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Behavior and Reproductive Physiology of Blood-sucking Snipe Flies (Diptera: Rhagionidae: *Symphoromyia*) Attacking Deer in Northern California

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At the University of California Hopland Field Station in Mendocino County, six species of hematophagous *Symphoromyia* attacked the Columbian black-tailed deer, *Odocoileus hemionus columbianus,* during the months of transition (April through June) from the rainy season to the drought season. Between 1964 and 1966, *S. pachyceras, S. cervivora, S. inconspicua, S. nana, S. truncata,* and *S. sackeni* had similar seasonal patterns of abundance, with each present 6 to 10 weeks.

Minimum temperature thresholds at which *Symphoromyia* attacked were determined for five species. The upper temperature threshold for attack by *S. sackeni* was between 34.4 and 37.2°C. Diverse wind and light conditions had little effect on the host-seeking behavior of the species studied.

Symphoromyia attacking deer were seldom attracted to hosts other than deer, and only *S. sackeni* and *S. pachyceras* fed on other hosts. The seasonal occurrence of snipe flies coincided with the annual spring shedding of winter pelage by the deer and, in bucks, with the growth of antlers. All *Symphoromyia* attacked only the face, ears, or antlers of deer after relatively direct approach, and most species engorged within 1 to 3 minutes. There was a direct relationship between snipe flies feeding on the ears and face and the more rapid loss of the woolly underhairs at these sites. The tilted posture of feeding snipe flies that angled the body upward between and above raised guard hairs permitted feeding on the outer ear surface, a site where most other blood-sucking flies are repulsed by the sensory guard hairs.

The number of *Symphoromyia* attracted to an individual deer and to the face or ears of an animal varied greatly. The tolerance to flies and the anti-biting fly behavior of individual deer (ear flicking, brushing flies from the face, and reducing the silhouette by lying down, lowering the head, flattening the ears, and extending the legs) contributed to variations in numbers of snipe flies on and around the hosts.

(Continued on inside back cover)

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INTRODUCTION AND OBJECTIVES

REPORTS OF ATTACKS on vertebrates by blood-sucking rhagionids of the genus *Symphoromyia* Frauenfeld have been made sporadically since Osten Sacken's (1877) original observation. Most reports are of man being attacked, but we became interested in these flies when observing large numbers of *Symphoromyia* attacking Columbian black-tailed deer (*Odocoileus hemionus columbianus* (Richardson)) in Mendocino County, California, during late spring of 1963. Since our initial studies of the behavior of selected species, detailed taxonomic studies of these *Symphoromyia* have been conducted by Turner (1974) and Turner and Chillcott (1973). In North America members of the family Rhagionidae are commonly known as snipe flies.

Evaluation of *Symphoromyia* as pests or vectors requires knowledge of the general biology of the group and of fly-host interactions. Such knowledge allows comparison between the genus *Symphoromyia* and other rhagionids and tabanoids, and may lead to a better understanding of the behavior of flies known to be vectors. Locally abundant outbreaks of *Symphoromyia* species during certain years can cause annoyance to humans, livestock, and game animals, but their potential medical and veterinary importance is unknown. Mills (1943) suggested that rhagionids might be vectors of tularemia and similar diseases, and the intermittent probing of individual flies attempting to take a blood meal (Shemanchuk and Weintraub, 1961) increases the probability of flies acting as mechanical vectors. Current urbanization and increasing recreational use of foothills in California intensifies the need for information on the hosts and feeding behavior of indigenous snipe fly species.

Apart from a basic interest in the vector potential of the *Symphoromyia* species at the study area, the major objectives of this study were to determine the following:

1) Number of species attacking deer.
2) Seasonal occurrence and abundance of each species attacking deer.
3) Spectrum of hosts attacked by the deer-feeding species, and their potential as pests of humans and domesticated animals.

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4) Daily biting activity, the feeding behavior of each species, and the resulting behavior of the hosts attacked.
5) Effect of weather on biting activity.
6) Reproductive biology and voltinism of each species.
7) Characteristics of nulliparous and parous females, and the parity of females attacking deer throughout the season.

Historical Review of Blood-feeding in the Family Rhagionidae

The Rhagionidae is a cosmopolitan family of flies that, according to Oldroyd (1964, p. 109), "... stand(s) at the base of the stem of evolution of all Brachycera..." Hematophagous members of the family have been reported from Australia, Europe, North America, South America, and Japan. The genus *Dasyomma* was the first recognized as having hematophagous species; but although Philippi reported *Dasyomma obscurus* Philippi biting in Chile in 1865, *Symphoromyia* was the first genus in the family to be widely recognized as hematophagous (Osten Sacken, 1877; Aldrich, 1915; Riley and Johannsen, 1915). The one other report of *Dasyomma* species biting vertebrates is the following footnote, signed by F. W. Edwards, on page 200 of Malloch (1932): "We observed this habit in two or three species, but unfortunately no exact record was kept of the observations. *D. coeruleum* and *D. humeralis* were taken on an ox used as bait for blood-sucking flies in the forest at Castro."

There is an unconfirmed report by Heim and Leprevost (1892) of *Rhagio scolopacea* L. and *R. strigosa* Meig. biting man. Paramanov (1962) stated that the genus *Spania* (=*Spaniopsis* in part) contains hematophagous members, as *Atrichops* and *Suragina* (Knab, 1912; Desportes, 1942). Malloch (1932) suggested that the genus *Austroleptis* was probably hematophagous, on the basis of its close relationship to *Spaniopsis,* but Chillcott (1963) placed *Austroleptis* in a generic grouping that does not include *Spania* or *Spaniopsis.*

Atrichops crassipes (Meigen) was suspected of transmitting a filarial worm of frogs after Desportes (1942) discovered that this species sucked blood from frogs. Although the hematophagous habit of *A. crassipes* was established as fact, development of infective nematode larvae did not occur in this species. Nagatomi (1962) reported two additional species of *Atrichops* feeding on frogs.

Suragina is another poorly studied genus whose members reportedly suck blood. Until quite recently (Stuckenberg and Young, 1973) only *Suragina longipes* (Bellardi) had been reported biting (Knab, 1912). Stuckenberg and Young (1973) reported *Suragina bivittata* (Bezzi) sucking blood from the upper eyelids of the Giant Eagle Owl (*Bubo lacteus* Temminck) in South Africa. The genera *Atrichops, Dasyomma,* and *Suragina* recently have been placed in the family Athericidae (Stuckenberg, 1973).

The genus *Spaniopsis* White is a "well-known pest of man" (Downes, 1958). However, this statement is undocumented as is Paramonov's declaration in 1962 that *Spania* (=*Spaniopsis*) is a biter of man. Tillyard (1926) referred to the genus *Spaniopsis* as "the biting flies," but again there is no documentation of a specific case of biting. White (1914) regarded the genus *Spaniopsis* as blood-sucking on the basis of a personal communication from Mr. G. H. Hardy.

Two authors have generalized about the acquisition or loss of the hematophagous habit within the Rhagionidae. Knab (1915) suggested that *Symphoromyia pachyceras* Williston was in a "transition state." He did not indicate

a direction of evolution, but quoted personal communication with W. H. Boyd, who reported that *S. pachyceras* "bites for itself on unprotected portions of animals, but seems to prefer to take blood oozing from a bite left by the larger fly" (*Tabanus*). Downes (1958), commenting in much broader terms on blood-sucking Diptera, said,

> "In all families certain species provide for the first maturation of the ovaries from internal reserves; they may or may not subsequently feed and lay again; similarly the mouth parts may or may not be reduced. The loss of the blood-sucking habit, with varying degrees of structural reduction, also occurs in larger groups (*Harpagomyia, Dasyhelea, Rhagio,* Chaoborinae, Psychodinae, Scepsidinae). The nonbiting species or groups are irregularly scattered within normal, biting taxa, and may reasonably be regarded as secondary."

Hematophagous behavior in the Genus *Symphoromyia*

The approach of two species of *Symphoromyia* prior to biting has been described as similar to that of the tabanid genus *Chrysops* (Aldrich, 1915; Shemanchuk and Weintraub, 1961). Specimens of *S. hirta* Johnson collected in Montana approach silently, and generally singly, and were easily picked off while they were taking blood (Knab and Cooley, 1912). *Symphoromyia hirta, S. kincaidi* Aldrich, and *S. atripes* Bigot have been observed to "swarm" around the host and, in the case of *S. hirta,* to produce an intense, loud hum (Ross, 1940; Shemanchuk and Weintraub, 1961; Frohne, 1959; Frohne and Williams, 1951).

Frohne (1959) described *S. atripes* and *S. kincaidi* as "purposeful biters," while Ross (1940) used the term "persistent" in describing the attack of *S. atripes* as did Knowlton and Maddock (1944) for *S. hirta,* but none of these authors made it clear whether the persistence applied to the approach or to the behavior after landing. In sharp contrast, Shannon (1915) stated that *S. hirta* from the eastern United States was very shy and remained on the host only a short time.

The host range of *Symphoromyia* is quite wide for certain species and narrow for others. Man is by far the most frequently reported host but, as the present study indicates, this probably reflects a lack of information about the genus. Various species of *Symphoromyia* have been reported biting hosts ranging in size from human babies (Frohne and Williams, 1951) to horses (Aldrich, 1915; Hearle, 1928) and cattle (U.S.D.A., 1958 and 1960; Shemanchuk and Weintraub, 1961).

Clear statements of host preference among *Symphoromyia* are rare. Aldrich (1915) suggested that *S. atripes* and *S. kincaidi* preferred horses, but would bite passengers in a stage coach. Frohne and Williams (1951) also reported a mixed population of *S. atripes* and *S. kincaidi* biting man and dog.

Shemanchuk and Weintraub (1961) found that *S. hirta* was not generally attracted to livestock but that some yearling and calf steers were attacked. Flies congregated about the head and to a lesser degree about a raw brand of a calf tethered in the brush. Yearling cattle in open and windy areas had no snipe flies, though they were attacked by horse, deer, and horn flies. Three horses on the windward side of buildings also attracted no snipe flies. Hearle (1938) reported that *Symphoromyia* spp. attacked pack horses and sheep in the higher plains of British Columbia.

Symphoromyia hirta has bitten humans on the head, neck, arms, and wrists (Knab and Cooley, 1912; Aldrich, 1915; Mills, 1943; Shemanchuk and Weintraub, 1961), as has *S. limata*

(Coquillett) (Hoy and Anderson, 1966).

Effects of biting flies of the Genus *Symphoromyia* on their hosts

Of the references cited above, only two (Shemanchuk and Weintraub, 1961; Frohne, 1959) gave more than cursory treatment to the attack and feeding behavior of the flies, and Frohne (1959) devoted most of his effort to correlation of biting rates with physical environment.

The psychological and physical reactions of the hosts are poorly reported in most cases. Frohne and Williams (1951) mentioned that *S. atripes* inflicts a "rather painful" bite. Ross (1940) was more emphatic. In 1959 Frohne suggested the bite of *S. atripes* was more painful than a mosquito bite. Aldrich (1915) described the trickling of blood from wounds inflicted on horses by the bites of *S. atripes*. Cockerell (Aldrich, 1915) and Cooley (Knab and Cooley, 1912) disagreed on the pain inflicted by the bite of *S. hirta,* the former saying that "The wound was not painful," and the latter describing the bite as "a painful wound" which caused swelling. Stanford (1931) reported that the bite of *S. hirta* was rather painful but did not cause swelling. Mills (1943) used the term "savage" to describe the bite. Shemanchuk and Weintraub (1961) presented detailed descriptions and photographs of the bite reaction to *S. hirta.* They described the bite as very painful but producing varied reactions among four individuals: one reacted violently; two had moderate inflammation and one was unaffected. Mills (1943) also reported variation in human reactions to bites of *S. hirta,* but the paper by Shemanchuk and Weintraub (1961) presents the most complete description to date of the bites and host reactions to *Symphoromyia.* The bite of *S. kincaidi* has been characterized as "rather painful" (Frohne and Williams, 1951), and *S. pachyceras* was reported to be a "vicious biter" by Riley and Johannsen (1915), citing the personal experience of Dr. J. C. Bradley. The only report of *S. sackeni* Aldrich regarding the pain of the bite is that of Wirth (1954) who described the bite as "painful." Sommerman (1962) associated two types of larvae (species "A" and "B") with adults that inflict painful bites.

MATERIALS AND METHODS

Location and description of the study area

All field work was conducted at the University of California Hopland Field Station (H.F.S.) in southeastern Mendocino County, California (about 160 km north of San Francisco and 64 km inland from the Pacific Ocean). The 1,890 hectares of land making up the Station are within a 4.8 × 7.6 km strip along the southwest slope of a ridge dominated by Cow Mountain and forming the eastern margin of the Russian River Valley. The elevation varies from 150 m along the west boundary to nearly 1,000 m along the northeast boundary. The topography can be summarized as rolling hills interspersed with ravines, thus producing many north- and south-facing slopes. According to Heady (1961), vegetation types are: woodland-grass (36.0%), grass (22.8%), dense woodland (21.8%), and chaparral (14.9%). The chaparral is primarily at higher elevations. In terms of community ecology, the area fits nicely into the concept of the Summer Drought or Broad Sclerophyll-Grizzly Bear Community (Shelford, 1963).

Heady (1961) reported nearly 400 species of plants collected on the Station and noted that the woodland-grass

vegetation type is "... an overstory of black oak (*Quercus douglasii* H. & A.), valley oak (*Q. lobata* Nee), and other trees and a grass understory that is similar to the grass type.... The dense-woodland type, primarily evergreen, has little grass under the trees. . . ." (Heady 1961). The canopy is liveoak (*Q. wislizenii* A. DC), bay (*Umbellularia californica* H. & A.), madrone (*Arbutus menziesii* Pursh.), and black oak (*Q. kelloggii* Newb.).

Domestic sheep and black-tailed deer are the predominant large mammals on the H.F.S., with jack rabbits (*Lepus californicus* Gray), coyotes (*Canis latrans* Say), skunks [*Mephitis mephitis* (Schreben) and *Spilogale gracilis* Merriam] and raccoons (*Procyon lotor* L.) common in the area. About 20 to 30 cattle were grazed on a couple of semi-open rangeland pastures each spring.

Biting flies are well represented by ceratopogonids, culicids, simuliids, tabanids, psychodids, and a wealth of rhagionids (Anderson and Hoy, 1972; Anderson, Olkowski, and Hoy, 1974; Weinmann et al., 1973).

The climate at H.F.S. is a Mediterranean type with a winter rainy season and a summer dought. The first effective rains (over 2.54 cm) and last effective rains (over 2.54 cm) occur around October 23 and April 21 respectively (Heady, 1961). The mean rainfall per season was 91.08 cm (35.86 inches) with a maximum of 153.49 cm (60.43 inches) and a minimum of 62.28 cm (24.52 inches) during the 13 seasons beginning 1951. Much of the rainy season is characterized by fog and drizzling rains, hence insolation is much reduced.

First frosts occur during October and early November, and last frosts between late March and mid-May (Heady, 1961).

Daily high and low temperatures differ by approximately 17°C (30°F) during the months of April through June. Daily highs occasionally reach 38°C during these months, but more commonly range from the low twenties to the low thirties. Relative humidity reaches 100 percent nearly every night during April, May, and June and falls to as low as 10 percent on the warmer days of that period.

Although daily variations in maximum wind speeds are quite pronounced, a pattern prevails of calm or light wind in the morning, followed by stronger winds in mid- and late afternoon and eventual evening calm.

Descriptions of fenced habitat areas

All observations of flies attacking deer were carried out in the two sets of specially constructed pens described below.

Four Deer Holding Pens of 0.5 ha each, all opening on a single corral, were used extensively during the 1964 season for study of tame deer and for study of flies attacking a group of wild range deer during the 1965 season. These pens were located 800 m east of Station headquarters at an elevation of 274 m. There is a 1.62-ha lake (Headquarters Lake) about 180 m south of the pens, which are otherwise surrounded by dense woodland on the west and north, and open woodland and grassland to the east and south. These pens permitted observation of individuals isolated from the remainder of the varying numbers of deer being held for other studies. Within the pens were madrone, oak, and liveoak as well as a wide selection of the local annual plants.

During the 1965 and 1966 seasons all studies involving the use of tame deer (see following section) were made at the "Parasite and Stress Pens" located approximately 1.6 km north of the Station headquarters at an elevation of 396 m. Two pens of 2.4 ha each were used. Each pen contained a 20 × 70-m enclosure adjacent to the other;

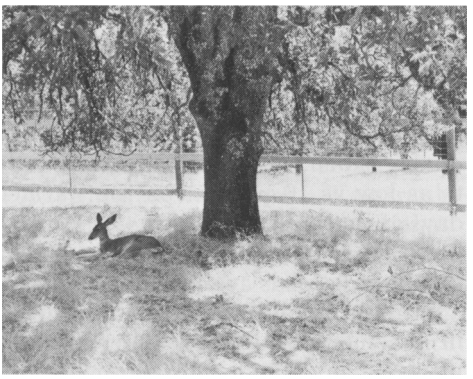

Fig. 1. Mixed sun and shade under a large oak tree in the Parasite and Stress Pens area.

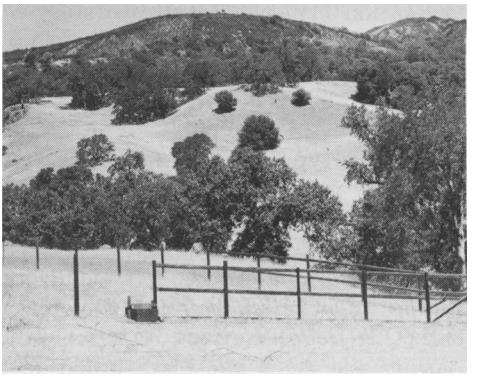

Fig. 2. Woodland-grass, woodland, and chaparral vegetation types on the hills directly northeast of the Parasite and Stress Pens.

Fig. 3. Typical ungrazed woodland-grass vegetation type within the Parasite and Stress Pens.

thus, deer could be limited to small areas for observation without being directly restrained.

The Parasite and Stress Pens were surrounded by areas of dense woodland, woodland-grass, and grassland. The pens enclosed woodland-grass vegetation. A moderate-sized stream runs adjacent to the north fence, and a second, smaller stream passes through the pens. Hagan Lake lies 495 m north of the pens. Both Hagan Lake and the small lake near the Deer Holding Pens are permanent bodies of water. The streams mentioned are dry 2 to 4 months of the year.

Figures 1 to 3 illustrate the types of terrain in and around the Parasite and Stress Pens.

Hosts utilized

To determine host range and specificity a variety of animals was observed. These animals were the coastal Columbian black-tailed deer, fallow deer [*Dama dama* (L.)], and domestic goats, sheep, horses, rabbits, and a dog. Limited observations of captive jack rabbits also were made. Moreover, man became one of the observed by his presence as an observer.

Seven tame black-tailed deer were used as bait during the 3 years of this study. Each of these individuals is described below:

Old Buck, 7 years old the spring of 1964, very large for a black-tailed deer, approximate weight 79 kg, approximate height at the withers 86 cm, reared on a bottle, moderately tame, died in June, 1964.

