STACKS

Hilgardia

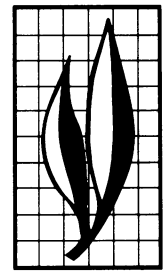
A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 57 • Number 2 • June 1989

Prevalence, Habitat Selection, and Biology of *Protocalliphora* (Diptera: Calliphoridae) Found in Nests of Mountain and Chestnut-backed Chickadees in California

Clifford S. Gold and Donald L. Dahlsten

UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURE AND NATURAL RESOURCES



ABSTRACT

Flies in the genus *Protocalliphora* are important nest parasites of chestnut-backed and mountain chickadees in El Dorado County and Modoc County, California. An undescribed *Protocalliphora* species was the predominant parasite at each site. Infestation rates of chickadee nests in nestboxes exceeded 95% in El Dorado County and 92% in Modoc County; a maximum of 273 larvae were recovered from a single nest. In contrast, only one of 84 chickadee nests was infested in Contra Costa County nestboxes.

The *Protocalliphora* species studied was univoltine, and both sexes overwintered as adults. Dissections of related species suggest multiparity with a maximum ovipositional potential of 90 eggs per gonotrophic cycle. Eggs were placed in the nest material, and females readily oviposited in previously parasitized nests. Oviposition occurred only when nestlings were present and without discrimination with regard to nestling age. Duration of the egg stage was less than 48 hours. The first instar lasted 1 to 2 days, the second instar 2 to 3 days, the third instar 7 to 10 days, the prepupa 2 to 3 days, and the pupa 10 to 36 days.

The undescribed *Protocalliphora* species was specific to cavity-nesting birds in forest habitats. The location and acceptance of potential hosts by various *Protocalliphora* species appear to be governed by two different sets of stimuli. *Protocalliphora asiovora* Shannon and Dobroscky and *P. sialia* Shannon and Dobroscky were attracted to, but never reared from, chickadee nests. Nest odor probably aids *Protocalliphora* females in nest location, but other short-range stimuli apparently determine which hosts are acceptable for oviposition.

Nest infestation levels of the undescribed *Protocalliphora* species were not related to differences in nest site environment, but they were related to nest size. Larger nests apparently provided the larvae with refuges from probing activities of adult chickadees, allowing maximum survival in these nests. Natural enemies did not appear to play a major role in the population dynamics of this *Protocalliphora* species.

THE AUTHORS:

Clifford S. Gold, formerly a graduate student, Division of Biological Control, Department of Entomological Sciences, University of California, Berkeley, is currently an entomologist for the International Crops Research Institute for the Semi-Arid Tropics, Patancheru P.O. Andhra Pradesh 502 324 India.

Donald L. Dahlsten is Professor of Entomology in the Division of Biological Control, and Entomologist in the Experiment Station, University of California, Berkeley.

Clifford S. Gold and Donald L. Dahlsten

Prevalence, Habitat Selection, and Biology of *Protocalliphora* (Diptera: Calliphoridae) Found in Nests of Mountain and Chestnut-backed Chickadees in California[1]

INTRODUCTION

Protocalliphora larvae are hematophagous parasites that attack the nestlings of a broad range of nidicolous birds. The genus is widespread geographically and occurs in many habitats. Nevertheless, only limited biological information, and even less quantified data, is available because of difficulties encountered in studying these flies. The nest environment is fragile and easily disrupted by handling. Direct observations are limited by the physical nature of the nest, and care must be taken to avoid adult abandonment, nestling trauma, or premature fledging. Adult flies have only been observed at nest sites or, rarely, overwintering (Somme 1961; Stiner 1969). Studies on *Protocalliphora* also have been constrained by the apparent randomness of parasite attack.

Early information concerning the biology of *Protocalliphora* came from the studies of Coutant (1915), Plath (1919a,b,c), Bezzi (1922), and Dobroscky (1925). Mason (1944) conducted the first ecological study of this genus, investigating the life history of the fly and comparing infestations on several species of birds. The most inclusive study involves the oviposition behavior and the effects of *P. azurea* (Fallen) on the great tit, *Parus major* L., in Holland (Dobben 1969; Kluyver and Eshuis-van der Voet 1970; Eshuis-van der Voet and Kluyver 1971; Eshuis-van der Voet 1972, 1975; Kluyver 1974; Eshuis-van der Voet and de Reede 1974; Eshuis-van der Voet and Houwink 1976).

Bennett (1957) extensively studied host and habitat preferences of *Protocalliphora* near Toronto, Canada, and investigated the biology and life history of several species under experimental conditions. Whitworth (1971, 1976) investigated host and habitat preferences of *Protocalliphora* found in Utah and also attempted to assess the effects on nestling birds through hematocrit and hemoglobin measurements. Surveys of bird nests show that host and habitat specificity for *Protocalliphora* vary by species (Bennett 1957; Whitworth 1976).

As far as is known, the larvae of all *Protocalliphora* species feed solely on avian blood. With the exception of *Protocalliphora braueri* (Hendel), which lives subcutaneously, all Nearctic species are intermittent ectoparasites that spend much of their time in the nest material (Zumpt 1965; Bedard and McNeil 1979). *Protocalliphora braueri* remains briefly on the hosts after the birds have fledged (Zumpt 1965). Otherwise all feeding by the parasitic larvae is confined to nestlings.

This study focused on the life history, behavior, and natural enemies of *Protocalliphora* parasitizing chestnut-backed chickadees (*Parus rufescens* Townsend) and mountain chickadees (*P. gambeli* Ridgeway) in previously established nestbox plots. The effects of *Protocalliphora* on their chickadee hosts have been reported elsewhere (Gold and Dahlsten 1983).

[1] Accepted for publication December 29, 1988.

The nesting biology and population dynamics of chestnut-backed and mountain chickadees have been studied in detail at two of the field sites used in this study (D. L. Dahlsten and W. A. Copper 1979, unpublished data for Blodgett Forest). Both species nest in cavities and readily utilize nestboxes. Nests are constructed of a moss or wood chip foundation and a fur cup. Eggs are laid one per day, and incubation begins only after the clutch is complete. Clutch size varies but is usually six to eight eggs. Incubation lasts 12 days with nestlings all hatching within a 24-hour period. The duration of the nestling period is 21 days.

Predation of entire clutches by weasels and snakes accounts for virtually all mortality that occurs in the nesting stage (Dahlsten and Copper, unpublished data). Calculations based on banding returns demonstrate that 85% of fledglings fail to survive the first year (Dahlsten and Copper 1979). Much of the high first-year mortality in passerine birds is believed to occur within the first few weeks after fledging (Lack 1966).

MATERIALS AND METHODS

Plot Design and Study Areas

We established nestbox plots in Modoc County, California, in 1966 and at Blodgett Forest (El Dorado County, California) in 1972. For each plot, 50 boxes were placed on trees, 1.5 m off the ground, and spaced in a grid of 10 north-south rows of 5 boxes. All boxes were placed at intervals of 100 m. Three plots were available for study at each site. In 1978, we placed 100 nestboxes in roadside stands of pine and oak in Contra Costa County, California.

