nests of other bird species within 100 yards of this colony had P. asiovora Shan. and Dob. and P. sialia Shan. and Dob. (both of which have been collected from Brewer's blackbirds elsewhere), indicating that these nests, for some reason, were unattractive to Protocalliphora. One of three nests examined the previous year in this location was infested with P. asiovora. Since seven species of Protocalliphora will infest Brewer's blackbird nests, it is strange that none infested some of these nests. Barn swallows nested primarily in site 9 (on bridges) and were infested primarily by species IV. However, in some colonies, species IV appeared to be rare, or at least reluctant to infest barn swallow nests. For example, only three nests in a colony which contained 66 nests were infested by Protocalliphora, all by species IV. This was my first collection of nests from that area and, thus, the low infestation was not the result of earlier reductions in the natural population through previous collections. There were notable regional differences in infestation in the nests of all colonial Passeriformes and the range in infestation between colonies commonly exceeded 50%. However, only in the Brewer's blackbird and barn swallow were differences so great that they resulted in a misleading overall infestation rate.

Some non-colonial birds had high infestation rates, due either to their regular occurrence in an area, their attractiveness, or both. Most cavity nesters (excluding woodpeckers) were commonly infested, usually by only one or two species of Protocalliphora. Since cavity-nesters are usually dependent upon old woodpecker nest holes they frequently renest in the same cavities, perhaps making their nests more easily located by Protocalliphora. The passerine cavity nesters in sites 3 and 7 (valley and mountain cavities) all had high infestation rates, i.e., purple martins 100%, tree swallows 77.3%, black-capped chickadees 100%, mountain chickadees 62.5%, house wrens 63.6%, starlings 69.7%, and mountain bluebirds 44.4 (Table 3). Infestations in these birds were primarily by species VIII, P. sialia, and species VI. Both their regularity of nesting in an area and their attractiveness to certain species of Protocalliphora probably influenced the high infestation rates in these cavity nesters.

Black-billed magpies, warblers, and flycatchers occurred in many habitats, yet were still infested frequently by a single species of Protocalliphora. Magpies were infested almost exclusively by P. asiovora in sites 2, 5, 6, 8, and 10 (mountain shrubs; valley arboreal, shrubs, marsh, and desert) and had an over-all infestation rate of 90.8% (Table 3). Empidonax flycatchers, wood pewees, and yellow and Audubon's warblers were infested exclusively by species II in sites 1, 2, 5, 6, and 8 (mountain and valley arboreal and shrubs, and valley marsh) and their respective rates of infestation were 75%, 71.4%, 55.6%, and 50%. In each of these groups (flycatchers, warblers, and magpies), the nests or nestlings were apparently so attractive that the Protocalliphora species found them regardless of where they were located.

The remaining passerines not discussed include the solitary nesters not regularly associated with a single species of Protocalliphora. Included are sparrows, finches, juncos, robins, and many other songbirds. They are mostly secretive nesters, and except for the robin, whose conspicuous nests were commonly collected, their nests were collected rarely. Robin nests in sites 1, 2, 5, 6, and 10 (mountain and valley arboreal and shrubs, and valley desert), were infested by five species of Protocalliphora, but only 25.7% of their nests were infested. This low infestation rate in robins suggests that low infestations may occur in other shrub-nesting solitary birds, but this needs to be substantiated by further study.

The last category consists of birds which appear not to attract Protocalliphora, this may be the case with the colonial nesting great blue heron and snowy egret. Only five nests of the former and three of the latter were examined, but none were infested. Since these birds are colonial and nest in an area frequented by Protocalliphora (site 5, valley shrub), perhaps their nests are unattractive to Protocalliphora. Heron and egret nests differ from most birds' nests infested by Protocalliphora in that they are usually covered with foul-smelling excrement, and their nesting sites have an odor peculiar to the nests of piscivorous birds. A single magpie nest near the heron colony was infested with P. asiovora, indicating that Protocalliphora were in the immediate vicinity. Considering the diversity of Protocalliphora species, it seems strange that they have not yet adapted to heron and egret nests.

Infestation in relation to Protocalliphora species

Eighteen species of Protocalliphora (seven described and 11 undescribed) were collected from 10 habitats (Table 4). Host selection by Protocalliphora species may be related to host specificity, habitat specificity, or a combination of these factors. P. chrysorrhoea (Meig.) and P. hirundo Shan. and Dob. had narrow host preferences and were collected primarily from a single species of bird in a single nest site. P. chrysorrhoea was found almost exclusively in bank swallow nests in site 7 (valley cavity) and the three nests of other bird species (two starlings, one mountain bluebird) found in that site were not infested. However, occasional infestation by this species in bird nests (house sparrows and barn swallows) in another nest site (site 9, structural) shows that it is not restricted to valley cavity nests. P. hirundo was collected primarily from cliff swallow nests under cliff overhangs (site 4). The only other nests infested by this species were those of 10 bank swallows in a colony near cliff overhangs. Until more nests of other bird species in nest site 4 are examined, it is not possible to determine whether this species is host specific or merely has narrow host preferences.

Table 4. Bird hosts of each species of Protocalliphora by habitat

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined[a] 1	2	3	4	5	6	7	8	9	10
aenea													
dipper	3	2	2		2/3								
Total			2		2								
asiovora													
blackbird, Brewer's	158	43	16					0/2	1/18		3/53		12/73
crow, common	2	2	2					2/2					
dove, mourning	5	1	1		0/1			1/1	0/1				0/2
eagle, golden	3	2	2					1/1					1/2
hawk, Cooper's	6	1	1	1/7									
hawk, ferruginous	17	14	14					1/1					13/8
goshawk	7	3	3	3/7									
hawk, red-tailed	8	7	7	1/1	1/1		1/1	2/2					2/3
hawk, Swainson's	2	2	2					2/2					
magpie, black-billed	141	128	128		11/11			110/122	1/1		4/5		2/2
owl, long-eared	1	1	1		1/1								
raven, common	7	6	6									2/2	4/5

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined[a] 1	2	3	4	5	6	7	8	9	10
asiovora (continued)													
robin	109	28	11	0/29	4/42			6/19	0/14				1/4
Total			194	5	17		1	125	2		7	2	35
chrysorrhoea													
sparrow, house	18	5	2					0/3				2/13	
swallow, bank	125	98	95							95/125			
swallow, barn	392	121	1									1/273	0/1
Total			98							95		3	
"gigantia"													
flicker, red-shafted	4	2	1			1/2				0/2			
goshawk	7	3	1	1/7									
hawk, red-tailed	8	7	2	1/2	0/1		1/2	0/2					0/3
hawk, sparrow	27	9	2							2/24		0/1	0/2
Total			6	2		1	1			2			
hesperia													
finch, Cassin's	2	1	1	1/2									
robin	109	28	11	5/29	4/42			1/18	1/14				0/4
sparrow, chipping	3	1	1		1/3								
unknown	1	1	1		1/1								
Total			14	6	6			1	1				

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined[a] 1	2	3	4	5	6	7	8	9	10
hirundo													
swallow, bank	125	98	10							10/55			
swallow, barn	392	121	3									3/27	
swallow, cliff	208	135	135				111/163					24/56	
Total			148				111			10		27	
hirudo													
blackbird, Brewer's	158	43	3					0/2	0/18		1/53		2/73
blackbird, yellow-headed	213	110	1								1/138		
magpie, black-billed	141	128	2					1/110	1/1				
starling	33	23	2			0/2				2/21			
wren, house	33	21	4			4/30				0/2			
wren, long-billed marsh	7	5	1								1/7		
Total			13			4		1	1	2	3		2
sialia													
blackbird, Brewer's	158	43	1					0/2	0/18		0/53		1/73
bluebird, mountain	9	4	4			1/4				3/5			
hawk, sparrow	24	9	7							7/24			

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined[a] 1	2	3	4	5	6	7	8	9	10
sialia (continued)													
kingbird, western	2	1	1					1/2					
martin, purple	6	6	1			1							
owl, flammulated	1	1	1			1/1							
owl, great horned	5	1	1	0/2				1/2					0/1
phoebe, Say's	5	3	1									0/1	1/4
raven, common	7	6	1									0/2	1/5
robin, common	109	28	2	1/29	0/42			1/18	0/14				0/4
sparrow, house	18	5	2					0/3				2/13	
starling	33	23	24				1/2			23/21			
swallow, bank	125	98	2							2/125			
swallow, violet-green	3	2	1							1/2			
swallow, barn	392	121	7									6/273	1/1
swallow, cliff	208	135	4				4/139					0/53	
swallow, tree	22	17	8			8/19							

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined: 1	2	3	4	5	6	7	8	9	10
sialia (continued)													
wren, house	33	21	3			3/30				0/2			
Total			71	1		14	5	3		36		8	4
sp. II													
Empidonax sp.	8	6	6	0/1	4/5						2/2		
goldfinch, American	5	2	2		2/3				0/2				
kingbird, eastern	6	2	2					0/1	2/4		0/1		
kingbird, western	2	1	1					1/2					
pewee, wood	7	5	5	5/6	0/1								
robin	109	28	1	0/29	1/42			0/18	0/14				0/4
swallow, barn	392	121	1									1/273	0/1
warbler, Audubon's	2	1	1	1/2									
warbler, yellow	10	7	7	1/2	2/3			4/6					
Total			26	7	9			5	2		2	1	
sp. III													
blackbird, Brewer's	144	43	8					0/2	2/18		0/53		6/73
blackbird, red-winged	85	17	2						1/37		1/40		

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined: 1	2	3	4	5	6	7	8	9	10
sp. III (continued)													
bunting, lazuli	5	1	1		0/1				1/4				
sparrow, fox	5	2	2		2/5								
sparrow species	9	3	2		1/8				0/1	1/1			
Total			15		3				4	1	1		6
sp. IV													
phoebe, Say's	5	3	3									0/1	2/4
swallow, barn	392	121	114									114/273	0/1
Total			116									114	2
sp. V													
blackbird, Brewer's	158	43	10					0/2	0/18		10/53		0/73
blackbird, redwinged	85	17	9						0/37		9/40		
blackbird, yellow-headed	213	110	119								119/138		
wren, long-billed marsh	7	5	5								5/7		
Total			138								138		

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined: 1	2	3	4	5	6	7	8	9	10
sp. VI													
chickadee, black-capped	5	5	5			5/5							
chickadee, mountain	8	5	5			5/8							
junco, Oregon	4	2	1		1/4								
wren, house	33	21	16			16/30				0/2			
Total			27		1	26							
sp. VII													
blackbird, redwinged	85	17	1						1/37		0/40		
robin	109	28	6	0/29	6/42			0/18	0/14				0/4
sparrow species	9	3	1		1/8				0/1				
Total			8		7				1				
sp. VIII													
martin, purple	6	6	5			5/5							
swallow, barn	392	121	1									1/273	0/1
swallow, cliff	208	135	4				4/139					0/53	
swallow, tree	22	17	10			10/19							
swallow, violet-green	3	2	1				1/1			0/1			
Total			21			15	5					1	

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined[a] 1	2	3	4	5	6	7	8	9	10
sp. X													
blackbird, Brewer's	158	43	3					0/2	0/18		0/53		3/73
swallow, barn	392	121	1									1/273	
Total			4									1	3
sp. XII													
blackbird, Brewer's	158	43	15					0/2	0/18		15/53		0/73
blackbird, redwinged	85	17	5						1/37		4/40		
blackbird, yellow-headed	213	110	2								2/138		
sparrow species	9	3	1		0/8				1/1				
Total			23						2		21		
sp. XV													
vireo, warbling	11	1	1	0/1	1/9				0/1				
Total			1		1								
undetermined													
flicker, red-shafted	4	2	1			1/2				0/2			
hawk, Cooper's	6	1	1	1/7									
junco, Oregon	4	2	1		1/4								
sparrow, white-crowned	6	1	1		1/6								

Table 4. Continued

Protocalliphora sp. bird species	Total nests of this bird examined	Total nests of this bird infested	Number infested by this species	Number of nests infested by this species / Total nests examined: 1	2	3	4	5	6	7	8	9	10
undetermined, (continued)													
swallow, bank	125	98	1							1/55			
swallow, tree	20	17	1			1/19							
warbler, species	2	2	1		1/1								
wren, house	33	21	1			1/30				0/2			
Total			8	1	3	3				1			

[a]1. mountain arboreal
2. mountain shrub
3. mountain cavities
4. mountain overhang
5. valley arboreal
6. valley shrub
7. valley cavity
8. valley marsh
9. valley structural
10. valley desert

Several species of Protocalliphora appear to be specific to certain bird groups, including P. "gigantia",[1] sp. II, sp. VI, and sp. VIII. P. "gigantia" was almost always restricted to the nests of Falconiformes, regardless of habitat. P. sp. II was found in a variety of nest sites, but was collected primarily from the nests of flycatchers and warblers. This was the only species infesting warblers and flycatchers, though other species were present in the area near their nests. P. sp. VI was usually restricted to the cavity nests of house wrens and chickadees. P. sialia and P. sp. VIII infested cavity nests of swallows in the same area as P. sp. VI, but only on three occasions did P. sialia infest wren nests, and P. sp. VIII never was found in wren or chickadee nests. P. sp. VIII infested cavity and open nests of swallows, but did not occur in other bird groups.

Three species of Protocalliphora (sp. V, sp. XII, and sp. IV) appeared to infest specific nest sites. Sp. V was found only in marsh habitats where it commonly infested nests of yellow-headed blackbirds. Sp. XII was also found around marsh habitats, usually toward the periphery, where its hosts were yellow-headed blackbirds, Brewer's blackbirds, and red-winged blackbirds. P. sp. IV was collected primarily under bridges from barn swallow nests, but it was not found in 63 cliff swallow nests under bridges (Table 3). This species may be somewhat host specific to barn swallows, but nests of different birds in stream habitats need to be examined before reaching this conclusion.

The distribution of some species of Protocalliphora appeared to be affected by both host and nest site preferences. P. asiovora was

[1] The species P. "gigantia" has not been formally described.

collected from eight nest sites and numerous hosts; however, it was never found in nests of some birds or in certain areas. It never infested the nests of small passerines, such as flycatchers, warblers, sparrows or swallows, and never was found in a cavity nest. P. asiovora was the primary species in corvid nests and only it and P. gigantia infested falconiform nests. P. sialia occurred in both cavity and open nests in a wide variety of bird species, but it was never found in the marsh habitat (site 8). P. hesperia Shan. and Dob. was found in three nest sites and three bird species' nests, although it commonly infested only robin nests. Records of it from a nest of a Cassin's finch and chipping sparrow indicate that it may also infest various small passerines. P. hirudo Shan. and Dob., a subcutaneous species, appeared to have no distinct host or site preferences, although most records of this species are from nests less than 5 feet above the ground. Nest site and host preferences of species of Protocalliphora are summarized in Table 5.

Mixed infestations

Mixed infestations of Protocalliphora occurred in 7.1% of the 869 nests examined (Table 6). Many Brewer's blackbird nests had mixed infestations. They were infested by seven species of Protocalliphora, but no one species occurred regularly in their nests. Robins also were infested by many species of Protocalliphora, including several which occurred in mixed infestations. Each of five species of swallows (Table 6) was regularly infested by a specific parasite. Most of the mixed infestations in these birds were the result of one swallow parasite "crossing over" to the nest of another swallow species. The remaining bird

Table 5. Summary of Protocalliphora species collected and their primary host and preferred nest sites

Protocalliphora species	Preferred nest sites (in parentheses)	Major hosts	Comments
aenea	two nests collected under bridge over mountain stream (2)	dippers	collected from many bird species in the east
asiovora	widespread, from high mountains to desert (1,2,5,8,10)	Corvids and Falconiformes	absent from cavity nests; also not found in nests of swallows, warblers, flycatchers and some other small passerines
chrysorrhoea	cavities in dirt banks (7)	bank swallows	rarely collected from other bird hosts, apparently specific to bank swallows
hesperia	forested areas in mountains (1,2)	robins	though seemingly less common in valleys (sites 5-10) fewer nests of the preferred hosts were collected there. Probably infests a variety of small passerine birds
hirudo	cavity and open nests (3,7,8,10)	blackbirds, starlings, wrens	rarely collect, this subcutaneous species probably infests a variety of hosts
hirundo	cliff overhangs (4)	cliff swallows	appears to favor cliff swallows though 4 of 8 bank swallow nests near cliff overhangs were infested by this species
"gigantica"	cavity and open nests	Falconiformes	not collected from hawk nests in the desert (site 10), not present in owl nests, present in a flicker nest which closely resembles that of a sparrow hawk
sialia	cavity and open nests, widespread (3,4,5,7,9,10)	starlings, mountain bluebirds, tree swallows	more widespread than P. asiovora, infesting nests in a wide variety of habitats, notably absent from the marsh (site 8)

Table 5. Continued

Protocalliphora species	Preferred nest sites (in parentheses)	Major hosts	Comments
sp II	widespread in open nests (1,2,5,6,8,9)	warblers, flycatchers	virtually the only species found in warbler and flycatcher nests, not found in cavities or desert habitats
sp III	in dry and moist habitats (6,10)	Brewer's and red-winged blackbirds	rarely collected; but present data indicates widespread distribution, usually in nests less than 5 feet above the ground
sp IV	under bridges (9)	barn swallows	common in barn swallow nests under bridges, probably more widespread than present data indicate
sp V	marsh (8)	blackbirds, marsh wrens	found in most marsh-nesting passerines, very common in yellow-headed blackbirds
sp VI	mountain cavity nests (3)	house wrens chickadees	never collected from nearby cavity nests of tree swallows, bluebirds, and starlings; probably also occurs in the valleys (sites 5-10) in the nests of favored hosts
sp VII	in forests (2)	robins	rarely collected; probably infests small passerines
sp VIII	cavity and open nests (3,4)	swallows only	taken from all of the swallows except the bank swallow, no other known hosts
sp X	dry habitats (10)	Brewer's blackbirds	rarely collected
sp XII	marsh habitats (8)	Brewer's and red-winged blackbirds	usually collected from peripheral marsh habitats, while sp V favored nests in central marsh habitats
sp XV	forest (2)	warbling vireos	from single nest

Table 6. Occurrence of mixed infestations of species of Protocalliphora in bird nests

Bird species	Usual parasite	Total nests infested by usual parasite	Number of nests with mixed infestations									
			asiovora	gigantia	hesperia	hirudo	hirundo	sialia	Sp. VIII	Sp. III	Sp. X	Sp. XII
blackbird, Brewer's	asiovora	43				3		1		3	2	2
	Sp. V		1									4
blackbird, yellow-headed	Sp. V	110										1
goshawk	asiovora	3		1								
hawk, red-tailed	asiovora	7		2								
magpie, black-billed	asiovora	128				2						
robin	hesperia	28	2									
	Sp. VII		1		1							
	asiovora							1				
starling	sialia	23						2				
swallow, bank	chrysorrhoea	105					10	1				
swallow, barn	Sp. IV	121				1	2	1	1		1	
swallow, cliff	hirundo	135						4	5			
swallow, tree	Sp. VIII	17						3				
wren, house	Sp. VI	21				3						
wren, marsh	Sp. V	5				1						
Total			4	3	1	10	12	13	6	3	3	7
Total nests with mixes infestations		62										
Percent of total infestation		$\frac{62}{869^a} \times 100 = 7.1\%$										

[a]From total in Table 3.

species listed in Table 6 usually were infested by a single species, and mixed infestations in their nests appeared to be incidental and uncommon. Only one species (P. hirudo) regularly occurred in mixed infestations. This subcutaneous species never infested any bird regularly, but it was the only species which occurred in magpies and starlings, other than their usual parasites, P. asiovora and P. sialia, respectively.

The observed low frequency of mixed infestations appears to be the result of selectivity by the adult fly. Bennett (1957) considered the possibility that larvae could not survive in the nests of hosts other than their own. He reared the larvae of several eastern species of Protocalliphora on bird hosts they did not normally infest in nature and found no reduced survival. I reared 20 P. sp. V and 40 P. sialia on nestling bank swallows and magpies, respectively, and they seemed to develop normally. Their usual hosts are blackbirds (P. sp. V) and starlings and other cavity nesters (P. sialia). Thus, larval specificity does not appear to prevent their maturity on other than normal hosts. This further supports the idea that the low number of mixed infestations is a result of adult selectivity.

Life History

Egg stages

Most viable Protocalliphora eggs were obtained from gravid field-collected females (early in my work a laboratory-reared P. asiovora laid viable eggs; however, this was never repeated). Eggs were obtained from two species (P. asiovora and P. chrysorrhoea). A female P. asiovora was captured in the vicinity of a magpie nest and placed in a small, capped vial. Within 1.5 hours she had laid 76 eggs. The eggs were scattered randomly and attached securely to the vial. The eggs were examined and breathed on at 24 hour intervals, since breathing on eggs will hatch the eggs of some Diptera (e.g. Cuterebridae). At 72 hours, breathing on the eggs stimulated hatching in most of them. Another female P. asiovora was captured in the field, but failed to lay eggs. Dissection after its death revealed 37 mature eggs.

A female P. chrysorrhoea was captured and placed in a plastic vial furnished with diluted honey and liver. It was observed laying eggs 32 hours later (2200 hours); it laid a total of 50 eggs. Unlike P. asiovora, eggs were deposited in clumps, and a number of eggs were inserted under a small watering vial placed with the fly. At 24 hours, the eggs were breathed on and exposed to warmth (sunlight), but no hatching occurred. At 38 to 43 hours, the eggs hatched without any special stimulus. Dissection of the fly upon its death revealed an additional 25 developed eggs. These limited data indicate that the incubation period of eggs is shorter in P. chrysorrhoea than in P. asiovora.

Three aditional P. chrysorrhoea were captured and fed the same diet as the above mentioned fly. Though they lived 5-7 days, none oviposited. Dissections showed two contained slightly over 100 mature eggs each and a third had 40 mature eggs. Six more female P. chrysorrhoea were captured and dissected immediately. Four had 77-104 developed eggs and two had undeveloped eggs. A single P. hirundo was also captured and dissected, but its eggs were undeveloped. Thus, in P. asiovora and P. chrysorrhoea, it appears the maximum number of eggs produced at one time is 100. Dissection revealed three immature eggs attached to each mature egg, which indicates a maximum fecundity of about 400 eggs.