517, doe, 2 years old the spring of 1964, approximately 66 cm at the withers in 1964 and 71 cm in 1965, weight approximately 32 kg, reared on a bottle, very tame.

Old Doe, 3 years old the spring of 1964, approximately 71 cm at the withers, weight approximately 34 kg, reared on a bottle, moderately tame,

died of undetermined cause in May, 1964, shortly after delivery of a fawn.

516, yearling buck in the spring of 1965, approximately 66 cm at the withers, weight approximately 22.5 kg in 1965, reared on a bottle, very tame.

New Doe, yearling in the spring of 1965, approximately 63 cm at the withers, weight approximately 26 kg in 1965, reared on a bottle, very tame.

380, doe, yearling in the spring of 1966, very tame.

381, buck, yearling in the spring of 1966, very tame.

During the 1965 fly season, six wild deer kept at the Deer Holding Pen were observed at various times. These deer are referred to in the results section as A through F, and their descriptions are summarized in Table 1.

TABLE 1

DESCRIPTION OF WILD DEER OBSERVED DURING 1965

Deer host	Sex	Estimated age	Estimated wt.	Ear tag code
		years	*kg*	
A	♂	4	43	FR61
B	♂	3	38	FR44
C	♂	4	59	RW411
D	♂	1	29	—
E	♂	1	27	RB22
F	♀	1	29	RB15

A pair of fallow deer (originally intended as experimental hosts) was purchased in early April, 1965. The male weighed approximately 90 kg and stood approximately 86 cm at the withers. He remained white throughout the period he was observed. The female was slightly shorter than the male and weighed an estimated 61 kg. Her color changed from medium brown in April to dark brown in July. These animals proved too wild to collect flies from, but they could sometimes be observed at distances of less than 3 m.

Five white domestic milk goats were kept in the Parasite Pens area during the 1965 season. Two mature females, approximately 71 cm at the withers, and three young of the year made up the group.

A bay gelding which stood approximately 152 cm at the withers was used as a bait animal at the Parasite Pens throughout the 1965 season. Before that time, limited collections of blood-sucking flies were made from several of the other horses kept at H.F.S.

Mature ewe sheep and lambs were observed sporadically throughout 1964 and 1965. For the comparative studies initiated in 1965, tame half-grown lambs were used.

A shorthaired mongrel bitch weighing approximately 13.5 kg also was used as a host during the 1965 season.

All comparative observations on the attractiveness of rabbits were made using a brown domestic hare weighing approximately 3 kg. Observations of captive jack rabbits were made at a site about 180 m from the Deer Holding Pens. These rabbits were in cages made of 2-mesh hardware cloth and wood, and were kept under an open shed where they received no direct sun.

Observational methods

Graphic records of *Symphoromyia* attacking and biting were made with still cameras and a motion picture camera. The activities of flies on and around hosts were observed from less than 1 m up to about 4 m, with 6 × 24 binoculars being used to observe and identify flies at the longer distances. In 1964, two taxidermically prepared heads of deer were hung on sawhorses draped with burlap and exposed within deer pens

only a few meters from deer being attacked by *Symphoromyia* species. In conjunction with related research (Weinmann et al., 1973), hobbled, anesthetized deer exposed in a lying-down position were observed for attacking *Symphoromyia* on several occasions from 1964 to 1966. To avoid possible confusion of techniques, the specific types of observations associated with different aspects of fly feeding behavior and host response to the flies are included with the results.

Collecting methods

Most specimens were collected by aspirating flies directly from hosts, but insect nets, rearing and CO_2-baited Malaise-type insect flight traps (Anderson and Hoy, 1972) were also used to secure specimens.

We used a tube-within-a-tube type of aspirator designed to give maximum suction. A sponge rubber pad surrounded the excurrent opening, providing a soft cushion for flies which struck the back of the chamber after being drawn in at great speed.

The most successful technique for collecting flies was to approach the fly from behind, holding the aspirator tube parallel to the long axis of the fly, and sucking in sharply as the tube came within 0.5 to 0.1 cm of the fly.

Nets were used to collect male *Symphoromyia* as they swarmed and to collect females when they were flying in great numbers around a tame host.

During 1965 special efforts were made to collect throughout the day at least 1 day of each week. In the 64 days from 25 April through 27 June 1965, 13 days were devoted to collecting the flies on deer throughout the period of fly activity. The maximum lapse of time between full-day collections was 12 days following 27 April. At no other time was full-day sampling more than 6 days apart. Some collecting was done on 4 and 5 May despite the cold weather prevailing during that week; hence some indication of the species active in the first week of May was recorded. Following 27 June, 9 days or parts of days were spent observing and/or collecting flies coming to deer. A period of intensive study from 27 May through 15 June, 1966, provided data on the relationship between host age and attack rate, and biting site preferences.

Storage methods

Living adult *Symphoromyia* were frozen within a few hours after collection, or they were held on ice for 24 to 48 hours before being frozen. This procedure provided a series of flies with which to study seasonal physiological age as well as species occurrence. All frozen material was held at –50°C until removed for study. Most penned specimens were refrozen and kept over desiccating salts in a desiccator jar, thus preserving the flies in a condition especially suitable for study.

Additionally, we maintained flies captured from hosts and swarms by holding them in 568-ml (one-pint) cylindrical cardboard containers stocked with water and commercially available sucrose cubes. The solid tops of these holding boxes were replaced by nylon mesh netting. During 1964 the live flies were held at prevailing laboratory temperatures and humidities (usually 18 to 24°C and 50 to 60 percent relative humidity). In 1965 a plant growth chamber[2] was used to hold flies in darkness at 12.8°C during 12-hour "night" periods and under artificial fluorescent light at 21°C for 12-hour "day" periods. Relative humidity was held at 60 ± 10%.

Handling of flies destined for dissection

Females for dissection were netted from or adjacent to male mating swarms, aspirated from deer, or (in

[2] Sherer-Gillet Model CEL 25-7.

1965 only) captured in CO_2-baited traps. For all dissected females, records were maintained of the date, time and site of capture, and of how the flies were maintained between capture and dissection. Some flies were chloroformed and examined during the evening of the day of capture and others were maintained alive in holding cages stocked with water and sucrose. Most were killed by exposure to –50°C in a low-temperature cabinet, after which they were stored therein until removed for dissection. Flies in the first category above were held alive in pill boxes without food or water, and were dissected and examined between 4 and 12 hours post-capture. Those in the second category were held in the plant growth chamber. Flies stored at –50°C were held in tape-sealed pill boxes, cork- or rubber-stoppered vials, or vials with plastic snap caps. All were stored in polyethylene bags tightly sealed with a rubber band. Frozen flies were thawed and dissected between 1 day and 4 years post-capture.

CO_2-baited flight trap catches were collected at 3-hour intervals and killed by freezing in dry ice chests. The frozen specimens were sorted into labelled snap-cap vials and stored on dry ice in sealed polyethylene bags (Anderson and Hoy, 1972). At about 3-day intervals, the frozen catches were transferred to the laboratory and stored at –50°C until specimens were examined at several weeks up to 4 years after capture.

On the day of examination frozen flies were removed in groups of 5 to 10 and allowed to thaw at room temperature for several minutes before dissection of the first fly in a series. As all flies from the CO_2-trap catches were killed by freezing between 1 and 4 hours after capture, when thawed and dissected they were considered physiologically equivalent to flies caught by other methods and dissected and examined within 1 to 4 hours post-capture.

The principal objective of dissecting females was to determine whether parous individuals could be distinguished from nulliparous ones. Therefore, the ovaries of all dissected flies were examined. In addition, the appearance and the condition of the intestines and rectal papillae were noted in about 60 percent of the dissected flies, and more sporadic observations were made on the appearance and condition of the diverticulae. Spermathecal squashes were examined from 68 nulliparous and 30 parous females captured from deer, from 15 nulliparous females captured in or near male swarms, and from 70 nulliparous and 25 parous females caught in CO_2-baited traps. The heads of 331 parous females were examined for the presence of filarial worms.

Dissection and manipulation of internal organs was done with fine-tipped jeweler's forceps. This, and the process of examination, usually proceeded as follows: 1) head and abdomen separated from thorax and transferred to a drop of Ringer's solution on a microscope slide; 2) ovaries removed and transferred to a separate drop of Ringer's solution and examined at a magnification of 8 or 32; 3) observation of intestines, rectal papillae, and diverticulae at magnifications of 8, 32, or 64, or at all three magnifications; 4) gross examination of ovaries at the above magnifications; 5) stretching of ovaries and separation of ovarioles into many small groups of 5 to 10; and 6) examination of individual ovarioles, rectal papillae, and portions of the intestines with a compound microscope at magnifications of 100 and 440. Spermathecae usually were removed and examined either prior to step 1 (above) or after step 5 or 6.

For nulliparous specimens having tiny, compact ovaries, ovariole separation was achieved with minuten-nadlen embedded in wooden handles. Prepara-

tions of rectal papillae, intestines, and ovarioles were examined both with and without coverslips. When spermathecae were examined, they were transferred to a separate drop of Ringer's solution, squashed under a coverslip, and examined at 100 and 440 ×. Heads were handled similarly except that a coverslip was not always used, the mouthparts were spread apart, and the heads were dissected and spread out under a dissecting microscope before being examined.

To supplement observational notes measurements of ovarioles and follicles were made with a calibrated ocular micrometer, and sketches of varying detail were made of most ovarioles examined. Photomicrographs of several dissected specimens were taken to illustrate the features measured and sketched.

Weighing

A semi-micro balance[3] was used to determine weights of individual flies. The declared accuracy of this balance was ± 0.02 mg in the optical range and ± 0.1 mg of the set of weights. All weighings were made without altering the set of weights; hence accuracy was within the ± 0.02-mg error of the optical range.

Specimens for use in the blood-meal study were collected during a 1-hour period, placed in a low-temperature cabinet within 10 minutes of the end of the collecting period, and kept in a frozen state until the time of weighing, 3 days later. Immediately after the specimens were weighed they were dissected to determine the degree of engorgement.

Identification of specimens

Specimens collected in 1963 and 1964 were sent to Dr. James G. Chillcott of the Canada Department of Agriculture for identification. He kindly returned a representative series of determined specimens and detailed suggestions for identification. Using these specimens and Dr. Chillcott's suggestions, we determined the specimens collected during the 1965 and 1966 seasons. Several species were undescribed at the time of our fieldwork but have since been described by Turner and Chillcott (1973).

Weather data sources

Weather information for this investigation was gathered from three sources: the U.S. Weather Bureau records, the H.F.S. lambing pasture weather station records, and our own weather equipment located at specific study sites.

During the 1964 fly season weather data in the study areas were taken on the hour. Weather data were recorded on the hour and half-hour during the 1965 and 1966 fly seasons. Incident light was recorded on the quarter hour on certain days. A hygrothermograph was located in a Stevenson screen which was within the Parasite Pens area. Also, a mercury thermometer was placed in permanent shade under a feeder shelter within 15 m of the Stevenson screen.

RESULTS

Seasonal distribution of *Symphoromyia* attacking deer

Species of the genus *Symphoromyia* attack and suck blood from deer at the H.F.S. from early April until early or mid-July. Since individual females of *S. pachyceras* Williston and *S. cervivora* Turner and Chillcott were not clearly determinable at the time of this study, these two species have been treated as one. Like other species of anautogenous Brachycera, only the females suck blood. *Symphoromyia pachyceras* and *S. cervivora* feed on deer

[3] Mettler Model H16.

TABLE 2
SUMMARY OF THE SEASONAL BITING ACTIVITY OF *SYMPHOROMYIA* FEMALES COLLECTED FROM DEER

Species	Year	First collected	Last collected	No. days present	Midpoint of occurrence
S. pachyceras-S. cervivora	1964	9 Apr.	21 May	43	30 Apr.–1 May
S. pachyceras-S. cervivora	1965	12 Apr.	20 June	70	17 May–18 May
S. truncata	1964	29 Apr.	21 May	23	10 May
S. truncata	1965	9 May	29 June	52	3 June–4 June
S. inconspicua	1964	29 Apr.	19 June	52	24 May–25 May
S. inconspicua	1965	9 May	27 June	50	3 June–4 June
S. nana	1964	21 May	19 June	29	4 June
S. nana	1965	16 May	7 July	53	11 June
S. sackeni	1964	14 May	1 July	49	9 June
S. sackeni	1965	11 May	20 July	71	15 June

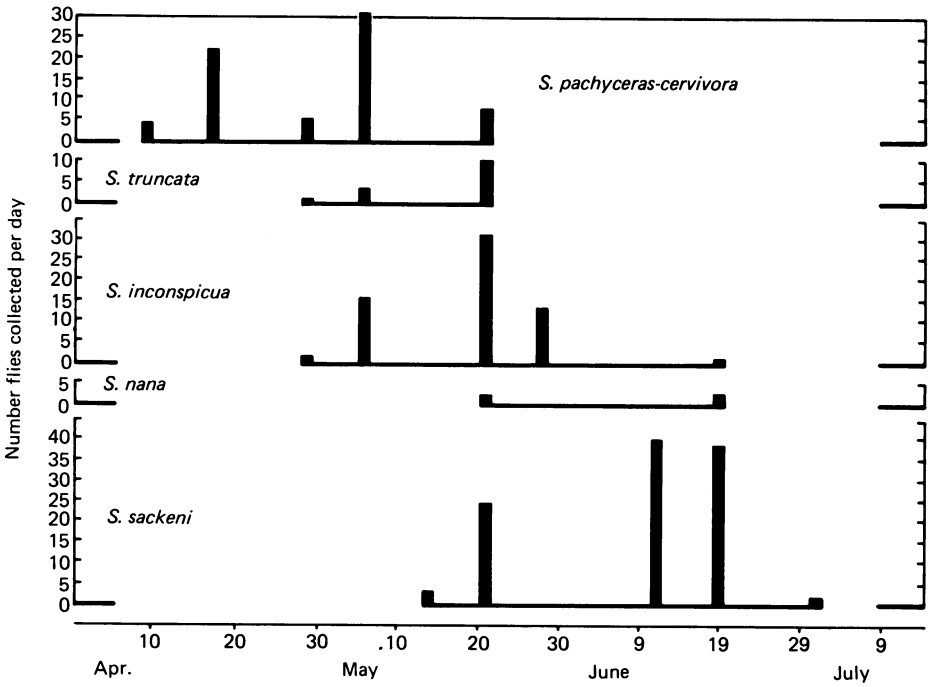

Fig. 4. Numbers of *Symphoromyia* imagines collected from deer at the H.F.S. during 1964.

from early April until mid-June, *S. truncata* Turner and Chillcott and *S. inconspicua* Turner and Chillcott attack from late April until mid-June, *S. nana* Turner and Chillcott from mid-May until late June, and *S. sackeni* Aldrich from mid-May until early or mid-July (Table 2). Representative densities of the species attacking at different times of the year are illustrated in Figs. 4 and 5. No *Symphoromyia* species were seen attacking deer from early to mid-July through the fall months. From this, coupled with a similar occurrence of male swarms and a seasonal shift to an all-parous popula-

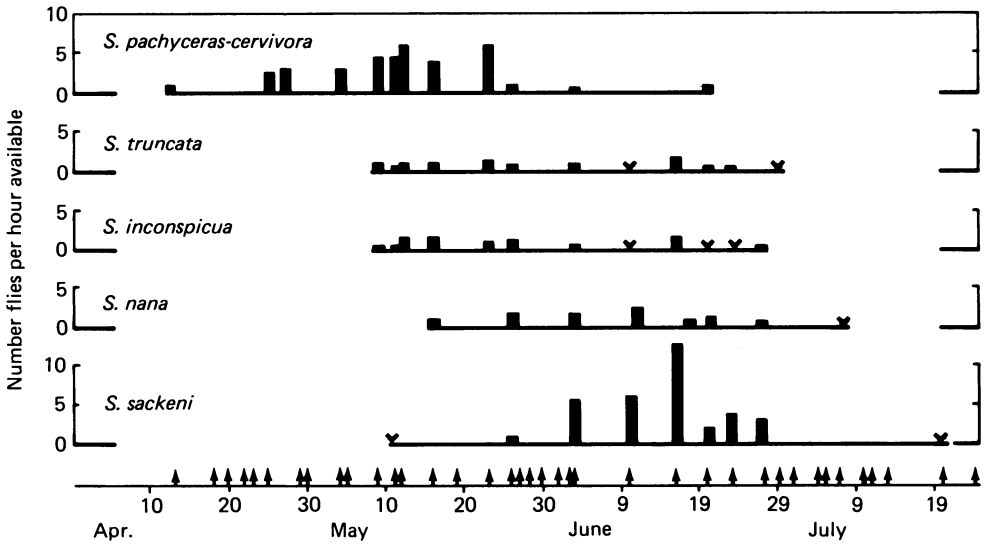

Fig. 5. Numbers of *Symphoromyia* imagines collected per hour during 1965 (within the known period of activity for given species). The small arrows on the time scale indicate the dates on which collecting efforts were made. The inverted carets indicate that only a single specimen was taken.

tion of females (see following sections), it is obvious that all of the above species are univoltine.

Species of *Symphoromyia* attracted to other hosts

On 3 and 23 June 1965, flies were collected from seven hosts simultaneously throughout each day. The hosts were two deer, one horse, one mature goat, one domestic rabbit, one dog, and one half-grown sheep. During the 2 days, two *S. pachyceras-cervivora*, six *S. truncata*, three *S. inconspicua*, 12 *S. nana*, and 20 *S. sackeni* were taken. Of the 43 flies collected, 38 were taken on deer and five were collected on or near the dog, goat, or horse. One specimen of *S. pachyceras-cervivora* and one *S. nana* were taken on and near the goat, respectively; two *S. sackeni* were taken on the horse; and one *S. inconspicua* was taken near the dog. Collecting flies that merely approached the dog or goat (an impracticality with the deer and horse) may have introduced a sampling bias in favor of those hosts.

Additional observation of the dog, other horses, range sheep, and caged jack rabbits at irregular intervals failed to disclose *Symphoromyia* attacking these animals. Moreover, swarms of *Symphoromyia*, almost exclusively males, were found within a few meters of the jack rabbit pens. Thus, except for the specimens taken on man, no *Symphoromyia* was seen actually feeding on any animal other than deer during 3 years of study.

During the entire 1965 season only one rhagionid, a specimen of *S. sackeni*, bit the senior author. Other people doing field work in the area have reported *Symphoromyia* attacks; however, only one of these reports was accompanied by the specimen involved, and again the species was *S. sackeni*. We also observed members of the *S. pachyceras* complex investigating human beings, but biting was recorded on only one occasion (Hoy and Anderson, 1966).

Symphoromyia plagens Williston has been collected several times at the H.F.S., most often in parked vehicles

with the windows opened, or partly opened. However, it was never collected on or observed approaching man or any of the other host animals. *Symphoromyia sackeni* and *S. pachyceras-cervivora* have also been found "trapped" in vehicles.