The Modoc County study plots were in Modoc National Forest near Adin. The forest is mixed conifer of mostly ponderosa pine (*Pinus ponderosa* Dougl.) and white fir (*Abies concolor* Gord. & Glend.), but incense cedar (*Calocedrus decurrens* Torr.) also is common. Blodgett Forest is a University of California research station 19.5 km east of Georgetown. The forest is mixed conifer composed of the above species plus sugar pine (*Pinus lambertiana* Dougl.), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), and several hardwood species. Tree stands are much denser at this site than in Modoc County. The Contra Costa County study site was adjacent to Orinda. Here, about half of the boxes were placed in even-aged Monterey pine (*Pinus radiata* D. Don) plantations, and the remainder in stands of California live oak (*Quercus agrifolia* Nee).

Nest Collection and Examination

In 1977, nests were collected within 5 days of termination of nesting (for example, because of abandonment, nest predation, or fledging). Nests were then transferred to Berkeley, where *Protocalliphora* larvae and pupae were removed and placed in rearing vials.

To evaluate pupal parasitism in 1978, we collected nests from Modoc County plots 14 to 19 days after the nestlings had fledged. This allowed us to collect nests before fly emergence but gave hymenopterous parasitoids maximal time to attack the pupae. Nests from Blodgett Forest, however, were collected as soon after fledging as possible because of overlap of breeding seasons and travel constraints.

Nests from both sites were placed in rearing containers, consisting of 3.79 L (1 gallon) cardboard cartons with an attached transparent vial. The containers were exposed to ambient conditions and thus approximated the nestbox environment. *Protocalliphora* densities were determined by the number of reared flies and puparia found within the nest material.

Nest Exchanges

It was not possible to observe *Protocalliphora* eggs and larval development in active nests. Therefore, to establish timing of oviposition and larval developmental rates, we made a series of nest exchanges. Chestnut-backed chickadee nests, taken from Contra Costa County nestboxes and found free of *Protocalliphora*, were placed in Berlese funnels to further clean them of arthropods. These nests were then used in nest exchanges in Blodgett Forest and Modoc County study plots. At these sites, boxes containing active nests were removed from trees and replaced with new ones containing cleaned nests. Nestlings were then cleaned of any *Protocalliphora* on them and placed in these new nests. Nestling ages during these exchanges ranged from 1 to 17 days. Removed nests were then examined for *Protocalliphora* larvae, which were identified to instar.

Species Determination

Identifications of *Protocalliphora* were made from a series of adults and associated immatures taken from nestboxes at the Modoc County and Blodgett Forest nestbox plots. Only puparia were available from Contra Costa County. *Protocalliphora* adults attracted to chickadee nests were collected off the nestbox with sweepnets and subsequently identified.

Host and Habitat Specificity

Host and habitat specificity for *Protocalliphora* species that attack chestnut-backed and mountain chickadees was investigated through examination of 160 nests of other bird species found within the nestbox plots and at selected habitats near the study sites. These habitats included (1) the Alturas Wildlife Reserve marshes in Modoc County, (2) woodlands and buildings around Adin, California, (3) buildings in Berkeley, California, Alameda County, and (4) Coyote Hills Regional Park marshlands in Alameda County.

Relationship of *Protocalliphora* Density to Nest and Habitat Parameters

Protocalliphora preferences in selecting chickadee nests were determined from data on the nest and nestbox environment. Data were taken for all nests that had remained active for at least 17 days after the eggs had hatched. The sample included all such nests at Blodgett Forest in 1977 and 1978 and a stratified random sample of similar nests at Modoc County for the same years, using year and *Protocalliphora* populations as stratifying variables.

Nest parameters were hatching date, dry nest weight, and nest volume. Habitat preferences were evaluated through site and stand measurements, taken in September and October 1978, for a circle around the nestbox of 11.33 m radius (= 0.04 ha). Site and stand parameters measured were tree species and diameter at breast height (DBH), the species composition of trees based on combined and specific basal areas (calculated from DBH) and population numbers, percentage of ground and canopy cover, the number and heights of canopy layers, the slope and aspect of the ground, and proximity to "flyways" such as trails, streams, or roads. The direction the nestbox faced and its topographical location were recorded.

Life History of *Protocalliphora*

Boxes with and without nests, with eggs, and with nestlings were all routinely observed for the presence of adult *Protocalliphora* during the collection of bird-nesting data and during the banding of birds. Bird banding often required observation of active nestboxes for up to 1 hour. Boxes where *Protocalliphora* adults were observed were subsequently watched for fly activity for up to an additional 4 hours.

To determine if cavity entrances were sufficient stimuli for attraction, we examined spider webs in empty boxes for *Protocalliphora* remains and applied stick-em to 76-by-127-mm (3-by-5-inch) cards that we then taped to the front, sides, and top of recently fledged or predated nestboxes as well as on empty boxes that had contained heavily infested nests the previous year.

To determine if oviposition required the presence of nestlings, we examined for calliphorid-type eggs and small *Protocalliphora* larvae the nests that had contained chickadee eggs but did not reach the nestling stage (because of abandonment or predation). Nest exchanges were used to help determine the youngest and oldest nestling ages associated with oviposition. In addition, recently fledged nests were examined for presence of eggs and small larvae. This would indicate whether or not *Protocalliphora* adults discriminated between nestling ages, thus ensuring sufficient time for larval development. Finally, we dissected 10 female *Protocalliphora* collected at active nests to record the number of ovarioles, ovariole development, and the presence of yellow bodies and second follicles.

Since it was not possible to make sequential observations of larval developmental rates within nestboxes in the field or to maintain nestling birds in field site laboratories, we assessed larval development through nest exchanges and examination of predated nests. Larvae from these nests were killed in KAA and determined to instar on the basis of characters provided by Bennett (1957). Larval development was related to the maximal time that the nest had been available for oviposition by *Protocalliphora* adults, although the exact timing of oviposition was not known.

The duration of the prepupal and pupal stages was determined for fully developed larvae that had been removed from nests within 24 hours of fledging and placed in vials. Since pupae were seldom found in nests at the time of fledging, we assumed that most larvae entered the prepupal stage when a food source was no longer available (for example, after fledging). Therefore, the length of the pupal stage could also be estimated by comparing dates of fly emergence from nests in rearing containers with the dates of fledging for the same nests.

Flies that emerged from collected nests were identified as to sex and placed in sleeve cages. These cages were exposed to ambient conditions, except rain, and received some direct sunlight during the day. Food was offered in the form of wet raisins, sugar cubes, and drops of protein amylase. Water was sprayed into the cages twice daily. Caged flies were observed for temperature activity thresholds, reactions to light, mating behavior, feeding choices, and any other conspicuous behavioral activities.

Ten caged females were dissected on four occasions to ascertain degree of ovariole development and presence of sperm in the spermatheca. Ten males were dissected once, in October, to note if their testes contained active sperm.

To see if nest odor encouraged mating and ovariole development, we transferred 24 *Protocalliphora* adults reared from Blodgett Forest nests to the Modoc County site and placed them in a sleeve cage with a recently fledged nest. After 2 weeks, the flies were dissected for ovarian examination. In a similar experiment, a cotton-stoppered vial containing 10 males and 10 females was placed in a nestbox under an active nest containing mountain chickadee nestlings, and the females were later dissected.

RESULTS AND DISCUSSION

Chickadee Nestling Presence

Protocalliphora reproductive biology is dependent on the breeding biology of their avian hosts. Parasite generation number and length of time females must overwinter are both influenced by the length of the host nesting season.