Larval stages

The larval stage of Protocalliphora was composed of two distinct types of larvae, the younger feeding larvae and the older, more sedentary, non-feeding prepupal stage (Bennett, 1957). Prepupae were identified as those large larvae with little or no blood in their crop.

The length of the larval developmental period was determined by observing the time from the first instar to the prepupa. Young larvae were obtained from nests in the field, and the time required for them to reach the non-feeding pre-pupal stage was determined. The exact ages of these larvae were unknown, but by comparing their size with that of newly hatched larvae from the laboratory, age estimates were made accurate to about 24 hours. These data are tabulated for five species of Protocalliphora (Table 7) and indicate that those species with larger larvae have longer developmental periods, as would be expected. P. chrysorrhoea, with the largest larvae (16-17mm)[1] of those studied, had the longest developmental period. P. asiovora, P. sialia, and sp. VI, each somewhat smaller (13-15mm), had shorter rates of development. P. sp. V, by far the smallest (7-9mm), had the shortest developmental period of the species studied. Larvae with short developmental periods often tend to infest nestlings which spend a shorter time in the nest. This is most obvious at the extremes where the host of P. chrysorrhoea, the bank swallow, has a 21-day nestling period, whereas the host of P. sp. V, the yellow-headed blackbird, fledges after 10 days. Considering the

[1]Measurements made on mature larvae which had been killed in K.A.A. Five larvae of each species were measured.

Table 7. Duration of larval, prepupal, and pupal periods of species of Protocalliphora

Protocalliphora species	Substitute host	Number of larvae and pupae	Length of[a] larval development (in days)	Prepupal period (in days)	Pupal[b] period (in days)	Total developmental period (days)
asiovora	magpie	32	7-8	3-4	10-11	20-23
chrysorrhoea	bank swallow	35	9-10	3-4	10-11	22-25
sialia	Brewer's blackbird	18	7-8	2-3	14-15	23-26
Sp. V	Brewer's blackbird	25	5-6	1-2	9-10	15-18
Sp. VI	Brewer's blackbird	20	6-7	3-4	12-13	21-24

[a]Larvae for this study were obtained from nests in the field and their ages were estimated, see the text for further discussion.

[b]Maintained at a temperature of 72 ± 3°F, relative humidity for 38 - 35%, and a photoperiod of LD 15-9.

probable time lag between hatching of nestlings and oviposition by the adult fly, as well as the time required for Protocalliphora eggs to hatch, most larger species of Protocalliphora would not reach maturity in yellow-headed blackbird nests before the young fledged.

Larval feeding habits

The literature on Protocalliphora larvae indicates that they spend most of their time in the nests (except P. hirudo) and occur on the nestlings only when feeding. However, my observations on P. asiovora, P. chrysorrhoea, and P. sialia indicate that at least some larvae spend much of their developmental period on the nestlings. The larvae of all three species have been observed in auditory and nasal cavities of nestlings. The presence of these larvae is often indicated only by the scab-like accumulations of larval excreta around cavity openings. In heavily infested nests, the nestlings often have many small larvae attached along the rear edge of their wings. They are usually wedged between the feather sheaths or between the folds of skin on the ventral side of the antebrachium (forearm). Since young birds do not flap their wings, these larvae are apparently quite secure and have been observed to remain in the same position for several days. As the nestlings mature and begin flapping their wings at feeding, this location becomes less secure, although smaller larvae can maintain their position. It is quite possible that larval survival is enhanced by their finding a secure location on the nestling and obtaining several blood meals before returning to the nest proper.

Older nestlings begin standing in the nests and, therefore, are less "available" to the larvae. At this time, larval feeding is concentrated on the nestling's naked lower abdomen, which becomes covered with scabs in heavily infested birds. Heavy feeding is usually less evident in younger nestling birds, because of the more scattered distribution of feeding spots. In addition, although blood wells up after a larva stops feeding, the resultant scab soon flakes off, leaving little evidence of blood-sucking. Only when repeated feeding occurs in the same site do feeding spots become conspicuous. Feeding spots caused by _Carnus hemapterus_ in magpies, starlings, and kestrels may also be conspicuous in heavily infested nestlings. Feeding by _C. hemapterus_ usually is most concentrated under the wings, and the whole undersurface may become covered with dried blood.

Pupae

Many of the _Protocalliphora_ collected in this study were in the pupal stage, since nests usually were examined after the young had fledged. Pupae were usually found in the cup of the nest, but in the flimsy nests of birds such as those of mourning doves and sparrow species, larvae often fell to the ground to pupate. Neff (1945) made numerous observations on _Protocalliphora_ on dove nests and, although many were infested, he never found pupae in the nests. Larvae infesting chickadee, wren, and warbler nests often wound themselves up in the nest material before pupating, forming a sort of "cocoon." Larvae of _P. hirundo_ often burrowed into the mud of cliff swallow nests before pupating. The precise function of such behavior (if any) is unknown, but it probably affords the pupae some protection from predators or parasites.

High temperatures were found to shorten the pupal developmental period, and high humidity greatly increased the number of adults emerging from puparia, as was also observed by Bennett (1957). The pupal period was determined for five species of Protocalliphora under controlled conditions (Table 7).

Adults

As discussed earlier, several gravid adults were captured in the field. However, caged females, reared from pupae taken in the field, very rarely contained mature eggs. Bennett (1957) provided caged adults with a variety of diets in an effort to stimulate ovarial development, but none laid fertile eggs.

Since it was generally thought that Protocalliphora overwinter as adults (Bennett, 1957), it was decided to test the effect of a cold period on ovarial development. Initially, adults obtained during midsummer were placed directly into a cooler for a two-month period at 46°F after feeding, watering, and mating had occurred. However, these flies suffered high mortality, and the ovaries were undeveloped in the few adult females which survived. The fact that the adults were not acclimatized before cooling probably accounted for much of the mortality observed.

In another experiment, about 50 adults of sp. VIII, collected as pupae July 23, 1972, were retained out-of-doors in a cage until October 28. Several females were dissected during this interval, but none were gravid. On October 28, about 15 adults were still alive, and sawdust was placed in the cage to serve as some protection from the elements. This cage was left outside, fully exposed to the elements, through the winter of 1972-73, when temperatures dropped to -20°F. On March 8, 1973, when the high was 44°F, three adult Protocalliphora were seen moving about in the cage (two males, one female). Dissections of the female showed that no ovarial development had occurred. However, this study did show tha Protocalliphora could overwinter as adults.

One possibility that has not yet been tested is whether ovarial development is prevented by some kind of behavioral inhibition. All adults reared to-date have been kept in relatively small cages and exposed to a simple environment. Perhaps if some flies were released into an environment-controlled greenhouse where conditions resembled the field, ovarial development would occur.

The adults of most species of Protocalliphora are rarely observed in the field. However, in bird species which are colonial and experience a high rate of infestation (i.e., bank and cliff swallows), adults can usually be observed around the colony. Since bank swallows were studied in detail, P. chrysorrhoea was observed on numerous occasions in the field.

During the day, some adults were usually seen resting on the vertical wall above the nest cavities. Early in the season, before adult Protocalliphora had developed in the bank swallow nests, most of the adult flies around the colony were gravid females, and adult males were uncommon (P. chrysorrhoea requires 22-25 days from larva to adult, Table 7). Later in the season, newly emerged flies of both sexes were observed in abundance near the nests early in the morning. By mid-day, most of these flies were gone, with only a few gravid females seen around the nests. Gravid females seemed most active at temperatures exceeding 80°F. Then they could be seen making short hopping flights from one burrow to another. They would usually land near the edge of a nest cavity, hesitate, then walk or fly into the burrow. Adults were observed entering burrows on many occasions, but attempts to observe the behavior of flies in the nest with a flashlight usually failed, since adults would fly out immediately. On one occasion, an adult was observed in a nest, walking from one nestling to another while dipping its abdomen. Eggs were laid on several nestlings in small clumps and were attached to the feathers. No eggs were found deposited on the nest material.

PART II

THE EFFECT OF SPECIES OF *PROTOCALLIPHORA* ON BLOOD LEVELS AND WEIGHT GAINS OF SPECIES OF NESTLING BIRDS

REVIEW OF LITERATURE

A preliminary review of the literature led to the selection of weight gain and blood values as parameters to be measured for monitoring the effects of larval feeding upon nestling birds. Two host species, the black-billed magpie and the bank swallow, were selected for detailed study. A search of the literature for information on weight gains in nestling magpies revealed only one report. Linsdale (1937) cited a brief study by Heinroth and Heinroth (1927) in Germany, in which two magpies were weighed 11 times between hatching and fledging. The lack of precise information necessitated basic weight gain studies on magpies. Later, this technique was dropped because it was very time-consuming and less sensitive to the effects of larval feeding than measures of blood levels. Therefore, rates of weight gain were measured only in magpies.

A variety of measurable blood parameters have been described in the literature. Lucas and Jamroz (1961) provided a thorough review of these factors, based on their study of the domestic chicken. Measurable blood values include: (1) hemoglobin levels, (2) hematocrit level, (3) erythrocyte numbers, (4) erythrocyte dimensions, (5) reticulocyte numbers, (6) leucocyte numbers, (7) differential leucocyte counts, and (8) Arneth counts. Each of these blood values was considered for use. Hemoglobin and hematocrit finally were selected, because samples could be obtained easily in the field. They also required little blood volume and the samples could be analyzed quickly.

A number of factors may affect hemoglobin and hematocrit values. These include: sex, age, season, elevation, laying condition, time of day, parasites, and disease. These factors have been studied much more extensively in domestic birds than in wild birds. Unfortunately, most such studies have dealt with adult birds, rather than with nestlings.

In most adult birds, there is a distinct sexual dimorphism in blood values, those of the male being slightly above those of the female. Large sexual differences (males and females had hemoglobin levels of 13.5 and 9.7g per 100cc and hematocrits of 40 and 31% respectfully) were found in white leghorns (Lucas and Jamroz, 1961). Much smaller differences were observed in a variety of wild passerines (Bennett and Chisholm, 1964). Little is known of the sexual differences in blood values (if any) in nestling birds. Sexes of most species of nestlings cannot be distinguished without dissection. The small standard deviations of nestling blood values observed within age groups in the bird species studied indicate differences are probably small.

Age also affects blood values, younger birds tending to have the lowest blood values. In altricial species, blood values are lowest at hatching and rise to adult values shortly after fledging. In the house sparrow, Bush and Townsend (1971) found that the hemoglobin and hematocrit levels rose steadily from 4g per 100cc and 20% at hatching to 14g per 100cc and 40% at 50-80 days. The red-winged blackbird had a similar steady rise, but blood values approached the adult level at 10 days of age, when the young fledged (Ronald, et al., 1968). It would, therefore, seem very important to determine the age of nestlings from which blood values are taken.

Season and reproductive state have been found to influence blood values in adult birds (Riddle and Braucher, 1934). However, they are of little importance in nestling birds (Ronald, et al., 1968).

Time of day may also be a factor affecting blood values. However, little work has been done on circadian rhythms of blood values in birds. A study of chickens revealed slight variations in hematocrits, the highest values being at midnight and the lowest around noon (Domm and Taber, 1946). These minor differences probably were not important to this study.

Blood values may also vary with elevation. McGrath (1971) compared the blood values of pigeons at sea level and a simulated elevation of 20,000 feet. He found the pigeons maintained at the higher altitude had somewhat higher blood values. However, the birds examined in the present study were from sites differing by, at most, a few thousand feet. Therefore, the effects of elevation on bird blood values are probably minimal.

The possible effects of disease and parasites on the blood values of birds were important, especially since I was interested in determining the effect of blood-sucking on the blood values of nestlings. However, surprisingly little information is available concerning this problem. Riddle and Braucher (1934) noted that "diseased" pigeons had substantially lower hemoglobin and red blood cell levels. Barlow (1927) found that pigeons with beri beri had hemoglobin and red blood cell counts 25% below normal.

The impact of blood-sucking ectoparasites on their hosts has been studied by several authors. Jellison and Kohls (1938) found that the wood tick (Dermacentor andersoni) caused severe anemia in rabbits. Hematocrits dropped from a normal 37% to a low of 8% just before death, when rabbits were exposed to large number of ticks. Moss and Camin (1970) studied the effect of blood-sucking mites on nestling purple martins (Table 3) and found that mite-feeding reduced nestling weights significantly. More recently, an excellent study was conducted by Chapman (1973) on the effect of swallow bugs (Oeciacus vicarius, Hemiptera: Cimicidae) on nestling cliff swallows. He found that feeding by this parasite affected fledging success, nestling mortality rates, and overall productivity in cliff swallows. He also observed a significant reduction in hemoglobin and hematocrit levels in infested nestlings.

The possibility that some internal parasites of nestlings might reduce blood levels was also considered. Clark (1966) found a variety of protozoan blood parasites in the yellow-billed magpie (Table 3). Possible pathogenicity of these parasites was not discussed, although he noted adults and nestlings had about equal numbers of parasites, and 99% of the birds had some parasites. Todd and Worley (1967) found black-billed magpies infested with several species of helminth parasites. They found helminths in 32% of the juveniles and 98% of the adults, but apparently observed no pathogenic effects caused by these parasites.

Sato (1960) observed the hematocrits of hen chickens with a variety of diseases. Those with visceral lymphomatosis, pullorum disease, blackhead, and coccidosis had hematocrits above normal. Those heavily infested with ascrids and cestodes had substantially lowered hematocrits.

METHODS

Nest Collections

The technique used for locating and examining bird nests was discussed in Part I Methods. However, in most of those nests, the young were allowed to fledge before larvae were removed. In the mortality studies, it was necessary to examine the nests while the nestlings were present. It also was desirable that the birds examined have a high rate of infestation and that their nests be abundant enough to provide a good sample. The nests of cliff and barn swallows were common and had a high infestation rate, but they were difficult to enter without destroying them. Cliff swallow nests had to be partly destroyed, simply to gain access to the nest proper. In barn swallows, a larval count could not be made without damaging the cup of the nest. Magpies and bank swallows finally were selected for intensive study. These birds were common and their nests were easily accessible. In addition, they experienced a very high rate of infestation. Some data also were gathered on starlings, but their nests were more difficult to find in large numbers. Information was also obtained on yellow-headed blackbirds and kestrels, which were fairly common, but experienced relatively low infestation rates.

Studies on the effect of Protocalliphora species on nestling birds consisted of two parts: 1) early efforts involved the weighing of nestlings and determining rates of weight gain; 2) later studies involved blood sampling of birds.

Nestling Weights, Identification and Aging

In the weight-gain studies, nestlings were weighed in the field to the nearest 0.1 gram on an Ohaus triple beam, balance scale. Nestlings were squeezed gently, which usually caused them to egest before weighing. Individuals were distinguished by color bands affixed to their legs. Initially, thread and rubber bands were used for leg bands, but they caused a serious constriction of the growing nestlings' legs. Finally, cut and shaped large fluffy pipe cleaners were found to make very good color bands. These were easily placed on the legs of young and the fuzzy material kept the bands tight, without causing constriction. However, when they were placed on birds too young to draw their legs under them, the nestlings usually were thrown from the nests by the adults. Birds were aged by measuring the length of the primary feather nest to the distalmost feather on the left wing and comparing this measurement to that of nestlings of known ages. Only the feather sheath (Pettingill, 1970) was measureable in very young birds. In older birds, when the rachis began to develop, only the exposed portion of the primary feather was measured.

Blood Sampling

Blood for analysis was collected from nestlings via the brachial vein, where it crosses the humerus on the underside of the wing (Bennett, 1970). In older birds, it was necessary to pluck some of the feathers around the vein to make it accessible. The vein was pricked with a number 1 insect pin. The pin was mounted in a cork and kept in alcohol when not in use.

After the brachial vein was pricked, blood flowed freely for a short time, after which a large embolism formed. This usually prevented further sampling for at least a day. When the blood was removed frequently from this region, it became heavily scarred and it was necessary to alternate wings for sampling.

Often, it was impossible to obtain blood from the veins of very young birds, in which case sampling was done by heart puncture with a five-eighths inch, size 23 hypodermic needle (Fisher Scientific, Chicago, Illinois). The needle was inserted into the heart via the top of the sternum, below the trachea. This type of sampling seldom caused nestling mortality. Initially, the anticoagulant, sodium oxalate (5% solution in 0.9% NaCl) was used to prevent coagulation, but it caused severe hemolysis of the blood sample. When heparinized vials (10 ml) were substituted, hemolysis was substantially reduced (Vials were prepared with 143 USP units of lithium heparin by BD Products, available from Van Waters, Salt Lake City, Utah). In some young birds, blood was obtained from a vein on the leg, where it crosses the front of the tarsometatarsus. This vein sometimes yielded more blood than the brachial vein, but, in older birds it was difficult to find, as the skin in that region is thick and scaly.

For hematocrit samples, 80-90 lambdas of blood were drawn directly into a Dade 100 lambda heparized microhematocrit tube. Tubes were kept in a cooler in the field to prevent hemolysis. Failure to keep the samples cool resulted in severe hemolysis in three to four hours at field temperatures of 80°-100°F. Samples were kept up to two days under refrigeration, with minimal hemolysis; however, it was best to run samples as soon as possible after withdrawing blood. Hematocrits were determined in the laboratory by heat-sealing one end of the tube, and spinning at 10,500 RPM's in an International Microhematocrit centrifuge. Hematocrits were determined by measuring (in mm) the amount of solid material, including erythrocytes and leucocytes, as compared to the amount of clear plasma (Johnston, 1955). The hematocrit is expressed as the percentage of the solid material in relation to the total length of the blood column. When hemolysis occurred, the normally clear plasma was cloudy and the solid portion of the sample was reduced, thus lowering the hematocrit readings.

Blood samples for hemoglobin analysis were taken directly from a hematocrit tube as soon as the sample was drawn. A Spencer Hemoglobinometer (American Optical, Model 1010D, available from Van Waters, Salt Lake City, Utah) was used to measure hemoglobin levels. Only a small drop of blood was required. This was stirred with a hemolysis stick (furnished by the manufacturer), which ruptured the blood cells. It was necessary to stir the drop thoroughly for about 60 seconds to achieve complete hemolysis. When hemolysis was complete, the droplet took on an identifiable transluscent appearance. The hemoglobin level was read by comparing the light absorption of the blood sample to a standard scale. It was found that readings could be made to the 0.10 level of accuracy, if done in subdued light. This technique was useful for field work with birds, because it required very little blood and could be completed immediately.

Quantifying Nest Material

In experiments with bank swallows, it was desired to determine the amount of feathers in each nest. Since feathers weigh so little per unit volume, it was decided that volumetric measurements would be most accurate. Feather volumes were measured in a jar 65mm in diameter and 160mm in height. The jar was calibrated with known volumes of water, and graduations were marked with a waterproof ink marker. Feathers were compressed to eliminate large air pockets before measuring.

Statistical Methods

The T-test for differences in means was used to determine whether significant differences existed between experimentals and controls. When testing for possible relationships between parameters, the correlations coefficient was used (Dixon and Massey, 1969).

The statistic used for calculating minimum normal blood levels was the tolerance limit (K), tabulated in Ostle (1963). The value of K is based on the sample size. By multiplying K times the standard deviation of the controls and subtracting this value from the mean for the control $[\bar{x} - (S.\ D.)(K)]$, a minimum normal blood value was obtained. This value was calculated for several age groups for hematocrit and hemoglobin of each bird species (see Appendix, Table 31). Any nestlings found with blood values below the calculated minimum normal were considered sick.

Models of hemoglobin and hematocrit for magpies and bank swallows were constructed by multiple regression. The importance of model elements was determined by stepwise regression (Ostle, 1963).

RESULTS AND DISCUSSION

Studies of the impact of larval feeding by Protocalliphora upon nestling birds were conducted during the summers of 1973 and 1974. A primary objective was to determine if high natural populations of larvae contributed to reduced survival rates in nestlings. It was also of interest to determine the effect of larval feeding upon blood levels and rates of weight gain, though weight gain studies were limited to nestling magpies.

Controls

The five species of birds selected for detailed study were magpies, bank swallows, starlings, yellow-headed blackbirds and kestrels. Control data were collected on several parameters for each species, including: 1) length of the second primary (counted from the wing tip,[1] 2) hematocrit level, and 3) hemoglobin level (see Appendix, Tables 25-29). Control data on weight gains in magpies were also gathered (Table 30, Appendix). Where nestling feather length was measured, the ages of the host individuals were known and age and feather length could be related. These data were used to estimate the age of nestlings, where exact ages were not known. In such nests, feather lengths of each bird were taken and these values converted to age. In this way, age data were obtained on all birds from which blood samples were taken.

---

[1]This is either primary number 8 or number 9, depending upon the bird species.

Some difficulties were encountered in obtaining control nests for blood values. I planned to use uninfested nests as controls. However, magpies, bank swallows, and starlings have very high rates of infestation and uninfested nests were not common. Initially, the use of a pesticide to "clean" the nests was considered, as was done by Chapman (1973) in cliff swallow studies. However, I wanted to eliminate only the effect of Protocalliphora and a pesticide would also destroy other hematophagous insects in the nests, thereby confounding the results. Therefore, some effort was made to remove larvae by hand. But, unless nests were regularly cleaned, new populations developed, which in some cases exceeded original population densities. Fortunately, natural larval populations varied considerably and a number of nests had so few larvae (10 or fewer) that their effect could be considered negligible. When data from these nests were combined with that from uninfested nests, a sizable control population was obtained for each bird species.

The Effect of *P. asiovora* on the Survival of Nestling Magpies

Detailed studies were conducted on magpie nests during the summers of 1973 and 1974. Thirty-seven nests were studied extensively during 1973 and 87 nests during 1974. Ninety-one percent of the magpie nests examined were infested by P. asiovora (Table 3), and my primary objective was to determine the impact of this species upon nestling magpies.

Data gathered on magpies included the number of eggs laid, the number hatched, the number surviving to 10 days, and the number fledging (Tables 32 and 33, Appendix). Data also were collected on the number of

Protocalliphora larvae in each nest. During 1973, rates of weight gain also were determined for nestlings in several nests and blood samples were gathered from nestlings in most nests during 1974.

In 1973, 182 (82%) of the 223 eggs laid by magpies hatched. Ninety-four percent (171) of these lived until their ninth primary was 1mm long and 77% (132) of these fledged (Table 32, Appendix). During 1974 only 232 (46.6%) of the 498 eggs laid hatched. Of these 87% (201) lived until their ninth primary was 1mm long, and 75% (151) of these survived to fledge. Thus, survival during both years was similar, except that hatching success was reduced by nearly 50% in 1974. Based on observations from previous years, the low hatching success of 1974 was definitely abnormal. However, I have no explanation for it.