Qualitative description of *Symphoromyia* attack

This part of the study represents a subjective and rather detailed description of the *modus operandi* of *Symphoromyia.* The description of the attack is subdivided into: the approach, the post-landing pre-engorging behavior, and the behavior at the feeding site. The last two categories overlap a bit; but the precise moment that a given individual begins to engorge is difficult, if not impossible, to determine. Following a general description of the attack are descriptions of exceptional types of behavior and particular variations of the attack with regard to *S. sackeni* and members of the *S. pachyceras* complex. (Since it is necessary to microscopically examine specimens to specifically identify the five "grey species" of *Symphoromyia,* i.e., *S. pachyceras, S. cervivora, S. truncata, S. inconspicua* and *S. nana,* flies landing or feeding on deer or flying about their heads were identified only as *S. pachyceras* complex or as *S. sackeni,* a yellowish species).

Approach.—The approach of a blood-seeking fly is quite direct and rapid. The fly is seldom noticed before landing or approaching within a few cm of the host. The first landing on the host occurs within a second or two of the initial approach. However, the number of other flies present and the initial landing site appear to influence the number of landings prior to engorging. Also, individual hosts differ in their tolerance of *Symphoromyia.* To repulse flies (see below), deer flick their ears in response to attack; while under heavy attack they become much more inclined to brush flies from their faces.

The speed of *Symphoromyia* on the wing is perhaps no greater than the speed of a typical tabanid; but the smaller size of *Symphoromyia,* coupled with their speed, enables them to fly within several cm of the host before being noticed. There appears to be no searching pattern of flight within the last few meters of the approach flight.

Hosts were observed continuously for 30 to 60 minutes rather than at short fixed intervals while determining the ending of fly-feeding activity for a day, and while recording quantitative measurements of attack behavior. During the latter type of observation, more than one fly approaching the host made observation of individual flies difficult. Then, and at other times of light fly attack (toward the end of activity), it appeared that periods of no attack were often followed by attack of more than one fly, suggesting that the host-seeking may be done in groups or that the attack by one fly in some way stimulates additional flies to attack. Efforts to confirm these observations were not attempted, but researchers have made similar observations for other blood-sucking flies, such as mosquitoes (Service, 1972).

Although two "decoy" deer (taxidermically prepared heads and burlap bodies) were in place within the deer pens and within a few meters of deer being attacked by flies for 6 weeks during the height of the 1964 fly season, at no time was any female *Symphoromyia* observed near them.

Post-landing and pre-engorging.—After the attacking *Symphoromyia* female has landed on the host, study of the behavior of the fly is complicated by the reactions of the host. The quantitative aspects of host-fly interaction will be discussed later; however, at this point, both social behavior of the deer

and individual reaction to fly attack should be recognized as potential influences on the flies' behavior.

Flies may be disturbed or physically dislodged several times before successfully taking a blood-meal. Characteristically, a *Symphoromyia* first lands on or near the ears of the prospective host deer. Although both the face and ears serve as feeding sites for all *Symphoromyia* species attacking deer, the face is generally the site where the meal is taken. Thus, from the ears the flies sometimes make short flights (at times little more than hops augmented by fluttering of the wings), working down across the frontal area of the head to a point about midway between the tip of the nose and a line drawn from eye to eye. Occasionally flies traversed the distance from near the ears to the bridge of the nose entirely on foot. The flies' movement is perhaps best described as dance-like. One gets the impression of increasing excitation as the fly progresses along a path that is more or less direct and always on the dorsal part of the head.

Flies on the ears appeared to move about less than those on the face, possibly because those flies which move about on the ears are flicked off.

Perhaps one fly in a hundred alighted on a part of the deer other than the head; such landings were usually on the hips. *Symphoromyia* were never seen on the legs or ventral surface of the body, sites that are attacked by other hematophagous Diptera. Likewise, the neck and flanks were not attacked by *Symphoromyia*. Generally those flies which land on the ears or other body surfaces equally well supplied with guard hairs, are flicked off or are so disturbed by the ear flicking or twitching of the raised guard hairs that they take flight.

All species observed attacking deer were strongly attracted to the head, but when they investigated human beings, these same species showed no special interest in any particular part of the body. Observations of the flies around humans were made near deer which were under attack. The impression that flies become excited after landing on the host and the fact of occasional attack of abnormal hosts when such hosts are near deer, suggest that partially excited flies may accidentally land on a bystander and proceed to bite.

Behavior at the feeding site.—Of the individual flies observed, many succeeded in drawing a blood-meal upon reaching the area along the bridge of the nose. Before engorging, the flies assumed a characteristic feeding position, i.e., with the long axis of their bodies held at a 45° angle from the substrate. As the abdomen filled with blood it became distended and drooped to nearly horizontal position (Hoy and Anderson, 1966, Figs. 1–3).

During feeding, the tarsi of all six legs are in contact with the host, and the legs are held in a relatively normal position. Upon trying to aspirate a feeding specimen, it becomes apparent that the legs or mouthparts have a firm grip on the host.

A "primary excretion" such as produced by tsetse flies (Glasgow, 1963), was never observed while flies were feeding.

Flies were sometimes observed feeding in clusters of three or more (Fig. 6). It was not determined whether the clusters were other than chance occurrences. However, clustering seemed more apparent on the ears, the site which seems to offer greatest potential feeding area based on overall observations.

Blood meals are taken within three areas of the head (if the host is a buck). Those areas are the developing antlers, the outside surface of the ears, and an elliptical area on the bridge of the nose. The area of attack is most clearly defined on the bridge of the nose. The elliptical area runs from the posterior

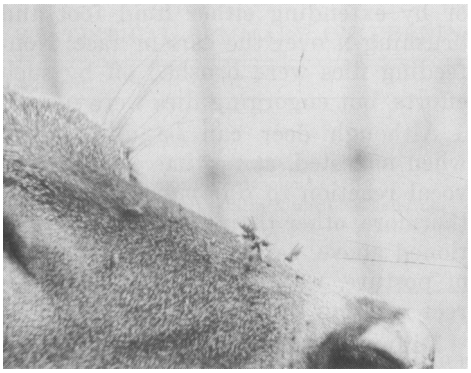

Fig. 6. A cluster of *Symphoromyia* females feeding on the face of a deer.

margin of the nose pad to a point on the mid-line of the head just anterior to the brow. The lateral extremes of the ellipse are no more than 2.5 cm from the dorsal mid-line of the head. Thus, on 2- or 3-year-old deer about 62 cm^2 of the face are used as a feeding site by *Symphoromyia* spp.

The constantly changing shapes and areas of the growing antlers make generalization difficult with regard to the area most often serving as a feeding site. However, during the period that the antlers are unbranched, attack seemed to be most prevalent at the "growing tip."

The entire outer surfaces of the ears are subject to occasional attack; however, most attacks on ears are made within the central one-half of these areas. Hence, a conservative estimate of ear surface that is regularly attacked is 77 to 97 cm^2/host. Although we observed and collected simuliids and ceratopogonids feeding in large numbers on the inner surfaces of the ears, *Symphoromyia* were never observed there.

Relatively little damage is done by the mouthparts of *Symphoromyia* species despite the fact that they are tabanoid in structure (Snodgrass, 1943). At most a small drop of blood may ooze from the bite after the fly has departed. The volume of the drop is never more than one-half the amount normally taken by the fly.

Small scabs, little more than scales of dried blood, form at the site of bites. After periods of heavy fly attack, as many as several hundred of these scabs may be seen on each ear and on the bridge of the nose (Figs. 6, 7).

The most striking aspect of biting behavior is the characteristic tilted posture assumed by a fly taking blood. This posture would appear to have little function when a blood-meal is being taken on the deer's face. However, when a meal is being taken on an ear, there are two ways that such a posture could be of value to the fly. The guard hairs on the ear lie and rise at such an angle that, mechanically, approach between the hairs might be easier with the angle of the body reducing contact with guard hairs and the ensuing flicking of the ear.

Effects of bites on the hosts.—As the fly season progresses there is a change in the amount of hair on the areas attacked by the rhagionids (compare Figs. 7, 8, 9). This change is due (in part) to the spring shedding of the winter pelage. However, the fine woolly underhair on the outer surface of the ears and on the face is lost more rapidly

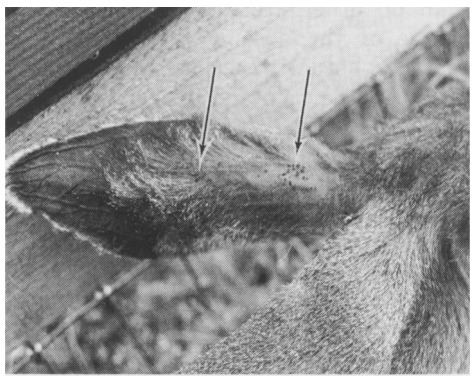

Fig. 7. Scabs (arrows) on the ear of a deer following heavy *Symphoromyia* attack. The bare area at the tip of the ear is caused by the tips of the ears rubbing together when both are flicked, rather than from fly attack.

Fig. 8. Condition of the ears and face at midseason. Note bare areas on outer ear surfaces and bridge of the nose.

than on other areas of the body. The bridge of the nose and the outer ear surfaces actually become nearly bare (Figs. 7, 8). Young deer, which are much less tolerant of flies on their ears than are the older deer, show this loss of hair to a lesser degree. Hence, fly attack may contribute significantly to the early loss of hair in these areas.

The deer normally did not respond to individual flies except when the guard hairs were disturbed. However, when fly attack was heavy, the deer became nervous and showed a greater tendency to attempt to dislodge flies from their faces either by brushing their head against an inanimate object or by extending either hind foot and brushing it over the ears or face. Nonfeeding flies were brushed off by such efforts, but engorging flies were not.

Although deer can be quite vocal when molested, at no time did we hear vocal reaction to *Symphoromyia*. Furthermore, other than the brushing mentioned above, ear flicking, and changes of posture, we did not observe any direct reaction to individual flies.

Differences between types of attack. —Some rather subtle differences exist between the behavior of *S. sackeni* and the other *Symphoromyia* species attacking deer. *Symphoromyia sackeni* females are more persistent in their approach to a host, hovering and returning re-

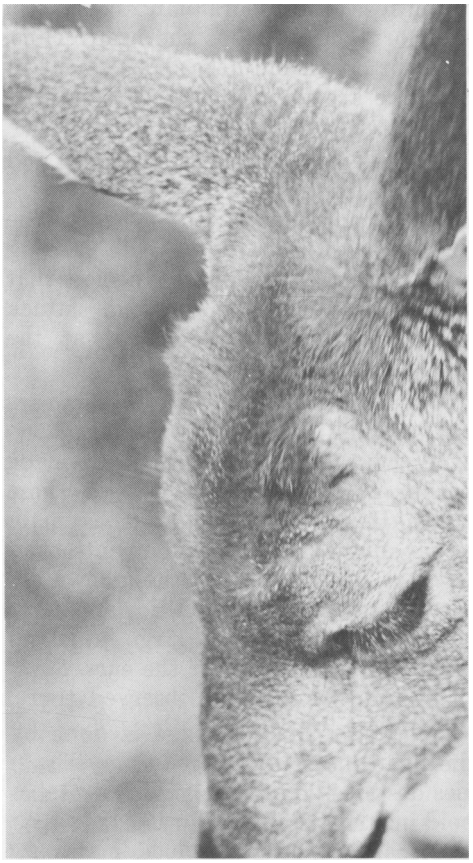

Fig. 9. Condition of the pelage of the face and ears before the beginning of the fly season.

TABLE 3
STATISTICAL SUMMARY ON FEEDING TIME (SECONDS) OF *SYMPHOROMYIA*

S. sackeni	N	$\bar{X}$	S.E.$\bar{X}$	Range
		seconds		
Elapsed time of attack*	13	141.1	32.2	74–417
Elapsed time after last landing*	34	75.4	2.8	47–114
Elapsed time after visible extension*	13	35.5	12.5	23– 59
Elapsed time from start of attack until last landing	13	69.7	34.0	1–356
S. pachyceras complex				
Elapsed time after last landing*	19	109.0	17.2	55–280

* To voluntary departure.

peatedly, whereas those of the other *Symphoromyia* species seemed more easily discouraged. However, once members of the latter group began engorging, they almost invariably took a full meal. *Symphoromyia sackeni* females were somewhat more easily disturbed while engorging.

Quantitative study of the feeding behavior of *Symphoromyia.*—Table 3 summarizes the data on three subdivisions of the total time spent by any *Symphoromyia* attacking a deer. The subdivisions are: a) the period from the first approach until the last time that the fly lands prior to feeding; b) the time from the last landing until voluntary departure after engorgement; and c) the time from the first visible distension of the fly's abdomen to voluntary departure.

The total amount of time spent by *S. sackeni* from the beginning to end of a successful attack was approximately 2.3 minutes (Table 3). Slightly more than one-half of that time was spent on the host after the final landing. Little more than 0.5 minute lapsed between the first visible distension of the fly's abdomen and departure with a full meal.

For the other *Symphoromyia* species only the times spent from "last landing" until "voluntary departure" were determined. The average time spent during that stage of attack was 109 seconds (Table 3).

Inasmuch as voluntary departure was allowed, specimens were not available for association with the behavior records. *Symphoromyia sackeni* is readily identifiable on the host; hence, the most intense study of biting behavior was concerned with that species.

The time spent around a host was studied 1) by a direct measure of the time spent after final landing and subtracting that time from the total period of attack, and 2) by comparing the number of flies around a host *vs.* those on a host at various times. The latter method depends on knowing the mean length of time that a fly is on the host.

The direct method was used only when observing *S. sackeni* attacking New Doe. Based on 13 observations, the mean "elapsed time from approach to last landing" was 69.7 seconds. These 13 observations were of flies which were successful in taking full meals. The elapsed times were highly variable; the standard error of the mean is 34.0 seconds.

Of 1,872 flies of the *S. pachyceras* complex observed on or around the two tame does during the 1965 season, 55.4 percent were *on* the deer (Table 4). Of 449 *S. sackeni* observed on or around the two deer during the 1965 season, 69.8 percent were *on* the hosts. In 1964, 66.5 percent of the *S. pachyceras* complex associated with a large buck were on the face, ears, or antlers, and 33.5 percent were flying around the head (Table 5).

TABLE 4
NUMBERS OF TWO TYPES OF FLIES *ON* AND *AROUND* THE HEADS OF TWO DEER* (1965)

Species	Flies on and around:						$\bar{x}$ % on head
	New Doe			517			
	Head alone		Total no. of flies	Head alone		Total no. of flies	
	No.	% of total		No.	% of total		
S. pachyceras complex	391	41.2	948	643	69.6	924	55.4
S. sackeni	132	54.3	243	176	85.4	206	69.8

* Based on data presented in tables 7 and 8.

TABLE 5
LOCATIONS OF FEMALES OF THE *S. PACHYCERAS* COMPLEX ON AND AROUND A LARGE BUCK (1964)

Day	Flies on:						Flies around head		Total flies
	Faces		Ears		Antlers				
	No.	%	No.	%	No.	%	No.	%	
27 Apr.	12	(14.8)*	6	(7.4)	31	(38.3)	32	(39.5)	81
29 Apr.	0	(0)	3	(14.3)	11	(52.4)	7	(33.3)	21
7 May	21	(17.8)	30	(25.4)	37	(31.4)	30	(25.4)	118
8 May	0	(0)	7	(25.0)	7	(25.0)	14	(50.0)	28
Totals:	33	(13.3)†	46	(18.6)	86	(34.7)	83	(33.5)	248

* Numbers in parentheses are percentages of the total counts/day/site.
† Numbers in parentheses are percentages of the total counts/site.

A quantitative study of preferred biting sites and attack rates

Data were gathered on the attack rate of *Symphoromyia* on each host, and these data were subdivided according to the flies' positions on or around the host. The rates are based on instantaneous counts of the number of flies on and around given hosts at regular intervals throughout major portions of days. At each count the numbers of flies on the face, on the ears, and around the head were recorded. The flies were recorded as the *S. pachyceras* complex, *S. sackeni,* or undetermined *Symphoromyia.* During 1964 observations were made at 15-minute intervals; in 1965 they were made at 7.5-minute intervals. During 1966, when four hosts were observed, 10-minute intervals were necessary because of the distance between hosts. Hence, when maximum fly-feeding activity coincided with maximum spacing of the deer in the pens, the full 10 minutes were required to make individual counts on all four hosts (Anderson and Hoy, 1972). Since the complete attack of a fly averaged 2.5 minutes, all of the above intervals insured that the same fly would not be counted twice.

Only the numbers of flies on the faces and around the heads of the wild deer were recorded, because wild deer usually faced the observer thus preventing observation of flies on the ears.

Biting site "preferences."—Throughout 1964, 1965, and part of 1966, the numbers of flies on the hosts were recorded according to location of the flies. During the first month of the 1964 season observations were made on a large black-tailed buck. Of the total number of the *S. pachyceras* complex recorded on and around the buck, 13.3 percent were on the face, 18.6 percent

TABLE 6
BITING SITE "PREFERENCE" ON FOUR HOST DEER DURING THREE SEASONS*

Fly species	Year†	Number of flies on:							
		517		New Doe		380		381	
		Face	Ears	Face	Ears	Face	Ears	Face	Ears
S. sackeni	1964	138	49	—‡	—	—	—	—	—
	1965	120	56	129	3	—	—	—	—
	1966	147	38	242	29	113	12	170	3
S. pachyceras complex	1964	86	138	—	—	—	—	—	—
	1965	384	257	324	66	—	—	—	—
	1966	31	53	67	48	21	9	36	6

* This table is based (in part) on data in Tables 7 and 8.
† Includes only those observations made on or after 13 May 1964 and 27 May 1966.
‡ Not available for observation.

on the ears, 34.7 percent on the antlers, and 33.5 percent were flying around the head. (See Table 5 for a comparison of days of observation.)

Extensive observations of four deer, three does, and a yearling buck that had no antlers during the fly season, have provided information on the biting site preferences of *Symphoromyia* (Table 6). In general, both *S. sackeni* and the *S. pachyceras* complex seem to favor the face as a feeding site, but the preference is more striking in younger hosts.

Because the 1964 observations of doe 517 began at mid-season and the 1966 observations began even later, data for the *S. pachyceras* complex are not fully comparable. The discrepancy between years may indicate a seasonal shift in the ratio of flies on the face to flies on the ears. This ratio (flies on face:flies on ears) does in fact change as the season progresses. During the early part of the 1965 season approximately 85 per-

TABLE 7
COMPARISONS OF *S. PACHYCERAS* COMPLEX IMAGINES OBSERVED *ON* AND *AROUND* TWO DOES DURING 1965*

Date	New Doe: flies—				Doe 517: flies—			
	On face		On ears	Around head	On face		On ears	Around head
	No.	%	No.	No.	No.	%	No.	No.
28 Apr.	39	89	5	68	47	39	72	44
30 Apr.	1	100	0	4	2	67	1	1
4 May	7	78	2	17	10	71	4	8
9 May	26	79	7	76	44	68	21	36
11 May	32	94	2	111	90	75	29	72
12 May	65	92	6	89	68	69	30	24
16 May	52	84	10	71	29	78	8	30
19 May	8	89	1	6	0	—	0	1
23 May	26	87	4	32	23	61	15	21
26 May	18	100	0	32	36	73	13	21
27 May	5	83	1	4	3	50	3	2
2 June	3	60	2	6	0	0	2	4
3 June	17	94	1	0	14	38	23	5
10 June	3	50	3	3	4	33	5	1
16 June	18	61	12	21	8	24	26	7
20 June	1	25	3	3	3	100	0	2
23 June	3	30	7	5	3	38	5	2
TOTAL				557				281

* Totals of the counts made at 7.5-minute intervals throughout the days.