In both Blodgett Forest and Modoc County nestbox plots, renests (second clutches) were uncommon, and chickadee nestlings were primarily present only within an 8-week period. A narrow nesting period is typical for chickadees at both study sites (Dahlsten and Copper 1979, and unpublished data). In Contra Costa County, nestling presence also was restricted primarily to an 8-week period (Gold and Dahlsten, unpublished data).

Nest Infestation Levels

Protocalliphora infested 95.1% of chestnut-backed and mountain chickadee nests in Blodgett Forest during the three years studied (table 1). Only two nests were free of *Protocalliphora* pupae, although larvae had been previously observed in one of these nests. The infestation rate of mountain chickadee nests in Modoc County during the two years studied was 92.9% (table 2). Parasite numbers varied considerably between nests at both sites.

In Contra Costa County nestbox plots, 29 chestnut-backed chickadee nests were examined in 1978, 30 in 1979, and 25 in 1980. In 1978 and 1980, all chickadee nests

Table 1. NUMBERS OF *PROTOCALLIPHORA* n. sp. LARVAE IN NESTS FLEDGING YOUNG OF CHESTNUT-BACKED AND MOUNTAIN CHICKADEES IN NESTBOXES AT BLODGETT FOREST, EL DORADO COUNTY, CALIFORNIA

Item	1977	1978	1979
Mean infestation levels			
Mean number of larvae	62.1	66.8	108.8
Range	0 - 273	0 - 144	20 - 238
Number of nests	21	15	11
Standard error	15.8	15.1	20.5
Infestation levels in individual nests			
No larvae	1	1	
1-10 larvae	3 (1)*	3	
11-20 larvae	1		
21-30 larvae	2	1	2
31-40 larvae	1	1	
41-50 larvae	4		1
51-60 larvae	(1)	(1)	
61-70 larvae	2	1	
71-80 larvae		1	
81-90 larvae		1	1
91-100 larvae	1	1	
>100 larvae	4	4	7
Total nests	19 (2)	14 (1)	11

*Numbers in parentheses indicate nests terminated prematurely by predation.

Table 2. NUMBERS OF *PROTOCALLIPHORA* n. sp. LARVAE IN NESTS FLEDGING YOUNG OF CHESTNUT-BACKED AND MOUNTAIN CHICKADEES IN NESTBOXES, MODOC COUNTY, CALIFORNIA

Item	1977	1978
Mean infestation levels		
Mean number of larvae	23.3	37.2
Range	0 - 162	0 - 164
Number of nests	73	80
Standard error	4.6	4.4
Infestation levels in individual nests		
No larvae	3 (15)*	6
1-10 larvae	22 (4)	15
11-20 larvae	4 (2)	14
21-30 larvae	6 (3)	12 (1)
31-40 larvae	2	7
41-50 larvae	3	4
51-60 larvae	2	4 (1)
61-70 larvae	1	2
71-80 larvae	2	2
81-90 larvae	(2)	1
91-100 larvae	1	3
>100 larvae	1	7 (1)
Total nests	47(26)	77 (3)

*Numbers in parentheses indicate nests terminated prematurely by predation.

were free of *Protocalliphora*; however, a Bewick wren (*Thryomanes bewickii* Audubon) nest taken from a box on the edge of an oak stand in 1978 contained 51 *Protocalliphora*. In 1979, a single chickadee nest was infested and contained 104 *Protocalliphora* puparia. Both infested nests were among the last nest attempts for that year. Emergence of adult *Protocalliphora* had occurred before nest collection, and in both cases the emergence rate was quite low. Only six flies had emerged from pupae found in the wren nest and five from pupae in the chickadee nest. Parasitization by a chalcidoid was responsible for the low emergence rate in the wren nest but was not a factor in the chickadee nest.

Species of *Protocalliphora* Associated with Chestnut-backed and Mountain Chickadees

Protocalliphora species in chestnut-backed and mountain chickadee nests during 1977 and 1978 were identified from a series of over 250 reared adults with associated puparia plus larvae of all instars. Identifications were also made from adults reared from a mountain chickadee nest in Blodgett Forest in 1979 and from puparia taken from a chestnut-backed chickadee nest in Contra Costa County in the same year. Adult *Protocalliphora* attracted to active chickadee nests were collected in Blodgett Forest and Modoc County in 1978.

Virtually all *Protocalliphora* collected from chickadee nests were identified as a single new species (= *Protocalliphora* n. sp.). This species had been previously collected by

Dahlsten from chestnut-backed and mountain chickadee nests in 1970 (unpublished data) at the Blodgett and Modoc sites and also from mountain chickadee nestboxes in Inyo County, California (C. W. Sabrosky, personal communication). Whitworth (1976) collected the same species in the nests of mountain and black-capped chickadees in Utah (Sabrosky, personal communication).

A single *P. braueri* adult was reared from the nest of a mountain chickadee at Blodgett Forest in 1978. Its subcutaneous habit suggests that other individuals may have been present in chickadee nests in this study but were carried away by fledglings. *Protocalliphora braueri* has a wide host range (Sabrosky, personal communication), but it is not known if its occurrence in chickadee nests was accidental.

Adults reared from the single mountain chickadee nest collected from Blodgett Forest in 1979 belonged to a second undescribed species of *Protocalliphora* (Sabrosky, personal communication). This nest was a renest, and the hatching and fledging dates were the latest at Blodgett Forest during the three years of study. It is therefore possible that temporal factors may be involved in the seasonal distribution of *Protocalliphora* species at this site.

Protocalliphora identified from the chestnut-backed chickadee and the Bewick wren's nest in Contra Costa County were also *Protocalliphora* n. sp. It is unclear why only two nests were infested by this species, whereas infestation rates of chickadee nests in Utah (Whitworth 1976), Blodgett Forest, and Modoc County were quite high. The lateness of the infested nests in Contra Costa County suggests that temporal factors also may affect *Protocalliphora* at this site.

Adults attracted to an active chestnut-backed chickadee nest in a snag in Blodgett Forest were all identified as *P. sialia* Shannon and Dobroscky. Eight females were collected leaving the nest cavity, and 30 individuals of both sexes were taken on the snag by the nest entrance. However, only *Protocalliphora* n. sp. was reared from this nest.

Male and female *Protocalliphora* collected at mountain chickadee nests in Modoc County were all *P. sialia* Shannon and Dobroscky. On two occasions, female *P. sialia* were collected from open nestboxes after they were observed crawling under nestlings. Nevertheless, this species was not reared from these or any other chickadee nests during the study.

Dissections of 10 *P. asiovora* and 10 *P. sialia* females revealed the presence of mature ovarioles, but these species apparently rejected chickadees as hosts. Both *P. asiovora* and *P. sialia* have relatively wide host ranges (Bennett 1957; Whitworth 1976). The nesting period of chickadees exceeds that of many reported hosts (Harrison 1978) and should provide sufficient time for larval development. Additionally, Bennett (1957) and Kluyver and Eshuis-van der Voet (1970) showed that *Protocalliphora* can develop on abnormal hosts and suggested that selective oviposition by the parasite determines host specificity. It appears that oviposition of these species did not occur in chickadee nests.

Protocalliphora sialia was reared from the nests of western bluebirds (*Sialia mexicana* Swainson) in snags at the same height as and in the vicinity of chestnut-backed chickadee nests in Modoc County nestbox plots. Similar results have been reported for *P. sialia* in Utah by Whitworth (1976). These results suggest that different sets of stimuli are involved in host finding and acceptance. Long-range stimuli may attract male and female *P. sialia* to active nest sites while other stimuli must be involved in host acceptance and oviposition. However, it remains unclear why chickadee nests, once discovered, were rejected.