Differences in Protocalliphora infestations were also observed between 1973 and 1974. In 1973, all 28 of the nests from which magpies fledged were infested, whereas, in 1974, all but two of the 46 nests from which birds fledged were infested. The average number of larvae per nest during 1973 was 170.6, whereas it was only 85.5 during 1974. However, a T-test run on the number of nestlings fledging from nests heavily infested with Protocalliphora (50 or more larvae) versus those with low infestations (fewer than 50 larvae) revealed no significant difference at the 95% level in either 1973 or 1974. Therefore, P. asiovora apparently had little impact on the survival of nestling magpies during these years. This finding contrasts with Chapman's (1973) study of swallow bugs (Oeciacus vicarius) in cliff swallows, in which he found that the bugs caused significant nestling losses before fledging.

Although P. asiovora apparently does not kill a significant number of magpie nestlings, I decided to conduct in-depth studies on the effect, if any, the larvae had on individual nestlings. Since large numbers of blood-sucking P. asiovora were frequently observed in nests, it appeared they must have some effect on nestlings. Therefore, weight gain and blood analysis studies were conducted.

The Effect of P. asiovora on Rates of Weight Gain in Nestling Magpies

Weights of nestlings in nine magpie nests were monitored daily during 1973. The first nestling hatched often had a distinct weight advantage over its younger cohorts. Thus, to compare daily weight gains, it was often necessary to shift weights of the oldest magpie back a day for statistical purposes. Sometimes two or more nestlings showed this advantage. This phenomenon was also observed in cliff swallows by Chapman (1973).

Two nests (1 and 2) were selected as controls (Table 30, Appendix) and were kept free of parasites by frequent cleaning. Natural populations of larvae were allowed to develop in the remaining seven nests. Mean weight gains are plotted in Figure 2. Mean weights for the experimentals were significantly lower than for controls (t-test, $P \leqq .05$) between seven and 20 days and 22 and 23 days (Table 8). Thus, the effects of Protocalliphora upon nestlings appear to be least when nestlings are very young or just before fledging. This corresponds to a time lag in very young birds in which larval populations have not yet had time to develop. In older birds, near fledging, larval impact is substantially

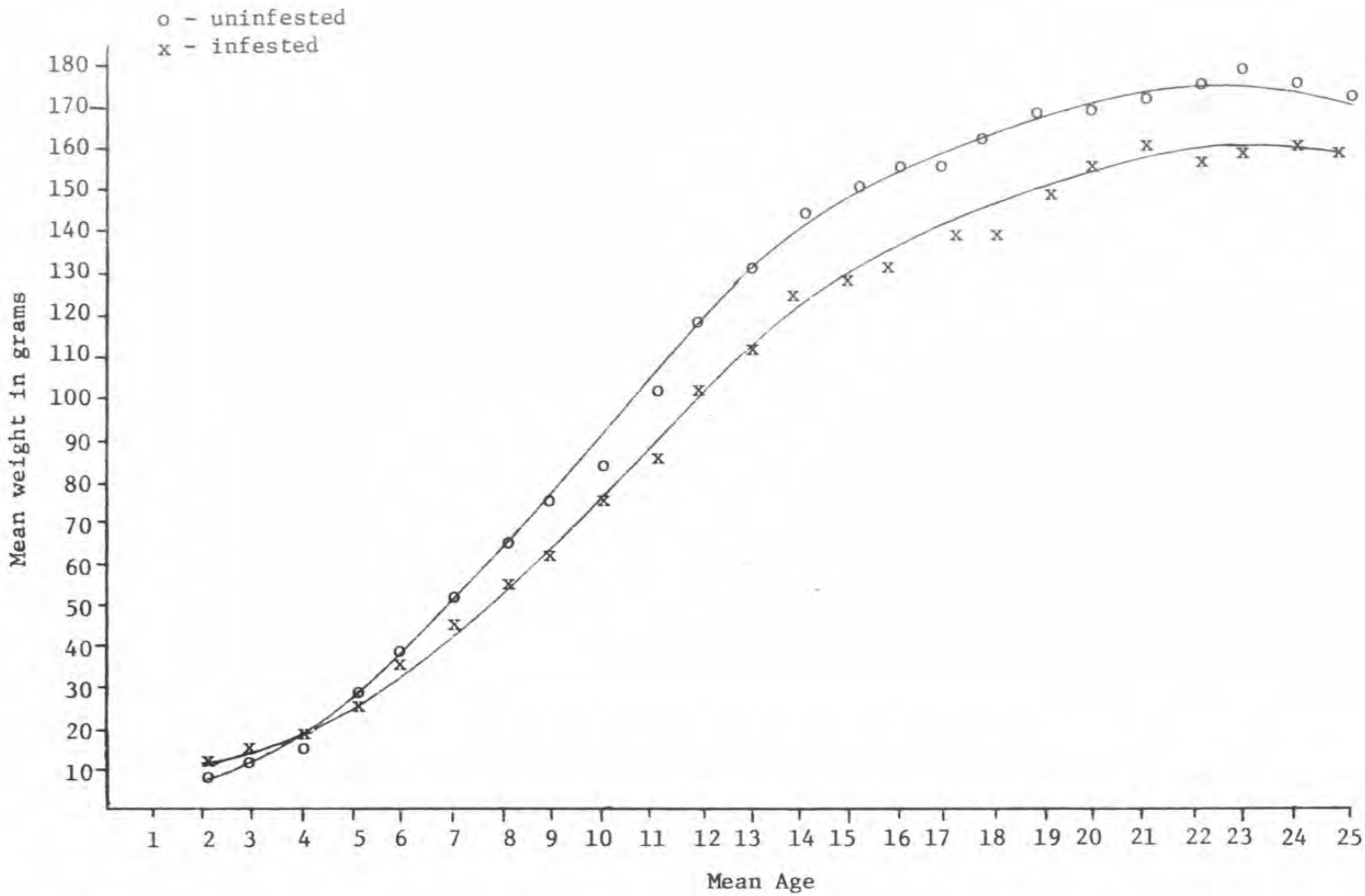

Figure 2. Comparison of daily weight gains in infested and uninfested nestling magpies

Table 8. Comparison of mean weight gains in uninfested and infested nestling magpies from 2 to 25 days old

Age days	Mean weight of uninfested birds (grams)	Mean weight of infested birds (grams)	T-test statistic	Degrees of freedom	Levels of significance			
					95%	97.5%	99%	99.5%
2	10.27	10.68	.57	11	n.s.			
3	13.66	13.85	.27	17	n.s.			
4	19.21	20.48	.95	22	n.s.			
5	28.29	25.64	1.34	30	n.s.			
6	39.33	34.44	1.60	32	n.s.			
7	51.33	44.03	2.20	34		✓		
8	65.10	54.75	2.56	35			✓	
9	73.90	66.12	1.97	34	✓			
10	86.03	76.43	2.19	34		✓		
11	103.57	87.73	3.03	32				✓
12	116.84	101.51	2.62	22			✓	
13	132.10	114.07	3.02	30				✓
14	141.81	125.97	2.48	24		✓		
15	151.41	129.14	3.15	23				✓
16	158.68	130.41	4.36	25				✓
17	156.87	139.69	2.06	22	✓			
18	162.99	140.59	2.36	22		✓		
19	168.03	149.93	2.13	20		✓		
20	171.24	155.61	1.82	20	✓			
21	173.76	161.33	1.25	18	n.s.			
22	177.30	154.50	2.48	11		✓		
23	177.93	156.84	2.47	10		✓		
24	173.60	161.13	1.16	6	n.s.			
25	173.40	161.52	.77	4	n.s.			

reduced, because birds begin perching in the nest and are no longer available to the larvae. It is unlikely that heavily infested nestlings actually "caught up" with the controls, as data in the graph indicate. Rather, during the latter part of the nesting period, fewer observations were made, and all birds began to lose weight just prior to fledging, which probably tended to obscure existing differences.

Two experimental conditions were tested in weight gain studies, the effect of naturally high larval populations and the effect of artificially overloading nests with Protocalliphora. In the first case, three nests (numbers 3, 4, and 5) were selected in which relatively high larval populations had developed naturally. The weight gains, number of nestlings, and minimum normals are given in Table 9.

The weights of some nestlings in all three nests were below normal. It would be expected that nests with the most larvae per nestling would have the most sick nestlings. However, nest 3, with 41 larvae per nestling, had only one nestling which was below normal over a long period (nestling B) and one which was only briefly sick (nestling A). Nest 4, which had 35 larvae per nestling, also had only one nestling sick over a long period (nestling A). It dipped below normal at 11 days of age and was dead at 19 days; no other nestlings in nest 4 appeared to be sick. Nest 5 had the fewest larvae per nestling (23), yet all birds in the nest had low weights. On the last day of observation, weights of six of the seven nestlings were below normal and one was dead. Unfortunately, observations then were discontinued on this nest. However, the nest was re-examined when the young were 22 days old and all six nestlings were still in the nest and appeared to be in good health.

Table 9. Weight gains of nestling magpies where larval populations developed naturally

Age in days	Minimum[a] normal weight	Nestling A	B	C	D	E	F	G	Number of active larvae per nestling
Nest number 3									41
2	5.24	12.1	9.5	11.1					
3	8.33	15.4	11.6	13.4					
4	10.33	19.5	13.0	18.9					
5	13.00	23.3	15.4	29.9					
6	24.48	30.4	22.3	36.2					
7	34.17	38.1	26.5	45.7					
8	48.07	46.8	30.5	60.6					
9	64.39	61.2	39.8	70.3					
10	81.58	71.6	46.6	83.3					
11	94.66	87.1	58.4	100.2					
12	101.58	101.4	66.8	108.6					
13	107.49	118.7	77.8	123.4					
14	118.77	131.3	85.5	127.7					
15	120.14	133.2	92.7	133.8					
16	124.95	140.0	100.3	141.2					
17	123.49	147.6	108.1	142.4					
18	122.38	152.0	112.0	147.6					
19	125.75	157.3	117.2	153.9					
20	120.98	161.1	121.9	155.8					
21	120.55	168.2	126.3	156.5					
22	122.96			158.3					
23	135.19			160.7					
Nest number 4									35
2	5.24	10.4		11.5					
3	8.33	12.5		15.8					
4	10.33	18.7	20.4	22.1	20.5				
5	13.00	28.5	27.0	33.5	27.5				

Table 9. Continued

Age in days	Minimum[a] normal weight	Nestling A	B	C	D	E	F	G	Number of active larvae per nestling
Nest number 4 (continued)									
6	24.48	36.1	34.7	41.2	35.9				
7	34.17	46.1	47.3	51.2	45.9				
8	48.07	55.4	58.4	63.3	59.5				
9	64.39	65.6	72.4	80.1	74.5				
10	81.58	82.7	87.1	95.2	89.1				
11	94.66	90.0	102.9	105.5	99.9				
12	101.58	101.9	113.3	118.7	115.8				
13	107.49	102.5	125.5	125.4	128.7				
14	118.77	110.4	141.2	136.7	140.8				
15	120.14	105.6	136.8	132.9	145.2				
16	124.95	104.7	140.6	122.3	152.3				
17	123.49	98.5	140.3	127.3	147.5				
18	122.38	92.9	132.3	134.2	141.1				
19	125.75	dead	140.5		151.1				
20	120.98		149.7		163.3				
Nest number 5									23
5	13.00	22.2	18.1	15.6	25.3	25.7	17.6	21.8	
6	24.48	33.3	25.3	21.7	32.2	36.0	25.8	30.1	
7	34.17	45.5	34.5	30.5	37.4	49.1	34.7	37.6	
8	48.07	59.6	47.2	40.9	46.2	58.4	46.5	46.9	
9	64.39	72.1	56.1	54.8	53.7	70.9	57.1	53.0	
10	81.58	81.2	66.1	59.6	72.2	81.9	66.7	65.3	
11	94.66	76.6	dead	69.2	87.7	91.1	95.9	73.9	

[a]Values derived from Table 31, Appendix.

The reason that nest 6 (with the least larvae per nestling) had the highest number of sick nestlings was not clear. However, analysis of blood value data later revealed that sickness in nestlings is influenced by a complex of factors, including number of larvae, number of active larvae, and age of nestlings. In nest 5, the larvae developed when the nestlings were somewhat younger than those in nests 3 and 4. This may explain the greater impact of larvae on them.

In four magpie nests (6, 7, 8 and 9), larval numbers were artificially increased to determine the effect upon nestling weight gains (Table 10). In nests 6 and 7, nestlings were weighed for several days. When nestlings were 17 days old, each nest was examined for natural larval numbers. Nest 6 contained about 100 larvae and nest 7 had about 60. At this time, 240 additional larvae were placed in nest 6 and 127 in nest 7. In nest 6, nestlings C and E, weights for which had been fairly low, dropped below normal the day following the addition of larvae; however, the following day their weights were again normal. In nest 7, no nestlings appeared to respond to the addition of larvae, although nestling B remained below normal, as it had been before the addition of larvae. It is probable that the reason the larvae had little effect on the nestlings is that the nestlings were perching by this age, and larval feeding was restricted to the feet and lower abdomen. Cases of illness caused by larvae were observed in older birds, but usually they had been heavily infested since they were quite young. The importance of perching behavior in aiding avoidance of larvae was further tested in the laboratory by placing a 25-day old magpie nestling in an enclosed area with about 300 larvae. After one night in the container, the nestling

Table 10. Weight gains of nestling magpies where larval populations were artificially increased

Age in days	Minimum[a] normal weight	Nestling A	B	C	D	E	F	G	No. of larvae added
Nest number 6									
2	5.24		9.5						
3	8.33		13.0						
4	10.33		18.9	25.7	20.5	26.7			
5	13.00	28.7	29.9	32.6	27.4	37.1			
6	24.48	38.8	36.2	46.9	41.4	49.9			
7	34.17	53.2	45.7	56.3	51.9	62.3			
8	48.07	62.6	60.6	65.4	63.7	73.9			
9	64.39	79.2	70.8	80.9	73.8	86.3			
10	81.58	97.2	83.3	86.3	83.1	93.1			
11	94.66	104.9	100.1	96.9	98.9	103.9			
12	101.58	119.8	108.6	105.2	107.1	117.7			
13	107.49	131.9	123.4	113.2	114.7	123.7			
14	118.77	139.7	127.5	120.1	120.5	130.4			
15	120.14	145.1	133.8	125.0	125.7	135.6			
16	124.95	155.2	141.2	130.2	129.1	138.9			
17	123.49	160.5	142.4	127.1	128.2	127.7			240
18	122.38	162.5	147.6	120.4	127.9	118.4			
19	125.75	167.4	153.9	126.6	130.1	129.5			
20	120.98	173.8	155.1	135.8	135.6	135.2			
21	120.55	186.6	156.4	146.1	140.2	141.5			
22	122.96	185.5	158.3	137.2	140.8	144.8			
23	135.19	187.2	160.1	139.5	147.5	149.9			
24	155.51	191.4		141.4	157.1	154.6			
Nest number 7									
13	107.49	120.5	128.7	125.7	101.2	123.7	146.0	107.6	
14	118.77	127.1	137.3	133.5	102.5	125.6	152.6	103.2	
15	120.14	133.7	146.9	139.2	104.7	dead	156.2	98.5	

Table 10. Continued

Age in days	Minimum[a] normal weight	Nestling A	B	C	D	E	F	G	No. of larvae added
Nest number 7 (continued)									
16	124.95	141.7	160.8	147.4	110.2		161.5	96.6	
17	123.49	156.2	171.9	159.4	118.5		171.2	dead	127
18	122.38	169.0	172.9	158.2	121.6		179.0		
19	125.75	175.5	178.6	159.5	127.4		180.5		
20	120.98	182.7	187.6	161.3	132.5		182.1		
21	120.55	183.8	192.9	175.4	131.3		192.1		
Nest number 8									
3	8.33	13.2	14.4	14.3	16.3	14.1	12.2		
4	10.33	19.2	22.9	20.1	22.8	20.3	17.9		
5	13.00	25.6	29.2	27.3	31.6	26.2	25.5		
6	24.48	37.4	39.0	37.1	43.7	37.6	35.8		148
7	34.17	43.4	47.7	45.5	50.4	43.9	41.7		
8	48.07	54.7	59.6	53.6	62.4	53.1	50.9		
9	64.39	69.0	68.3	dead	68.6	67.9	66.4		212
10	81.58	75.2	76.7		79.4	75.1	65.5		
11	94.66	81.5	83.1		92.6	78.3	68.1		
12	101.58	89.4	91.5		94.6	85.4	79.8		
13	107.49	98.2	99.1		95.5	94.4	88.1		
14	118.77	all nestlings dead							
Nest number 9									
7	34.17	48.1	51.3	28.1	37.4				54
8	48.07	60.9	60.9	36.4	48.9				69
9	64.39	68.2	68.7	42.4	59.3				122
10	81.58	77.8	79.2	51.1	68.5				
11	94.66	91.4	92.5	59.9	78.1				
12		all nestlings dead							

[a]Values derived from Table 31, Appendix.

showed little sign of feeding by larvae and appeared quite healthy. However, the next night the nestling was hobbled so that it could not perch; it was found dead the following morning. There was evidence of heavy larval feeding on the bird and it seems probable that larval feeding contributed to the nestlings' death. The reason for the increased feeding the second night is thought to be that the bird was more accessible because it could not perch.

In two nests (8 and 9) containing relatively young nestlings, a considerable number of larvae were added. In nest 8, 148 first and second instar larvae were added when the nestlings were six days old, and an additional 212 were added three days later (Table 10). By the ninth day, the rate of weight gain showed some drop, and by 10 days all birds were below normal. At 14 days of age, all nestlings were dead. This larval population was quite large for such young birds and it seems surprising that they survived as long as they did; however, the larvae used were not fully developed when placed in the nest and did not reach their maximum size until the day the birds died. In nest 9, 245 nearly mature larvae were added to the nest over a three-day period (Table 10). The day following the last larval addition, all the nestlings were below normal. Two days later, all were dead. These data indicate that large larval populations can be lethal to young magpies. However, field data reveal this rarely happens with magpies in nature. Factors which prevent large larval population build-ups will be considered in a subsequent section (factors regulating larval populations).

The Effect of P. asiovora on Blood Levels of Nestling Magpies

Although weight gain studies provided some information on the effect of larval feeding on nestlings, it was felt a more precise and simple technique was needed. Therefore, studies on the effect of larval feeding on nestling blood levels were initiated.

The effect of larval feeding on the blood of nestling birds was unknown, although it was suspected that hematocrit and hemoglobin levels would be reduced in heavy infestations. Therefore, a preliminary laboratory experiment was conducted in which two nestling magpies were exposed to a very high population of active P. asiovora larvae. The average number of active larvae was maintained at about 100 throughout the four-day experiment. Hematocrits and weights were measured daily in these two birds, as well as in two uninfested controls of the same age (Table 11). All four birds were brought to the laboratory at 17 days of age and the first larvae were not introduced until weighing and blood sampling at the end of the eighteenth day. Table 11 shows that, during the first two days in captivity, all four birds lost weight and showed a drop in hematocrit. However, after the larvae were introduced into the nest of the experimentals, their hematocrits and weights dropped much more rapidly than in the controls. In the last day of the experiment, one bird had a hematocrit of only 10.3%, one-fourth of normal for its age. It died shortly after the blood sample was taken. This bird's blood was so thin and watery that it no longer looked like bird blood. It is likely that a hematocrit of 10% is very near the minimum level at which a young magpie can survive. In several uncontrolled

Table 11. Blood levels and weight gains in heavily infested nestling magpies compared with those of uninfested nestlings

	Age in days					
	17	18	19	20	21	22
Control 1						
hematocrit	48.0	42.0	36.8	35.8	36.5	33.2
weight	148.2	140.7	120.6	121.6	105.4	118.3
Control 2						
hematocrit	43.0	44.0	41.5	34.6	39.2	36.5
weight	133.7	121.5	120	109.6	98.2	114.6
Experiment 1						
hematocrit	45.0	43.0	31.1	19.3	17.6	18.6
weight	157.1	136.8	118.9	114.6	106.2	108.5
Experiment 2						
hematocrit	42.0	39.0	24.0	25.9	13.5	10.3
weight	133.4	121.4	103.6	99.4	101.1	95.3

experiments, heavily infested nestlings were unable to recover when their hematocrits fell below 20%, even when larvae were removed. However, the blood in the other experimental bird in this study had a hematocrit of only 18.6 when the larvae were removed and it recovered fully. Recovery was rather slow, however, and three days after the larvae were removed, its hematocrit measured only 30.5%, and by six days 38% (normal for this age is 40-45%). This indicates that the hematocrit is quite sensitive to larval feeding. It also indicates that wild birds brought to the laboratory experience considerable stress. Therefore, whenever possible, studies were carried out in the field.

During 1974, blood samples were taken from 143 infested nestling magpies from 37 nests to determine the effect of blood-sucking _P. asiovora_ on young magpies (Table 34, Appendix). The sampling program was also expanded to include hemoglobin, as well as hematocrit measurements. Results were categorized into control and experimental nests, based on the number of larvae present in the nest. The control data in Table 31 (Appendix) were divided into two age categories for hemoglobin (sheaths 1mm to feathers 5mm and feathers 6-75mm) and three age categories for hematocrit (sheaths 1-10mm, feathers 1-10mm, feathers 11-75mm). The blood values of the uninfested birds in Table 25 (Appendix) were compared with the infested birds in Table 34 (Appendix) within age groups by a t-test (Table 35, Appendix). Differences were not significant at age 1 for hemoglobin or hematocrit, but they were highly significant (t-test $P \leq .05$) at age 2 for hemoglobin and ages 2 and 3 for hematocrit. The reason for no significance at age 1 is that nestlings were quite young and most had few larvae at that age. In addition, blood levels of such young birds tended to be unstable, which obscured any possible effects of *Protocalliphora* on the nestlings.

Blood levels for nestlings and deviations from normal are also given in Table 34 (Appendix). The relative sensitivity of hemoglobin and hematocrit levels to larval feeding can be determined from these data. Of the 37 nestlings from which blood was taken, 24 had low hemoglobin and 33 had low hematocrit. There were several instances where one blood level was below normal in a particular bird, while the other was not. A bird was considered "sick" if either blood level was below normal.