TABLE 8

COMPARISON OF *S. SACKENI* COMPLEX IMAGINES OBSERVED ON AND AROUND TWO DOES DURING 1965*

Date	New Doe: flies—				Doe 517: flies—			
	On face		On ears	Around head	On face		On ears	Around head
	No.	%	No.	No.	No.	%	No.	No.
26 May	2	100	0	1	1	8	11	1
27 May	8	100	0	3	1	100	0	0
2 June	3	100	0	0	0	—	0	0
3 June	12	100	0	18	21	64	12	4
10 June	8	89	1	26	17	71	7	6
16 June	58	98	1	47	54	75	18	11
20 June	7	100	0	1	2	100	0	0
23 June	21	100	0	8	16	70	7	4
24 June	0	—	0	0	2	100	1	0
27 June	10	91	1	7	6	100	0	4
TOTAL	129		3	111	120		56	30

* Totals of the counts made at 7.5-minute intervals throughout the days.

cent of the *S. pachyceras* complex were on the face, but by late in the season less than 50 percent of the flies usually were on the face (Table 7 and Fig. 10).

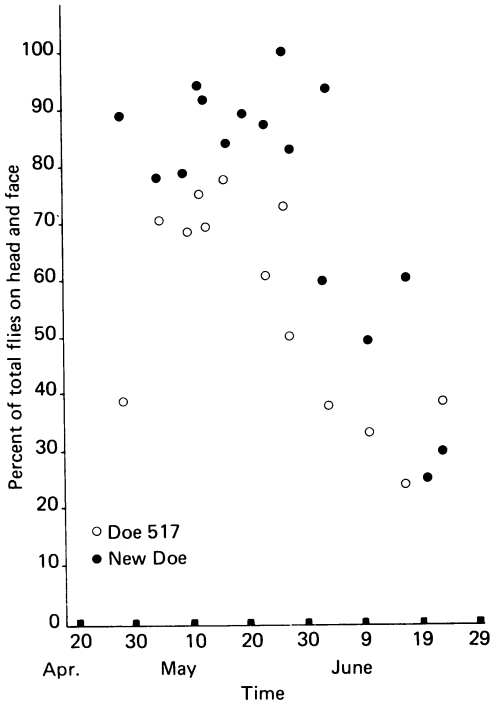

Fig. 10. Seasonal shift of the percentage of the total number of *S. pachyceras* complex imagines observed on the face.

No seasonal shift in the ratio of flies on the face *vs.* flies on the ears was observed for *S. sackeni* (table 8).

Attack rates relative to individual hosts.—On 11 and 23 May 1965, the herd of wild deer was observed to determine if individual hosts were attacked at different rates. On the first day three mature bucks and one yearling were observed and on the second day, two mature bucks and three yearlings. Attack rates were recorded in terms of the number of flies on the face and the number of flies around the head/observation. On the bases of collection records and close range observations of tame deer on 11 and 23 May 1965, it is certain that these figures apply to the *S. pachyceras* complex and probably more specifically to *S. pachyceras* or *S. cervivora*, which are prevalent early in the season. On both days the number of flies/observation was roughly 20 times greater *on* the faces of the mature deer than on the faces of the yearlings (Table 9). However, the numbers of flies *around* the heads did not differ greatly. The greatest contrast was between hosts A and D (mature and yearling bucks, respectively).

The total numbers of *Symphoromyia*

TABLE 9

COMPARISON OF FLY ACTIVITY ON SIX PENNED, WILD BLACK-TAILED DEER

Item	Mature deer			Yearling deer		
	A♂	B♂	C♂	D♂	E♂	F♀
Flies on face						
11 May 65						
Flies/obs.	2.62	1.40	3.16	0.11	—†	—
No. of obs.	49	45	49	45	—	—
No. of flies	128.5*	63.0	155.0	5.0	—	—
23 May 65						
Flies/obs.	1.82	—	2.55	0.06	0.29	0.06
No. of obs.	17	—	18	18	17	17
No. of flies	31	—	46	1	5	1
Flies around head						
11 May 65						
Flies/obs.	2.14	1.22	1.66	1.07	—	—
No. of obs.	49	47	46	46	—	—
No. of flies	105.0	57.5	76.5	49.0	—	—
23 May 65						
Flies/obs.	2.34	—	2.03	1.97	2.00	1.41
No. of obs.	17	—	18	18	17	17
No. of flies	40.0	—	36.5	35.5	34.0	24.0

* When fly activity was reported as falling within a certain range, the median of that range was used when summing the observations; hence counts of "half" flies.
† Blank spaces indicate no observations made on that day.

TABLE 10

SYMPHOROMYIA ON AND AROUND HOSTS ACCORDING TO YEARS AND FLY SPECIES

Location	Year	Species	Number of flies:			
			517	New Doe	380*	381*
Around hosts	1965	*sackeni*	206	243	—	—
		pachyceras	924	948	—	—
	1966	*sackeni*	222	393	194	221
		pachyceras	102	137	45	55
On hosts	1965	*sackeni*	176	132	—	—
		pachyceras	643	391	—	—
	1966	*sackeni*	185	271	125	173
		pachyceras	84	115	30	42
$\frac{\text{On hosts}}{\text{Around hosts}}$ (100)	1965	*sackeni*	85%	54%	—	—
		pachyceras	70%	41%	—	—
	1966	*sackeni*	83%	69%	64%	78%
		pachyceras	82%	84%	67%	76%

* No observations were made on hosts 380 and 381 until 1966.

observed at hosts during 1965 and 1966 are summarized in Table 10. Comparisons can be made only among hosts by fly species and by years. The "at host" data include flies around the host as well as those on the head. The "on host" data are more meaningful in that a nervous host keeps a swarm of flies at bay, thus appearing to be more attractive. However, once the flies land, the time required to engorge is probably constant regardless of host. Hence the difference between a datum "at host" and a datum under "on host" may be a measure of the evasive nature of the host. Perhaps this measurement is best expressed as "percent allowed on host," i.e., the number on the host divided by the number at the host times 100.

New Doe bore twins on either 26 or

27 May 1966. On 4 June, *Symphoromyia* were observed attempting to bite the fawns; on 11 June a series of 10 observations revealed that both *S. sackeni* and the *S. pachyceras* complex were successful in attacking the fawns. Five *S. sackeni* and three *S. pachyceras* complex were observed on the two fawns. During the same 10 observation periods, 31 *S. sackeni* and six *S. pachyceras* complex were observed on the four older hosts (517, New Doe, 380, and 381). The small size of the fawns (estimated weight 4.5 to 5.5 kg) emphasizes the host-finding abilities of these flies.

Host behavioral patterns relative to fly attack

General behavioral patterns of the hosts.—The black-tailed deer displayed a variety of behavioral patterns, some of which were in response to fly attack. The relationship between a fly landing on the ear and the flicking of that ear is evident. However, the relationships between an attacking fly population and the posture or resting place of a host are not so evident. Below is an outline of certain behavioral patterns which conceivably could influence, or be influenced by, the rate of fly attack.

Ear flicking, the rapid forward movement of the ear, is the most conspicuous response to insects landing on or flying near the ear. The ear sometimes swings far enough forward to come into contact with the bridge of the nose; however, this is not readily noticed until slow motion pictures of the flicking have been studied. Occasionally the ears touch each other, causing a slapping noise. Ear flicking seems to be triggered by insects touching the guard hairs on the ears. A similar response could be elicited by touching these hairs with a blade of grass. The sensory function of the guard hairs also has been noted by Cowan and Raddi (1972).

Rate of ear flicking, however, does not readily serve as an index of attack rate because it reaches an asymptotic maximum when four to six flies approach a host simultaneously and does not increase above that frequency with more flies. Furthermore, as noted below, ear-flicking rates vary with age of host.

Closely resembling ear flicking is the shuddering or rippling of the skin in an area where a fly has landed. This type of response is familiar to anyone who has observed horses under fly attack. The sudden movement of the skin follows the landing of an insect on any dorsal body surface of the deer. Like ear flicking, this response appears to be involuntary.

The deer sometimes brush flies from their faces, either with their hind feet or by brushing against an inanimate object. A flat surface of the ground may

Fig. 11. A yearling doe simultaneously flicking her right ear and beginning to brush a fly from the bridge of her nose.

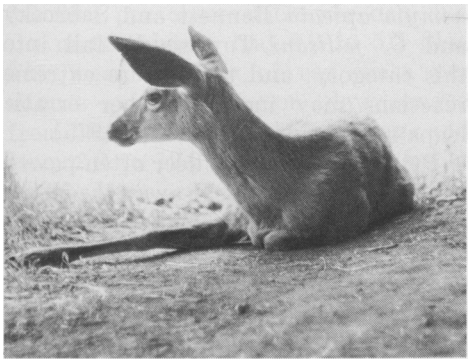

Fig. 12. Normal resting posture with regard to head and neck.

Fig. 14. "Head-down" and "legs-out" posture.

serve this purpose although the deer must assume a rather awkward position during the maneuver (Fig. 11). On flat ground the neck is fully extended in line with the body as the head is brushed against the ground in a rapid sweeping motion.

Other postural changes (Figs. 13, 14, 15) also occur when deer are attacked by *Symphoromyia* species. Figure 12 illustrates the posture assumed much of the time when flies are not attacking deer, except that both forelegs are usually folded under the body. Figure 13 illustrates a lower head posture that is induced by attacking *Symphoromyia*. The lowering of the head reaches an extreme when the lower mandible is in contact with the ground (Fig. 14).

In the absence of flies the deer normally lie with their legs drawn up near or beneath their bodies and with the body proper nearly vertical. Figure 15 shows a small doe under fly attack in a posture that is an extreme deviation from that described above. When the legs are in the extended position, the head is generally down. The converse

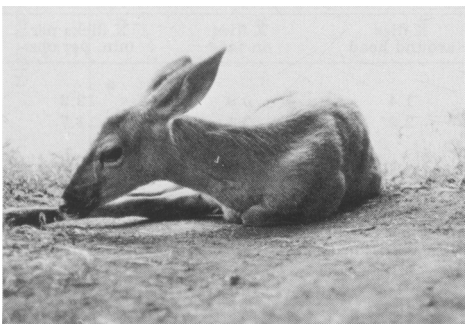

Fig. 13. "Head-down" posture under fly attack.

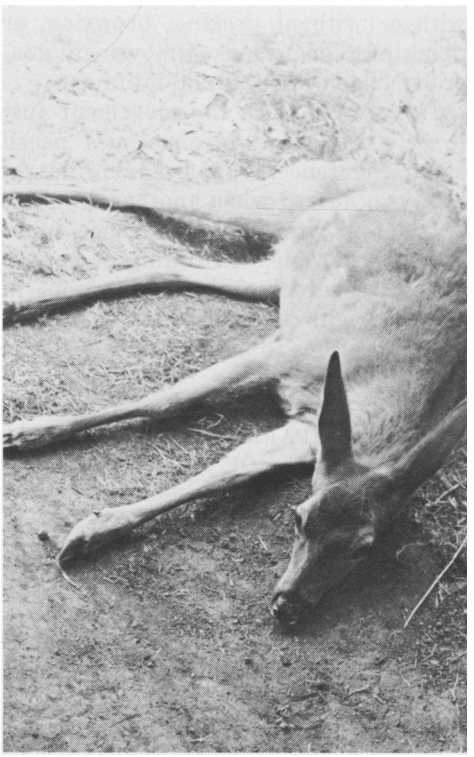

Fig. 15. "Head-down" and "legs-out" posture, with the body showing the lowest possible profile.

is not so often the case; the legs are not always (or usually) extended when the head is lowered.

Normally the ears are held so that the tips are anterior to, and well above, the bases. When under fly attack (as well as when the deer is in an aggressive mood) the ears are held with the tips posterior to the bases and with the axes of the ears nearly in line with the axis of the head. (Compare Fig. 12 with Figs. 13 to 15).

The deer observed in this study spent a great portion of the day lying either in the shade or in mixed sun and shade. The latter type of resting place is illustrated in Fig. 1. At 1- to 2-hour intervals the deer moved to alternate resting sites. These moves sometimes appeared to be in response to changing exposure to the sun. The movement was usually at a slow walk, seemingly aimless, and with or without grazing, browsing, or drinking. The periods of movement generally lasted less than 30 minutes.

In contrast with the movement just described, deer also sometimes paced along the fence. This behavior nearly always occurred when another deer was on the opposite side of the fence. More vigorous movement, running or bounding, was characteristic of situations in which fright was probably involved. Some reactions to nose bot flies (*Cephenemyia apicata* Bennett and Sabrosky and *C. jellisoni* Townsend) fall into this category, and these more extreme reactions may include rather erratic leaps to the side (Anderson, 1975).

Prior to lying down deer often pawed the ground as if to clear away the leaves or grass. The pawing motion was sufficiently vigorous to not only clear away vegetable material, but also to break the surface of the soil, sometimes forming a "bed" 0.09 to 0.36 m^2.

Ear flicking.—Ear flicking was quantified in this study by counting the number of flicks within 72 periods ranging in length from 30 to 60 seconds. All periods were timed with a stopwatch but varied because hosts under attack frequently lowered or otherwise moved their heads from view. Observation periods of less than 30 seconds were discarded so that chance errors were reduced. The relatively large number of flicks/minute reduces the importance of "rounding" errors created by having observation periods of various lengths.

The mean numbers of *Symphoromyia* around the heads of four deer (two 4-year-old bucks and two yearlings) observed on 2 days ranged from 1.2 to 2.0 flies/observation. However, with regard to the numbers of flies *on* the faces of these hosts, the yearlings had 0.0 to

TABLE 11

COMPARISON OF EAR-FLICKING RATES AND TWO MEASURES OF ATTACK RATES FOR FOUR HOSTS (1965)

Host	Date	No. of observations	$\bar{X}$ flies around head	$\bar{X}$ flies on face	$\bar{X}$ flicks per min. per obs.
A					
(4-year-old	23 May	7	1.4	0.9	12.2
male)	10 June	7	2.0	2.1	11.7
C					
(4-year-old	23 May	13	1.5	3.0	7.0
male)	10 June	10	1.4	5.2	2.2
D					
(yearling	23 May	13	1.7	0.0	39.9
male)	10 June	11	1.2	0.2	36.7
F					
(yearling	23 May	2	1.2	0.0	41.3
female)	10 June	9	1.6	0.0	30.2

0.2 flies per observation per day and the mature bucks had 0.9 to 5.2 flies. The mean number of ear flicks per minute per observation day ranged from 30.2 to 41.3 for the yearlings and from 2.2 to 12.2 for the mature bucks (Table 11).

Postural changes.—Only when attacking flies became numerous (5 to 10 flies at once) did deer brush the flies from their faces. Postural changes were observed to occur before brushing started. The lowered head and change of position of the ears were frequently seen when fly attack was moderate (1 to 4 flies at once), whereas the extended-leg reclining posture was more characteristic of deer under heavy attack. Although the limited observations of the latter type of behavior make generalization difficult, we suspect air temperature and/or soil temperature may have contributed to the posture assumed. The above-mentioned postural changes were most apparent in yearling hosts.

Movement.—Throughout this study, simultaneously with observations of flies, records were kept of the position of deer relative to the sun and of the movements of deer between observation periods. Position relative to the sun was recorded as in the shade (sh), in mixed sun and shade (s-sh), and in the sun (s). Movement, directly observed or inferred, was indicated in the field notes without regard for direction or degree. The time of movement was recorded simply as between given observation periods.

During 17 days of observation, both New Doe and 517 were in the shade half or more of the times observed, 50.3 percent for the former and 70.1 percent for the latter. Neither host spent more than one-twelfth of her time in the sun. New Doe spent 45.3 percent of her time in the mixed sun and shade,

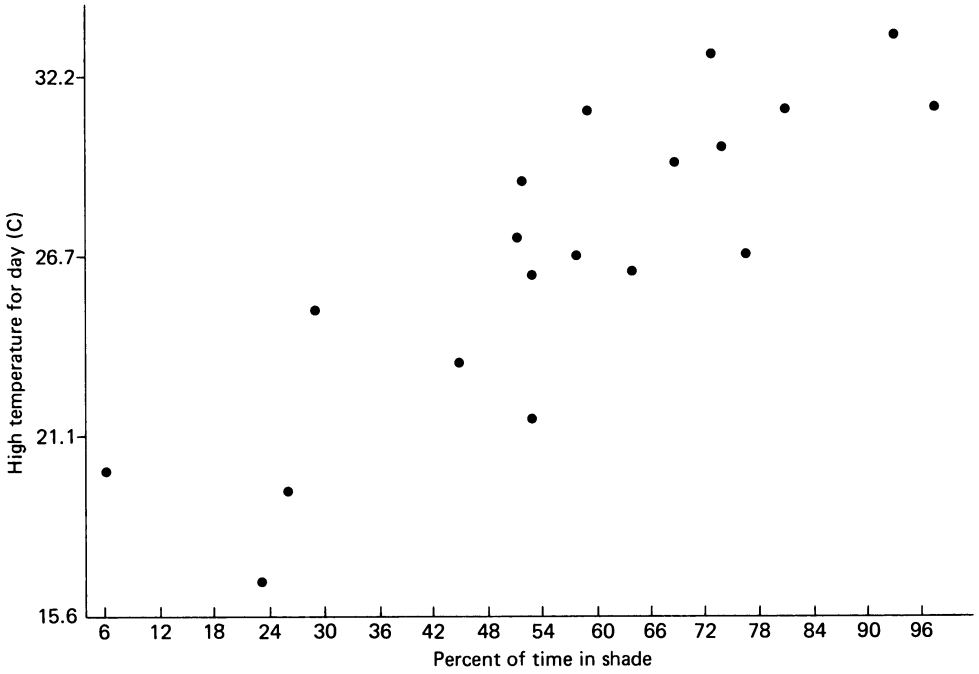

Fig. 16. Relationship between the maximum air temperature on 19 days in 1965 and the mean percent time spent in the shade by the host deer.