Also unclear is why we never saw *Protocalliphora* n. sp. adults coming to active chickadee nests. Possibly this species was active during early morning or crepuscular hours when observations were not made.

Host Specificity of *Protocalliphora* in Nests of Bird Species Other than Chickadees

We collected 170 nests fledging young from 28 species of birds outside of nestboxes (table 3). In addition to chestnut-backed and mountain chickadees and a Bewick wren, hosts for *Protocalliphora* n. sp. included a brown creeper (*Certhia americana* Bonaparte) and a barnswallow (*Hirundo rustica* L.). Dahlsten (unpublished data) had previously collected this species in the nest of a red-breasted nuthatch (*Sitta canadensis* L.) in California, and Whitworth (1976) also reported it in the nests of house wrens (*Troglodytes aedon* Vieillot) and an Oregon junco (=dark eyed junco) (*Junco hyemalis* [L.]).

Hosts of *Protocalliphora* n. sp. are primarily cavity-nesting birds in forests. Attack of cup nesters was uncommon and also associated with forest habitats. The infested barn swallow nest was under a bridge at the edge of Modoc National Forest, while barn swallow nests several kilometers from the forest contained other species of *Protocalliphora*. The infested junco nest reported by Whitworth (1976) was from a forest understory. Nests outside forests were free of this species.

Protocalliphora n. sp. has been reported from seven species of cavity-nesting birds, but the fact that it did not attack western bluebird nests in Modoc National Forest suggests that it does not indiscriminately attack all birds in tree holes.

In Contra Costa County, starlings (*Sturnus vulgaris* L.), barnswallows, and cliff swallows (*Petrochelidon pyrrhonota* Vieillot) were all free of *Protocalliphora*, although high infestation rates in nests of these birds occurred at other localities in this study and have been reported elsewhere (Bennett 1957; Whitworth 1976). Variability in *Protocalliphora* attack was noted by Whitworth (1976), who reported infestation rates in nests of barn swallows and Brewer's blackbirds that ranged from 0 to 100% for different sites. Similarly, Owen (1954) reported large yearly fluctuations in infestation rates by *Protocalliphora* in the nests of great tits.

Factors Influencing *Protocalliphora* Numbers Within Nests

Hatching dates in 1977 and 1978 for nests in Blodgett Forest and Modoc County plots were available for a total of 162 nests in which at least one nestling reached the age of 17 days. Site and stand data were collected for 34 of these nests at Blodgett Forest and for 50 nests at Modoc County. Nest volumes and weights were measured for all 84 nests active in 1978. Since not all parameters were measured for each nest, the data were analyzed through a series of regressions.

Protocalliphora n. sp. densities were significantly higher in Blodgett Forest chickadee nests than in Modoc County nests during 1977 ($p < 0.001$). Densities were not significantly different in 1978, although *Protocalliphora* numbers in Blodgett Forest nests remained almost twice as high as those in Modoc County (tables 1, 2). Higher parasite densities in Blodgett Forest could have resulted from a concentration of ovipositing females among the lower density of chickadee nests at this site.

Nest volume ranged from 5 to 440 cm^3 and was highly correlated with *Protocalliphora* n. sp. numbers ($p < 0.001$). Whitworth (1976) also reported correlation of *Protocalliphora* populations with nest size and believed that variability in *Protocalliphora* levels resulted from larval competition for resting spaces within the nest. He noted that larval and bird excrement were toxic to larvae and that buildup of these wastes in smaller nests reduced the available space suitable for larvae. Larvae withdrawing from crowded and contaminated portions of the nest may have increased chances of falling out of or otherwise leaving the nest.

Table 3. *PROTOCALLIPHORA* INFESTATION OF BIRD NESTS OTHER THAN CHESTNUT-BACKED AND MOUNTAIN CHICKADEES IN VICINITY OF STUDY SITES

Host species	Locality*	Nest type	Infestation	Species
Contra Costa County				
Barn swallow	CH	Cup	0/10	
Bewick wren	CCP	Cavity	1/3	*P.* n. sp.
Black phoebe	CH	Cup	0/2	
Brown towhee	BER	Cup	0/2	
Cliff swallow	BER	Gourd	0/17	
House finch	CH	Cup	0/2	
House sparrow	BER	Cavity	0/19	
Plain titmouse	CCP	Cavity	0/5	
Starling	CH	Cavity	0/6	
Western bluebird	CCP	Cavity	0/2	
Winter wren	CCP	Cavity	0/2	
Total			1/70	
Blodgett Forest				
Alder flycatcher	BF	Cup	2/4	*P. hesperoides*
American robin	BF	Cup	0/5	
Brown creeper	BF	Cavity	2/3	*P.* n. sp.
Dark-eyed junco	BF	Cup	0/8	
Steller's jay	BF	Cup	0/2	
Warbling vireo	BF	Cup	0/2	
Western flycatcher	BF	Cup	1/1	*P. sialia*
White-headed woodpecker	BF	Cavity	0/3	
Total			5/28	
Modoc County				
Barn swallow	MOD	Cup	9/12	*P. asivora* *P. hesperia* *P. hirundo* *P.* n. sp. *P. sialia*
Brewer's blackbird	ALT	Cup	0/1	
Chipping sparrow	MOD	Cup	0/3	
Cliff swallow	MOD	Gourd	5/6	Unidentified
House finch	ALT	Cup	2/2	Unidentified
House wren	MOD	Cavity	1/1	Unidentified
Long-billed marsh wren	ALT	Reed	0/12	
Red-breasted nuthatch	MOD	Cavity	1/1	Probably *P.* n. sp.
Starling	MOD	Cavity	1/4	Unidentified
Tree swallow	ALT	Cavity	2/2	*P. sialia*
Western bluebird	MOD	Cavity	2/3	*P. sialia*
White-breasted nuthatch	MOD	Cavity	0/1	
White-headed woodpecker	MOD	Cavity	0/1	
Yellow-headed blackbird	ALT	Cup	8/13	New species
Total			31/62	

* ALT: Alturas Wildlife Reserve
BER: Berkeley, California and Berkeley Hills
BF: Blodgett Forest
CH: Coyote Hills Regional Park
CCP: Contra Costa County Plots
MOD: Modoc Forest and Adin, California

We believe that, in chickadee nests, contamination was not a factor in determining parasite densities. Adult chickadees removed the fecal sacs of their young and, as a result, the nests were quite clean and dry. We found that larval wastes were, in fact, toxic to *Protocalliphora* n. sp. larvae held in petri dishes but did not appear to be important in chickadee nests. Additionally, parasite densities seldom approached the maximal levels recorded in a few nests, indicating that space availability was not a factor. Thus, a different mechanism must account for the relationship between chickadee nest volume and densities of immature *Protocalliphora.*

Bennett (1957) suggested that *Protocalliphora* has evolved on avian hosts because of the inability of nestlings to defend themselves against parasites. However, Kluyver (1974) speculated that parent birds actively search their nests for and feed on *Protocalliphora* parasites.

We were unable to observe adult chickadee behavior within the nests. Nevertheless, the hypothesis posed by Kluyver (1974) is consistent with the relationship we found between nest volume and the number of *Protocalliphora* larvae present. Larger nests afford larvae more material in which to hide from the probing activities of adult chickadees. In contrast, nests composed of very little material (less than 100 cm^3) were invariably free of *Protocalliphora.* Additionally, larvae commonly were found on the box bottom, underneath the nest material. A negative phototactic or geotactic response may have evolved as a defense against the probing activities of adult birds. This may also explain the preference of this species for cavity nests.