Examination of magpie blood data (Table 34, Appendix) revealed that feeding *P. asiovora* larvae had the greatest impact when they were in their last three days of development (7-8 day development period, Table 7).

At this age they had reached maximum size and fed frequently. I have referred to this age category as the active larval stage. Active larvae were identified in the field by their large size and the presence of fresh blood in their crops.

As blood data were collected on nestling magpies, it became evident that blood values were low in some birds with low populations of Protocalliphora. With further study, it was found that another blood-sucking ectoparasite which frequently occurred in magpie nests also caused lowering of blood values. The parasite Carnus hemapterus Nitzch (Diptera: Milichiidae) is a small fly that is blood-sucking as an adult and whose larvae are thought to be saprophagous in the nest material. The life history of this species was reviewed by Capelle and Whitworth (1973). This parasite's presence tended to confound the data and made it necessary to divide the nest data into four categories: 1) high Protocalliphora, low Carnus, 2) high Protocalliphora, high Carnus, 3) low Protocaliphora high Carnus, and 4) low Protocalliphora, low Carnus. (Table 12 is a summary of data in Table 34, Appendix.) High Protocalliphora was defined as 10 or more active larvae per nestling. As Carnus was not countable, because of their small size and elusiveness, the degree of Carnus infestation was judged by the amount of feeding evident under the wings and on the stomach of the nestlings. Levels of Carnus infestation were placed in three categories, I being the smallest infestation and III being the largest.

In the first category, low Carnus and high Protocalliphora numbers, 12 of 17 nests had some sick nestlings. Of those nests with sick nestlings, 30 of 56 (53.6%) of the nestlings were sick. In the nests with

Table 12. Number of sick nestlings in relation to degree of infestation by P. asiovora and C. hemapterus

Nest no.	Average feather length of nestlings (in mm)	Fraction of sick nestlings in nest	Number of active larvae per nestling
With 10 or more active P. asiovora larvae per nestling and few or no C. hemapterus			
1	15	1/4	29
2	24	1/2	17
3	24	1/1	18
4	27	5/5	20
5	30	1/7	18
6	35	5/6	31
7	40	3/6	11
8	41	2/5	30
9	44	1/4	13
10	50	3/7	11
11	55	2/4	24
12	55	5/5	22
13	25.7	0/3	22
14	35	0/4	20
15	35	0/5	15
16	39	0/2	35
17	50	0/6	20
With 10 or more active P. asiovora per nestling and moderate to high infestations of C. hemapterus			
1	10	2/4	27
2	16	1/4	10
3	35	1/4	40
4	43	1/2	11
With moderate to high infestations of C. hemapterus and few or no P. asiovora			
1	3	3/5	5
2	7	3/6	0
3	16	1/1	0
4	17	1/2	4
5	22	3/3	7
6	27	2/3	0
7	16	0/2	7
8	4[a]	0/5	3

Table 12. Continued

Nest no.	Average feather length of nestlings (in mm)	Fraction of sick nestlings in nest	Number of active larvae per nestling
With few *P. asiovora* and few *C. hemapterus*			
1	1	0/6	8
2	18	0/6	7
3	35	0/5	5
4	40	0/3	8
5	58	0/2	0
6	60	0/2	5
7	60	0/1	4
8	65	0/2	4

[a]Refers to the sheath rather than the feather.

high *Protocalliphora* and high *Carnus* numbers, all four nests had some sick nestlings and five of 14 nestlings (35.7%) were sick. In the nests with high *Carnus* and low *Protocalliphora* numbers, six of eight nests had sick young, and 11 of 20 nestlings (55%) in the six nests were sick. There were eight nests with low *Protocalliphora* and low *Carnus* numbers, and none of the 27 nestlings in them were sick. A question arising from these data is, Why were only some of the nestlings within a nest sick? Since there is considerable variation in apparent ages (as determined by feather length) within a nest, a t-test was made on the hematocrit and hemoglobin levels between the youngest and oldest birds in the nests (from data in Table 34). Both were significant at the 95% level. This indicates that younger birds are probably fed on more heavily than older ones. Perhaps younger birds get pushed into the center of the nest, where they are more available to parasites. Also, younger birds have less plumage, are less mobile, and may provide more area for feeding by parasites.

A correlation test was run between the number of sick nestlings and the number of active larvae in each nest to see if nests with high numbers of active larvae had more sick nestlings. The correlation was based on the data in Table 12, and included nests with high *Protocalliphora* and low *Carnus*, as well as those with low *Protocalliphora* and low *Carnus*. The result was a correlation of .600, indicating some relationship. When the interaction of age and active larvae versus number sick was compared, the correlation rose slightly to .614.

The presence of *Carnus* in many magpie nests (22/37) tended to confound the effects of *Protocalliphora*. However, as demonstrated in Table 12, only four nests had both high populations of *Carnus* and *Protocalliphora*. This was because high *Carnus* infestations tended to occur in very young nestlings, while heavy *Protocalliphora* populations were in older birds. The average primary length of nestlings heavily infested with *Carnus* (II and III) was 19.6mm, while that of birds with high *Protocalliphora* was 37.6mm (Table 12).

In summary, *P. asiovora* does not appear to cause substantial mortality in nestling magpies. Other factors such as bad weather and poor food supply may be more important. However, both *P. asiovora* and *C. hemapterus* appear to have a definite effect on nestling magpies, as weight gain and blood studies revealed. The blood data indicated that 68% of the infested nests examined had some sick birds and 32% of all nestlings in these nests were sick (see Table 34, Appendix). However, under natural conditions, nestlings are usually able to overcome anemia caused by these parasites and fledge normally. Birds which fledge in an anemic condition might experience higher than normal mortality rates, but this is beyond the scope of the present investigation.

The Effect of P. chrysorrhoea on Blood Levels of Nestling Bank Swallows

The effects of P. chrysorrhoea on its primary host, the bank swallow, was studied in detail during the summers of 1973 and 1974. Ninety bank swallow nests were examined, and larval and nestling numbers were determined in each nest. In 39 nests, nestling numbers, larval populations, and blood values were determined. Of these 39 nests, 12 with low larval numbers were used as controls (Table 26, Appendix), 13 had high larval numbers (Table 13), and in 11 nests conditions were manipulated and the resultant impact on larvae and nestlings was observed (Tables 15, 16, and 23). In the remaining 54 nests, only numbers of nestlings and larval populations were determined (Table 17).

The blood values of nestlings in 13 bank swallows nests with moderate to high infestations of P. chrysorrhoea are given in Table 13. In nests numbers 1-7 both hemoglobin and hematocrit were measured. In nests 8-13, only hematocrit was determined. The blood levels of the control birds (Table 26) were compared with the infested birds (Table 13) within age groups by a t-test (Table 26, Appendix). The values were significantly different at the 97.5-99.5% level. Thus, P. chrysorrhoea larvae caused a significant reduction in hematocrit and hemoglobin levels in infested bank swallow nestlings.

The nestling survival rates and larval populations in 21 bank swallow nests are given in Table 14. The fraction of nestlings surviving from the age where their eighth primary was 1mm long to the age of fledging was compared by a t-test among the six nests with no larvae

Table 13. Blood levels of bank swallow nestlings infested with P. chrysorrhoea

Nest no.	Nestling feather length	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum[a] normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum[a] normal level	Hematocrit: Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest
1	65	15.60	12.47		61	47.05		49	7
	55	13.40	12.47		59	47.05			
	50	11.75	12.47	.72	52	47.05			
	58	12.00	12.47	.47	49	47.05			
	62	12.80	12.47		48	47.05			
2	1	10.75	8.69		51	41.48		115	25
	1	9.50	8.69		47	41.48			
	2	6.50	8.69	2.19	33	41.48			
	3	12.25	8.69		60	41.48			
3	30	11.25	12.47	1.22	47	47.05	.05	68	8
	22	7.50	11.10	3.60	41	41.48	.48		
	20	8.25	11.10	2.85	36	41.48	5.48		
	25	9.50	11.10	1.60	42	41.48			
	25	7.50	11.10	3.60	35	41.48	6.48		
4	1	8.50	9.69	.19	46	41.48		38	19
	1	8.50	8.69	.19	48	41.48			
5	3	8.60	8.69	.09	43	41.48		100	17
	5	9.50	8.69		45	41.48			
	1	6.70	8.69	1.99	39	41.48	2.48		
	4	8.50	8.69	.19	47	41.48			
	2	10.50	8.69		54	41.48			
6	2	8.25	8.69	.44	40	41.48	1.48	32	6
	1	11.00	8.69		51	41.48			
	1	11.25	8.69		51	41.48			
	2	10.40	8.69		50	41.48			
7	2	8.00	8.69		48	41.48		58	12
	1	6.90	8.69		32	41.48	9.48		
	1	6.00	8.69		29	41.48	12.48		
8[b]	5	—	—	—	36	41.48	5.48	45	8
	5	—	—	—	41	41.48	.48		
	5	—	—	—	52	41.48			
	5	—	—	—	43	41.48			
9	1	—	—	—	48	41.48		12	4
	1	—	—	—	53	41.48			
	1	—	—	—	47	41.48			
10	7	—	—	—	52	41.48		57	10
	7	—	—	—	40	41.48	1.48		
	7	—	—	—	39	41.48	2.48		
	7	—	—	—	40	41.48	1.48		

Table 13. Continued

Nest no.	Nestling feather length	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum[a] normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum[a] normal level	Hematocrit: Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest
11	8	--	--	--	42	41.48		96	16
	8	--	--	--	55	41.48			
	8	--	--	--	42	41.48			
	8	--	--	--	36	41.48	5.48		
12	4	--	--	--	50	41.48		143	20
	4	--	--	--	41	41.48	.48		
	4	--	--	--	34	41.4-	7.48		
	4	--	--	--	46	41.48			
	4	--	--	--	42	41.48			
13	8	--	--	--	46	41.48			
	8	--	--	--	44	41.48		58	7
	8	--	--	--	58	41.48			
	8	--	--	--	44	41.48			
	8	--	--	--	44	41.48			

[a]Derived from Table , note minimum level varies with age of nestlings.

[b]Hemoglobin not taken and data on individual bird ages missing on nests 8-13.

Table 14. Losses in nestling bank swallows from hatching to fledging during 1973 and 1974

Nest no.	No. of Eggs	No. of eggs hatching	Number of nestlings surviving to a feather length of 1 mm[b]	Number of nestlings surviving to fledge	Number of[c] larvae in each nest
1	--[a]	5	3	3	11
2	--	5	4	4	1
3	--	5	5	5	75
4	--	5	5	5	115
5	6	6	6	6	68
6	--	2	2	2	50
7	--	1	1	0	30
8	--	5	5	4	0
9	--	4	4	4	32
10	--	4	4	4	4
11	--	2	2	0	5
12	--	2	2	2	38
13	5	0	0	0	0
14	--	5	5	4	71
15	--	3	3	3	0
16	--	5	5	4	0
17	--	4	4	4	32
18	5	1	1	1	0
19	--	5	4	4	20
20	--	4	4	0	9
21	--	5	5	4	20
Totals		78	74	67	581

[a]Nest not found until after egg hatched.

[b]Eighth primary

[c]*P. chrysorrhoea*

(or one larva) and the 15 infested nests. The t-statistic was only 0.09, not significant at the 95% level. Based on this limited sample, *P. chrysorrhoea* do not reduce the number of nestlings surviving to fledge. However, nothing is known of the survival rate of a recently fledged nestling bank swallows with low blood values. In the period just after fledging, birds normally suffer high mortality; perhaps those weakened

Table 15. Effect of high larval populations on blood levels of nestling bank swallows

Days observed	Nestling feather length (mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum normal level	Hematocrit: Deviation below normal	Total larvae per nest	Number of active larvae per nestling
1	1	9.50	8.69			41.48		118	35
	1	11.50	8.69			41.48			
2	3	6.80	8.69	1.89	35	41.48	6.48	118	30
	3	8.75	8.69		47	41.48			
4	8	9.50	11.10	1.60	39	41.48	2.48	214	45
	9	8.75	11.10	2.35	44	41.48			
5	11	8.30	11.10	.39	47	41.48		252	45
	12	11.00	11.10	.10	60	41.48			
7	20	9.50	11.10	1.60	53	41.48		331	35
	22	10.00	11.10	1.10	50	41.48			
9	28	6.25	12.47	6.22	31	41.48	10.48	440	30
	33	8.00	12.47	4.47	38	47.05	9.05		
10	35	7.40	12.47	5.07	29	47.05	18.05	440	40
	39	9.10	12.47	3.46	49	47.05			
12	45	8.75	12.47	3.72	46	47.05	1.05		
	49	10.50	12.47	1.97	49	47.05			
14	fledged								

Table 16. Effect of removing 3 of 5 nestling bank swallows and maintaining a high larval population on the blood levels of nestling birds

		Hemoglobin			Hematocrit				
Days observed	Nestling feather length	Observed level (g/100cc)	Minimum normal level	Deviation below normal	Observed level (%)	Minimum normal level	Deviation below normal	Total larvae per nest	Number of active larvae per nestling
1	1	9.00	8.69		39	41.48	2.48	115	40
	2	7.00	8.69	2.69	45	41.48			
2	4	7.75	8.69	.94	39	41.48	2.48		
	7	8.60	11.10	2.50	45	41.48			
4	8	8.50	11.10	2.60	43	41.48			
	12	9.60	11.10	1.50	47	41.48			
5	15	9.00	11.10	2.10	50	41.48		76	14
	16	11.00	11.10	.10	52	41.48			
7	25	13.00	11.10		54	41.48			
	23	12.90	11.10		55	41.48			
9	38	13.25	12.47		51	47.05		70	5
	31	14.25	12.47		57	47.05			
10	41	14.25	12.47		58	47.05			
	36	12.60	12.47		53	47.05			
12	54	15.20	12.47		65	47.05		65	0
	47	16.20	12.47		62	47.05			

Table 17. Age (expressed as feather length), number of nestlings, and number of *P. chrysorrhoea* observed in bank swallow nests during 1973 and 1974

Nest no.	Average feather length of nestlings (mm)	Number of nestlings in each nest	Total number larvae in each nest	Number of larvae per nestling	Number of active larvae per nestling
1	50	5	4	1	0
2	10	5	69	14	10
3	55	5	58	12	8
4	5	3	4	1	0
5	50	5	3	2	0
6	1	6	15	3	0
7	1	2	21	10	10
8	55	2	60	30	20
9	5	5	20	4	4
10	45	7	43	6	0
11	10	4	29	7	6
12	30	5	87	17	12
13	1	4	11	3	2
14	35	5	91	18	8
15	15	4	113	28	15
16	1	3	88	26	11
17	35	4	41	10	9
18	40	6	31	5	0
19	15	5	0	0	0
20	1	3	51	17	9
21	5	4	61	15	7
22	50	3	25	8	1
23	10	4	21	5	2
24	30	4	33	8	1
25	20	5	12	2	2
26	25	4	6	2	1
27	55	4	35	9	3
28	5	4	30	8	5

Table 17. Continued

Nest no.	Average feather length of nestlings (mm)	Number of nestlings in each nest	Total number larvae in each nest	Number of larvae per nestling	Number of active larvae per nestling
29	30	4	1	0	0
30	35	6	10	2	1
31	50	5	49	10	8
32	25	4	32	8	5
33	40	6	10	2	1
34	55	5	85	17	9
35	50	5	26	5	2
36	45	4	7	2	0
37	50	3	27	9	8
38	35	5	37	7	7
39	30	5	34	7	6
40	50	5	30	6	5
41	45	3	8	3	0
42	55	3	19	6	0
43	55	3	27	9	1
44	40	3	43	14	2
45	30	3	40	13	4
46	45	4	20	5	0
47	5	5	20	4	4
48	10	5	58	12	8
49	1	3	9	3	2
50	5	4	42	11	8
51	1	5	51	10	3
52	1	5	43	9	7
53	2	5	47	9	6
54	5	3	5	2	1

from blood loss may experience a disproportionate amount of mortality. Eleven of the 13 nests in Table 13 contained sick nestlings, with a total of 25 of the 54 nestlings sick. A correlation test between the number of active larvae and the number of nestlings sick showed they were not significantly related (r = 0.06). This may have been due in part to the fact that, in young nestlings with many active larvae, the blood levels had not yet lowered with increased larval feeding. In older birds, which had been fed on heavily over a long period of time, the blood levels might not have recovered fully, although the larvae had stopped feeding. Both of these phenomena would tend to lower the correlation between the number of active larvae and the number of birds sick.

In the seven nests cited above in which both hemoglobin and hematocrit were measured, hemoglobin seemed much more sensitive to larval feeding than hematocrit. Seventeen birds had low hemoglobin levels, while only nine had low hematocrit. This contrasts with the magpie data, where hematocrit appeared to be slightly more sensitive than hemoglobin. I presently am unable to explain this discrepancy.

In two bank swallow nests, the larval populations were increased by adding larvae. In one experiment, active larvae were added to a nest every two-three days over a period of 11 days. The nests had two nestlings and a total of 440 larvae were added to the nest. The active larval population was, thereby, maintained at 35-45 larvae per nestling. The primary objective of this experiment was to determine the effect of prolonged heavy feeding on nestling birds (Table 15). Results indicate that nestling blood values were somewhat low at the beginning of the experiment and by the third day both young were well below normal and remained there for the duration of the experiment. However, the birds did manage to fledge.

Since blood loss and tissue damage resulted from the frequent removal of blood, a control group of four nestlings of the same age was also selected for regular sampling. The mean hemoglobin values of these were compared to those of the two experimental nestlings (Figure 3). Also shown are the expected blood values from the controls in Table 26 (Appendix). The controls, from which blood was removed regularly, had blood levels slightly above the regular controls. This indicates that a regimen of blood removal about every two days does not in itself reduce nestling blood values. Both control groups were well above the experimental birds. The rise of hemoglobin in the controls was continuous with age, whereas it fluctuated in a cyclic fashion in the experimentals.

This experiment indicates that nestling bank swallows are very resiliant and seem to be able to survive high blood losses. It would be interesting to see if a nest with four or five nestlings and an equal number of larvae per nestling could survive as well. Perhaps the presence of only two birds in the nest resulted in the nestlings receiving abundant food and, thus, they were able to regenerate blood more rapidly than nestlings which received less food. Since Chapman (1973) observed that blood-sucking could reduce rate of primary growth, the feather growth of the two experimental birds were compared with the four controls by a t-test. Although feather growth with increasing age was somewhat lower in the experimentals, the difference was not significant.

In another experiment, a nest was found with a high larval population. Three of the five young nestlings were removed to determine the larval

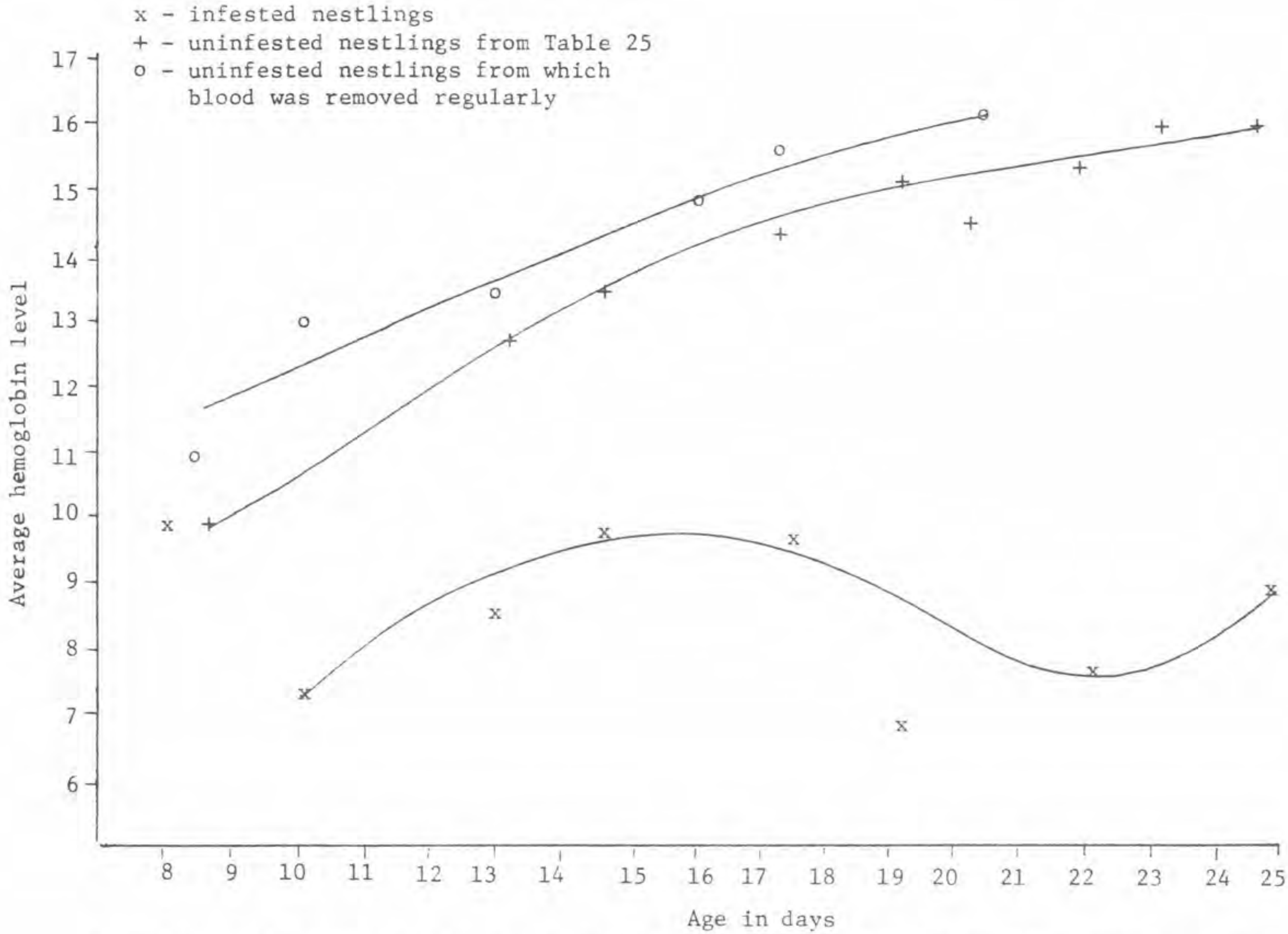

Figure 3. Effect of high larval populations on blood levels of nestling bank swallows

impact upon the two remaining nestlings. Blood levels of these birds are presented in Table 16. The hemoglobin level for these two birds were compared to those for the control birds from which blood was removed regularly (Figure 4). At the beginning of the experiment, the birds were seven days old and there were 55 active larvae in the nest, plus 20 medium-sized larvae and 40 small larvae. The larvae were allowed to develop normally and no additional larvae were added. The climb in hemoglobin was less erratic than in Figure 3. By the time the nestlings were 11 days old, there were only 21 active larvae remaining in the nest and most of the rise in hemoglobin beyond this point represented recovery, since the majority of the larvae had stopped feeding.