TABLE 12

PERCENT TIME SPENT IN SHADE, SUN-SHADE, AND SUN BY TWO DEER AND THE PERCENTAGES OF THE TOTAL FLIES COLLECTED FROM EACH HOST (1965)

Date	New Doe					517				
	Shade	Sun-shade	Sun	Tot. no. obs.	% of tot. flies	Shade	Sun-shade	Sun	Tot. no. obs.	% of tot. flies
28 Apr.	68.8	18.8	12.5	48	40.7	46.8	38.8	14.9	47	59.3
4 May	30.3	42.4	27.3	33	54.2	16.7	66.7	16.7	36	45.8
9 May	57.4	33.8	18.2	68	51.9	70.6	26.5	2.9	68	48.1
11 May	72.4	27.6	0.0	76	43.3	75.0	22.4	2.6	76	56.7
12 May	36.5	59.5	4.1	74	56.7	82.2	17.8	0.0	73	43.3
16 May	25.0	75.0	0.0	64	66.5	80.6	16.4	3.0	67	33.5
19 May	8.5	85.1	6.4	47	93.8	2.6	30.8	66.7	39	6.2
23 May	44.7	48.9	6.4	47	51.2	61.7	21.3	17.0	47	48.8
26 May	83.1	16.9	0.0	77	41.4	79.2	20.8	0.0	77	58.6
27 May	95.2	4.8	0.0	21	72.2	100.0	0.0	0.0	21	27.8
2 June	11.8	88.2	0.0	17	68.2	47.1	47.1	5.9	17	31.8
3 June	9.1	90.9	0.0	33	42.4	92.2	8.8	0.0	34	57.6
10 June	89.7	10.3	0.0	29	52.2	96.6	3.4	0.0	29	47.8
16 June	36.0	60.0	4.0	75	57.4	67.5	28.6	3.9	77	42.6
20 June	48.4	51.6	0.0	31	68.2	96.8	3.2	0.0	31	31.8
23 June	68.1	27.7	4.3	47	54.9	85.1	14.9	0.0	47	45.1
27 June	57.7	38.5	3.8	26	59.0	80.8	15.4	3.8	26	41.0
				813					812	

whereas 517 spent 22.6 percent of her time there.

Great day-to-day variation occurred in the proportions of time spent in the three types of location. The relationship between the maximum air temperature for the day and the amount of time spent in the shade appears to be direct (Fig. 16). The deer spent all of the time in shade when the maximum temperature exceeded 35°C and no time in shade on days when the maximum was less than 15.6°C. The collections of flies in relation to deer resting sites and movements are summarized in Table 12.

The relationship between the time spent in the shade and the percentage of flies observed on or around each of two hosts is indicated in Figure 17. "Percentage of total flies" refers to the number of flies on one host calculated as a proportion of the total number of flies observed on both hosts. "Percentage ± mean time in shade" refers to time spent in the shade by a single host as a deviation (in percent) from the mean percentage time spent in the shade by both hosts.

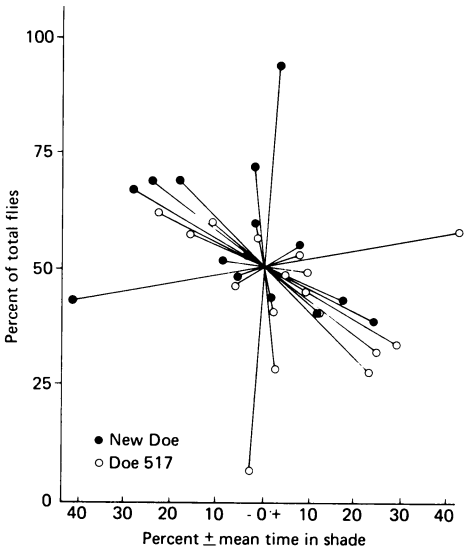

Fig. 17. Relationship between the percentage of total flies attracted to each of two does and the percentage of time spent in the shade by each of those hosts. See text for full definitions of the factors plotted.

For example, the uppermost point on Fig. 17 indicates that on 1 day, 93.8 percent of the flies observed were on New Doe, and that host was observed in the shade slightly more than the mean number of times that both hosts were observed in the shade on that day.

For a given day, regardless of the absolute amount of time spent in the shade by the two hosts, the host spending the lesser amount of time in the shade tended to have more flies around her (Fig. 17). This was true for 13 of 17 days.

Effects of weather on biting activity of *Symphoromyia* species

Air temperature.—The threshold of activity was determined for the individual species of the *S. pachyceras* complex on the basis of specimens collected in half-hour lots and the lowest air temperature during the half hour. Since specimens of *S. sackeni* are easily identified on the wing, observations of the beginning of activity were from field notes rather than from specimens. The mean lower temperature thresholds for species of *Symphoromyia* attacking deer at the H.F.S. were as follows: *S. pachyceras* and/or *S. cervivora,* 19.9°C; *S. inconspicua,* 21.7°C; *S. sackeni,* 22.6°C; *S. truncata,* 22.8°C; *S. nana,* 23.7°C (Table 13).

Few data were obtained on high-temperature thresholds. On 4 consecutive days in late June, 1964, the maximum air temperature exceeded 37.8°C (100°F) at the H.F.S. *Symphoromyia* activity was studied on the last 3 days of that period. Observations were also made the day following the heat wave, at which time the maximum air temperature was 27.8°C. On 3 days during which *S. sackeni* stopped attacking during the middle of the day the temperature was between 34.4° and 37.2°C. On days that the temperature failed to

TABLE 13

MEAN LOWER TEMPERATURE THRESHOLDS AND RELATED STATISTICS* AT WHICH *SYMPHOROMYIA* SPECIES WERE FIRST OBSERVED ON AND AROUND DEER

Species	$\bar{X}$ (in °C)	2 × SE$\bar{x}$	No. of days*	No. days during 1965 with max. temp. above threshold	Days over threshold divided by total days in season × 100
S. sackeni	22.6	±1.4	11	58	82
S. nana	23.7	±5.2	5	37	70
S. inconspicua	21.7	±2.2	8	39	78
S. truncata	22.8	±1.8	8	38	73
S. pachyceras and/or *S. cervivora*	19.9	±5.0	9	46	66

* The lowest temperature at which each species was first seen at deer was: *S. pachyceras-S. cervivora*—17.2, *S. inconspicua*—19.4, *S. sackeni*—20.0, *S. truncata*—20.6, *S. nana*—20.0. For the data associated with each individual fly see: Hoy, J. B. 1966. The behavior of the genus *Symphoromyia* attacking deer in Northern California (Diptera: Rhagionidae). Univ. Kansas, Ph.D. thesis, 162 pp.

reach 34.4° no mid-day cessation of fly activity occurred.

Wind.—Wind speeds recorded on 21 days during 1965 and the numbers of flies observed during quarter-hour periods were compared for the 3 days with the highest rate of fly activity (11 May, 12 May, and 16 June) and for 3 days with highly variable wind condition (4 May, 23 May, and 15 June). The purpose of these comparisons was to explore relationships between the wind and fly activity. Despite consideration of lag effects (of wind conditions during the 14 minutes preceding fly observations) and possible positive *or* negative effects of low wind speeds, no generalizations can be made. Likewise, gusty periods seemed to have no effect on the activity despite maximum speeds of 32 to 37 kmph.

Light.— Intensive study of the rate of fly attack as related to the light conditions on 4 days (9 May, 19 May, 16 June, and 23 June), days representing many possible combinations of cloud cover and light intensity, together with more general studies for 15 additional days, revealed no trends in fly activity that are not more easily explained in terms of fly response to temperature.

No *Symphoromyia* were caught in battery-operated light traps which captured phlebotomines, ceratopogonids, or mosquitoes on six nights when temperatures might have allowed snipe fly activity.

Other factors.—Although continuous records of the black globe temperature, soil temperature, and wet bulb temperature were available for the entire period of this study, none of these measures of the environment gave a more accurate basis for prediction of initial *Symphoromyia* activity than did air temperature. Likewise, the various measures of atmospheric water failed to have predictive value greater than that of air temperature.

The above remarks apply to prediction of the beginning of fly activity, rather than the magnitude of activity. Positive correlations between the magnitude of activity (attack rate) and measures of temperature often occur.

Insemination of attacking females

All nulliparous females collected while biting deer, and whose spermathecae were examined, were found to be inseminated. This included 22 specimens of the *S. pachyceras* complex and

TABLE 14

RELATIONSHIP BETWEEN WING LENGTH AND FLY WEIGHT

Specimen	(Wing length)^3 1 unit = 0.4 mm X	Fly weight in mg Y
1	2326	6.24
2	2433	6.07
3	3688	9.40
4	2024	4.70
5	2833	8.92
6	2955	6.24
7	2894	7.84
8	1838	4.72
9	1772	6.48
10	2300	5.68
Total	25063	66.29

$\overline{X} = 2506$
$\overline{Y} = 6.63$
$b = .002195$
$Y = 1.3 + 0.002195X$

Anova

	d.f.	SS	MS
Total	9	23.23	2.58
Explained	1	15.24	15.24**
Error	8	7.99	1.00

** Significant at the 1 percent level.

14 *S. sackeni* examined in 1964, 31 (mixed species) examined in 1965, and 1 *S. sackeni* from 1966. All 70 nulliparous females collected in CO_2-baited traps in 1966 and examined for sperm also were found to be inseminated, as were 25 parous females (Anderson and Hoy, 1972). All of 30 parous females (mixed species) collected from deer in 1965, and whose spermathecae were checked, also were inseminated. Noninseminated females were caught only from mating swarms.

Amount of blood taken by *Symphoromyia sackeni*

Weights were determined for 10 unengorged females of *S. sackeni* collected while landing on deer; hence they were in a physiological condition similar to that of others collected after the initiation of feeding. The mean weight of the unengorged specimens was 6.63 mg (range 4.70 to 9.40 mg; see Table 14).

Wing lengths of these unengorged specimens were also measured. Fly weight was then regressed on wing length cubed. The resulting relationship can be expressed as $Y = a + bX$, where Y is the fly's weight, a is the Y-intercept, X is wing length cubed, and b is the slope of the regression line. We found with $N = 10$: $Y = 1.13 + 0.02195\ X$. Analysis of variance of fly weight in relation to wing length is significant at the 1% level. Two flies, three-quarters engorged, were studied further. Setting confidence limits of 95 percent on estimates of Y with X's of 3275 and 2248, it becomes apparent that the larger fly took between 46.9 and 98.3 percent of its estimated unengorged weight in blood. The smaller fly took between 25.5 and 90.0 percent of its expected body weight in blood. These two flies were selected from a series of nine partially engorged flies. The degree of engorgement within a series of nine specimens ranged from a trace to three-quarters engorged.

The actual weight of blood taken, within 95 percent confidence limits,

would be 4.48 to 6.96 mg for the larger fly and from 1.86 to 4.34 mg for the smaller fly. Hence, an average-sized, fully engorged *S. sackeni* might be expected to take about 5.5 mg of blood per meal, or about 90 percent of its pre-engorging body weight.

Evidence for gonotrophic concordance and for anautogenous development of eggs

We experienced considerable difficulty in keeping large numbers of engorged and partly engorged females alive in the laboratory for more than a few days. In a mixed group of the *S. pachyceras* complex[4] aspirated from deer on 15 May 1964, five were dead 4 days after capture, and 15 at 11 days after capture. The latter were too decomposed to yield information, but two of five flies dead at 4 days post-capture showed from one-third to one-half digestion of their blood meals and primary follicles about one-half matured. The other three apparently had just begun to feed when caught and had no ovarian development. Of eight flies still alive on the 11th day post-capture, one small grey (nulliparous) and two large grey specimens (one nulliparous, one undetermined) had mature eggs. The intestines of two other small grey specimens, however, were still about one-fourth to one-half filled with blood, and their primary follicles were only one-fourth to one-half developed. The three other survivors were non-blood-fed nullipars, probably *S. nana,* whose primary follicles were as illustrated in Fig. 18A.

The above flies were not observed between 21 May and 26 May because of field work. Therefore, most dead flies found on 26 May were either too dessicated or decomposed to yield information on the condition of their internal organs. Twenty other specimens of the *S. pachyceras* complex collected feeding on deer between 21 and 25 May also died in the laboratory at 4 to 7 days post-capture. About one-half of these latter females had their midguts about half-full of blood and their primary follicles about one-fourth to one-half developed; the other half consisted of non-blood-fed, nulliparous females with undeveloped ovaries. Other attempts in 1964 to hold engorged females in the laboratory until completion of oogenesis were unsuccessful.

Sixteen non-blood-fed, nulliparous *S. sackeni* held in the laboratory in 1964 for 4 to 8 days on sucrose and water, had no further follicular development than illustrated in Fig. 18A. Ten non-blood-fed, nulliparous specimens of the *S. pachyceras* complex held in the laboratory 4 to 7 days and three such females held 11 days also had no ovarian development beyond that illustrated in Fig. 18A. In 1965, four *S. pachyceras* or *S. cervivora* and 12 *S. sackeni* collected from deer, and all non-blood-fed and nulliparous, were held in the laboratory for 3 to 11 days with no autogenous development of the ovaries. The same was true for two *S. sackeni* females collected from male mating swarms and held 2 days before dissection and examination.

Four engorged *S. pachyceras* or *S. cervivora* aspirated from deer on 29 April 1965, had, respectively, 105, 112, 113, and 168 mature eggs when dissected on the 7th day after capture from deer. Three non-blood-fed *S. pachyceras* or *S. cervivora* aspirated from deer on 12 April 1965, and dead 3 and 4 days later, had no more development of the primary follicle than illustrated in Fig. 18A. In another group of 20 *S. pachyceras* or *S. cervivora* col-

[4] When these flies were dissected in 1964, the extent of the species complex for the grey *Symphoromyia* species was unknown. Hence the specimens dissected during 1964 were classified only as "small grey" or "large grey" species. All large grey flies from this date probably were *S. pachyceras-cervivora,* and the small grey flies probably *S. inconspicua.*

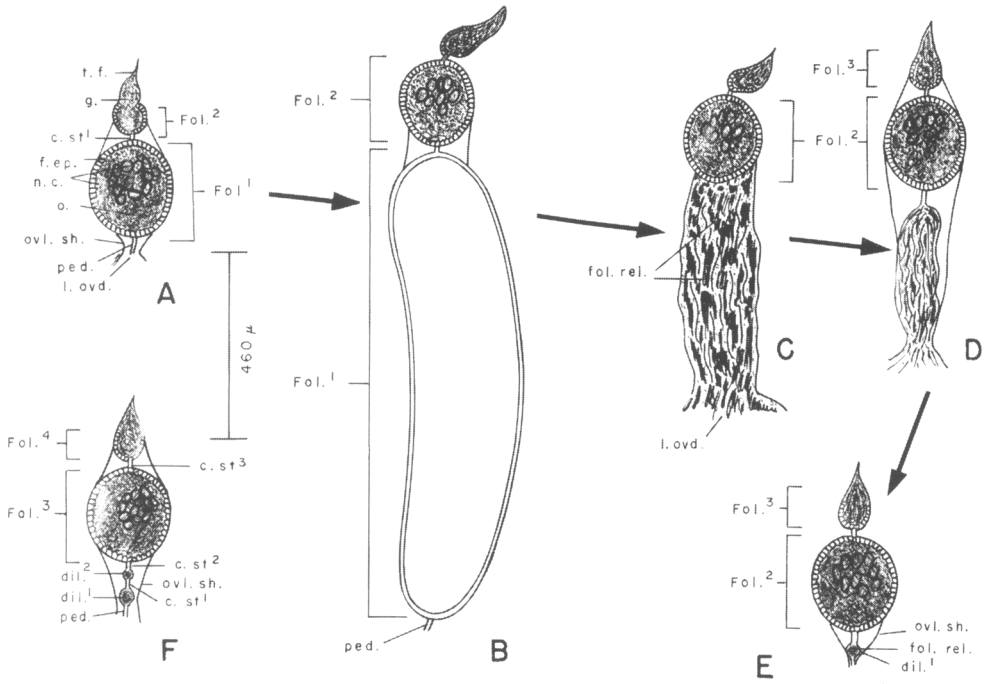

Fig. 18. Morphological changes occurring in the ovarioles of the six *Symphoromyia* species studied: A) Ovariole of a nulliparous female (primary follicle at stage II); B) Ovariole of a nullipar with the primary follicle containing a mature egg (stage V); C) Ovariole shortly after oviposition, showing saccate dilatation packed with follicular relics; D) Ovariole with dilatation about one-half contracted; E) Ovariole of uniparous female showing one fully contracted dilatation containing some follicular relics; F) Ovariole of biparous female with two fully contracted dilatations. c. st.^{1,2,3}-first, second, and third connecting stalks, respectively; dil.^{1,2}-first and second dilatations, respectively; f. ep.-follicular epithelium; Fol.^{1,2,3,4}-first (primary), second, third, and fourth follicles, respectively; f. rel.-follicular relics; g—germarium; l. ovid.—lateral oviduct; n. c.—nurse cells; o—oocyte; ovl. sh.—ovariole sheath; ped.—pedicel.

lected from deer on 9 May 1965, four survived for 8 days. Of these survivors, only two females had mature eggs (72 and 195, respectively). The third female had partially developed eggs (stage III), and the fourth had no follicular development despite evidence of an almost full (but undigested) blood meal. All of these 1965 females, plus 12 dissected, non-engorged ones aspirated from deer on these two dates, were nulliparous.

Of 13 blood-fed *S. sackeni* collected from deer on 3 June 1965, four of five survivors had mature eggs when killed and examined 9 days later. The other survivor had eggs at stage IV of development. Eight of the above group of flies were found dead on the 4th day post-capture. One live non-engorged specimen was also killed and dissected at that time. Except for the last fly, these dead females all contained partially digested blood meals and had various degrees of ovariole development. All of the above *S. sackeni* were nulliparous.

Although we experienced difficulty in keeping caged females alive in the laboratory, 15 blood-fed nullipars sur-

vived for 7 to 11 days before they were dissected and examined. The fact that 13 of these females contained clutches of mature eggs, and two had nearly mature eggs, indicated that these *Symphoromyia* species exhibited gonotrophic concordance (i.e., each blood meal of an unknown minimum quantity gave rise to one batch of matured eggs). As with many other nulliparous females that died 4 to 8 days after feeding on deer, when the blood meal was one-third to one-half digested, the primary follicles likewise were one-third to one-half developed. All other field-collected females dissected and examined further support this conclusion; none of the nullipars captured from hosts or in CO_2-baited traps (Anderson and Hoy, 1972) was found with its primary follicles at intermediate stages of development. In fact, except for one gravid female caught in a CO_2-baited trap, all of the 1347 females (nulliparous and parous) caught in traps or captured from hosts had the most advanced follicles in stage II (Figs. 18A, and 18C–F). The only flies with ovarioles at intermediate stages of development were two *S. sackeni* females collected in the vicinity of male swarms, and having follicles at stage IV.

In the species studied, therefore, ovarian development was an all-or-none phenomenon initiated by the attainment of, and completed with the digestion of, one blood meal. If the blood meal was of sufficient size to provoke oogenesis but not large enough to support the development of all ovarioles, then only a percentage of a fly's total ovarioles produced mature eggs. The primary follicles of those ovarioles that did not function in the first gonotrophic cycle remained about the same size (and no more than doubled) as in unfed nulliparous females.