Protocalliphora n. sp. population density in nests was not correlated with any measured site and stand parameter, despite habitat preferences of their avian hosts within the forest (Sturman 1967; Dahlsten, unpublished data). It is possible that the strong dispersal capability of calliphorids might make nest cues more important than habitat features per se.

Life History of *Protocalliphora* n. sp.

Timing of oviposition

We examined 66 nesting efforts that terminated during the egg stage as a result of predation, abandonment, or mortality of adult chickadees. The absence of calliphorid eggs and *Protocalliphora* larvae in these nests indicates that oviposition of *Protocalliphora* n. sp. does not occur before chickadee eggs hatch. Oviposition only in the presence of nestlings is probably an adaptive feature. Emergence of *Protocalliphora* larvae before hatching of its host would leave adult birds as the only food source. Larvae attacking adult birds would be vulnerable to preening or to being carried away from the nest.

Oviposition of *Protocalliphora* n. sp. could occur immediately after the eggs hatch. First-instar larvae were detected in nests containing 2- and 3-day-old nestlings. These findings contrast with those of Bennett (1957), who believed that oviposition did not occur until the nestlings were 5 to 7 days old. We observed third-instar *Protocalliphora* n. sp. larvae in nests with 5-day-old birds and pupae in a nest where predation occurred with 6- or 7-day-old nestlings.

Protocalliphora n. sp., as well as *P. sialia*, continued to oviposit throughout the nestling period up to the time of fledging, even though oviposition in older nests provides larvae insufficient time to complete development. Examination of fledged chickadee and western bluebird nests occasionally revealed the presence of *Protocalliphora* eggs and first-instar larvae. To verify that these *Protocalliphora* were the result of late oviposition and not of delayed hatch, we exchanged a nest containing 17-day-old chickadee nestlings with a clean nest taken from Contra Costa County. When the

chickadees fledged 2.5 days later, this new nest contained more than 20 eggs and first-instar *Protocalliphora* larvae.

Multiple infestations

Most nests contained a range of *Protocalliphora* n. sp. larval sizes and instars indicating multiple infestation. For example, the presence of *Protocalliphora* eggs and first-instar larvae in recently fledged nests supporting high densities of mature larvae demonstrated that ovipositing females were not deterred by prior parasite presence. In addition, some infestation levels clearly surpassed the fecundity of any one female. We were unable to obtain gravid *Protocalliphora* n. sp. to determine egg potential for this species. However, dissections of *P. asiovora*, *P. sialia*, and *P. hirundo* females revealed that ovipositional capacity for one gonotrophic cycle was 90 eggs. *Protocalliphora* n. sp. densities in nests frequently exceeded this number (tables 1, 2) with a maximum density of 273.

Egg stage

Eggs commonly were encountered in collected nest materials, indicating that flies oviposited directly into the nest. Additionally, female *P. sialia* were observed entering open nestboxes and crawling directly into the nest material without investigating the nestlings. The egg size of *Protocalliphora* n. sp. and *P. sialia* averaged 0.11 by 0.02 mm, making it difficult to determine if eggs were ever placed directly on nestling birds. Most eggs in nest materials had been deposited singly.

Protocalliphora n. sp. eggs removed from nests hatched under ambient conditions within 36 hours, suggesting an egg stage of 1 to 2 days. The presence of larvae in nests 2 days after chickadee hatching and soon after nest exchanges further indicated an egg stage of less than 48 hours. Whitworth (1976) reported an egg stage of 38 to 43 hours in *P. chrysorrhea* (Meigen) and 72 hours in *P. sialia*.

Larval stage

The duration of the larval instars was estimated from the earliest appearance of each instar within a nest after chickadee hatching and after nest exchange. We assumed that the earliest oviposition occurred on the day the nestlings hatched and that the egg stage of the parasite lasted about 48 hours.

Protocalliphora n. sp. larvae obtained in four nest exchanges were measured, and instar determined (table 4). One nest, exchanged when the nestlings were 5 days old, already contained several small third-instar larvae. These data suggest that the first two instars may be completed in as little as 3 days. Based on larval sizes found within each instar (table 4), we believe that the first instar lasts 1 to 2 days, and the second instar 2 to 3 days.

Protocalliphora n. sp. third-instar larvae removed from nests containing 7-day-old nestlings successfully pupated and emerged as adults. Thus, it appears that the third instar can be completed in as little as 2 days. However, these pupae were undersized, and success of the small adults that emerged may have been reduced. Nevertheless, it appears that larval development in the third instar is rapid. Larvae in nests with 6- to 7-day-old nestlings had attained 60% to 70% of the maximal length for this stage.

Despite rapid development in the third instar, pupation of *Protocalliphora* n. sp. before chickadee fledging was uncommon. Pupae were seldom encountered in nests collected immediately after fledging although, on one occasion, pupae were found in a nest exchange involving 17-day-old nestlings. No pupae were ever observed in nests

Table 4. SIZES OF *PROTOCALLIPHORA* n. sp. EGGS OR LARVAE FROM CHICKADEE NESTS COLLECTED DURING NEST EXCHANGES IN WHICH MAXIMAL TIME FOR LARVAL DEVELOPMENT WAS KNOWN, MODOC COUNTY, CALIFORNIA, 1978

	Number of *Protocalliphora* at different stages* in nests															
	Nest 1 5 days◊				Nest 2 6 days◊				Nest 3 7 days◊				Nest 4 12 days◊			
Length of larvae	E	1	2	3	E	1	2	3	E	1	2	3	E	1	2	3
mm																
0 - 0.3	5	1											1			
0.4 - 0.7		19				1	1								1	
0.8 - 1.1			1				1								14	
1.2 - 1.5							3								31	
1.6 - 1.9							3				2				38	
2.0 - 2.3				2			3	1			3				28	1
2.4 - 2.7			1	2			3	3			3	2			16	17
2.8 - 3.1								5				2			11	22
3.2 - 3.5								3				4			2	11
3.6 - 3.9								5				7				18
4.0 - 4.3								2				5				14
4.4 - 4.7								3				5				10
4.8 - 5.1								2				5				5
5.2 - 5.5								4				2				
5.6 - 5.9								2				2				1
6.0 - 6.3																3
Total	5	20	2	4	0	1	14	30	0	0	8	34	1	0	141	102

* E = egg stage; 1 = first instar; 2 = second instar; 3 = third instar.
◊ Nestlings' age.

containing birds younger than 17 days. Therefore, larvae from infestations occurring early in the nesting cycle must have spent at least 10 to 12 days in the third instar and prepupal period.

Oviposition in nests containing older nestlings did not allow *Protocalliphora* n. sp. larvae sufficient time to complete development. Although Bennett (1957) reported that third-instar larvae could successfully pupate after one blood meal, we found that most smaller pupae (under 6 mm) failed to produce adult flies. Upon removal from nests, larger larvae entered the prepupal stage more quickly than smaller larvae. This stage was marked by a reduction in activity and a change in larval color from gray to white. The prepupal stage of *Protocalliphora* n. sp. lasted 2 to 3 days.