Fifty-four bank swallow nests were examined where blood values were not determined, but the number of nestlings and number of active larvae were recorded (Table 17). Assuming that any nests with eight or more active larvae per nestling had some sick nestlings, 15 of the 54 nests should have had some sick birds. The number eight was selected, since all nests in Table 13 with eight or more active larvae per nestlings had some sick nestlings. Many of the nests in Table 22 had high larval numbers, but, when examined, the larvae had either not reached the active stage, or had passed through it. Assuming that all larvae would reach the active stages simultaneously (which is not always true), and applying the same criteria as above, 27 of the 54 nests should have had some sick nestlings. Thus, extrapolating to the whole colony, perhaps as many as half the nests in the colony could have contained some sick young.

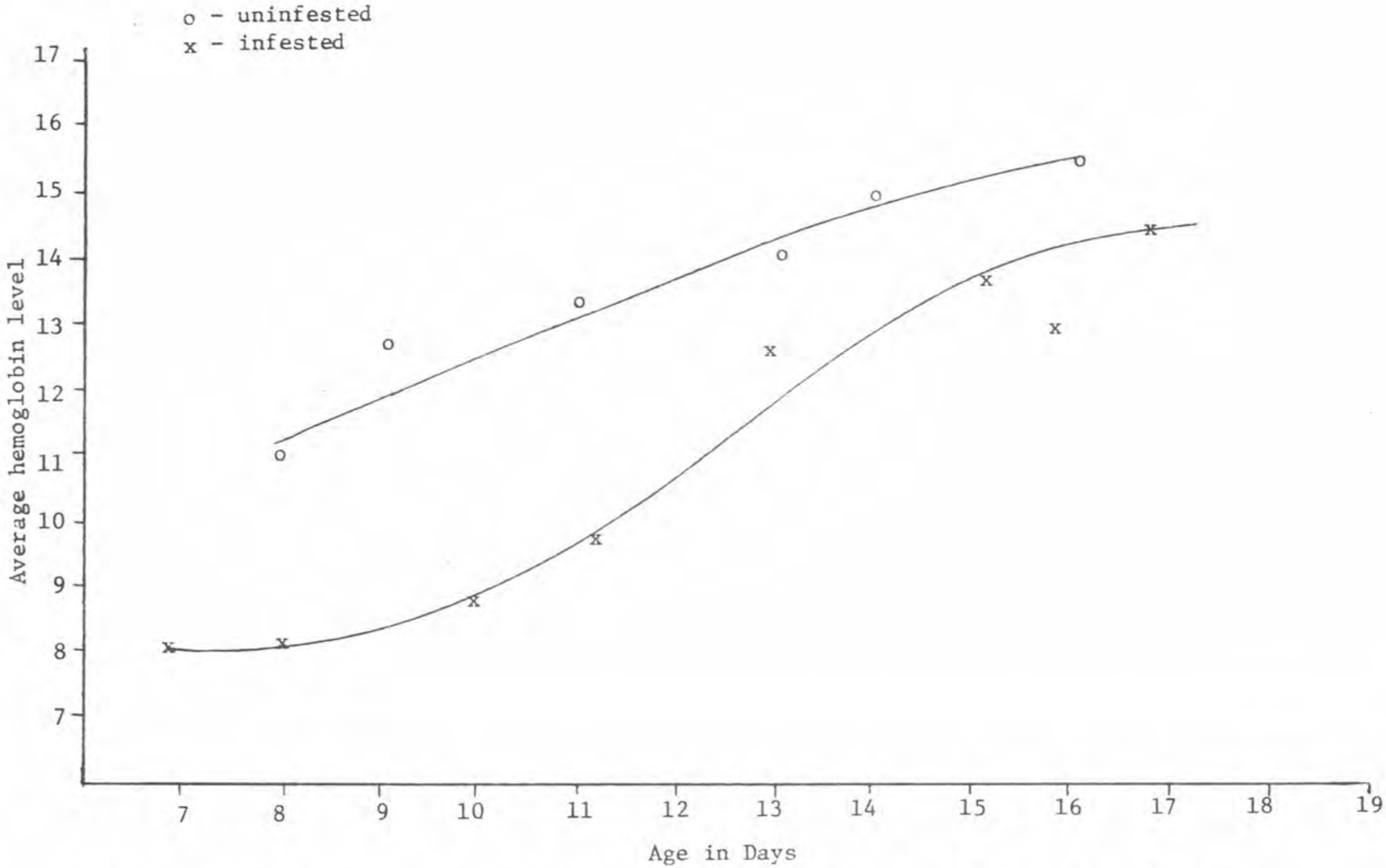

Figure 4. Effect of removing 3 of 5 nestlings and maintaining a high larval population on the blood levels of nestling bank swallows

Efforts to Model the Effect of Host-Parasite Interactions on Nestling Blood Levels

An attempt was made to model the effect of P. asiovora larvae on the blood levels of 77 nestling magpies. The dependent variables were hemoglobin and hematocrit. The independent variables were: 1) primary feather length, 2) number of larvae four days old, 3) number of larvae eight days old, 4) number of prepupae, 5) number of active larvae per nestling, 6) number of nestlings, 7) level of C. hemapterus. The r^2 values for hemoglobin and hematocrit were 0.14 and 0.15, respectively. These low values provided poor predictability. The models generated are as follows:

$$\text{hemoglobin} \quad \hat{Y}i = 236.66 - 0.01\,x_1 - 0.35x_2 + 1.93\,x_3 + 0.12x_4 - 7.87x_5 - 28.81x_6 + 11.01x_7$$

$$\text{hematocrit} \quad \hat{Y}i = 89{,}713.80 - 44.94x_1 + 2{,}358.60x_2 - 2{,}364.46x_3 - 364.84x_4 + 9{,}174.13x_5 + 34{,}221.00x_6 - 12{,}646.10x_7$$

Efforts were also made to model the effect of P. chrysorrhoea larvae on hemoglobin and hematocrit levels of 80 nestling bank swallows. Again, the dependent variables were hemoglobin and hematocrit. The independent variables were: 1) primary feather length, 2) number of larvae of all ages, 3) number of active larvae, 4) number of prepupae, 5) number of active larvae per nestling, 6) number of nestlings, 7) depth of nest in inches, 8) quantity of sand in milliliters, 9) quantity of feathers in milliliters.

The r^2 values for hemoglobin and hematocrit were 0.80 and 0.04, respectively. The model for hemoglobin appeared to provide high predictability. Both models are as follows:

$$\text{hemoglobin} \quad \hat{Y}_i = 11.2 + 0.01x_1 + 0.01x_2 - 0.04x_3 - .29x_4 + 0.02x_5 + 0.33x_6 - 0.03x_7 - 0.01x_8 - 0.01x_9$$

$$\text{hematocrit} \quad \hat{Y}_i = 1{,}987.60 + 0.89x_1 + 305.10x_2 - 313.30x_3 + 309.90x_4 + 613.50x_5 - 274.10x_6 - 384.50x_7 - 48.60x_8 + 48.60x_9$$

Since hemoglobin had such a high r^2 value, a stepwise regression was conducted to determine the relative importance of the model elements. Results revealed that only age was of much importance in blood level predictions ($r^2 = 0.67$). Larval populations contributed only .01 to the overall r^2. This model, therefore, would predict hemoglobin levels well for normal birds, but poorly for heavily infested birds. Since the sample size for both models was small (magpies 77, bank swallows 80), it could probably be improved considerably with more samples and by manipulating the variables.

Estimates of Larval Blood Consumption and the Potential Impact of Larval Feeding on Nestling Magpies and Bank Swallows

The number of larvae required to make a nestling sick can be related to the size of the larvae feeding and the amount of blood they consume in a single meal. By determining the amount of blood a larva consumes in a single meal and the total amount of blood in a nestling bird, it is possible to estimate the number of larvae required to make a nestling sick or to kill it. Two of the most common and largest *Protocalliphora* species were selected for this study, *P. asiovora* (common in magpies) and *P. chrysorrhoea* (common in bank swallows). Blood samples were taken directly from the larval crop in a coagulated clump. Only the bright red blood from the most recent blood meal of the larvae was weighed; older, darker blood was not included. The blood samples were weighed on a Mettler (S5 semimicrobalance) scale readable to 0.00005 grams. Samples probably contained some digestive juices, which were included in the blood weights. Blood was removed from eight large third-instar P. asiovora and five third instar P. chrysorrhoea. P. asiovora blood weights ranged from 0.0064 to 0.0344 g ($\bar{x}$ = 0.0165 g). In P. chrysorrhoea, blood weights ranged from 0.0156 g to 0.2010 g ($\bar{x}$ = 0.0809 g). Differences in weights for both species were due primarily to the fact that some larvae were freshly engorged, while others had not fed recently. Differences between species are due to the substantially larger size of P. chrysorrhoea.

According to Sturkie (1954), about 4% of a chicken's body weight is blood. Assuming a similar percentage for magpie and bank swallow nestlings, their blood volume can be estimated. Twenty, 13-day-old magpie nestlings (half grown) weighed an average of 123.1 g and would contain a mean of about 4.9 g of blood each. Assuming only large larvae were feeding, those capable of consuming the maximum observed (0.0344 g), 144 larvae could consume all of a bird's blood. In humans, a blood loss of 20-40% is considered very serious, so a nestling would probably die long before all of its blood was consumed. In bank swallows six, 18-day old nestlings (near fledging) weighed an average of 11.3 g. Thus each should contain about .45 g of blood. Assuming only large P. chrysorrhoea fed, with a capacity of .201 g, only two larvae could consume almost the entire blood supply of a nestling. Since bank swallows are small birds and are infested by large larvae (P. chrysorrhoea), it would be expected that they would have relatively few larvae or have high nestling mortality rates. Since P. asiovora occurs in nests of large birds, it would be expected that larger larval populations could be supported. Both of these expectations were borne out when the average number of larvae occurring in each of these species were compared (Table 20). The maximum blood capacity of larvae is not the only factor influencing the number of larvae a nest can support. Observation has revealed larvae often do not feed to maximum capacity at each feeding. In addition, feeding is often an extended process of up to an hour's duration, during which time the birds are generating new blood. It would seem that stress would be greatest at night, when larvae are feeding upon them.

Factors Affecting Blood Levels in Nestling Starlings

Eleven starling nests were infested by the primary starling parasite, P. sialia. Four nests had low infestations and were used as controls to calculate minimum normal blood values (Table 27, Appendix). Blood levels for the young in the remaining nests are given in Table 18. Five of the seven remaining nests had some young with blood values below normal. Dead or dying nestlings were found in two of these seven nests. In both cases, Protocalliphora larvae appeared to be implicated in the nestlings' illness and death. In one heavily infested nest with six young birds (10 days old), all the nestlings were dead. An examination of the nests revealed 215 active Protocalliphora in the nest. In another nest with four young (8-days old), three of the young had died and a fourth bird had extremely low blood values and signs of heavy larval feeding. This nest contained 88 active larvae. The most heavily infested

Table 18. Blood levels of nestling starlings heavily infested by _P. sialia_

Nest no.	Nestling feather length (in mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum normal level	Hematocrit: Deviation below normal	Total larvae per nest	Number of active larvae per nestling	Level of C. hempaterus infestation
1	S3[a]	7.50	3.67		36	25.54		49	10	3
	S1	6.50	3.67		33	25.54				
2	1	4.50	3.67		22	25.54	3.54	88	88	3
3	5	6.75	8.70	1.95	28	31.39	3.39	35	8	3
	5	4.50	8.70	4.20	26	31.39	5.39			
	5	4.50	8.70	4.20	28	31.39	3.39			
	5	6.00	8.70	2.70	30	31.39	1.39			
4	13	7.50	8.70	1.20	33	31.39		39	5	2
	16	7.20	8.70	1.50	33	31.39				
	15	6.60	8.70	2.10	28	31.39	3.39			
	21	9.90	8.70		42	31.39				
	22	7.25	8.70	1.45	33	31.39				
5	37	11.25	8.70		48	31.39		145	12	0
	37	11.00	8.70		39	31.39				
	33	10.00	8.70		39	31.39				
	40	13.50	8.70		43	31.39				
	16	8.00	8.70	.70	36	31.39				
6	47	9.20	8.70		47	31.39		441	50	0
	42	7.40	8.70	1.30	44	31.39				
	35	8.10	8.70	.60	41	31.39				
	40	7.80	8.70	.98	42	31.39				

[a] S refers to measurement of sheath rather than feather length.

[b] _Carnus hemapterus_ numbers expressed as an index, 2 = moderate level of infestation; 3 = high level of infestation.

starling nest found had four nestlings near fledging (20 days old) and 381 larvae and 60 puparia. Three of the four nestlings were sick, but all were surprisingly healthy. Of course, they could have been quite sick when younger and other nestlings in the nest may have died. These limited observations indicate that the impact of Protocalliphora is more severe on starlings than on magpies and bank swallows.

The parasite Carnus hemapterus was also found in nine of eleven starling nests. As in the magpie, the effect of its feeding was most evident in very young birds (feeding spots under wings, etc.), and the presence of this parasite tended to confound the blood analysis data. Levels of C. hemapterus in each nest are given in Table 18, with I representing the fewest Carnus and III representing the most. Blood-sucking mites also were observed occasionally in some nests; but only one starling was heavily infested with them. According to Moss and Camin (1970), blood-sucking mites have the potential to cause anemia. However, my limited observations indicate mites have little impact on nestling starlings in this area.

Factors Affecting Blood Levels in Nestling Kestrels

Thirteen kestrel nests were examined for the presence of Protocalliphora and other blood-sucking parasites. Only five nests were infested by Protocalliphora, all P. sialia, and the most heavily infested contained only 17 larvae. Protocalliphora probably had little or no impact on the nestlings observed. However, two kestrel nests examined in 1972 were heavily infested with P. gigantia.

All nestling kestrels examined that were less than 20 days old were infested by C. hemapterus. The lack of uninfested birds in this age group prevented a t-test comparison between infested and uninfested birds. However, none of the birds had exceptionally low blood values. Parasites apparently had little impact upon the nestling kestrels observed.

Blood values were determined for all kestrels examined and, since they appeared to be uniform, the results were recorded in Table 28 (Appendix) as controls. Minimum normal blood values were calculated in Table 31 (Appendix).

Factors Affecting Blood Levels in Nestling Yellow-Headed Blackbirds

Twenty-four yellow-headed blackbird nests were examined and 12 nests infested with P. sp. V were found. The 12 uninfested nests were used for controls (Table 29, Appendix). Minimum normal values for yellow-headed blackbirds were calculated in Table 31 (Appendix). The blood levels of infested birds are shown in Table 19. None of the birds examined was below normal. This is not surprising, since the greatest number of larvae per nestling observed was five. Large infestations were occasionally found in nests examined during previous years, and some mortality, probably related to Protocalliphora feeding, was observed. However, in the most recently examined colony, Protocalliphora seemed to have little impact. A blood-sucking mite also was occasionally observed in these nests. However, its numbers were so low they appeared to have little impact on nestlings.

Table 19. Blood levels of nestling yellow-headed blackbirds infested with P. sp. V

Nest no.	Nestling feather & sheath length (in mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum normal level	Hematocrit: Deviation below normal	Total larvae per nest	Number of active larvae per nestling
1	S2	7.25	5.70	0	33	25.46	0	20	3
	4.5	7.25	5.70		36	25.46			
	6	8.00	5.70		40	25.46			
2	S6	8.50	5.70	0	36	25.46	0	31	4
	3	8.00	5.70		36	25.46			
	10	8.75	5.70		38	25.46			
3	S7	9.25	5.70	0	50	25.46	0	4	1
	4.5	8.25	5.70		42	25.46			
	S8	8.40	5.70	0	38	25.46	0	7	3
	13	8.50	8.35		40	25.46			
4	F2	9.80	8.35	0	35	25.46	0	11	2
	6	9.50	8.35		38	25.46			
	1	9.25	8.35		41	25.46			
5	F5	10.00	8.35	0	30	25.46	0	5	5
6	F11	9.00	8.35	0	33	25.46	0	7	2
7	F6	12.50	8.35	0	41	25.46	0	5	2
	12	12.20	8.35		40	25.46			

Factors Regulating Larval Populations in Nestling Birds

As the preceding studies revealed, Protocalliphora at times is capable of developing high, even lethal, populations in some bird species nests. However, an analysis of the larval populations in each bird species' studied indicated that near-lethal numbers are uncommon under natural conditions (Table 20). Highest larval populations were observed, as expected, in large birds with sturdy nests, such as magpies, crows, and ravens. The larval populations of hawks, owls, and eagles were small, considering the size of their nests. Reasons for this are unknown. Smaller birds, with relatively sturdy open nests, also harbored fairly high larval populations. These included warblers, flycatchers and kingbirds. Many cavity nesting birds also were heavily infested. Starlings and chickadees constructed very compact nests, in which large populations of larvae developed. House wrens, tree swallows, and mountain bluebirds usually constructed their nests on a deep layer of twigs laid in a loose latticework to support the nest. The nest proper was quite small and, in these birds, many larvae would have to rest at the bottom of the nest cavity and ascend through the latticework to feed. Thus, the larval populations in these nests were usually lower than in the more compact cavity nests of starlings and chickadees.

The nests of some bird species examined seemed suitable for larval development, but had few or none. This was the case in kestrels and woodpeckers. The nests of these cavity-nesting birds are relatively clean during the first few days of nestling development, and larvae then may be found in these nests. However, as the nestlings mature, the cavities become very foul-smelling from an accumulation of their excrement.

Table 20. Number of larvae and nestlings in the nests of various bird species

Bird species	Average[a] number of nestlings observed	No. of nests examined with young birds	No. of nests[b] examined with 10 or more larvae per nestling	% of total infested nests with 10 or more larvae per nestling	Total nests examined	Number of larvae per nest in infested nests of each bird species: 1–25	26–50	51–75	76–100	101–150	151–200	201–300	301–400	401–600
blackbird, Brewer's	3	2	4	10	41	36	4	1						
blackbird, red-winged	2	17	2	12	17	15	1	1						
blackbird, yellow-headed	3	8	17	15	111	93	9	6	1	1		1		
bluebird, mountain	4	4	0	0	4	4								
bunting, lazuli	4	1	0	0	1	1								
chickadee, black-capped	5	4	2	40	5	3		1	1					
chickadee, mountain	6	4	4	100	5	1	1	3						
crow, common	3	1	2	100	2				1				1	
dipper	5	2	0	0	2	2								
dove, mourning	2	1	0	0	1	1								
eagle, golden	2	1	0	0	2	2								
finch, cassins	4	1	0	0	1	1								
flicker, red-shafted	6	2	1	50	2	1	1							
Empidonax, flycatcher	3	3	4	67	6	2	4							
goldfinch, American	3	4	1	50	2	1	1							
hawk, Cooper's	4	2	0	0	1	1								
hawk, ferruginous	4	13	2	14	14	12	2							
goshawk	3	3	0	0	3	3								
hawk, red-tailed	2	5	1	14	7	7								
hawk, sparrow	5	6	0	0	8	7	1							
hawk, Swainson's	2	2	0	0	2	2								
junco, Oregon	4	2	0	0	2	2								
kingbird, eastern	4	1	1	50	2	1				1				
kingbird, western	4	1	0	0	1	1								
magpie, black-billed	5	127	62	49	126	45	18	13	12	16	8	6	6	2
martin, purple	4	6	2	25	6	3	3							
owl, flammulated	2	1	1	100	1	1								
owl, great horned	2	1	0	0	1	1								
owl, long-eared	1	1	1	100	1	1								
pewee, wood	3	3	1	20	5	4	1							
phoebe, Say's	5	2	1	33	3	1	2							
raven, common	5	6	3	50	3	2	1			1			1	1
robin	3	5	4	15	27	23	2	2						
sparrow, chipping	2	1	0	0	1	1								
sparrow, fox	3	2	0	0	2	2								
sparrow, house	3	2	0	0	5	5								
sparrow, white-crowned	3	1	0	0	1	1								
starling	5	18	7	32	22	6	10	1	2	1	1			1
swallow, bank	4	90	33	33	101	44	29	15	5	8				
swallow, barn	3	7	28	22	125	85	22	6	4	5	1	1	1	
swallow, cliff	3	5	7	9	78	65	10	2						
swallow, tree	5	11	2	12	17	13	2		2					
swallow, violet-green	4	2	0	0	2	2								
vireo, warbling	2	1	1	100	1		1							
warbler, Audobon's	3	1	0	0	1	1								
warbler, yellow	3	1	1	20	5	4		1						
wren, house	5	9	1	5	20	16	3		1					
wren, long-billed marsh	4	3	3	60	5	1	1		2	1				

[a] Average rounded off to nearest whole number.

[b] Nests with ten or more larvae per nestling usually had some sick nestlings. The number of sick nestlings will be overestimated where reinfestations occurred and larvae did not mature simultaneously.

Excreta accumulates to some extent in all cavity nests, but the nests of kestrels and woodpeckers consist of little or no nest material, which causes their nests to become very foul and saturated with excreta. Apparently this condition is unsuitable for the larval development of Protocalliphora. It may also discourage Protocalliphora adults from ovipositing in the nests of older nestlings.

Several additional factors may operate in a nest to regulate larval populations. They fall into four main categories: 1) selective oviposition by the adult female, 2) predation and parasitism on larvae and puparia in the nest, 3) interspecific competition between Protocalliphora larvae and other nest inhabitants, and 4) intraspecific competition among Protocalliphora larvae for feeding and resting sites.