None of the 76 non-blood-fed, nulliparous females developed eggs autogenously when held in the laboratory for 3 to 11 days with constant access to sucrose cubes and water. This included two *S. sackeni* from male swarms that were held for 2 days before dissection; and from deer, 12 held for 3 to 11 days, and 17 held for 4 to 8 days before dissection and examination. For *S. pachyceras* or *S. cervivora* three were held for 3 to 4 days, 12 were held for 8 days, and four were held for 3 to 11 days before dissection and examination. Twenty-six others identified as members of the *S. pachyceras* complex were held 4 to 11 days without developing eggs autogenously. Nulliparous females held 11 days had no more development of the primary follicles than did 2-day-old females.

Egg maturation time and number of eggs produced

When flies were held at a relative humidity of 60 percent ± 10 percent, and in darkness at 12.8°C during 12-hour "night" periods and under artificial light at 21.1°C for 12-hour "day" periods, eggs were matured between 7 and 11 days after the flies had engorged on deer. Because frequent field trips in 1964 and 1965 prevented our examining laboratory-held flies on a regular basis, we were not able to determine the minimum time required to complete oogenesis.[5] From the previous section one will note that four *S. pachyceras* or *S. cervivora* had mature eggs at 7 days post-feeding, and that two had mature eggs at 8 days after feeding on deer. Four *S. sackeni* had mature eggs at 9 days post-feeding, and three specimens of the *S. pachyceras* complex had mature eggs at 11 days post-feeding. Perhaps because they were not able to obtain full blood meals before they were aspirated, the number of mature eggs produced by the blood-fed flies

[5] We have since determined that, at a constant temperature of 23.3 to 23.9°C, *S. sackeni* can mature its eggs in as little as 4 days after obtaining a blood meal from deer.

TABLE 15

CHARACTERISTICS OF NULLIPAROUS AND PAROUS FEMALES*

Item	Nulliparous	Parous
Ovarioles	Tightly bunched and difficult to separate.	Loosely bunched and easily separated.
Ovariole pedicels and lateral oviducts	Transparent (no visible follicular relics).	Follicular relics present in saccate ovariole pedicels, lateral oviducts and dilatations.
Size of ovariole pedicels	Short, narrow, and tubular (Fig. 19A).	Either long and dilated (Figs. 19C, D) or with distinct dilatations on the tubular pedicels (Figs. 19E, F).
Intestines	Frequently containing a greenish meconium.	Always with residual blood evident.
Rectal papillae	Clear, or containing a white granular material.	Tinted light to dark red and almost always with hematin granules.

* In addition to these characteristics, the diverticulae of both nulliparous and parous flies commonly contained a clear, viscous fluid.

held in the laboratory was always less than the number of eggs seen in gravid, wild-caught females. For example, the numbers of eggs produced by the four *S. sackeni* held in the laboratory were 54, 56, 68, and 68, respectively, whereas the numbers of eggs in seven gravid, wild-caught females were 88, 88, 102, 108, 110, 114, and 118. Similarly, the number of eggs in laboratory-held *S. pachyceras-cervivora* ranged from 72 to 195, but a gravid female trapped in 1966 had 238 eggs. The total number of ovarioles in eight *S. pachyceras-cervivora* ranged from 132 to 240 ($\bar{x} = 190$). The total number of ovarioles in 30 *S. sackeni* ranged from 64 to 132 ($\bar{x} = 107$), but most of these were collected from mid to late June 1965 when specimens were somewhat smaller than earlier in the season. Total ovariole counts in other species were: *S. truncata,* 126 to 138; *S. nana,* 114 to 150; and in one *S. inconspicua,* 112.

Recognition of nulliparous and parous females

As females of known ages and histories could not be studied because the flies' larval habitats were unknown, the interpretation of morphological changes occurring in ovarioles during and following oogenesis was inferred from results obtained for other hematophagous Diptera (e.g., Beklemishev et al., 1959; Davies, 1961, 1963; Detinova, 1962; Duke, 1960; Kuzina, 1950; Lewis, 1960 *a, b;* Lutta, 1964; Gillies and Wilkes, 1963; Samarawickrema, 1962). In compensating for the above, illustrations were made of the ovarioles of many females caught during the early, middle, and late fly season. We soon found that parous flies of all five *Symphoromyia* species could readily be distinguished from nulliparous specimens by comparing the morphology of the ovarioles of females caught at different times of the year. Ovarian structures (Fig. 18) and post-oviposition changes in the ovarioles (Table 15) were the same in all five species. The morphology of the ovarioles of the *Symphoromyia* species studied (Fig. 18) is like that of other hematophagous Nematocera and Brachycerca (e.g., see same references cited in first sentence of this section). Hence, stages I to V of Christophers (see Bertram, 1962) were arbitrarily selected for classifying the state of oogenesis a female was in (see Bertram, 1962, for a descriptive analysis of these stages and a morphological description of a generalized mosquito ovariole).

The capture of teneral, non-inseminated nullipars and gravid females of *S. sackeni* in and near male swarms proved indispensable for establishing

the morphological features of nulliparous flies. All females aspirated from deer early in the season were nullipars with ovarioles morphologically identical with those of nullipars captured in male swarms (Fig. 18A and Table 15). Collections from deer yielding parous females with one or more mature eggs remaining after completion of a previous gonotrophic cycle likewise allowed the unequivocal establishment of the morphological features of parous females. The following numbers of the indicated species were found with one or more retained (relic) eggs: ten *S. sackeni;* three *S. inconspicua;* two *S. pachyceras* or *S. cervivora;* one *S. nana;* one *S. truncata.* One fly had one egg in a lateral oviduct; all other eggs were retained in ovarioles. Ten flies contained only one egg, four had two eggs, two had three eggs, and one had four eggs.

The results in this section, and those in several of the preceding ones, are based on the dissection and microscopic study of the following species and numbers of snipe flies per year: 1964—46 specimens in the *S. pachyceras* complex (27 nulliparous, 16 parous, 3 undetermined), 16 *S. sackeni* (nullipars); 1965—16 *S. inconspicua* (15 parous, 1 undet.), 20 *S. pachyceras* or *S. cervivora* (12 nulliparous, 5 parous, 3 undet.), 22 *S. nana* (1 nullipar, 21 parous), 25 *S. truncata* (2 nullipars, 23 parous), 187 *S. sackeni* (53 nullipars, 130 parous, 4 undet.), 1966—3 *S. inconspicua* (2 nullipars, 1 parous), 285 *S. pachyceras* complex (6 nulliparous, 279 parous), 727 *S. sackeni* (69 nullipars, 658 parous).

The several more important characters for distinguishing nulliparous from parous flies are summarized in Table 15. Of the 1347 females dissected from 1964 to 1966, only 11 could not definitely be classified as nulliparous or parous. In all cases the unclassified flies were partially engorged females that had died in the laboratory and whose ovaries were permeated with blood and badly decomposed.

Morphological features of follicular development typical of various stages seen in nulliparous and parous flies are depicted in Fig. 18. The developing follicles of the *Symphoromyia* species studied differed from those of certain mosquitoes (Bertram, 1962) in that the primary follicles of nullipars were already at stage II at the time females were captured from male swarms, or coming to a host for their first blood meals. The developing follicles of anautogenous mosquitoes usually do not proceed to stage II until after digestion of a blood meal has begun. The evidence against autogeny occurring in the *Symphoromyia* species studied is presented in the two preceding sections.

There was essentially no difference in the sizes of the largest developing follicles of flies attracted to deer or CO_2-baited traps regardless of whether these happened to be the primary follicles of a nullipar or the secondary, tertiary, etc., follicles of a parous female (Fig. 18). At the time eggs were matured, the next developing follicles were at stage II (Fig. 18B), and were about the same size as the largest developed follicles seen in blood-seeking females.

As the largest developed follicles seen in all flies caught, whether captured from hosts, male swarms, or in CO_2-baited traps, were at stage II, this confirmed the laboratory-obtained evidence (see previous sections) that oogenesis in these species is associated with gonotrophic concordance. No females with ovarioles at stage III were captured because the resting sites of engorged, digesting females were not discovered. Except for two gravid females (an *S. pachyceras* or *S. cervivora* and an *S. sackeni*) captured in insect flight traps, other gravid and near-gravid females (all *S. sackeni*) were captured only while sweeping vegetation in the vicin-

ity of male swarms. The latter included two females with developing follicles at stage IV, and four gravid females (stage V) (Table 18). Also, one dead female was found in the grass at one of the male swarming sites.

The primary follicles of nulliparous *S. sackeni* females (Fig. 18A) ranged from 131 × 166 μ to 207 × 276 μ regardless of whether the flies were obtained from male swarms, deer, or in CO_2-baited traps. Differences in follicle sizes were associated with different sized flies. Follicles in *S. pachyceras* or *cervivora* (slightly larger species than *sackeni*) ranged from 138 × 173 μ to 221 × 304 μ, whereas those of *S. inconspicua, S. nana,* and *S. truncata* (all smaller species than *sackeni*) ranged from 124 × 152 μ to 173 × 235 μ. Nulliparous females were primarily identified (Table 15) by the appearance of the short, narrow, transparent ovariole pedicels, the compactness of the ovary, and the absence of characteristics associated with parous females. Details of ovariole morphology, particularly in nullipars, were more easily seen when the ovarioles were separated into groups of five to ten. In part, because of the tightness of the ovarian tracheation, it was difficult to separate the tightly bunched ovarioles so that entire individual ovarioles could be studied. Conversely, individual ovarioles of parous females (see below) were easily separated for study.

After oviposition the follicles which gave rise to mature eggs (Fig. 18C) were clearly distinguished as large, sac-like structures immediately below the follicles at stage II. While viewing wet preparations from gravid females, the follicles and pedicels of ovarioles from which eggs had just passed out were observed to contract almost immediately to a size about one-half as long as a mature egg and slightly wider than the next developing follicle. Most host-seeking, parous females had expanded sacs about one-fourth to one-half the length of a mature egg, about as wide as the next developing follicle, and packed with follicular relics (Fig. 18 C). The lateral oviducts of such females also commonly contained large quantities of follicular relics. Parous females at this stage could readily be identified with only a stereoscope (nevertheless many preparations also were examined under a compound microscope) because the "loose" nature of the ovaries made it easy to see the wide, sac-like follicles. Under a stereoscope these follicles appeared filled with a white to greyish material. The fact that almost all parous females captured from deer or in CO_2-baited traps, and dissected the same evening of the day of capture or frozen at 1 to 4 hours post-capture and later thawed and dissected, had ovarioles as in Fig. 18C, indicates that these flies are extremely efficient at again finding hosts soon after ovipositing.

Figure 18D depicts an ovariole of a parous female estimated at about 30 to 48 hours post-oviposition. The fly from which this illustration was made was held alive and dissected 22 hours after capture from a deer. Twelve other parous females maintained alive until examination at about 24 hours after capture had ovariole sacs contracted to approximately this state. The only times when flies with ovariole sacs about one-half contracted were captured from deer were on days preceded by one or more days which had temperatures below the minimum to elicit host-seeking. This indicates that flies such as these (and those with ovarioles as in Figs. 18E,F) probably oviposited on a day when the temperature was high enough to elicit oviposition but not the seeking of a host or that there had been a brief period when oviposition and search for a host occurred but only oviposition was achieved.

In comparison with certain mosquitoes in which complete contraction oc-

curs in 12 to 36 hours post-oviposition (Detinova, 1962; Samarawickrema, 1962) or 36 to 48 hours post-oviposition (Gillies and Wilkes, 1963), contraction of the sac-like follicles and associated structures proceeds relatively slowly in the *Symphoromyia* species studied. In fact, the minimum time required for complete contraction of the follicular sacs of parous *Symphoromyia* was not determined. Complete contraction to the point of showing distinct dilatations (Figs. 18E,F) was seen in only three parous females examined 5 days after capture from deer. Unfortunately, the few flies surviving long enough to determine the time needed for engorged flies to mature eggs were all nulliparous. However, supplanting the observations of distinct dilatations in the ovarioles of the above three parous flies, complete contraction (with one or more distinct dilatations present) was seen in 15 females captured from hosts or in CO_2-baited traps and killed and frozen within 1 to 10 hours after capture. Also, on a few occasions one or more dilatations were observed in the ovarioles of parous females containing mature relic eggs not laid at the last oviposition.

As for many mosquito species (see Detinova, 1962; Gillies and Wilkes, 1965; Kurihara and Hayashi, 1965; Samarawickrema, 1962) and other Diptera (Davies, 1961, 1963; Detinova, 1962, 1968; Linley, 1965), the elasticity of the follicle and of associated ovariole structures permits post-oviposition contraction to proceed until only a small dilatation is apparent on the narrow, tubular pedicel and connecting stalks. The original position of a follicle which has previously produced an egg is marked by a small, roughly circular distention or dilatation. Almost all such dilatations contain follicular relics (Figs. 18E,F). The number of dilatations present, therefore, as for some *Culicoides,* black flies, and many species of mosquitoes, undoubtedly indicates the number of eggs produced/ovariole and, therefore, the number of gonotrophic cycles completed by the female. Follicles interpreted as abortive (degenerating) were larger than dilatations and they usually contained considerable quantities of yellowish yolk granules irregularly dispersed throughout.

As the *Symphoromyia* species studied are characterized by gonotrophic concordance, it is apparent that several gonotrophic cycles can be completed during the life of a fly. However, because these flies are such efficient host finders, most parous flies arrive at hosts (or CO_2-baited insect flight traps) with a single, large, sac-like dilatation packed with follicular relics. All one is able to do with such flies is classify them as parous. To determine the number of gonotrophic cycles completed by such parous females, the flies should be maintained alive for several days before they are examined. The maximum number of dilatations seen was three in *S. sackeni.* The only occasion on which a few parous flies with ovarioles in the fully contracted state were captured was on 1 and 3 June 1966 (Anderson and Hoy, 1972), following a prolonged cold spell of 4 days during which the low temperatures inhibited host-seeking activity.

Storage of collected flies at –50°C proved an excellent technique for determining parity long after females were captured. All flies frozen within 30 minutes after death were found upon thawing to have all internal organs in the same condition as in specimens dissected immediately after being killed, regardless of whether frozen flies were thawed at 3 weeks or up to 4 years after their initial freezing. Also, as long as thawed flies remained at room temperature for no longer than an hour, frozen flies could be thawed and refrozen several times with little adverse

TABLE 16

SEASONAL CHANGES IN THE NUMBERS OF NULLIPAROUS AND PAROUS FLIES ATTACKING DEER (1965)

Date collected	*S. pachyceras* and *cervivora*	*S. inconspicua*	*S. nana*	*S. truncata*	*S. sackeni*
29 April	4/0*	—†	—	—	—
4 May	4/0	—	—	—	—
9 May	3/0	—	—	—	—
23 May	0/2	—	—	—	—
28 May	0/1	—	—	—	—
3 June	0/0	—	—	2/0	26/0
10 June	0/0	—	0/1	0/0	1/0
16 June	0/0	0/12	0/14	0/18	10/87
20 June	0/2	0/1	0/2	0/1	2/3
27 June	—	0/2	0/4	0/4	0/16
29 June	—	—	—	—	0/19
13 July	—	—	—	—	0/2
20 July	—	—	—	—	0/2

* Number of nulliparous females/parous females.
† No flies seen.

effect on the condition of the internal organs.

Seasonal changes in the parity of flies attacking deer

During 1965, 262 *Symphoromyia* were categorized as being either parous or nulliparous, with the parity of eight females designated as undetermined. As shown in Table 16, 245 females whose parity was determined were collected from deer. Most other females were collected in or adjacent to male swarms of *S. sackeni,* including one nulliparous *S. nana* caught on 28 May and 14 nulliparous *S. sackeni* caught between 28 May and 15 June.

The population of *S. sackeni* females attacking deer was largely parous by mid-June, as were the populations of *S. inconspicua, S. nana,* and *S. truncata.* The *S. pachyceras* and *S. cervivora* population probably became largely parous during mid-May (Table 16). Collection and dissection of *S. sackeni* females that attacked deer on 16 June 1965 revealed no shifts in the ratio of nulliparous to parous flies (Table 17).

TABLE 17

NULLIPAROUS AND PAROUS *S. SACKENI* ATTRACTED TO DEER ON 16 JUNE 1965

Pacific Standard Time	Number of nulliparous/parous
1030	1/2
1100	0/1
1130	0/4
1200	0/2
1230	0/3
1300	1/7
1330	2/6
1400	1/10
1430	1/8
1500	1/12
1530	1/13
1600	2/9
1630	0/3
1700	0/6
1730	0/1

Search for infective filarial worm larvae

In 1965 the heads and mouthparts of 53 parous *Symphoromyia* were dissected in a saline solution and examined under a compound microscope (35×) for the infective stages of filarial worms. All tissues were negative. The specimens were five *S. pachyceras* or *S. cervivora,* four *S. inconspicua,* seven *S. nana,* seven *S. truncata,* and thirty *S. sackeni.* Twenty of the *S. sackeni* specimens were collected on 29 June 1965, the latter part of the season and a time when the maximum number of a vector species would be infective. Be-

fore determination of parity in dissected females, the heads of 28 other specimens were examined, all of which were negative.

In 1966 we examined the dissected heads and mouthparts of 10 parous *S. sackeni* collected from deer, as well as of 72 parous flies in the *S. pachyceras* complex and 196 parous *S. sackeni* collected in CO_2-baited traps (Anderson and Hoy, 1972). These flies were likewise negative for filarial worms. Also, no mature or developing worms were seen in the abdomens of flies examined for parity. The deer on the Hopland Field Station are often parasitized by three species of filarial worms (Weinmann et al., 1973).

Symphoromyia mating swarms

On 21 May 1964, a small swarm of *Symphoromyia* males was discovered within the Deer Holding Pens. Four specimens were taken, two *S. sackeni* and two *S. plagens*. The following day 11 *S. plagens* males were collected from another swarm formed at the same place.

During the 1965 fly season we observed *Symphoromyia* swarms for a total of 33.5 hours on 10 different days when flies were active at swarming sites. The first swarms were seen on 28 May, the last on 14 July. No swarms were seen on 20, 22, 23, 26, and 28 July, nor on 5 August or 4, 5, 11, 19, and 20 May. Of the May dates, however, only the 4th and the 11th were warm enough for swarming to have occurred. Since we caught only inseminated females at deer or in CO_2-baited traps, and since one female was collected from deer on 11 May, small numbers of males obviously were present from about 10 May onward.

In 1965, nearly all flies collected from swarms were *S. sackeni* males. *Symphoromyia plagens* males were never taken, but two females and a few males belonging to the *S. pachyceras* complex were caught in the sweep net collections from the large swarms of *S. sackeni*. Although the swarms consisted mostly of *S. sackeni* males throughout the season, by collecting large numbers of flies from swarms we caught 18 females (about 1 for every 75 males). It should be pointed out, however, that this seasonal sex ratio is misleading with respect to these swarms being mating swarms, for it is well known that males of numerous species are present at mating sites both before and after females. Furthermore, virgin females generally are present at mating swarm sites only for the few minutes necessary to be inseminated (Downes, 1969).