During the many daylight hours in which we monitored nestboxes, observations of chickadee nestlings being attacked by *Protocalliphora* were uncommon. Those few larvae found on birds quickly released themselves during handling or disturbance of the nestling. The *Protocalliphora* n. sp. larvae probably were not nocturnal feeders per se, since light and temperature conditions within the nest cavity remain fairly constant throughout the day. It is more likely that the larvae attacked nestlings at night because their hosts were less active at that time.

On the occasions that larval feeding was evident, red feeding marks were most commonly observed along new feather tracts, especially on the back and along the wing. Feeding marks were also seen on the feet, on the legs, and around the eyes. On several occasions, larvae entered the ears, and in one case this appeared to have led to the death of the nestling.

Protocalliphora n. sp. larvae were also observed feeding in the viscera of dead nestlings and in the stomach, thorax, and ears of adult chickadees killed by weasels. However, only once were *Protocalliphora* n. sp. encountered feeding on a dead bird

in the presence of live nestlings. At that time, four third-instar larvae were removed from the bird's brain cavity. Attack of dead nestlings in the absence of blood from living birds supports Bennett's (1957) suggestion that the evolution of a parasitic life style in Protocalliphora involved a shift from dead to live nestlings.

Pupal stage

Pupation of *Protocalliphora* n. sp. occurred from 4 days before host fledging until 7 days after the hosts left the nest. Most *Protocalliphora* n. sp. pupated within 2 to 3 days after fledging, suggesting that the prepupal stage began soon after hosts were no longer available.

Prepupae normally wrapped themselves with protective coverings constructed from nest material within which pupation occurred. Most often these pupal coverings were made of fur, but in nests containing little fur, sawdust or nest debris was used. On rare occasions, pupal coverings were formed from moss, and about 15% of the parasites pupated without any covering. As a result, pupal distribution was not random within the nest; most were found in the fur layer. Pupae were normally in clusters, and pupation within these clusters occurred more or less synchronously.

In 1978, *Protocalliphora* n. sp. adults reared from Blodgett Forest nests emerged an average of 25 days (range 15 to 36 days) after the nestlings had fledged. Assuming a prepupal stage of 3 days, the pupal period averaged 22 days.

Duration of the pupal stage differed considerably between the first and second halves of the 1978 nesting season in Modoc County. For nests fledging before July 11, the average elapsed time between fledging and fly emergence was 22.6 days, and less than 2% of the flies emerged within 17 days of fledging. In contrast, for nests fledging after July 11, 56% of the flies had already emerged before nest collection, 16 to 19 days after fledging, and flies were observed emerging from nests as early as 7 days after fledging. The average time of emergence for the remaining 44% of *Protocalliphora* n. sp. pupae was 20.7 days after fledging.

Since pupae were observed in nests with 17-day-old nestlings, the duration of the pupal period would be at least 11 days and at most 33 days. Undoubtedly, the duration of the pupal period was affected by timing of pupation and ambient temperature. Parasites pupating while nestlings were still present would have the advantage of elevated temperatures within the nestbox before fledging.

Emergence of adults

Peak emergence of *Protocalliphora* n. sp. adults occurred between 0900 and 1500 Pacific Standard Time. Emergence of adults from some nests was concentrated into one or a few days, while in other nests emergence was spread out over as many as 20 days. On average, females tended to emerge 1 to 2 days ahead of males. This suggests the need for prenuptial development by females.

The male:female sex ratio for *Protocalliphora* n. sp. reared from chickadee nests in Blodgett Forest in 1978 and 1979 and from Modoc County in 1978 was 1:1.71 (N = 2,750). Earlier emergence of females and the fact that many flies had emerged before collection of nests in Modoc County during the second half of 1978 suggest that the sex ratio may be weighted even more toward females.

Adult behavior in captivity

Reared *Protocalliphora* n. sp. adults, maintained in sleeve cages, had temperature thresholds of 15.5°C for activity and 17.5°C for full flight capability. During the day, the flies tended to congregate in the parts of the cage exposed to direct sunlight.

Sugar cubes and raisins were accepted food sources, while liquid protein amylase and bird excrement were rejected. The blood diet of larvae may have rendered additional protein sources superfluous, although it is not known if supplemental protein would be necessary for egg production. Dissections of males revealed that they were capable of producing motile sperm. However, caged females did not produce eggs.

Mating was not observed in either *Protocalliphora* n. sp. or in *P. sialia* (reared from western bluebird nests). Three to 4 months after emergence, the spermathecae in *Protocalliphora* females did not contain sperm, confirming that mating did not occur. These results contrast with those of Bennett (1957), who observed frequent mating and courtship behavior in *P. sialia* and other species, which commenced soon after emergence.

Absence of mating in newly emerged *Protocalliphora* n. sp. adults may be related to a univoltine life cycle. While chestnut-backed and mountain chickadee breeding cycles are not entirely synchronous at the California study sites, they are sufficiently so that most breeding is completed by the time the first *Protocalliphora* adults emerge from chickadee nests. Late nests (principally renests and second clutches) account for only a small percentage of chickadee nest efforts (Dahlsten and Copper 1979). The host specificity of this species precludes the possibility of switching to other bird hosts that nest later in the season.

Newly emerged *Protocalliphora* n. sp. adults were transferred from Blodgett Forest to Modoc County which, due to differences in elevation, had a later nesting season. These adults were placed in vials stoppered with gauze, which in turn were put in active chickadee nests. Such exposure to chickadee nestlings failed to induce mating or ovarial development. Additional *Protocalliphora* n. sp. reared from Blodgett nests and confined in a sleeve cage with a recently fledged nest likewise failed to stimulate reproductive behavior. These results further suggest that *Protocalliphora* n. sp. is univoltine.

Dissections of 10 *P. sialia* females, collected at nests, showed that this species is at least biparous. Whitworth (1976) found females of *P. asiovora* and *P. chrysorrhea* to have three immature follicles attached to each mature ovariole. We did not observe adult *Protocalliphora* n. sp. coming to active chickadee nests and so were unable to determine its parity. *Protocalliphora* n. sp. is probably multiparous with a single generation of flies responsible for infestations of both early and late nests.

Longevity and overwintering of adults

Adult *Protocalliphora* n. sp. maintained in sleeve cages survived for up to 130 days, even though they were kept in an artificial environment and were damaged in flying against the sides of the cage. In late October, dissected flies contained a buildup of fat bodies, indicating preparation for entering diapause. Longevity of caged males and females was equal. Thus it appears that both sexes overwinter and mate in the spring.

Field observations of adult *Protocalliphora* attracted to nestboxes

Adults were observed at an active chestnut-backed chickadee nest within a snag near the nestbox plots at Blodgett Forest. In 45 observations of adult flies over a 2-day period, greatest *Protocalliphora* activity occurred when the nest was exposed to full sunlight. Of 31 adults collected from the snag, 16 were male. Females were observed entering the nest, but no *P. asiovora* were reared from either this nest or any other chickadee nest in Blodgett Forest.

In Modoc County plots, *P. sialia* adults of both sexes were observed on nestboxes containing active mountain chickadee nests. On two occasions, female flies entered

an open nestbox while we were counting chickadee nestlings. Both times the fly crawled underneath the nestlings into the fur cup. These flies were collected and identified as *P. sialia*. *Protocalliphora sialia* was not reared from either of these nests, and we believe that oviposition did not take place.