The role of host-finding mechanisms (if any) in adult female Protocalliphora is poorly understood. The females must first find a nest and then determine if it is suitable for oviposition. Once a nest is found, it is not known if oviposition occurs immediately or if the female somehow determines whether the nestlings are young enough that eggs laid would mature before the nestlings fledged. Young larvae have rarely been observed in nests containing older birds. Perhaps the fly is simply not attracted to older birds. Several adult P. chrysorrhoea in a bank swallow colony seemingly testing the air in various burrows (discussed in the Life History section of this paper) may indicate an ability to determine nestling age by detecting odors of nestlings.

Since Protocalliphora larvae may kill nestlings, if they develop large populations in a nest, it seems plausible that adult females may limit the number of eggs which they deposit according to the number of nestlings present in the nest. This limitation of larvae per nest could be accomplished if the eggs were deposited directly on the nestling and a small number of eggs were laid consistently on each nestling. Some blowflies, however, do not do this. Andrewartha and Browning (1961) cited an example of blowflies laying far more eggs on a sheep carcass than it could support. Counts on the number of eggs laid by Protocalliphora in bird nests have never been made. However, larvae of many age groups, indicating multiple infestations by Protocalliphora, have been observed in many nests of various species. Such repeated infestations would tend to negate the regulatory effect of a single female Protocalliphora, even if she did limit the number of eggs per nestling.

Both predation and parasitism may reduce the number of larvae in nests. Birds with long developmental periods in the nest, such as magpies, starlings, and bank swallows, seem to acquire fairly large insect faunas other than Protocalliphora. I studied in detail only the fauna of magpie nests. Common insects in magpie nests include adult and larval dermestids, adult staphylinids, and adults histerids (Coleoptera), all of which are potential predators on Protocalliphora larvae and puparia. Several individuals of each of these groups were dissected and blood was found in the intestines. Initially, when blood was found, it was assumed they had fed on Protocalliphora larvae, since their mouthparts are not adapted for feeding upon nestling birds. However, the blood may have come from their scavenging upon dead larvae or dried blood in the nest, rather than from actual predation. Therefore, a series of tests were conducted to see if these insects would take live larvae. Small groups of third instar P. asiovora were isolated in one-pint jars with groups of dermestids and histerids. The jars were about half-filled with nest debris. Since very few staphylinids were available, they were not studied. Four histerids consumed 6 of 10 larvae in 24 hours and a total of 8 larvae in 48 hours. Ten larval dermestids consumed 11 of 15 Protocalliphora larvae in 24 hours. Five adult dermestids consumed only one of 15 Protocalliphora larvae in a 48-hour period. Based on these observations, it would appear that adult histerids and larval dermestids may be important predators on Protocalliphora larvae. Dermestid larvae will also consume pupae and must be removed carefully from nest material when Protocalliphora larvae are brought to the laboratory for rearing to the adult stage.

Virtually all species of Protocalliphora found were, at least occasionally, parasitized in the pupal stage by Nansonia vitripennis (Walk.) (Hymenoptera: Pteromalidae). It rarely parasitized pupae during May, but by mid-June and thereafter it was common in several bird species. It was extremely common in yellow-headed blackbird nests and parasitized a high number of the P. sp. V pupae occurring there. It probably had considerable impact on the general abundance of adults of this species. It was much less common in the nests of other bird species, but when it occurred in a nest, it often parasitized 90-95% of the puparia therein. Since this parasite occurred only in the puparial stage of the host, its primary effect in limiting larval populations was that it reduced the total adults available to oviposit in bird nests. Other paraistes were not observed in any other stages of Protocalliphora.

Several species of blood-sucking arthropods coexist in magpie nests with Protocalliphora and interspecific competition may occur. Carnus hemapterus (Diptera: Milichiidae) and Culicoides sp. (Diptera: Ceratopogonidae) are common in magpie nests. C. hemapterus also occurs regularly in the nests of starlings, kestrels, and woodpeckers. Oeciacus vicarius Horv. (Hemiptera: Cimicidae) is common in the nests of cliff and barn swallows and can often make nestlings quite ill (Chapman, 1973). Large numbers of fleas (Ceratophyllus sp.) develop in the nests of most bank swallows. Fleas occur less frequently in starling and tree swallow nests. Blood-sucking mites have also been observed in the nests of yellow-headed blackbirds, barn swallows, and starlings. Moss and Camin (1970) cite instances of high mite populations causing illness in nestling purple martins. Although all of these arthropods feed on the same source as Protocalliphora (i.e. nestling birds), I have no evidence of actual competition between them.

Intraspecific competition between Protocalliphora larvae may also regulate larval populations. It has been observed in at least two forms: 1) competition for feeding and resting places on nestlings, and 2) competition for resting places within the nests. If competition for food in the nest is severe enough to regulate larval populations, a relationship should exist between the number of larvae and the number of nestlings in a nest (assuming nestlings are about equally available). Since considerable data of this sort were gathered on magpies and bank swallows, a correlation test was conducted between larval and nestling numbers. There was some correlation between these factors in the magpie ($r = .32$, significant at 99%), and a slightly lower correlation in the bank swallow ($r = .27$, significant at 95%) (Tables 21 and 22). Thus, it is possible there is some relationship between the number of larvae in the nests and the number of nestlings. This then may be the reason why large overpopulations of larvae are rare. In-depth data on how this happens are lacking, but several postulates have been formulated.

In P. asiovora, the newly hatched first instar larva is very fragile until it receives a blood meal. As mentioned earlier, many young P. asiovora larvae are observed along the rear edge of magpie wings, as well as at the base of the body feathers. They often get wedged into a secure position on the bird and remain there several days, until they have passed through the first and second instars. Such spaces on the nestlings are limited, and larvae which gain a secure position may have enhanced their chances for survival. Meanwhile other young larvae, which must fend for themselves in the nest, may be at a distinct disadvantage. Similar competition for feeding places may also occur in older larvae when young magpies begin perching in the nest. At this time, only the lower abdomen and feet of the nestlings appear to be "available" to the larvae. This is evident in perching nestlings, since feeding spots from larvae are concentrated almost exclusively on these body regions. In heavily infested magpie nests, dead and dying larvae frequently are observed, which may be the result of starvation because of the severe competition for food.

There is also evidence of competition among larvae for resting places in the nest. Resting places in flimsy nests (e.g. mourning doves) obviously are quite limited, but all of the space in large nests is not

Table 21. Comparison of nestling and larval numbers found in magpie nests during 1971, 1973, and 1974

1971		1973		1974	
Number of nestlings	Total larval numbers	Number of nestlings	Total larval numbers	Number of nestlings	Total larval numbers
1	9	5	4	3	19
2	6	7	290	3	20
2	21	4	15	2	34
2	49	5	25	3	63
2	77	6	158	2	3
2	157	6	93	3	0
2	111	4	368	1	5
3	215	4	311	3	156
3	322	4	100	2	114
3	46	4	77	5	911
3	3	5	116	1	0
3	6	2	6	5	239
4	368	6	74	3	229
4	311	7	16	4	435
4	100	4	19	2	72
4	77	7	48	4	334
4	19	4	29	4	783
4	29	7	539	6	423
4	17	6	141	5	228
4	234	8	529	4	256
4	187	7	166	3	2
4	87	4	17	1	4
4	73	4	234	7	12
4	100	4	187	6	326
4	117	4	84	5	35
5	116	5	2	6	278
5	2	3	52	2	56
5	153	4	73	6	72
5	204	6	219	4	264
6	158	4	100	3	175
6	93	6	200	7	147
6	74	3	322	5	200
6	141	7	4	6	120
6	219	7	114	2	70
6	200	2	21	2	60
6	100	1	9	5	55
7	290	2	49	4	86
7	48	3	46	4	564
7	539	5	153	2	78
7	166	2	77	6	204
7	4	5	204	2	62
7	114	4	117	6	1
8	529	8	338		
8	338	6	100		

Table 21. Continued

1971		1973		1974	
Number of nestlings	Total larval numbers	Number of nestlings	Total larval numbers	Number of nestlings	Total larval numbers
		2	157		
		2	111		
		3	3		
		3	6		
Total for all years	r = .32350				

necessarily suitable for resting places. Specific portions of nests tended to house the majority of the larvae, depending primarily on the type of nest. Robin nests have a mud cup, which contains only a small quantity of grass and feathers in the center, which is suitable for larvae. Barn swallows build a nest almost identical to that of the robin, but usually line it with a thick layer of feathers. They tend to harbor much larger populations of Protocalliphora. Magpies build their nests with a mud cup base, a deep layer of sticks, and a smaller layer of rootlets, grasses, and feathers just beneath the nestlings. Larvae are rarely found in the layer of sticks. They usually are found either in the layer just beneath the nestlings or at the bottom of the nest, next to the mud cup, where dandruff from the nestlings accumulates. These ideal locations often become unsuitable for larval habitation in heavily infested nests, as the nests become matted with larval excreta. The excrement is a sticky substance with a blood-like consistency and has a strong ammonia odor. It appears to be toxic to the larvae when it accumulates in high concentrations. To verify this observation, an

Table 22. Comparison of nestling and larval numbers found in bank swallow nests during 1973

Number of nestlings	Total larval numbers	Number of nestlings	Total larval numbers
6	10	3	88
5	33	2	51
4	32	4	41
6	10	6	31
5	85	3	51
5	26	3	1
4	7	4	61
3	27	3	25
5	37		
5	34	4	21
5	38	4	33
3	8	5	12
5	3	4	6
3	19	5	6
3	27	5	36
3	50	4	3
2	29	4	53
3	24	5	34
3	43	3	12
3	45	1	8
4	20	4	30
5	4	1	1
5	69	2	2
5	58	4	57
3	4	5	96
5	3	5	143
6	15	4	1
2	21	5	52
6	100	5	115
5	20	6	68
7	43	2	30
4	29	4	32
5	87	2	5
4	25	2	38
4	11	5	15
5	91	4	50
4	113	4	32
2	27	3	35

$r = .26602$

experiment was conducted with three groups of active P. asiovora larvae. Each group consisted of 10 larvae which were placed in three separate vials. One group was provided with normal nest material as a control, another contained very wet soil to determine the effect of moisture, and the last group was not provided with any material, allowing larval excreta to accumulate. After several days, all of the controls and nine of those placed in the wet soil had pupated. Seven of the larvae with no absorbent also pupated, but most of the puparia appeared abnormal. Adults emerged from all of the puparia found in groups I and II, but only one adult emerged from the vial which lacked an absorbent. The apparent toxicity to larvae at high concentrations may reflect a sensitivity to much lower concentrations in the nest. This phenomenon may explain some of my observations in the early phases of my mortality studies on magpies, when efforts were made to determine the effect of high larval populations on nestling magpies. Larval populations were increased artificially by the addition of larvae from other nests. However, high larval populations could not be maintained, because many larvae fell from the nests when a nest was overloaded. To estimate how many larvae may be lost from a nest, a magpie nest and its nestlings was brought into the laboratory. The nest was placed in a large Berlese funnel (without a light) and 368 P. asiovora larvae were placed in the nest. Within 12 hours, 264 larvae had fallen from the nest. Admittedly some of the larvae may have been displaced and accidentally fallen from the nest, but it is possible that many were attempting to escape the highly crowded situation in the nest. I previously reported (Whitworth, 1971) finding 75 larvae of P. asiovora in the soil below a heavily infested raven nest, indicating that larvae will also fall from overcrowded nests under natural conditions.

Detailed observations have also been made on the relationships between the amount of nest material and larval populations of P. chrysorrhoea on the bank swallow. Bank swallows nest in horizontal cavities, 16-30 inches deep. Their nests are usually situated at the end of the cavity and are composed of a small feather and straw cup over a loose sandy base. In early mortality studies, efforts were also made to overload bank swallow nests, but, as in magpies, many larvae crawled from the nest and fell to the ground. In two experimental nests, larvae of P. chrysorrhoea were added at regular intervals for several days, until the populations should have approached 300 larvae in each nest. However, the nestlings showed no ill effect, and when the nests were re-examined, they contained only 25-50 larvae each. It was later found that by adding additional nest material (primarily feathers), large larval populations could be maintained in the nest. Larval excreta did not seem to accumulate in bank swallows nests, since there was much loose, absorbent sand directly below the nest. Therefore, other explanations for the larval decrease were sought. The temperature of the feathers directly beneath the nestlings, where almost all of the larvae were observed, was quite warm, about 36°C. However, the sand 10mm below an occupied bank swallow nest measured only 23°C, 1°C above the temperature of the sand in the rest of the burrow. The ambient temperature was 36°C. Thus, the sand around the nest remains quite cool, probably below the temperature preferendum of larval P. chrysorrhoea. Feathers are easier to keep warm than sand, and, therefore, the addition of feathers in the nest allowed larger larval populations to develop. To verify the importance of feathers in the nest, tests were made on larval populations in bank swallow nests using large and small amounts of feathers. An average bank swallow nest contained about 150 ml of loose sand and 75 ml of loosely packed feathers and straw.

In four nests, feathers were increased from normal to 250-400 ml. In five nests, all feathers were removed (Table 23). The larvae were removed from the nine nests. When the nests were reexamined at a later date, only one of the nests with no nest material had any larvae, and it contained only four. Larval populations redeveloped in three of the four nests with much nest material, although none had exceptionally large populations. The presence or absence of feathers did not seem to affect nestling survival. If the nests with no nest materials were also reinfested, the lack of feathers probably greatly reduced larval survival. A correlation test was conducted on 18 bank swallows nests between the quantity of feathers and the number of larvae in a nest. The coefficient of correlation was 0.40, which because of the low sample size, was not significant ($P \leq .05$). If this test was conducted with a larger sample size, perhaps a significant relationship between the amount of feathers and the number of larvae would be found.

In review, it is not known if female Protocalliphora limit the number of eggs deposited in each nest. If they do, the effect is somewhat dampened by frequent reinfestations in bird species which are heavily infested. Andrewartha and Browning (1961) found Lucilia sp. (Diptera: Calliphoridae) females often deposited more eggs on sheep carcasses

Table 23. Bank swallow nests where conditions were altered to determine the effect on larval populations of P. chrysorrhoea

Nest no.	Nest condition	Age[b] in days	Number of nestlings	Volume of sand (in ml)	Volume of feathers (in ml)	Number of larvae
Feathers added						
1	original[a]	7	4	300	25	1
	new				300	0
	re-examination	18	4	300	250	4
2	original	9		100	75	106
	new		5		250	0
	re-examination	20	4	100	225	0
3	original	9	5	50	175	51
	new				400	0
	re-examination	20	5	75	350	72
4	original	6	5	50	75	15
	new				400	0
	re-examination	17	4	100	375	61
Feathers removed						
5	original	8	2	100	150	38
	new				5	0
	re-examination	17	2	100	0	0
6	original	8	4	150	40	5
	new				0	0
	re-examination	17	4	200	0	0
7	original	9	2	100	30	15
	new				0	0
	re-examination	18	2	100	0	0
8	original	6	3	200	10	0
	new				0	0
	re-examination	17	3	250	0	0
9	original	8	4	50	150	32
	new			250	0	0
	re-examination	20	4	300	0	4

[a] Original refers to the condition when first examined; new refers to the condition created by removing larvae and adding or removing sand; re-examination refers to the conditions found after a specified interval had passed.

[b] Determined from feather length recorded in Table 26, Appendix.

than the food supply could support. Female *Protocalliphora* may be similar behaviorally. Predators definitely may limit *Protocalliphora* larval populations, at least in the magpie. However, in Ullyett's (1950) study, predation enhanced larval survival by reducing intraspecific competition for the limited food supply. It is possible that the influence of predators on *Protocalliphora* is more beneficial than detrimental to the larvae. Evidence indicates that intraspecific competition is the most important factor in limiting *Protocalliphora* larval populations in nests. Ullyett (1950) made similar observations on factors regulating *Lucilia* populations. In the magpie, larvae appear to compete for feeding spaces on the nestling birds and for suitable resting places in the nest. It seems likely that this form of competition occurs in heavily infested nests of most bird species. A special case of larval population regulation was observed in the bank swallow, where the amount of feathers in a nest may have been a factor in regulating larval populations. The number of puparia emerging as adults is limited by the puparial parasite *Nansonia vitripennis*, and, in heavily infested species like *P*. sp. V, it may have a severe impact on overall populations.

SUMMARY

The host and habitat preferences of 18 species of *Protocalliphora* were studied, 11 of which were undescribed. A total of 1,819 bird nests were examined, representing 68 bird species. Of these, 869 (47.8%) nests of 51 bird species were infested.

Factors affecting infestation rates in various bird species were considered. Most colonial (cliff and bank swallows and yellow-headed blackbirds) and cavity nesters (tree swallows, wrens, chickadees, and starlings) and some solitary open nesters (magpies and warblers) experienced high rates of infestations and were infested regularly by a single species of *Protocalliphora*. One colonial nester (red-winged blackbird) and many solitary open nesters (sparrows, finches, juncos, and robins) experienced lower rates of infestation, apparently because they were not regularly infested by a single species. Brewer's blackbirds and barn swallows (both colonial) experienced high infestations in some colonies and much lower infestations in other colonies, resulting in reduced overall infestation rates. Infested nests of great blue herons and snowy egrets were never found and their nests may have been unattractive to species of *Protocalliphora*.

Host selection by species of *Protocalliphora* appeared to be related to host specificity, habitat specificity, or a combination of these factors. Two species of *Protocalliphora* had narrow host preferences, *P. chrysorrhoea* and *P. hirundo* in bank swallows and cliff swallows, respectively.

Several species were specific to certain bird groups in a variety of habitats. P. gigantia was found almost exclusively in the nests of Falconiformes. P. sp. II occurred primarily in warbler and flycatcher nests and was the only species of Protocalliphora found in their nests. P. sp. VI was usually restricted to the cavity nests of house wrens and chickadees. P. sialia parasitized many cavity nesters, including starlings, kestrels, tree swallows, and mountain bluebirds, but never infested chickadee nests.

Three species of Protocalliphora appeared to be habitat specific: sp. V, sp. XII, and sp. IV. Sp. V and XII were found exclusively in marsh habitats, infesting yellow-headed blackbirds and Brewer's blackbirds, while sp. IV occurred around bridges and barns in barn swallow and Say's phoebe nests.

The distribution of P. asiovora appeared to be affected by both habitat and host preferences. It occurred in many habitats and the nests of several large birds, but never infested cavity nests. One species P. hirudo, seemed to have no distinct host or habitat preferences.

Mixed infestations of Protocalliphora were found in 7.1% of the infested nests examined. Host species lacking a specific parasite, such as Brewer's blackbirds and robins, commonly experienced mixed infestation. A considerable amount of "crossing over" was observed between the usual parasites of five species of swallows. P. hirudo was the only species of Protocalliphora which regularly occurred in mixed infestations. Most mixed infestations appeared to be incidental, and their low number seemed to be a result of selectivity by the adult fly.

The life histories of several species of Protocalliphora were studied. Field-collected P. asiovora and P. chrysorrhoea laid eggs in the laboratory and egg developmental periods were determined. Larval and pupal developmental periods were determined for five species: P. asiovora, P. chrysorrhoea, P. sialia, P. sp. V, and P. sp. VI. Observations were made on larval and adult behavior.

Both rates of weight gain and blood levels (hemoglobin and hematocrit) were determined in magpies, while only blood levels were determined in bank swallows, starlings, kestrels, and yellow-headed blackbirds. Weight gains and blood levels of uninfested and infested magpies were significantly different by a t-test. However, when the number of young fledging from each nest was compared, there was no significant difference, indicating that heavy infestations of Protocalliphora do not cause a significant amount of mortality. Similar observations were made on nestling bank swallows. However, it was noted that many nestlings had blood levels below normal at fledging and they may have experienced reduced survival rates after fledging. The nests of several starlings were examined and two nests had young dead or dying from the feeding of Protocalliphora sialia. However, too few data were available to show a significant difference in the number of nestlings that fledged. The kestrel and yellow-headed blackbird nests examined experienced very low infestations of Protocalliphora, and the blood values of infested and uninfested birds did not differ significantly.

Three primary factors appeared to regulate larval populations of Protocalliphora in nests. They were: 1) selective oviposition by the adult female fly, 2) interspecific competition between Protocalliphora and other nest inhabitants, 3) parasitism and predation on

Protocalliphora larvae, and 4) intraspecific competition among _Protocalliphora_ larvae for feeding and resting sites. Selective oviposition by the female fly could regulate the number of eggs laid, but repeated infestations by other flies would seem to negate any regulatory effect on larval populations. Interspecific competition could occur between _Protocalliphora_ larvae and other blood feeders in the nests. However, I found no evidence for this. Dermestid larvae and histerid adults were commonly found in magpie nests, and tests revealed they can be predatory on _Protocalliphora_ larvae. However, predation may enhance larval populations, rather than regulate them, because it reduces intraspecific competition. _P._ sp. V was heavily parasitized by _Nansonia vitripennis_ in the pupal stage, and adult populations (of sp. V) may be reduced substantially by it. _N. vitripennis_ also occurs in other species of _Protocalliphora_, but in much lower numbers. Intraspecific competition was observed in at least two forms, competition for feeding places on the nestlings and for resting places in the nest. The limited data available at the present time indicate that intraspecific competition may be the most important factor regulating _Protocalliphora_ larval populations.

LITERATURE CITED

American Ornithologist Union Committee. 1957. Checklist of American birds. American Ornithologists Union. 691 p.

Andrewartha, H. G., and T. O. Browning. 1961. An analysis of the idea of "resources" in animal ecology. J. Theoret. Biol. 1:83-97.

Barlow, O. W. 1927. Studies on the anemia of rice disease. Amer. J. Physiol. 83:237-244.

Barlow, O. W., and R. W. Whitehead. 1928. The relation of the blood specific gravity to cell count, hemoglobin level, cell volume, and total blood volume in pigeons. Amer. J. Physiol. 87:51-57.

Bennett, G. F. 1957. Studies on the genus Protocalliphora (Diptera: calliphoridae). Unpub. PhD dissertation. Univ. Toronto, Ontario, Canada. 166 p.

Bennett, G. F. 1970. Simple techniques for making avaian blood smears. Can. J. Zool. 48:585-586.

Bennett, G. F., and A. E. Chisholm. 1964. Measurements on the blood cells of some wild birds of North America. Wild. Disease 38:1-22.

Bush, F. M., and H. I. Townsend. 1971. Ontogeny of hemoglobin in the house sparrow. J. Embryol. and Exp. Morph. 25:33-45.