With the above points in mind, we note that all female *S. sackeni* were caught between 28 May and 17 June, a period in which we captured 231 males. Only males were seen and caught on 24 and 29 June and on 1 and 14 July. Thus females comprised 7 percent of the flies caught between 28 May and 17 June, but, as shown in Table 18, not all females caught in sweep net collections from swarms may have been in the area to mate. Since *S. sackeni* is an anautogenous species, and since all host-seeking flies were inseminated, the 6 (of 9) females caught on 15 and 16 June, and having mature or nearly mature eggs, probably were attracted to oviposit in the same areas where swarming occurred. Of the ten females judged to be recently emerged nullipars, five were not inseminated (Table 18). If we eliminate the 16-June catch because most females were older, gravid individuals, then mate-seeking females comprised about 5 percent of the flies (180 males: 10 females) caught from 28 May through 15 June.

Detailed observations revealed that females fly through the swarms and are pursued by males. This response by the males is also directed at small stones thrown through the swarms. Two pairs of *S. sackeni in copulo* were netted from

TABLE 18

FOLLICLE DEVELOPMENT AND INSEMINATION OF NULLIPAROUS FEMALE *S. SACKENI* NETTED IN OR ADJACENT TO MALE SWARMS*

Date	Time	Stage of follicle development	Inseminated (?)	Notes and observations
28 May	1030	II	Yes (1 lobe†)	Dissected 12 h post-capture
28 May	1030	II	No	As above
28 May‡	1300	II	Yes (1 lobe†)	Some greenish-brown meconium in mid-gut; rectal papillae clean
28 May‡	1330	II	No	As above
10 June	0930	II	Yes	Diss. 24 h. post-capture. Some greenish meconium in mid-gut
10 June	1000	II	No	As above
10 June	1000	II	No	As above
15 June	1120	IV	Yes	88 maturing eggs
15 June	1120	II	No	
16 June	1140	II	Yes	Diss. 48 h. post-capture; no autogenous dev. of follicles
16 June	1220	V	Not determined	88 matured eggs
16 June	1240	II	Yes	Diss. 48 h. post-capture; no autogenous dev. of follicles
16 June	1240	V	Yes	102 matured eggs
16 June	1320	V	Yes	108 matured eggs
16 June	1430	IV	Yes	118 maturing eggs
16 June	1450	V	Yes	114 matured eggs

* Only 14 of the 18 females caught in 1965 were dissected and examined. The 2 females netted while flying *in copulo* were pinned with their respective males instead of being dissected.

† These 2 females were only partially inseminated; in both, sperm was seen in only one (the central) of the three spermathecal lobes. All other inseminated females had abundant sperm in all lobes. Complete insemination may have been prevented when copulation was disrupted by mixing with other flies in the net.

‡ 1966 dates; all others 1965.

swarms, and another pair was seen flying out of a swarm *in copulo* and descending into the grass. The latter flies were searched for but not found. The two partially inseminated females noted in Table 18 may have been flying *in copulo* or flushed from the grass and then been caused to uncouple by mixing and disruption by other flies in the net.

The following remarks apply to swarms of *S. sackeni:*

On 28 May we saw numerous swarms of 5 to 10 males form at 1000 hours (P.S.T.). These swarms increased to 25 to 35 males/swarm during the next hour, and then decreased in number shortly before swarming ceased at 1215 hours. The level of activity was about the same on 1 June, but on 10, 15, and 16 June, individual swarms consisted of as many as 100 males during peak swarming hours. Swarms of males also persisted for 2 to 3 hours longer on 15 and 16 June, but this also may have been influenced by cool temperatures (see below). On 29 June swarms of 25 to 30 males still were common during peak swarming hours. On 1 July the individual swarms were reduced to only 6 to 15 males/swarm during peak activity, and on 14 July only five smaller swarms were seen during 3 hours and 15 minutes of observation.

The two areas where the largest numbers of *S. sackeni* males were seen swarming, and where the swarms were first and last seen, were located 1) about 270 m north of the Deer Holding Pens (along the margin of a stream in an area of oak and madrone trees interspersed with open patches of grassland), and 2) about 360 m WNW of the Deer Holding Pens in a similar type of area adjacent to dense woodland but with no stream present. Smaller swarms were observed in similarly sparse to moderately wooded areas located from 4 to 9 m outside the Deer Holding Pens

and at sites up to 1.6 and 3.2 km from the pens.

The swarms formed in late morning or early afternoon, giving some indication of forming as the air temperature approached 21.1°C. The lowest temperature at which swarming was observed was 19.4°C. On this date (15 June), the first males were seen swarming at 1120 hours (observations began at 1010 hours). Similarly, on 24 June when the temperature was 18.3°C at 0915, swarming did not begin until the temperature warmed to 21.1°C at 1050 hours. Male swarms were not observed on days cooler than 19.4°C. On warmer days males were seen swarming as early as 0930 hours when the temperature was 21.1°C. Limited observations indicated that swarming stops in late afternoon or earlier. Swarming ceased between 1215 and 1330 hours on 4 days when the temperature had reached 29.4 to 30°C by these times, but on 2 days (15 and 16 June) it continued until 1500 and 1640 hours at temperatures of 21.1 and 24.4°C, respectively. Diminishing light conditions and warm temperatures appeared to be associated with cessation of swarming.

The number of flies in the swarm appears to contribute to the volume of the swarm. A swarm of approximately 100 flies would be roughly spherical with a diameter of about 1 m. A swarm of 10 flies would be about half that diameter. The center of the swarm was generally about 1 m above the ground. No conspicuous movement was made by the swarm as a whole, although over a period of time it may follow the movement of the sun relative to the margin of a tree or shrub.

All swarms were close to trees; none was seen in patches of open grassland and none was seen more than 0.3 to 0.9 m from the peripheral margins of oak or madrone trees. Generally the swarms formed at the margin of shade from a tree with flies hovering in the area between the tips of the lowest branches and the ground. In the more densely wooded areas swarms often occurred in a column or patch of sunlight filtering through a surrounding dense canopy of leaves. In exposed areas flies faced into the wind, but in sheltered areas they might be facing in any direction.

Where grass was 0.6 to 0.9 m high, the bottom members of a swarm hovered just a couple of cm or so above the grass. Where the grass or other vegetation was only several cm high, the bottom males of a swarm hovered about 0.3 m above the ground. Depending somewhat on the size of the swarm, the top males usually would be 1.2 to 1.5 m above the ground. Less commonly, a few individuals at the tops of swarm would hover as high as 3 to 5 m above the ground.

Within swarms individual males often "bounced" between positions several cm apart and changed positions frequently. In darting from one position to another they often rose slightly and then dropped, thus following an arc pattern. They also bounced in an up-and-down pattern and often chased one another in an upward spiral fashion. When flies chased small pebbles tossed through the swarm from the side, they also followed the arched flight path of the pebble. Males also chased stones upward and then down when stones were thrown up through the bottom of the swarm. Depending on the size of the swarm, one to two to six to eight flies would dart after a stone as it passed through a swarm.

On numerous occasions, several flies were observed to suddenly dart in unison in one direction. Since identical behavior was provoked by tossing small pebbles through swarms, and since coupled pairs were only seen flying beyond the edge of a swarm, it seems likely that such movement resulted from a group of males pursuing a female that had passed through the swarm. Within the all-male swarms,

males generally pursued other males for several seconds when: 1) two hovering males came within 10 to 15 cm of one another; 2) a male changed his flight pattern from hovering to flying; and 3) a male rejoined a swarm or a new male flew into a swarm.

A typical swarm of males would react as follows. Beginning with a spacing distance of about 0.5 to 1.5 m, the males bounce about in a hovering position and tolerate the presence of other males up to a distance of 10 to 15 cm. When they approach closer than this, one male will pursue the other. This usually results in several adjacent males joining the chase once the hovering pattern is interrupted momentarily. This behavior results in a rapid darting, circling, or spiraling movement of several males, lasting for several seconds. After a short chase of about 0.5 to a few meters, the now more dispersed swarm reassembles in the typical hovering, bouncing pattern. The individuals then gradually move closer together until two males interact again, thus momentarily setting off a change in the activity and structure of the swarm. The male-male chases generally moved laterally, but upward spiral pursuits between two, and then several, males were not uncommon. When a person rushed forward and swept through the swarms, the flies dispersed in both lateral and lateral-upward directions. The latter rose to heights of 3 to about 6 m, then after a few minutes they gradually descended.

Inasmuch as males of *S. hirta* (Shemanchuk and Weintraub, 1961), and now of *S. sackeni,* are known to swarm, it was not unusual to find males of other *Symphoromyia* species swarming at the H.F.S. and elsewhere (Turner 1971, 1974).

Bailey (1948), in his review of reports of hovering and mating of tabanids, found that 11 of the 13 species studied mated between 0800 and 1200 hours. Tabanids swarm at a variety of sites, i.e., over wooded hammocks (Snyder 1917), openings in woods (Blickle, 1959), and near high towers (Corbet and Haddow, 1962). Utilizing openings between shrubs and trees, *Symphoromyia hirta* and *S. sackeni* swarm in morning and afternoon. For the latter species our catches from swarms, at certain times, comprised 5 to 7 percent females, whereas *S. hirta* swarms contained approximately 12 percent females (Shemanchuk and Weintraub, 1961).

Our emphasis on the feeding behavior of females left little time to search for male swarms of other species at sites very far from the deer pens. Turner (1971, 1974) has since discovered the species-specific swarming sites of many other *Symphoromyia* species and has described the swarming behavior of the males.

DISCUSSION

Seasonal distribution and population dynamics

Table 2 shows the observed lengths of biting seasons for females of six species of *Symphoromyia.* The early-season limit of occurrence of the earliest species (*S. pachyceras* and *S. cervivora*) and the late-season limit of the latest species (*S. sackeni*) are probably less accurate estimates than are the other seasonal limits. Increased sampling and less extreme variation in weather contributed to the greater accuracy of the seasonal limits occurring near the middle of the total *Symphoromyia* season. (The greater uniformity of weather in midseason contributed to more uniform sampling during that time.)

The observed midpoints of seasonal occurrence of the six species differed

between years (1964 and 1965) from 6 days for *S. sackeni* to 24.5 days for *S. truncata*. For all six species the midpoints occurred later the second year. Also, the first (except for *S. nana*) and last records of each species were later in 1965 than in 1964.

Study of Fig. 4 and especially of Fig. 5 reveals that fly populations, as determined by attack rates, do not have early peaks followed by gradual declines (as reported for several species of tabanids by Tashio and Schwardt, 1953). This lack of early peaks in abundance indicates either long-lived adults emerging over a relatively short period of time or additions of short-lived individuals throughout a long period. Since we are dealing with univoltine species, the latter phenomenon would tend to cause a mid-season population peak, whereas the former phenomenon would demand relatively low losses due to predation and mishap and thereby have a less well-defined and relatively longer period of the population plateau. Neither Fig. 4 nor Fig. 5 shows clearly defined midseason peaks for any species, although *S. sackeni* during the 1965 season might be interpreted as having such a peak.

Although the histograms (Figs. 4 and 5) suggest the type of survivorship curve one might expect for a given cohort of the population, information on the physiological age of specimens taken during the season can add greatly to the accuracy of a hypothetical survivorship curve. Also, the period of adult emergence and length of time for conversion of blood to eggs can then be indirectly inferred from ovarian data if the sampling is well placed. Furthermore, the period of time required to utilize a blood meal determines the number of meals that may be taken in the lifetime of one individual and hence the vector potential.

Results of the parity determinations summarized in Table 16 reveal that nulliparous specimens are predominant in collections only during the early weeks a species is present. For *S. sackeni* (the only species for which many data are available) the period during which the first parous specimens occurred was probably the first week of June, and the period when the population became wholly parous was quite likely the 4th week of June.

Without discussing details of the effects of weather on the census data (illustrated in Fig. 5) or on the physiology of the insects, we propose a hypothetical model of *S. sackeni* adult population dynamics based on the following data: a) seasonal occurrence; b) period during which no nullipars were found; c) period when the population was wholly nulliparous; and d) apparent shape of the survivorship curve. Figure 19 illustrates the steps in construction of a graphic model depicting the proposed population dynamics and age-structure as related to gonotrophic cycles. Before discussing the logic on which Fig. 19 is based, however, one point should be made clear regarding the length of the season of *S. sackeni*. Although one specimen was observed on 11 May 1965, no other was observed until 26 May. During the 15 days between the first and second observed specimens, 2 full days of observation (each of which had several hours above the temperature threshold for *S. sackeni* activity) failed to produce a record of *S. sackeni*. Furtherfore, 6 of the 7 days preceding 26 May were cool with maximum temperatures below the temperature threshold for *S. sackeni* activity. Thus very few blood meals could have been taken before 25 or 26 May and the first parous specimens collected probably fed on or after 25 May. That day is therefore accepted as the beginning of the season of *S. sackeni*. Likewise, that day is a realistic date from which to work in terms of the beginning of emergence. The total season of occur-

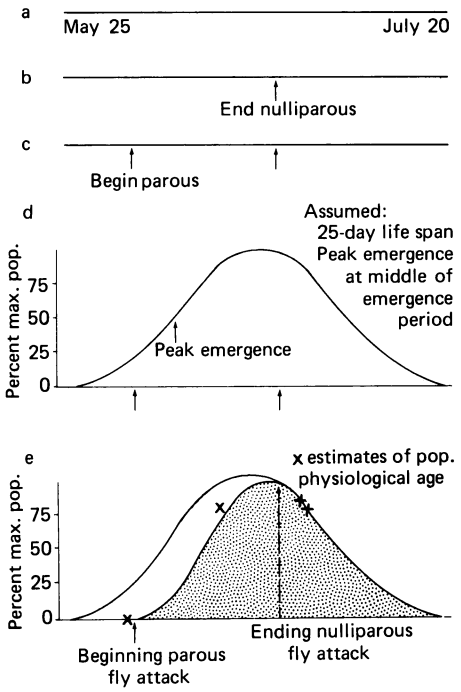

Fig. 19. Stepwise presentation of estimated population dynamics of imaginal *S. sackeni* during 1965. See text for the logic upon which each step is based.

rence of adults thus becomes aproximately 8 weeks, a period also supported by CO_2-trap catches and observations of deer in 1966 (Anderson and Hoy, 1972).

The logic behind the construction of Fig. 19 follows. Step (a) establishes the base line of the adult population which lasts for 8 weeks. Step (b) shows the date after which nulliparous specimens no longer appear. The difference between this date and the date of the last observed adults suggests the life span of adult females of *S. sackeni,* i.e., 25 days. Step (c) indicates when parous specimens first appear in the population. This point, some 10 days after the first adults come to the hosts, indicates that a complete gonadotrophic cycle may be completed in 1 to 2 weeks. (*Symphoromyia sackeni* held in the laboratory develop eggs in about 9 days.) Step (d) of Fig. 19 is based on a 25-day life span as imagined and a 30-day period of adult emergence for *S. sackeni.* Emergence of adults is assumed to be maximal at the midpoint of that 30-day period. If emergence is normally distributed, the population build-up would follow a sigmoid curve with maximum rate of increase at mid-curve. Therefore, the peak numbers of adult *S. sackeni* should occur at a time between the first natural mortality and the last adult emergence, a period of 6 days. A very limited number of flies would be expected to die of old age during this period, hence the growth curve would deviate only slightly from the classical sigmoid curve. Likewise, the decline of the adult population might be expected to follow a reverse of the sigmoid pattern of growth, perhaps slightly attenuated as a result of slight natural mortality before the end of emergence. Step (e) is the addition of an estimate of the make-up of the population in terms of physiological age. Determination of parity (age-grouping) on the basis of ovarian morphology was used to determine the time of onset of attack by parous specimens and the end of attack by nulliparous specimens. Study of the percentage of parous flies in two samples taken at times between a 100 percent nulliparous and a 100 percent parous population indicated that by mid-season approximately 95 percent of the fly population was parous. Since field collections and parity determinations do not contradict the assumption of normally distributed emergence, we believe that the curve is logical.

The scheme presented in Fig. 19 does not take into account weather variations, host-finding efficiency, losses due to predation or accidents, or the intrinsic variations in the life spans of the imagines. Adjustment for the first of these factors would require a much

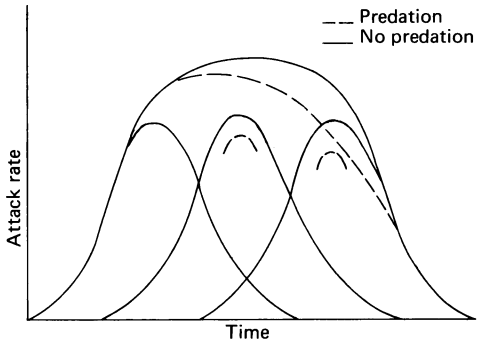

Fig. 20. Hypothetical effects of predation on the attack rate. See text for explanations.

greater understanding of the effects of weather on the physiology of *S. sackeni* than we now have. The host-finding efficiency of *S. sackeni* can be estimated only after further study. For the present discussion, however, it is assumed that the efficiency is very high. The life span of *S. sackeni* might be assumed to have a coefficient of variation of 10 percent without greatly changing the shape of the curve in Fig. 19.

Losses due to predation and accident have been regarded as negligible. If this assumption is wrong, what change would occur in the shape of the curve in Fig. 19? Although the height of the peak would be reduced, a more significant change would be a shift of the peak to the left (Fig. 20). Collection and

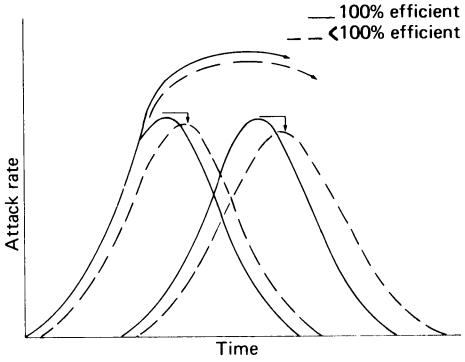

Fig. 21. Hypothetical effects of lowered host-finding efficiency on the attack rate. See text for explanation.

parity data do not support this type of curve.

What effect would low host-finding efficiency have on the shape of the proposed curve? If, in fact, host-finding efficiency were low, the peak of attack would come well after the peak of emergence (see Fig. 21), but before the end of emergence. Furthermore, the estimate of the emergence period would be longer than the actual period, inasmuch as the estimate is based on the assumption of host-finding activity immediately upon or very soon after emergence. Lag in completion of the attack cycle due to low host-finding efficiency would imply an earlier *emergence* peak than if efficiency were high (see Fig. 21). A shorter, earlier period of emergence, coupled with a lag in completion of the first cycle of attack, would demand that attack rates be highest when the maximum number of flies was searching (very near the end of the emergence period). The curve, assuming low host-finding efficiency (Figs. 21 and 22), is clearly opposed by the seasonal pattern of attack rates shown in Fig. 5.