Adult *Protocalliphora* were observed at first nests in both sites. The appearance of both male and female *Protocalliphora* at these nests confirms the overwintering of both sexes and suggests that mating occurs near nest sites. The chestnut-backed chickadee nest in the Blodgett Forest snag was the earliest nest encountered at this site. When first discovered, it contained nestlings approximately 14 days old. Female *P. asiovora* collected at this time had mature ovarioles, and fully developed larvae of *Protocalliphora* n. sp. were found in the nest upon its collection a week later. It seems likely that stimuli from chickadee nests during egg brooding stimulates mating behavior and subsequent egg production in *Protocalliphora*.

Protocalliphora attacking cavity-nesting birds do not appear to be attracted to cavity holes per se. During the many days we spent monitoring nestboxes, we did not observe flies on empty boxes or in spiderwebs within empty boxes. Stick-em traps on empty boxes that had contained high *Protocalliphora* densities the previous year were likewise free of *Protocalliphora*. Additionally, male *P. asiovora* and *P. sialia* at active nests were observed in the nest vicinity but were not seen inspecting the cavity itself.

Several observations suggest that *Protocalliphora* use odor in locating active nests. A male *P. asiovora* and a female *P. sialia* were collected at recently fledged nests. Additionally, an unidentified female *Protocalliphora* was observed on the interior of a nestbox in which weasel predation had occurred earlier in the day. Since live chickadees were no longer present at these nests, such stimuli as $C0_2$, heat, and sound could not have served as attractants, although nest odor would still be present. Nest odor may vary among bird species and may aid in directing the parasite to a suitable host.

Natural enemies of *Protocalliphora* n. sp. in nestboxes

In 1978, parasitism of *Protocalliphora* n. sp. pupae in mountain chickadee nests in Modoc County was determined by exit holes or, where no exit holes were present, by dissection. Since absolute numbers of *Protocalliphora* n. sp. could be determined per nest by puparial remains, parasitization rates provide an accurate picture of true parasitism. Known parasitoids of *Protocalliphora* are pupal parasitoids; therefore, parasitization rates were affected by the timing of nest collection and, hence, exposure time of the *Protocalliphora* pupae to parasitoids in the field.

Three parasitoids attacked *Protocalliphora* n. sp. The dominant one was the pteromalid *Nasonia vitripennis* Walker (= *Nasonia brevicornis* and *Mormoniella vitripennis*). This species was common in both Blodgett Forest and Modoc County chickadee nests in 1977 and 1978. This parasitoid has a wide host range (Peck 1963). Its biology has been described by Schneiderman and Horowitz (1958) and Whiting (1967).

A second pteromalid, *Morodora armata* Gahan, was reared from a single puparium, from a Blodgett Forest nest, in 1977 but was fairly common in both Blodgett Forest and Modoc County plots in 1978. As far as is known, this parasitoid is specific to *Protocalliphora* and has been reported only from *P. avium* (C. W. Sabrosky, personal communication) and *Protocalliphora* n. sp. No biological information is available for this species.

The encyrtid *Tachinaephagus zealandicus* Ashmead was reared from *Protocalliphora* n. sp. collected from a Bewick wren nest in the Contra Costa County plots. This species had been introduced into California from New Zealand (Olton and Legner 1974), and parasitization of *Protocalliphora* n. sp. represents a new host record (Gold

Table 5. FATES OF *PROTOCALLIPHORA* n. sp. PUPARIA, WRAPPED OR NOT WRAPPED IN PUPAL COVERS CONSTRUCTED OF NEST MATERIAL, IN NESTS IN BLODGETT FOREST AND MODOC COUNTY, 1978

Puparia	Emerged		Parasitized		Dead	
With pupal covers	999	(78.2%)	155	(12.1%)	124	(9.7%)
Without pupal covers	269	(61.3%)	100	(22.8%)	70	(15.9%)

Emerged and parasitized only, chi square: 37.4 ($p < 0.01$).
Emerged and (parasitized + dead), chi square: 43.22 ($p < 0.01$).

and Dahlsten 1981). *Nasonia vitripennis* and *M. armata* were also reared from the same nest.

Parasitization of *Protocalliphora* n. sp. in mountain chickadee nests in Modoc County in 1978 was 9.02%, and only 30.3% of chickadee nests containing *Protocalliphora* n. sp. showed any parasitization at all. This parasitization rate was quite low compared with that found in other studies (for example, Johnson 1927, 1932; Whitehead 1933; Boyd 1936) where parasitization exceeded 88%. Additionally, in Modoc County, parasitization of *Protocalliphora* in tree swallow and yellow-headed blackbird nests exceeded 90%.

Nasonia vitripennis and *M. armata* are gregarious ectoparasites. Parasitoid numbers ranged from 3 to 28 per puparium but were most often between 15 and 20 per puparium. Emergence of non-overwintering parasitoids averaged 12.6 days after emergence of the last *Protocalliphora* n. sp. adult from a given nest. Seventy-eight percent of the parasitoids overwintered as larvae within *Protocalliphora* n. sp. puparia. Overwintering larvae were found in both early and late nests. On occasion, several parasitoids emerged from a given puparium while others overwintered. Overwintering *N. vitripennis* and *M. armata* emerged in March and April of the following year.

Nasonia vitripennis and *M. armata* oviposited in housefly pupae (*Muscus domesticus* L.) in the laboratory. Both parasitoids exhibited host feeding before and/or after parasitization, and mortality of pupae not producing parasitoids was greater than 70%. In contrast, housefly pupae controls had nearly 100% emergence.

In one experiment, nine *Protocalliphora* n. sp. pupae were exposed to a single *N. vitripennis* female found in a mountain chickadee nest in Blodgett Forest in 1979. Emergence of wasps began 18 days after first exposure, and a total of 89 wasps emerged from six pupae. The remaining three pupae died and dissection revealed no signs of parasitization, suggesting host feeding as the source of mortality.

Pupal coverings provided *Protocalliphora* n. sp. protection against parasitization. In nests with substantial parasitization, 22.8% of pupae without coverings were parasitized compared with 12.1% for those with cases (Chi square = 37.4; $p < 0.01$) (table 5). Eshuis-van der Voet (1975) observed a similar trend for parasitization of "wrapped" and "unwrapped" *P. azurea*.

Carpenter ants, *Camponotus modoc* Wheeler, tunneled in nest material soon after nestlings fledged but were not present in active nests. We observed these ants removing marked pupae placed in nests. The presence of pupal cases is not believed to be a deterrent to the foraging of carpenter ants (G. C. Wheeler, personal communication). Since many ants were present in some nests, it is possible that they may significantly reduce the number of adult flies that emerge.

Predators of minor importance include clerids and spiders. Clerid larvae occasionally were encountered in nests. These accepted *Protocalliphora* n. sp. pupae in the

laboratory. Orb-web spiders, building webs in boxes after nest termination, were observed feeding on emerging adult *Protocalliphora.*

All recorded natural enemies of *Protocalliphora* are active in nests only after the parasite's hosts have fledged. Thus the effect of parasitoids and predators will be limited to an influence on the size of the overwintering population of flies.

FUTURE RESEARCH CONSIDERATIONS

The importance of *Protocalliphora* as a limiting factor in chickadee populations remains unclear. Parasitization of nestling birds by *Protocalliphora* spp. may result in nestling death or reduced post-fledging success (Whitworth 1976; Gold and Dahlsten 1983). Field determination of the effects of different parasite densities on chickadee survival is virtually impossible to ascertain, since first-year birds disperse from study sites. However, relating fledgling survival to parasite load may be determined through banding returns for bird species that remain in original nesting sites.