Capelle, K. J. and T. L. Whitworth. 1973. The distribution and avian hosts of Carnus hemapterus (Diptera: Milichiidae) in North America. J. Med. Ent. 10:525-526.

Chapman, B. R. 1973. The effects of nest ectoparasites on cliff swallow populations. Unpub. PhD dissertation. Texas Tech. Univ. 70 p.

Clark, G. W. 1966. Incidence and seasonal variations in blood and tissue parasites of yellow-billed magpies. J. Protozool. 13:108-110.

Coutant, A. F. 1915. The habits, life history, and structure of a blood-sucking larva (Protocalliphora azurea). J. Parasitol. 1(3):135-150.

Dixon, W. J. and F. J. Massey. 1969. Introduction to statistical analysis. McGraw-Hill Book Co., N. Y. 638 p.

Dobroscky, I. D. 1925. External parasites of birds and the fauna of birds' nests. Biol. Bull. Marine Biol. Lab. 48(4):274-281.

Domm, L. V., and E. Taber. 1946. Endocrine factors controlling erythryocyte concentration in the blood of domestic fowl. Physiol Zool. 19:258-281.

Hall, D. G. 1948. The blowflies of North America. Thomas Say Foundation, Monumental Printing Co., Baltimore, Md. 477 p.

Heinroth, O., and M. Heinroth. 1927. Die vögel mitteleuropas in allen legens-und entwicklungsstufn photographisch aufgenommen und in ihrem seelenlebenbeider aufzucht von ei ab beobachtet von Dr. Oskar und Frau Magdalena Heinroth. 1:1-339 (original not seen, cited in Linsdale, 1937).

Hill, M. H., and T. H. Work. 1947. Protocalliphora larvae infesting nestling birds of prey. Condor 49:74-75.

Jellison, W. L., and G. M. Kohls. 1938. Tick-host anemia: a secondary anemia induced by Dermacentor andersoni Stiles. J. Parasitol. 24:143-154.

Jellison, W. L., and C. B. Philip. 1933. Faunae of nests of the magpie and a crow in western Montana. Can. Entomol. 65(2):26-31.

Johnson, C. W. 1929. The injury to nestling birds by larvae of Protocalliphora. Entomol. Soc. Am. Ann. 22(1):131-135.

Johnston, P. M. 1955. Hematocrit values for the chick embryo at various ages. Amer. J. Physiol. 180:361-362.

Linsdale, J. M. 1937. The natural history of magpies. Cooper Ornithological Club, Berkeley, Calif. 234 p.

Lucas, A. M., and C. Jamroz. 1961. Atlas of avian hematology. Agric. Monogr. 25, Dept. Agric. Wash., D. C. 234 p.

Mason, E. A. 1936. Parasitism of birds' nests by Protocalliphora at Groton, Mass. Bird-Banding 7:112-121.

McGrath, J. J. 1971. Acclimation responses of pigeons to simulated high altitude. J. Appl. Physiol. 31:274-276.

Moss, W. W., and J. H. Camin. 1970. Nest parasitism, Productivity, and clutch size in purple martins. Science 168:1000-1003.

Neff, J. A. 1945. Maggot infestation of nestling mourning doves. Condor 47:73-76.

Ostle, B. 1963. Statistics in research. Iowa St. Univ. Press, Ames. 585 p.

Owen, D. F. 1954. Protocalliphora in bird nests. Brit. Birds 47(7):236-243.

Owen, D. F., and J. S. Ash. 1955. Additional records of Protocalliphora (Diptera) in birds' nests. Brit. Birds 48:225-229.

Peterson, A. 1959. Entomological techniques. Edwards Brothers, Inc., Ann Arbor, Michigan. 435 p.

Pettingill, O. S. 1970. Ornithology in laboratory and field. Burgess Pub. Co., Minneapolis, Minn. 524 p.

Plath, O. E. 1919. Parasitism of nestling birds by fly larvae. Condor. 21:30-38.

Riddle, O., and P. F. Braucher. 1934. Hemoglobin and erythrocycte differences according to sex and season in doves and pigeons. Am. J. Physiol. 108:554-566.

Ronald, K., M. E. Foster, and M. I. Dyer. 1968. Physical properties of blood in the red-winged blackbird. Can. J. Zool. 46:157-163.

Sabrosky, C. W., and G. F. Bennett. 1958. The utilization of morphological, ecological, and life history evidence in the classification of Protocalliphora (Diptera: Calliphoridae). Proc. Tenth Internat. Congr. Entomol. 1:163-164. Abstr.

Sato, K. 1960. Hematocrit of chickens; with special reference to visceral lymphomatosis. Poultry Sci. 39:1126-1130.

Stoner, D. 1936. Studies on the bank swallow, Riparia riparia riparia (Linnaeus) in the Oneida Lake region. Roosevelt Wildl. Annals. 4:126-233.

Sturkie, P. D. 1954. Avian physiology. Cornell Univ. Press, Ithaca, N. Y. 766 p.

Todd, K. S., and D. E. Worley. 1967. Helminth parasites of the black-billed magpie Pica pica hudsonia (Sabine, 1823), from southwestern Montana. J. Parasitol. 53:364-367.

Ullyett, G. C. 1950. Competition for food and allied phenomena in sheep-blowfly populations. Phil. Trans. of the Roy Soc. of London. Series B. 234:10-174.

Whitworth, T. L. 1971. A study of the biology of the species of Protocalliphora in the northern Wasatch range. Unpub. MS thesis, Utah State Univ., Logan, Utah 58 p.

Wigglesworth, V. B. 1967. The principles of insect physiology. Methuen and Co., London. 741 p.

Willson, M. F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Monogr. 36(1):51-77.

Zumpt, F. 1965. Myiasis in man and animals in the Old World. Butterworth, Inc., Washington, D. C. 267 p.

APPENDIX

Table 24. A list of bird species whose nests were examined for *Protocalliphora*[a]

Order Family	Common name	Scientific name
Ciconiiformes		
Aredeidae	snowy egret	*Leucophoyx thula*
	great blue heron	*Ardea herodias*
Coraciiformes		
Alcedinidae	belted kingfisher	*Megaceryle alcyon*
Columbiformes		
Columbidae	mourning dove	*Zenaidura macroura*
	rock dove	*Columba livia*
Falconiformes		
Accipitridae	golden eagle	*Aquila chrysaetos*
	Cooper's hawk	*Accipiter cooperii*
	ferruginous hawk	*Buteo regalis*
	goshawk	*Accipiter gentilis*
	marsh hawk	*Circus cyaneus*
	red-tailed hawk	*Buteo jamaicensis*
	sharp-shinned hawk	*Accipiter striatus*
	Swainson's hawk	*Buteo swainsoni*
Falconidae	sparrow hawk	*Falco sparverius*
	prairie falcon	*Falco mexicanus*
Passeriformes		
Tyrannidae	dusky flycatcher	*Empidonax oberholseri*
	western flycatcher	*Empidonax difficilis*
	eastern kingbird	*Tyrannus tyrannus*
	western kingbird	*Tyrannus verticalis*
	western wood pewee	*Contopus sordidulus*
	Say's phoebe	*Sayornis saya*
Hirundinidae	purple martin	*Progne subis*
	bank swallow	*Riparia riparia*
	barn swallow	*Hirudo rustica*
	cliff swallow	*Petrochelidon pyrrhonota*
	tree swallow	*Iridoprocne bicolor*
	violet-green swallow	*Tachycineta thalassina*
Corvidae	common crow	*Corvus brachyrhynchos*
	black-billed magpie	*Pica pica*
	common raven	*Corvus corax*
Paridae	black-capped chickadee	*Parus atricapillus*
	mountain chickadee	*Parus gambeli*
Troglodytidae	house wren	*Troglodytes aedon*
	long-billed marsh wren	*Telmatodytes palustris*
Mimidae	catbird	*Dumetella carolinensis*
Turdidae	mountain bluebird	*Sialia currucoides*
	robin	*Turdus migratorius*
Cinclidae	dipper	*Cinclus mexicanus*

Table 24. Continued

Order Family	Common name	Scientific name
Passeriformes (continued)		
Sturnidae	starling	Sturnus vulgaris
Vireonidae	warbling vireo	Vireo gilvus
Parulidae	Audubon's warbler	Dendroica auduboni
	yellow warbler	Dendroica petechia
Ploceidae	house sparrow	Passer domesticus
Icteridae	Brewer's blackbird	Euphagus chyanocephalus
	red-winged blackbird	Agelaius phoeniceus
	yellow-headed blackbird	Xanthocephalus xanthocephalus
	Bullock's oriole	Icterus bullockii
Fringillidae	lazuli bunting	Passerina amoena
	Cassin's finch	Carpodacus cassinii
	American goldfinch	Spinus tristis
	black-headed grosbeak	Pheucticus melanocephalus
	pine grosbeak	Pinicola enucleator
	Oregon junco	Junco oreganus
	Brewer's sparrow	Spizella breweri
	chipping sparrow	Spizella passerina
	fox sparrow	Passerella iliaca
	savannah sparrow	Passerculus sandwichensis
	song sparrow	Melospiza melodia
	vesper sparrow	Pooecetes gramineus
	white-crowned sparrow	Zonotrichia leucophrys
	green-tailed towhee	Chlorura chlorura
Piciformes		
Picidae	red-shafted flicker	Colaptes cafer
	yellow-bellied sapsucker	Sphyrapicus varius
	Williamson's sapsucker	Sphyrapicus thyroideus
	hairy woodpecker	Dendrocopos villosus
Strigiformes		
Strigidae	flammulated owl	Otus flammeolus
	great horned owl	Bubo virginianus
	long-eared owl	Asio otus

[a]Common and scientific names from the American Ornithologist Union checklist (1957).

Table 25. Growth of primaries, hemoglobin level, and hematocrit level with age in uninfested nestling magpies

	Length of ninth primary					Hemoglobin level				Hematocrit level			
Age in days	Mean[a] sheath length (in mm)	Mean[b] feather length (in mm)	Standard deviation	Number of obser- vations	Range	Mean hemoglobin level g/100cc	Standard deviation	Number of obser- vations	Range	Mean hematocrit level (in %)	Standard deviation	Number of obser- vations	Range
1	0	small, naked, helpless											
2	0	faint feather tracts visible											
3	0												
4	0	feather tracts distinct											
5	0	feather sheaths breaking through skin											
6	.50	--	0	2	--								
7	1.25	--	.35	2	1-1.5								
8	1.30	--	.45	5	1-20								
9	3.30	--	1.80	5	2-50	9.40	1.60	8	7.00-11.00	35.6	5.6	8	26-42
10	4.80	--	1.90	5	3-80								
11	7.40	--	1.80	5	5-10	9.40	1.20	2	8.50-10.25	33.5	.7	2	33-34
12	10.30	--	2.50	3	8-13								
13	--	1.50	2.10	5	0-50	9.60	1.20	6	8.50-11.50	40.8	3.0	6	38-46
14	--	3.50	1.30	4	2-50								
15	--	6.25	1.70	4	4-80	11.80	.63	4	11.00-12.50	40.5	1.7	4	39-42
16	--	9.25	2.20	4	7-12								
17	--	12.00	2.60	4	9-15	10.90	.14	3	10.75-11.00	43.0	1.4	2	42-44
18	--	14.25	2.50	4	11-17								
19	--	15.80	1.50	4	14-17	12.40	1.00	4	11.50-13.50	46.3	4.7	4	42-45
20	--	24.50	2.60	4	22-28								
21	--	29.50	3.40	4	25-33	14.00	0	1	--	48.5	.7	2	48-49
22	--	38.50	1.90	4	36-40	11.50	0	1	--	40.0	0	1	--
23	--	44.00	2.60	4	41-47	12.50	2.12	2	11.00-14.00	45.0	2.8	2	43-47
24	--	49.00	2.40	4	46-51	12.10	.90	3	11.25-13.00	46.3	1.5	3	45-48
25	--	52.80	1.90	4	50-54								
26	--	56.30	2.50	4	53-59	12.00	1.40	2	11.00-13.00	51.0	4.2	2	48-54
27	--	62.50	0	1	--	13.50	0	1	--	43.0	0	1	--

[a]The sheath is the basal portion of the primary feather referred to as the calamus.

[b]The feather is the distal portion of the primary feather with vanes called the rachis. In very young birds only the sheath is measurable, in older birds when the rachis began to appear only this portion of the primary feather was measured.

Table 26. Growth of primaries, hemoglobin level, and hematocrit level with age in uninfested nestling bank swallows

	Length of the eighth primary					Hemoglobin level				Hematocrit level			
Age in days	Mean sheath length (in mm)	Mean feather length (in mm)	Standard deviation	Number of obser-vations	Range	Mean hemoglobin level (in g/100cc)	Standard deviation	Number of obser-vations	Range	Mean hematocrit level (in %)	Standard deviation	Number of obser-vations	Range
1		tiny, naked, eyes closed											
2		eyes open											
3													
4		primary sheaths beginning											
5	1.33	0	.58	3	1-2	11.25	.68	4	11.00-12.25	53.60	6.7	8	44-65
6	6.00	0	1.73	3	5-8								
7	—	.80	.84	5	0-2	11.00	0	1		49.30	3.2	3	48-53
8	—	2.25	.96	4	1-3								
9	—	4.13	1.81	8	4-7	12.40	.66	8	11.00-13.00	50.80	4.1	8	45-57
10	—	8.00	1.31	8	6-10								
11	—	11.38	1.69	8	8-12	12.60	.65	7	11.50-13.50	50.70	3.1	7	49-54
12	—	15.75	.89	8	15-17	13.40	.70	8	12.50-14.75	52.00	5.0	8	43-61
13	—	20.00	1.20	8	19-22	13.20	.80	8	12.00-14.40	52.10	5.0	8	40-56
14	—	24.55	2.08	11	23-27	14.40	1.50	4	12.60-15.90	51.00	6.6	4	45-58
15	—	30.88	2.36	8	27-33	15.20	.82	8	14.25-16.75	59.50	5.8	8	52-70
16	—	36.57	2.88	7	31-39	14.10	1.50	4	12.60-16.00	56.50	5.3	4	51-62
17	—	42.00	3.27	7	36-44	15.40	.81	6	14.25-16.40	55.80	2.1	6	52-58
18	—	45.50	2.87	4	42-49	16.10	.71	2	15.60-16.60	59.00	1.4	2	58-60
19	—	50.50	4.95	2	47-54	15.50	.39	2	15.20-15.75	59.50	7.8	2	54-65
20		fledged											

Table 27. Growth of primaries, hemoglobin level, and hematocrit level with age in uninfested nestling starlings

	Length of the ninth primary					Hemoglobin level				Hematocrit level			
Age in Days	Mean sheath length (in mm)	Mean feather length (in mm)	Standard deviation	Number of obser-vations	Range	Mean hemoglobin level (in g/100cc)	Standard deviation	Number of obser-vations	Range	Mean hematocrit level (in %)	Standard deviation	Number of obser-vations	Range
11	4.50		.71	2	4-5	6.00	0	1	--	34.00	0	1	--
12	--	1	0	4	--	6.50	.71	4	5.50-7.00	36.25	2.87	4	32-38
13	--	5	1	3	4-6								
14	--	9.30	2.08	3	7-11								
15	--	15.30	3.06	3	12-18	11.06	.97	4	9.75-12.00	42.00	1.73	3	40-43
16	--	20.30	3.79	3	16-23								
17	--	26.30	3.06	3	23-29	11.25	.71	2	10.75-11.75	42.00	1.41	2	41-43
18	--	31.00	2.64	3	28-33								
19	--	36.80	2.87	4	33-40								
20	--	44.50	10.61	2	37-52								
21	--	48.50	12.02	2	40-57	11.38	.88	2	10.75-12.00	48.50	3.54	2	46-51

Table 28. Growth of primaries, hemoglobin level and hematocrit level with age in uninfested nestling kestrels

Age in days	Length of the ninth primary: Mean feather length (in mm)	Standard deviation	Number of obser-vations	Range	Hemoglobin level: Mean hemoglobin level (in g/100cc)	Standard deviation	Number of obser-vations	Range	Hematocrit level: Mean hematocrit level (in %)	Standard deviation	Number of obser-vations	Range
15	—	—	—	—	10.25	0	1	—	36.00	0	—	—
16	2.60	1.14	5	1-4	11.13	.99	8	9.25-12.25	43.88	5.33	8	39-56
17	6.50	2.89	4	3-10	11.63	.67	6	10.50-12.50	48.80	5.07	5	42-56
18	11.25	.96	4	10-12	11.11	.63	7	10.20-12.00	49.33	6.86	6	39-58
19	15.50	1.29	4	14-17	11.00	0	1	—	39.00	0	1	—
20	20.00	1.83	4	18-22	11.75	0	1	—	47.00	0	1	—
21	24.00	1.83	4	22-26	12.80	1.13	2	12.00-13.60	48.50	10.61	2	41-56
22	28.75	2.63	4	26-31	12.00	0	1	—	47.00	0	1	—
23	33.67	4.04	3	29-36	12.25	.66	3	11.75-13.00	48.00	1.00	3	47-49
24	38.00	4.36	3	33-41	12.00	0	1	—	46.00	0	1	—
25	42.00	4.36	3	37-45	12.08	.46	2	11.75-12.40	48.50	2.12	2	47-50
26	51.00	5.70	4	44-57	11.94	.43	4	11.50-12.50	44.25	2.50	4	41-47
27	55.75	7.89	4	45-63	12.08	.58	3	11.00-13.00	46.67	1.15	3	46-48

Table 29. Growth of primaries, hemoglobin level, and hematocrit level with age in uninfested yellow-headed blackbirds

Age in days	Mean[a] primary length	Hemoglobin level: Mean hemoglobin level (in g/100cc)	Standard deviation	Number of observations	Range	Hematocrit level: Mean hematocrit level (in %)	Standard deviation	Number of observations	Range
2-1/2	0.2	8.15	.65	6	7.30-8.75	34.60	3.21	5	30-38
3-1/2	1.9								
4-1/2	5.7	9.12	1.12	5	7.60-11.00	38.00	3.46	4	33-41
5-1/2	10.7	11.43	.25	2	11.25-11.60	41.50	6.36	2	37-46
6-1/2	16.7	10.01	.28	4	9.75-10.25	36.75	1.26	4	35-38
7-1/2	23.2	10.98	.96	4	9.75-11.40	40.25	5.19	4	33-44
8-1/2	29.4	12.60	0	1	--	38.00	0	1	--
9-1/2	34.6	12.08	.38	3	11.75-12.50	46.67	3.06	3	44-50
10-1/2	40.5								

[a]From Willson (1966), measuring the eighth primary.

Table 30. Calculation of the minimum normal weights of nestling magpies up to 24 days of age

Age in days	Weight in grams							Mean weight in grams	Standard deviation	(K)[a]	=	Minimum normal weight
	Nest number 1			Nest number 2								
	Nestling A	Nestling B	Nestling C	Nestling A	Nestling B	Nestling C	Nestling D					
0	7.9	6.1	8.2	7.6	8.4	9.5	8.7	8.06	1.06	3.399		4.40
1	9.2	9.2	10.3	9.1	9.8	13.2	11.1	10.27	1.48	"		5.24
2	11.5	13.7	14.5	12.0	13.0	16.1	14.8	13.5	1.53	"		8.33
3	15.3	18.8	20.5	17.6	18.1	23.3	20.9	19.2	2.61	"		10.33
4	22.3	25.5	28.2	26.7	28.9	36.4	30.1	28.1	4.43	"		13.00
5	36.6	35.8	44.5	38.8	37.1	46.0	36.5	39.2	4.23	"		24.48
6	56.3	52.2	52.2	51.4	47.1	57.4	42.7	51.4	5.06	"		34.17
7	58.5	60.9	64.6	58.6	55.1	69.1	62.3	61.7	4.02	"		48.07
8	68.8	74.4	74.3	73.6	73.3	78.8	74.4	73.6	2.72	"		64.39
9	83.8	84.6	86.3	86.9	86.6	87.3	86.7	86.0	1.31	"		81.58
10	103.7	99.6	100.5	105.4	106.7	104.2	104.9	103.6	2.60	"		94.66
11	117.9	115.1	113.1	114.4	118.5	125.8	113.1	116.8	4.47	"		101.58
12	134.7	126.0	127.8	128.1	144.9	137.6	125.6	132.1	7.24	"		107.49
13	149.7	135.6	140.1	135.8	149.5	147.4	134.6	141.7	6.75	"		118.77
14	159.8	151.2	143.2	144.5	163.5	157.6	140.1	151.3	9.18	"		120.14
15	164.4	155.1	146.2	158.6	169.4	170.2	146.8	158.7	9.92	"		124.95
16	165.3	152.6	148.3	151.4	163.5	171.5	145.5	156.9	9.83	"		123.49
17	173.2	164.3	156.4	150.2	173.4	176.4	147.0	163.0	11.95	"		122.38
18	181.7	165.1	162.7	155.4	177.9	182.1	151.3	168.2	12.48	"		125.75
19	190.8	167.5	160.1	158.5	181.3	185.5	155.0	170.8	14.66	"		120.98
20	195.6	165.3	165.7	161.1	185.2	188.7	154.7	173.6	15.61	"		120.55
21	200	171.4	163.2	166.2	188.7	191.9	159.7	176.9	15.88	"		122.96
22		173.6	168.5	171.4	192.3	194.8	167.2	177.7	12.50	"		135.19
23		174.9	169.8	175.4			174.3	172.8	3.36	5.145		155.51
24		175.4	171.7					173.0	2.83	7.655		151.34

[a]Value tabulated in Ostle (1963), based on the number of observations.

Table 31. Major age groups and calculations of minimum normal blood values in five species of nestling birds

	Hemoglobin							Hematocrit						
Bird species	Primary length (in mm)	Mean in g/100cc −	Standard deviation x	K[a] =	Minimum normal level	Number of observations	Range	Bird age	Mean in % −	Standard deviation x	K =	Minimum normal level	Number of observations	Range
black billed magpie	$S_1^b-F_5^c$	9.50	1.33	2.523	6.14	16	7.0-11.5	S_{1-10}	35.2	5.01	2.911	20.62	10	26-42
	F_{6-75}	12.15	1.06	2.329	9.68	23	10.5-14.0	F_{1-10}	40.7	2.50	2.911	33.42	10	39-46
								F_{11-75}	45.7	2.32	2.453	37.58	18	40-49
bank swallow	S_1-F_5	11.20	.60	4.202	8.69	5	10.8-12.3	S_1-F_{30}	51.6	4.84	2.092	41.48	45	40-70
	F_{5-25}	12.90	.82	2.200	11.10	31	11.0-14.8	F_{31-80}	57.7	4.60	2.309	47.05	24	51-70
	F_{26-80}	15.13	1.26	2.249	12.47	28	12.6-16.8							
yellow-headed black-bird	S_1-S_{10}	8.59	1.03	2.815	5.70	11	7.3-11.0	S_1-F_5	37.0	3.74	2.566	27.40	15	30-46
	$S_{11}-F_{20}$	11.12	1.06	2.614	8.35	14	9.8-12.6	F_{6-20}	42.3	5.24	3.188	25.46	8	33-50
starling	S_4-F_1	6.40	.65	4.202	3.67	5	5.5-7.0	S_4-F_1	35.8	2.68	4.202	25.54	5	32-38
	F_{15-50}	11.20	.78	3.188	8.70	8	10.8-12.0	F_{16-50}	43.9	3.67	3.399	31.39	7	40-51
kestrel	S_1-F_{65}	11.60	.85	2.126	9.79	40	9.3-13.6	S_1-F_{20}	46.0	6.43	2.371	30.76	21	36-58
								F_{21-65}	46.8	3.29	2.453	38.76	18	41-56

[a] K is tabulated in Ostle (1963), and is a statistic based on the sample size.
[b] Length of primary sheath (calamus).
[c] Length of rachis.

Table 32. Survival of young magpies from egg to fledging during 1973

Nest no.	Number of eggs laid	Number of eggs hatched	Number surviving to feathers 1 mm[a]	Number fledged	Fraction surviving from feather 1 mm to fledging	Number of larvae
1	5	5	0			
2	6	6	6	5	.83	4
3	7	7	7	7	1.00	290
4	5	4	4	0	0	245
5	2	0				
6	7	6	5	5	1.00	25
7	4	0				
8	5	5	0			
9	7	7	6	6	1.00	158
10	7	7	6	6	1.00	93
11	7	7	7	4	.57	368
12	7	6	6	4	.67	311
13	6	6	6	4	.67	100
14	7	6	5	3	.60	10
15	6	0				
16	6	5	5	4	.80	77
17	8	7	7	5	.71	116
18	3	3	2	2	1.00	6
19	6	0				
20	7	6	6	6	1.00	74
21	7	6	6	0	0	240
22	7	7	7	7	1.00	250
23	5	4	4	4	1.00	19
24	7	7	7	7	1.00	48
25	7	6	5	4	.80	29
26	7	7	7	7	1.00	539
27	7	6	6	6	1.00	141
28	8	8	8	8	1.00	529
29	8	7	7	6	.86	215
30	7	7	7	6	.86	166
31	7	6	4	4	1.00	234
32	7	6	6	4	.67	187
33	7	6	6	4	.67	84
34	7	0				
35	7	6	6	4	.67	219
Sum	223	182	171	132		4777
Percent		82	94	77		
Average						170.6

[a]Ninth primary

Table 33. Survival of young magpies from egg to fledging during 1974

Nest no.	Number of eggs laid	Number of eggs hatched	Number surviving to feathers 1 mm	Number fledged	Fraction surviving from feather 1 mm to fledging	Number of larvae
1	4	1	1	1	1.00	38
2	8	0				
3	7	6	3	0	0	12
4	-	-	3	3	1.00	13
5	-	-	2	2	1.00	20
6	-	-	3	3	1.00	32
7	5	2	2	2	1.00	3
8	7	0				
9	7	0				
10	3	3	3	0	0	274
11	4	0				
12	8	0				
13	5	1	1	1	1.00	5
14	6	5	4	3	.75	91
15	8	6	5	2	.40	69
16	7	6	0			
17	1	0				
18	7	2	0			
19	7	0				
20	6	5	5	4	.80	488
21	5	0				
22	9	0				
23	7	0				
24	7	0				
25	6	5	5	5	1.00	136
26	7	5	3	0	0	20
27	4	3	3	3	1.00	119
28	7	0				
29	6	6	5	4	.80	263
30	7	0				
31	8	0				
32	6	4	4	2	.50	51
33	6	0				
34	4	2	0			
35	7	0				
36	6	3	0			
37	6	0				
38	6	5	4	1	.25	26
39	5	4	4	0	0	12
40	7	7	5	4	.80	135
41	7	6	6	4	.67	463
42	4	0				
43	8	7	7	6	.86	239
44	8	6	6	5	.83	133

Table 33. Continued

Nest no.	Number of eggs laid	Number of eggs hatched	Number surviving to feathers 1 mm	Number fledged	Fraction surviving from feather 1 mm to fledging	Number of larvae
45	6	5	4	0		
46	4	4	4	4	1.00	183
47	4	0				
48	6	4	3	3	1.00	2
49	7	2	2	1	.50	4
50	6	0				
51	8	7	7	7	1.00	7
52	7	7	7	6	.86	178
53	7	6	5	3	.60	22
54	5	3	2	2	1.00	0
55	8	6	4	4	1.00	4
56	6	0				
57	8	0				
58	6	5	4	3	.75	58
59	7	0				
60	6	6	6	6	1.00	44
61	6	5	4	4	1.00	151
62	6	0				
63	7	7	6	4	.67	90
64	3	0				
65	7	0				
66	7	7	7	7	1.00	86
67	7	6	6	5	.83	108
68	8	0				
69	7	3	2	2	1.00	0
70	7	6	3	3	1.00	5
71	7	6	6	5	.83	59
72	7	0				
73	4	0				
74	7	6	6	6	1.00	70
75	4	3	3	2	.67	33
76	7	0				
77	7	6	6	2	.33	35
78	4	0				
79	6	6	6	5	.83	29
80	6	6	5	4	.80	52
81	3	0				
82	6	4	3	2	.67	70
83	4	0				
84	7	6	6	6	1.00	1
Sum	498	232	201	151		3933
Percent		46.6	87	75		
Average						85.5

Table 34. Blood levels of nestling magpies infested with P. asiovora

Nest no.	Nestling feather length (in mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum[a] normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum[a] normal level	Hematocrit: Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest	Level of[b] Carnus infestation	Average feather length of nestlings by nest
1	13	8.00	9.68	1.68	33	37.58	4.58	13	3.5	III	16.5
	20	12.00	9.68		40	37.58					
2	17	11.25	9.68		46	37.58		31	7	III	16.0
	15	11.75	9.68		45	37.58					
3	30	10.75	9.68		41	37.58		91	22	I	25.7
	30	14.00	9.68		49	37.58					
	17	10.75	9.68		40	37.58					
4	35	10.25	9.68		47	37.58		488	30	0	41.4
	40	8.75	9.68	.93	41	37.58					
	40	11.25	9.68		47	37.58					
	47	11.25	9.68		42	37.58					
	45	8.50	9.68	1.18	43	37.58					
5	29	8.25	9.68	1.43	41	37.58		136	20	I	27.2
	19	6.25	9.68	3.43	30	37.58	7.58				
	26	9.00	9.68	.68	47	37.58					
	32	6.00	9.68	3.68	34	37.58	3.58				
	30	7.25	9.68	2.43	38	37.58					
6	2	9.00	6.14		32	20.62		45	3	III	4.4
(sheath	4	8.75	6.14		35	20.62					
length)	7	9.25	6.14		—	20.62					
	4	10.25	6.14		34	20.62					
	5	10.00	6.14		35	20.62					
7	43	10.25	9.68		39	37.58		263	40	III	35.0
	25	9.75	9.68		34	37.58	5.58				
	35	10.50	9.68		39	37.58					
	37	11.50	9.68		47	37.58					
8	42	8.00	9.68	1.68	37	37.58	.58	51	11	III	43.5
	45	11.00	9.68		39	37.58					
9	24	8.00	9.68	1.68	27	37.58	10.58	26	18	II	24.0
10	12-19	11.00	9.68		43	37.58		135	29	0	15.5
	12-19	9.75	9.68		33	37.58	4.58				
	12-19	9.75	9.68		42	37.58					
	12-19	8.38	9.68	1.30	35	37.58	2.58				
11	30-40	12.50	9.68		53	37.58		401	20	0	35.0
	30-40	11.50	9.68		48	37.58					
	30-40	12.25	9.68		44	37.58					
	30-40	13.00	9.68		48	37.58					

Table 34. Continued.

Nest no.	Nestling feather length (in mm)	Hemoglobin Observed level (g/100cc)	Hemoglobin Minimum[a] normal level	Hemoglobin Deviation below normal	Hematocrit Observed level (%)	Hematocrit Minimum[a] normal level	Hematocrit Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest	Level of[b] *Carnus* infestation	Average feather length of nestlings by nest
12	40-60	14.00	9.68		62	37.58		234	20	0	50.0
	40-60	14.00	9.68		49	37.58					
	40-60	13.75	9.68		46	37.58					
	40-60	12.00	9.68		46	37.58					
	40-60	11.00	9.68		38	37.58					
	40-60	11.25	9.68		44	37.58					
13	30-40	12.00	9.68		40	37.58		132	15	I	35.0
	30-40	12.00	9.68		44	37.58					
	30-40	12.00	9.68		40	37.58					
	30-40	13.00	9.68		44	37.58					
	30-40	11.25	9.68		39	37.58					
14	55	10.25	9.68		37	37.58	.58	183	24	0	55.0
	50	9.25	9.68	.43	36	37.58	1.58				
	55	10.75	9.68		52	37.58					
	60	10.25	9.68		44	37.58					
15	32	10.75	9.68		39	37.58		2	0	III	27.7
	30	10.00	9.68		34	37.58	3.58				
	21	8.50	9.68	1.18	34	37.58	3.58				
16	16	7.50	9.68	2.18	37	37.58	.58	4	0	III	16.0
17	30-40	8.50	9.68	1.18	31	37.58	6.58	178	31	0	35.0
	30-40	7.00	9.68	2.68	30	37.58	7.58				
	30-40	7.25	9.68	2.43	29	37.58	8.58				
	30-40	7.50	9.68	2.18	29	37.58	8.58				
	30-40	11.50	9.68		40	37.58					
	30-40	9.25	9.68	.43	38	37.58					
18	1-5	--	6.14		17	33.42	16.42	20	5	III	3.0
	1-5	9.00	6.14		33	33.42	.42				
	1-5	9.50	6.14		34	33.42					
	1-5	8.25	6.14		30	33.42	3.42				
	1-5	10.25	6.14		44	33.42					
19	60	11.25	9.68		38	37.58		139	4	0	60.0
20	55	11.00	9.68		42	37.58		56	0	0	57.5
	60	12.50	9.68		47	37.58					
21	15-20	11.50	9.68		44	37.58		44	7	II	17.5
	15-20	11.00	9.68		42	37.58					
	15-20	11.50	9.68		43	37.58					
	15-20	11.50	9.68		43	37.58					
	15-20	11.00	9.68		43	37.58					
	15-20	13.00	9.68		46	37.58					

Table 34. Continued

Nest no.	Nestling feather length (in mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum[a] normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum[a] normal level	Hematocrit: Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest	Level of[b] Carnus infestation	Average feather length of nestlings by nest
22	5-15	8.75	9.68	.93	40	37.58		151	27	III	10.0
	5-15	8.50	9.68	1.18	40	37.58					
	5-15	11.00	9.68		47	37.58					
	5-15	11.75	9.68		49	37.58					
23	35-45	11.50	9.68		43	37.58		90	8	I	40.0
	35-45	11.00	9.68		40	37.58					
	35-45	11.50	9.68		40						
24	50	11.00	9.68		38	37.58		86	11	0	50.0
	50	13.00	9.68		41	37.58					
	50	11.00	9.68		40	37.58					
	50	13.00	9.68		36	37.58	1.58				
	50	9.50	9.68	.18	36	37.58	1.58				
	50	10.50	9.68		32	37.58	5.58				
	50	12.00	9.68		39	37.58					
25	50-60	8.50	9.68	1.18	33	37.58	4.58	108	22	II	55.0
	50-60	7.75	9.68	1.93	29	37.58	8.58				
	50-60	9.50	9.68	.18	38	37.58					
	50-60	8.25	9.68	1.18	34	37.58	3.58				
	50-60	7.50	9.68	2.18	35	37.58	2.58				
26	40	11.00	9.68		38	37.58		70	11	0	40.0
	40	11.50	9.68		36	37.58	1.58				
	40	12.50	9.68		49	37.58					
	40	13.00	9.68		37	37.58	.58				
	40	12.00	9.68		47	37.58					
	40	13.00	9.68		37	37.58	.58				
27	70	11.75	9.68		46	37.58		33	4	I	65.0
	60	11.00	9.68		49	37.58					
28	43	11.50	9.68		55	37.58		35	10	0	39.0
	35	11.50	9.68		43	37.58					
29	30-40	13.00	9.68		--	37.58		29	5	I	35.0
	30-40	11.00	9.68		38	37.58					
	30-40	11.75	9.68		42	37.58					
	30-40	12.00	9.68		40	37.58					
	30-40	13.50	9.68		48	37.58					
30	10	8.50	9.68	1.18	35	33.42		52	10	III	16.3
	15	11.50	9.68		47	37.58					
	20	11.50	9.68		49	37.58					
	20	12.00	9.68		44	37.58					

Table 34. Continued

Nest no.	Nestling feather length (in mm)	Hemoglobin: Observed level (g/100cc)	Hemoglobin: Minimum[a] normal level	Hemoglobin: Deviation below normal	Hematocrit: Observed level (%)	Hematocrit: Minimum[a] normal level	Hematocrit: Deviation below normal	Total number larvae in nest	Number of active larvae per nestling in each nest	Level of[b] *Carnus* infestation	Average feather length of nestlings by nest
31	1	11.00	6.14		41	33.42		50	8	0	1
	1	11.00	6.14		39	33.42					
	1	12.50	6.14		42	33.42					
	1	11.00	6.14		36	33.42					
	1	11.00	6.14		35	33.42					
	1	9.00	6.14		36	33.42					
32	40	10.50	9.68		38	37.58		311	13	0	44.3
	45	11.00	9.68		35	37.58	2.58				
	52	11.00	9.68		41	37.58					
	40	11.75	9.68		40	37.58					
33	20	9.75	9.68		43	37.58		70	17	II	23.5
	27	7.25	9.68	2.43	37	37.58	.58				
34	20-40	11.50	9.68		41	37.58		134	18	0	30.0
	20-40	11.50	9.68		41	37.58					
	20-40	10.50	9.68		32	37.58	5.58				
	20-40	12.50	9.68		39	37.58					
	20-40	10.00	9.68		41	37.58					
	20-40	12.00	9.68		39	37.58					
35	60	13.00	9.68		47	37.58		31	5	0	60.0
36	5	10.25	6.14		39	33.42		1	0	III	6.8
	7	9.50	9.68	.18	39	33.42					
	8	10.50	9.68		39	33.42					
	8	9.00	9.68	.68	34	33.42					
	6	10.25	9.68		39	33.42					
	7	9.50	9.68	.18	37	33.42					
37	30	8.50	9.68	1.18	41	33.42		21	7	III	21.7
	15	8.50	9.68	1.18	38	33.42					
	20	9.50	9.68	.18	39	33.42					

[a] From Table 31, note minimum level varies with age of nestling.

[b] 1 indicates the fewest *Carnus* and 3 indicates the most.

Table 35. Comparison of blood values between uninfested nests and nests infested with _P. asiovora_ in nestling magpies

Hemoglobin levels in g/100cc				Hematocrit levels in percent					
Sheaths 1 mm to feathers 5 mm		Feathers 6 mm to feathers 75 mm		Sheaths 1 mm to 10 mm		Feathers 1 mm to 10 mm		Feathers 11 mm to 75 mm	
Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings
10.50	9.00	11.75	8.00	42	32	43	17	42	33
11.00	8.75	11.00	12.00	41	35	39	33	44	40
7.00	9.25	12.50	11.25	36	34	38	34	42	46
7.00	10.25	12.00	11.75	26	35	40	30	45	45
9.00	10.00	11.00	10.75	30	17	46	44	45	41
10.25	9.00	10.75	14.00	39	33	39	35	49	49
9.75	9.50	11.00	10.75	38	34	39	41	48	40
10.50	8.25	13.50	10.25	33	30	42	39	40	47
8.50	10.25	13.00	8.75	33	44	39	42	47	41
10.25	11.00	11.50	11.25	34		42	36	43	47
10.50	11.00	11.50	11.25				35	48	42
9.75	12.50	14.00	8.50				36	46	43
8.50	11.00	11.50	8.25				39	45	41
8.75	11.00	14.00	6.25					48	30
11.50	9.00	11.00	9.00					54	47
8.75	10.25	12.00	6.00					43	34
		11.25	7.25					45	38
		13.00	10.25					49	39
		13.00	9.75						34
		11.00	10.50						39
		13.50	11.50						47
		12.75	8.00						37
		13.00	11.00						39
			8.00						27
T-statistic	1.22		11.00		.91		2.32		43
			9.75						33
Degrees of	30		9.75		17		21		42
freedom			8.30						35
Level of	Not significant		12.50	Not significant			97.5%		53
significance			11.50						48
			12.25						44

Table 35. Continued

Hemoglobin levels in g/100cc					Hematocrit levels in percent							
Sheaths 1 mm to feathers 5 mm		Feathers 6 mm to feathers 75 mm			Sheaths 1 mm to 10 mm		Feathers 1 mm to 10 mm		Feathers 11 mm to 75 mm			
Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings		Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings		
		13.00	8.50	12.00					48	40	35
		14.00	11.00	10.50					62	47	41
		14.00	11.75	11.00					49	49	40
		13.75	11.50	11.00					46	43	43
		12.00	11.00	11.75					46	40	37
		11.00	11.50	9.75					38	40	41
		11.25	11.00	7.25					44	38	41
		12.00	13.00	11.50					40	41	32
		12.00	11.00	11.50					44	40	39
		12.00	13.00	10.50					40	36	41
		13.00	9.50	12.50					44	36	39
		11.25	10.50	10.00					39	32	41
		10.25	12.00	12.00					37	39	39
		9.25	8.50	13.00					36	33	37
		10.75	7.75	10.25					52	29	39
		10.25	9.50	9.50					44	38	39
		10.75	8.25	10.50					39	34	34
		10.00	7.50	9.00					34	38	39
		8.50	11.00	10.25					34	36	37
		7.50	11.50	9.50					37	49	41
		8.50	12.50	8.50					31	37	38
		7.00	13.00	8.50					30	47	39
		7.25	12.00	9.50					29	37	39
		7.50	13.00	11.50					29	46	39
		9.25	11.00	11.75					40	49	38
		11.25	11.50	11.00					38	43	55
		12.50	13.00	11.50					42	38	47
		11.50	11.00	11.00					44	40	42
		11.50	12.00	11.75					42	48	43
		11.50	13.50	11.00					43	49	46
		13.00	8.50	8.75					46	44	43
		11.50	11.50						40	38	
T-statistic		4.06							3.49		
Degrees of freedom		145							139		
Level of significance		99.5%							99.5%		

Table 36. Comparison of blood values between uninfested nests and nests infested with *P. chrysorrhoea* in bank swallow nestlings

Hemoglobin levels in g/100cc						Hematocrit levels in percent			
Sheaths 1 mm to feathers 5 mm		Feathers 5 mm to 25 mm		Feathers 26 mm to 80 mm		Sheath 1 mm to feather 30 mm		Feather 31 mm to 80 mm	
Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings
11.00	10.75	13.00	7.50	13.75	15.60	52	51	52	61
10.75	9.50	13.00	8.25	12.60	13.40	48	47	58	59
11.00	6.50	13.00	9.50	15.90	11.75	52	33	65	52
12.25	12.25	11.00	7.50	15.25	12.00	52	60	70	49
11.00	8.50	12.25		14.50	12.80	44	41	55	48
	8.50	12.25		15.00	11.25	59	36	62	47
	8.60	12.30		15.00		57	42	57	
	9.50	12.50		15.25		69	35	57	
	6.70	12.50		16.00		48	46	60	
	8.50	13.50		16.75		53	48	62	
	10.50	12.60		14.75		47	43	51	
	8.25	12.25		14.25		56	45	53	
	11.00	11.50		14.75		57	39	55	
	11.25	13.20		16.00		52	47	57	
	10.40	12.75		13.25		48	54	52	
		13.00		12.60		45	40	57	
		12.50		14.75		50	51	56	
		13.50		15.25		50	51	58	
		13.00		16.00		48	50	58	
		14.00		16.40		49		60	
		13.50		15.80		53		54	
		13.10		14.25		45		65	
		14.75		16.60		50		56	
		12.25		15.60		54		54	
		12.00		15.75		53			
		14.25		15.20		51			
		13.75		16.75		53			
		13.40		15.75		43			
		14.40				61			
		13.00				51			
		12.90				54			
						51			
						50			
						53			
						40			
						53			
						54			
						52			

Table 36. Continued

Hemoglobin levels in g/100cc						Hematocrit levels in percent			
Sheaths 1 mm to feathers 5 mm		Feathers 5 mm to 25 mm		Feathers 26 mm to 80 mm		Sheath 1 mm to feather 30 mm		Feather 31 mm to 80 mm	
Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings	Uninfested nestlings	Infested nestlings
						53			
						56			
						54			
						55			
						45			
						47			
						58			
						55			
T. statistic									
2.37		10.79		4.30		4.30		2.24	
Degrees of freedom									
18		33		32		63		27	
Level of significance									
97.5%		99.5%		99.5%		99.5%		97.5%	

VITA

Terry Lee Whitworth

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Host and Habitat Preferences, Life History, Pathogenicity and Population Regulation in Species of Protocalliphora Hough (Diptera: Calliphoridae)

Major Field: Biology

Biographical Information:

Personal Data: Born in Burlington, Iowa, September 23, 1946, son of Robert L. and Wilma J. Whitworth; married Faye Marie Attaway May 20, 1966.

Education: Attended elementary school in Burlington, Iowa and Martinstown, Missouri; graduated from Unionville High School in 1964; received the Bachelor of Science degree in Education from Northeast Missouri State College, with a major in zoology, in 1968; received the Master of Science degree at Utah State University in 1971; completed requirements for a Ph.D. at Utah State University in 1975.