Chestnut-backed and mountain chickadees produce far more offspring than will survive the first year (Dahlsten and Copper 1979). Increased mortality rates for those fledglings weakened by parasite attack may be compensated for by relaxed density-dependent processes. More information is needed on the effects, if any, of *Protocalliphora* on the population densities of host birds. It is clear, however, that this type of information would be quite difficult to obtain.

ACKNOWLEDGMENTS

William Copper and Katharine Sheehan provided much advice in working with chickadees and helped in the collection of data. Paul Gutierrez and Carol Bortfeld Stine also assisted in data collection. We are grateful for the critical comments on earlier versions of this manuscript offered by John R. Anderson, Stephen F. Bailey, Curtis W. Sabrosky, and two anonymous reviewers. David L. Rowney and Susan M. Tait assisted with proofing.

We thank Curtis Sabrosky and Gordon F. Bennett for identification of *Protocalliphora* and E. E. Grissell for identification of parasitoids. Leonard Marascuilo and David Rowney provided suggestions in the analysis of site and stand data.

Harry Dano of the East Bay Municipal Utility District permitted us to use District land for establishment of the Contra Costa nestbox plot. We also thank the following people for permission to collect nests: E. Clark Bloom at the Alturas Wildlife Refuge, Wallace Cromwell at Coyote Hills Regional Park, Charles Crabbe for use of nestboxes at the University of California, Davis, and Jennifer White at the Lawrence Hall of Science.

LITERATURE CITED

BEDARD, J., and J. N. McNEIL
1979. *Protocalliphora hirudo* (Diptera: Calliphoridae) infesting Savannah Sparrow, *Passerculus sandwhichensis* (Aves: Fringillidae) in eastern Quebec. Can. Entomol. 111:111-12.

BENNETT, G. F.
1957. Studies on the genus *Protocalliphora* (Diptera: Calliphoridae). Ph.D. dissertation. Univ. Toronto.

BEZZI, M.
1922. On the dipterous genera *Passeromyia* and *Ornithomusca* With notes and bibliography on the non-pupiparious Myiodaria parasitic on birds. Parasitology 14:29-46.
BOYD, A. W.
1936. Report on the swallow enquiry, 1935. British Birds 30:98-116.
COUTANT, A. F.
1915. The habits, life history, and structure of a blood sucking muscid larva (*Protocalliphora azurea*). J. Parasit. 1:131-50.
DAHLSTEN, D. L., and W. A. COPPER
1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and its impact on selected forest insects. *In*: The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J A. Jackson, and J. C. Croll, eds.), pp. 217-60. New York: Academic Press.
DOBBEN, W. H. van
1969. Institute of Ecological Research Progress Report 1968. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 58:24-32.
DOBROSCKY, I. D.
1925. External parasites of birds and the fauna of birds' nests. Biol. Bull. Woods Hole 48:274-81.
ESHUIS-van der VOET, C. W.
1972. Parasitism by *Protocalliphora azurea* (Fall). Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 61:73-74.
1975. Parasitism by *Protocalliphora* spp. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 66:81-84.
ESHUIS-van der VOET, C. W., and E. HOUWINK
1976. Parasitism by *Protocalliphora* spp. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 67:116.
ESHUIS-van der VOET, C. W., and H. N. KLUYVER
1971. Parasitism by *Protocalliphora azurea* Fall. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 60:50-51.
ESHUIS-van der VOET, C. W., and R. H. de REEDE
1974. The effect of parasitism by *Protocalliphora*. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 63:77-79.
GOLD, C. S., and D.L. DAHLSTEN
1981. A new host record for *Tachinaephagus zealandicus* (Hym: Encyrtidae). Entomophaga 26:459-60.
1983. Effects of parasitic flies, *Protocalliphora* spp. on nestlings of Mountain and Chestnut-backed Chickadees. Wilson Bull. 95:560-72.
HARRISON, C.
1978. A Fieldguide to the Nests, Eggs, and Nestlings of North American Birds. Glasgow: William Collins. 416 pp.
JOHNSON, C. W.
1927. Further studies of *Protocalliphora* infesting nestling birds. Bird Banding 3:77-82.
1932. Notes on *Protocalliphora* during the summer of 1931. Bird Banding 3:26-29.
KLUYVER, H. N.
1974. The behavior of Great Tits toward the parasite *Protocalliphora azurea* (Fall). Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 63:77.

KLUYVER, H. N., and C. W. ESHUIS-van der VOET
1970. Parasitism by *Protocalliphora* sp. Verh. K. Ned. Akad. Wet. Afd. Natuurk. de Tweede Reeks 59:48.
LACK, D.
1966. Population Studies of Birds. Oxford: Clarendon Press. 341 pp.
MASON, E. A.
1944. Parasitism by *Protocalliphora* and management of cavity-nesting birds. J. Wildl. Mgmt. 8:232-47.
OLTON, G. S., and E. F. LEGNER
1974. Biology of *Tachinaephagus zealandicus* (Hymenoptera: Encyrtidae), parasitoid of synathropic diptera. Can. Entomol. 106:785-800.
OWEN, D. F.
1954. *Protocalliphora* in birds' nests. Brit. Birds 47:236-43.
PECK, O.
1963. A catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). Can. Ent. Supplement 30:1-1092.
PLATH, O. E.
1919a. Parasitism of nestling birds by fly larvae. Condor 21:30-39.
1919b. A muscid fly of the San Francisco Bay region which sucks the blood of nestling birds. Publ. Univ. Calif. Berk. Zool. 19:191-200.
1919c. The prevalence of *Phormia azurea* (larva parasitic on nestling birds) in the Puget Sound region and data on two undescribed flies of similar habit. Ann. Entomol. Soc. Amer. 12:378-81.
SCHNEIDERMAN, H. A., and J. HOROWITZ
1958. The induction and termination of facultative diapause in chalcid wasps *Mormoniella vitripennis* (Walker) and *Tritneptis klugii* (Ratzeburg). J. Exper. Biol. 35:520-51.
SOMME, F. M.
1961. On the overwintering of house flies (*Musca domestica* L.) and stable flies (*Stomoxys calcitrans* L.) in Norway. Norsk. Ent. Tidssh. 11:192-223.
STlNER, F. M.
1969. Overwintering by *Protocalliphora metalica* (Diptera: Calliphoridae). Ann. Entomol. Soc. Amer. 62:1205-6.
STURMAN, W. A.
1967. Description and analysis of breeding habits of the chickadees, *Parus atricapillus* and *P. rufescens*. Ecology 49:418-31.
WHITEHEAD, W. E.
1933. Parasites from a bird's nest. J. Econ. Entomol. 26:292-93.
WHITING, A. R.
1967. The biology of the parasitic wasp *Mormoniella vitripennis* (= *Nasonia brevicornis*) (Walker). Q. Rev. Biol. 42:333-406.
WHITWORTH, T. L.
1971. A study on the biology of the species of *Protocalliphora* in the northern Wasatch Range. M.S. thesis. Logan: Utah State University.
1976. Host and habitat preferences, life history, pathogenicity and population regulation in species of *Protocalliphora* Hough (Diptera: Calliphoridae). Ph.D. dissertation. Logan: Utah State University.
ZUMPT, F.
1965. Myiasis in man and animals in the Old World. Washington, D.C.: Butterfield. 267 pp.