One aspect of host-finding efficiency is host density. Clearly, a high density of hosts could improve the chance that all searching flies would find hosts. The H.F.S. is an area where a large, managed deer population afforded opportunities for a high level of attack. During 1964 to 1966, Connolly (1970) estimated the average numbers of deer/2.56 km^2 (one square mile) on the H.F.S. as being 62 in April, 95 in May, 91 in June, and 89 in July (April and May differences are due to the spring birth of fawns). These densities range from 21 to 31 more deer/km^2 than in the remainder of Mendocino County (Anderson et al., 1974), and they are about 50 percent greater than that which Taber and Dasman (1957) considered high in neighboring Lake County. On the H.F.S., marked deer

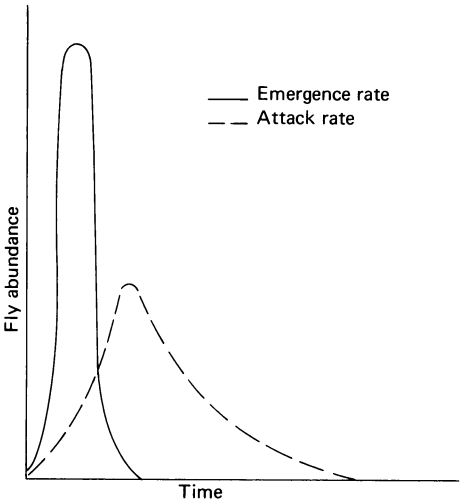

Fig. 22. Illustration of the relationship between the emergence rate curve and the attack rate curve when host-finding efficiency is low. Arrows indicate the shifts in peaks with lower host-finding efficiency.

had home ranges of 0.8 to 1.2 km in diameter, and they retained the same home range the year round (Brook, Connolly, and Longhurst, 1972).

The reliability of the physiological age-grouping data is critical to this discussion. Inasmuch as Duke (1960) found that peaks of attack by parous and nulliparous tabanids can differ in time of day, the time of collection of *Symphoromyia* specimens might have influenced the proportions of nulliparous and parous specimens taken. No diurnal variation was discovered for *Symphoromyia,* however; hence the hours at which specimens were collected for age-grouping studies are not critical.

This study is the first in which age-grouping techniques (based largely on distinguishing nulliparous from parous flies) have been applied to *Symphoromyia.* The general applicability of these techniques to orthorrhaphous hematophagous flies is now well established (Detinova, 1968).

Since Lutta (1964), a number of workers (Lutta, 1970; Morris and DeFoliart, 1971; Paenko, 1966, 1969; Pavlova, 1968; Skuf'in and Paenko, 1967; Thomas, 1972, 1973) have distinguished the parity of many species of Tabanidae. All evidence obtained in this study indicates that hematophagous *Symphoromyia* also exhibit gonotrophic concordance, i.e., production of one batch of eggs/blood-meal.

Symphoromyia sackeni and *S. pachyceras* and/or *S. cervivora* were by far the most common species attacking deer at the H.F.S. They accounted for approximately three-quarters of the specimens collected during two seasons. Despite their abundance, or perhaps because of it, *S. sackeni* and the latter two species appear to have very little temporal overlap. When the hypothesis that the seasons are identical is tested by means of the Mann-Whitney U test, it is estimated that the probability is less than 0.0013. Rejecting that hypothesis leads one to accept that *S. pachyceras* and/or *S. cervivora* occur earlier than *S. sackeni.* The factors responsible for such a clear separation of the two seasons are better discussed after the reactions of the hosts to *Symphoromyia* have been examined.

Quantitative description of *Symphoromyia* attack

The striking uniformity of times spent in the final phase of attack by all flies (Table 3) suggests that the behavioral patterns are quite fixed after the final landing and that the blood supply is rapidly tapped. Gordon and Lumsden (1939), in their classic study of the feeding behavioral of *Aedes aegypti* (L.), reported that complete engorgement required as long as 10 minutes when mosquitoes fed from blood pools and 3 minutes when they fed directly from capillaries. Nagatomi (1962) reported that two specimens of *Atherix* (*Atrichops*) *moromotoi* Nagatomi required 37 to 79 minutes, respectively, to

completely engorge on frogs. Certain Phlebotomine species which feed on cold-blooded vertebrates also require a long time (60 to 75 minutes) to engorge (Chaniotis, 1967) whereas species which feed on warm-blooded vertebrates usually require only a few minutes to fully engorge (Adler and Theodor, 1931; Johnson and Hertig, 1961). *Glossina swynnertoni* Austen commonly take 1 to 3 minutes to feed; but they sometimes require 10 minutes, according to Glasgow (1963). Various tabanids commonly require about 4 minutes to engorge (Philip, 1931). Hence, the engorging time for *S. sackeni* (75 seconds) compared with that required by other blood-sucking flies of approximately the same size is quite rapid.

Only engorging times (from last landing to voluntary departure) were obtained for members of the *S. pachyceras* complex. The mean time from last landing to full engorgement and voluntary departure was 109.0 seconds and the standard error of the mean was 17.2 seconds. Four of the 19 observations were approximately twice the mean, suggesting that at least two species of the complex were represented in the above measurements. The mean engorgement rate for the *S. pachyceras* complex was about 30 percent greater than for *S. sackeni.*

Direct measurement of the amount of time successful flies had spent in attack prior to final landing was achieved only for *S. sackeni.* The mean time was 69.7 seconds with a standard error of the mean of 34.0 seconds, slightly less than the time from final landing to full engorgement. (Fifty-two percent of the attack time was spent after the final landing.) However, when the numbers of *S. sackeni* observed on and around the heads of deer during the 1965 season are compared, one finds that 69.8 percent were on the head which indicates that approximately 17.8 percent of the total attack time was spent on the head before the final landing. If time after final landing was 75.4 seconds (and 52.0 percent of the total attack time) and an additional 17.8 percent (or 25.8 seconds) of the total attack time was spent on the host, then 30.2 percent (or 43.8 seconds) of the total attack time must have been spent flying about the host. This conclusion is based on the assumption that unsuccessful flies spent the same proportions of their attack time on and around the head as did successful flies. Either unsuccessful flies must be few in number or they must be spending time on the host in proportions similar to time spent by successful flies; otherwise the season-long ratio would favor numbers around the head.

The precision of the above statements is reduced somewhat by the difficulty in identifying the flies in flight. Although attacking flies stay within 25 to 38 cm of the host, approximately 10 percent of the flies recorded as "around head" were listed as undetermined *Symphoromyia.* If a major portion of the undetermined flies were *S. sackeni,* the season-long ratio of *S. sackeni* on the head to those around the head could in actuality be lower than estimated. However, female *S. sackeni,* being yellow, would probably seldom be classified as undetermined; therefore, little shift from the original estimate would be expected.

Based on season-long observations, 55.4 percent of the *S. pachyceras* complex were observed *on* the head, a lower figure than the 69.8 percent for *S. sackeni.* If the major portion of undetermined *Symphoromyia* around the head were of the *S. pachyceras* complex (as suggested), the 55.4 percent figure might be reduced slightly. Even with this lower proportion of time on the head and a longer mean time (109 seconds) from final landing to full engorgement for the *S. pachyceras* complex, very few flies would be counted twice with observations at 7.5-minute intervals.

The apparent clustering of biting *Symphoromyia* can be explained as an intrinsic attraction of the flies to dark or raised objects, such as other flies, on a surface (Garcia and Radovsky, 1962). A less parsimonious explanation might involve a local anesthetic effect by the first fly feeding, thus making the landing of a second fly less noticeable to the deer. The fact that clustering was most obvious on the ears lends support to this hypothesis inasmuch as an anesthetic effect would promote clustering if the function of the guard hairs was nullified.

The published reports of *Symphoromyia* attack on humans fail to show a strong biting site preference in any species. In contrast, those species observed attacking deer at the H.F.S. fed only on the ears, antlers, and face. Although this site specificity might be explained by the types of pelage on the various parts of the deer, only about 1 percent of the *Symphoromyia* attacking deer did not initially land on the head, an indication that the silhouette of a deer releases a specific behavioral pattern in the fly. Certain observations of the deer's behavior while under heavy attack also support the latter speculation, e.g., lowering the head.

Biting-site 'preference'

Four days' observations of flies on a mature buck (Table 5) revealed that on all days more flies were on the antlers than on either the ears or the face. Furthermore, the 4-day totals of observed flies were greater for the antlers than for the ears and face combined. At the time of observation the antlers were 2.5 to 5 cm long, hence the surface area was nearly equivalent to the normally attacked area of the ears. The differences could be due to the absence of guard hairs on antlers or to longer engorging times for flies on the antlers. The blood supply to the "velvet" of the antlers may be limited enough that engorging takes significantly longer, but we did not investigate this possibility. Likewise, differences in blood supplies could contribute to differences in numbers observed on the ears and the face.

The difference between the 1964 and 1965 seasons in distributions of flies on the ears versus those on the face of "517" was striking for the *S. pachyceras* complex, but not for *S. sackeni* (Table 6). The former comparison is not fair, however, because only part of the 1964 season for the *S. pachyceras* complex was included. As shown in Fig. 10, the number of flies on the face decreased in relation to the number on the ears as the season progressed; therefore, only full seasons' observations can be compared.

Observations of 517 included the entire 1964 season for *S. sackeni;* hence the number of *S. sackeni* on the face relative to that on the ears may be compared for 1964 and 1965. The similarity in this percentage between the 2 years' observations of 517 (73.8 *vs.* 73.9%) contrasts with the great difference between 517 and New Doe (73.8 *vs.* 97.7%). The preponderance of *S. sackeni* on the face of New Doe probably resulted from a higher rate of ear-flicking by that host, then a yearling, than by 517, who was 3 years old. A similar distribution of *S. pachyceras* complex females is noted when 517 and New Doe are compared; the latter having 83.0 percent of total flies on her face, whereas 517 had only 59.6 percent of the total flies on her face. Observations in 1966 of yearlings and older hosts confirmed this relationship (Tables 6, 10).

From these two types of comparison it is evident that both the species of fly and individual variation among hosts contribute to the ratio of flies observed on the ears and on the face.

The seasonal decrease in the percentage of the total *S. pachyceras* complex observed on the face (Fig. 10) may be

explained by behavioral differences among different species of the complex, seasonal changes in the pelage of the hosts, seasonal changes in the behavior of the hosts, or combinations of these or other factors. The first-mentioned seems (in light of the difference in site preference between *S. sackeni* and the *S. pachyceras* complex) a good possibility, with the late season species "displaced" by the large numbers of *S. sackeni* feeding on the face. As for pelage changes, certainly loss of the woolly underhairs makes attack on the ears more feasible. However, although we believe that fly attacks contribute to the rapid spring loss of hair on the face and ears, the majority of shedding is completed so early in the fly season that this could not be a major factor in the observed shift of feeding site for the late season members of the *S. pachyceras* complex. Also, in spite of the loss of hair from the ears, *S. sackeni* feeds predominantly on the face. The evidence against a seasonal shift in behavior of the hosts (with respect to an increased tolerance of flies on the ears) is only that no shift was apparent within the series of observations on *S. sackeni* (assuming that *S. sackeni* would be affected by a shift in host behavior). Data on *S. sackeni* are limited, however, on all but 4 or 5 days/season.

The pelage of black-tailed deer adults consists of large and intermediate guard hairs, mane-type hairs, and woolly underhairs, with the large guard hairs having a sensory function (Cowan and Raddi, 1972). The spring molt is incomplete in that only guard hair follicles are involved; the woolly undercoat is shed by breakage and not replaced during the summer (Cowan and Raddi, 1972). As we also noted, shedding of the short hairs on the face (and the ears) was diffuse in the spring. At Vancouver, British Columbia, new large guard hairs were appearing by April, and they continued to grow for about 3.5 months. Such hairs were larger, straighter, and more slender than those in the winter pelage, and Cowan and Raddi (1972) postulated that these hairs ". . . lying at an inclined angle to the skin, appears designed to shade the skin and to provide for easier heat loss." In view of their sensory nature these large summer guard hairs may also be more effective in repelling certain biting insects. As noted previously, the tilted posture of feeding snipe flies allows the body to angle upward between and above a raised guard hair. This may account for the successful feeding of *Symphoromyia* species on the outer ear surface, a feeding site where few other blood-sucking flies were seen.

There were slight differences in the numbers of *Symphoria* observed on the faces of 517 and New Doe (Table 6), whereas great differences between hosts occurred in the number of flies on the ears. This difference should be kept in mind during the discussion of attack rates relative to individual hosts. In effect, attack rates on the face were equal and attack rates on the ears were unequal.

Jones and Anthony (1964), generalizing on the biting sites of Floridian Tabanidae, reported that *Chrysops* and four species of *Tabanus* attack the head, neck, and shoulders of livestock, with occasional attacks on the legs. Three other species of *Tabanus* are characterized as feeding on the lateral surfaces and back. A group of three *Tabanus* species was reported feeding principally on the lower legs and belly, whereas 2 others preferred the inner surfaces of the hind legs. More recently Smith, Davis, and Golini (1970) also reported specific feeding sites for species of Tabaninae and Chrysopsinae feeding on moose and deer in eastern Canada. Hence biting site specificity apparently is common also in many tabanid species.

In contrast with the tilted biting pos-

ture of *Symphoromyia,* all tabanids (nine species in five genera) observed biting deer (Anderson, Olkowski, and Hoy, 1974) kept the long axis of their bodies parallel to the surface on which they rested. Furthermore, only an occasional *Chrysops* species was observed biting the ears, but several were seen on the face. *Silvius notatus* (Bigot) and *S. gigantulus* (Loew) usually bit on the lower rear legs, whereas other larger tabanids attacked the neck, back, or face. The areas in which the tabanids bite deer are all characterized by short, sparse pelage. Breyev (1950) made much the same observation for the tabanids attacking reindeer in Russia where he also noted a relationship between the time of year shedding occurred and the maximum densities of tabanids and other blood-sucking flies attacking the animals.

Attack rates relative to individual hosts

Data discussed above indicate not only variation in the sites attacked, but also in the total numbers of flies observed on individual hosts. The total numbers of *S. sackeni* observed on 517 and New Doe during 1965 differed significantly ($X^2 = 6.00$ and $0.02 > P > 0.01$). The total numbers of the *S. pachyceras* complex observed on 517 and New Doe differed even more.

Reference to Table 9 reveals an approximate 10-fold difference between the numbers of flies on the faces of the mature deer and the numbers on the yearlings. Yet little, if any, difference existed in the numbers *around* the heads of the two age categories. These differences emphasize the danger of lumping data such as flies upon, and flies around, the heads of hosts.

Host behavior relative to fly attack

Of the behavioral patterns of deer described above, only ear flicking and choice of resting sites readily lend themselves to quantification. Brushing flies from the head and lowering the head are most significant in that such behavior is seldom observed and is evident only when *Symphoromyia* attack is intense. These two behaviors therefore can be regarded as the most typical anti-snipe fly behavior reactions (ear flicking also being provoked by tabanids).

If the temperature of the substrate is related to the number of times the deer changes resting site or to the posture assumed at the resting site, the soil temperature and related behavioral patterns may be of importance in the study of *Symphoromyia.*

Perhaps more directly related to the behavior of the fly are the postural changes displayed by the deer when under fly attack. Although leg-extending and head-lowering are different patterns of behavior, the net result is a lowering of the profile. Head-lowering carried to the extreme reduces the profile to that of an unconscious deer, a form remarkably unattractive to *Symphoromyia.* (On several occasions when snipe flies were attacking normal deer, we looked for *Symphoromyia* attracted to prone, anesthetized deer in the same pens; but no flies were attracted to such animals.) However, since the extreme "head down and legs out posture" taken by deer when they are being attacked by maximum numbers of *Symphoromyia* seems remarkably similar to the "freeze," hiding, or predator concealment position taken by infant cervids and certain other ungulates (e.g. Lent 1971, McCullough 1969), the taking of this position by adults may not reflect a specific anti-snipe fly behavior.

When ear-flicking data are reduced to the number of flicks/minute, an inverse relationship between the rate of flicking and the number of flies on the face becomes apparent (Table 11). These data were collected with six deer together and at times when fly activity was moderate to heavy. It should be

noted that the ear-flicking rate bears no relationship to the number of flies *around* the head.

The linear relationship between maximum air temperature for the day and mean time spent by deer in the shade may indicate cause and effect. Regardless of the cause, it is apparent that on warm days more time is spent in the shade than on cool days. Within the temperature range of *Symphoromyia* activity on deer at the H.F.S. (17.2 to 35°C), time spent in the shade varied from less than one-fifth to more than four-fifths of the total.

The relationship between the relative time spent in the shade and the percentage of flies observed on or around each of two hosts is illustrated in Fig. 17. The cause(s) for the generally inverse relationship has not been determined. On days having temperatures in the lower parts of the temperature range, hosts in the shade might be in an area cooler than the threshold(s) of activity of *Symphoromyia,* thus lowering the total number of attacks. On warmer days, however, moderate attack on hosts in the shade may induce movement (and temporary exit from shade) which may in turn attract more flies. This would in effect mean that the more tolerant hosts stay in the shade longer and are thereby attacked by fewer flies.

Effects of weather on fly attack

From the first weeks of this study the certainty of *Symphoromyia* attack above certain temperatures was striking. Despite relatively low numbers of flies and sampling at half-hour intervals, estimates of the thresholds for *S. inconspicua* and *S. truncata* have relatively low standard errors (Table 13). Sampling in half-hour lots introduces the possibility of a two- or three-degree error inasmuch as such increments are not uncommon during the late morning hours when the rate of temperature change is greatest. The temperature at the beginning of the half-hour period during which the first collections were made was designated as the threshold for that day. A single record of *S. pachyceras* or *S. cervivora* activity beginning at more than 21.1°C (70°F) is entirely responsible for the large standard error found for that group.

Only for *S. sackeni* are there data that indicate an upper temperature, or temperature-related, threshold for fly attack. For this species it is quite certain that attack ceases when temperatures reach 34.4 to 37.2°C.

The number of days during the 1965 fly season with maximum air temperatures above the mean lower thresholds for the six *Symphoromyia* species are given in Table 13. Likewise the percentage of total days in the season above the threshold is shown. Each species of fly had a threshold low enough that well over 50 percent of the days of any species' season were sufficiently warm for activity to occur.

The lack of apparent effect of mean wind speeds of 9.6 to 11.2 kmph on the rate of attack by *Symphoromyia* indicates that few days of any season at the H.F.S. would be windy enough to influence fly attack, for mean wind speeds are seldom that great. Furthermore, gusty winds did not appear to affect the attack rate. Inasmuch as *Symphoromyia* is a montane genus, it is not surprising that winds under 32 kmph had little or no influence on the attack behavior. The occurrence of the adults during the months of transition from rainy season to dry season would seem to call for adaptation to a windy environment.

Members of the *S. pachyceras* complex have been observed attacking with the incident light measured at as little as 750 ft-c. However, biting activity almost always was reduced before light intensity decreased to 750 ft-c. At this

time in the afternoon the temperature is usually above the threshold at which activity began earlier in the day. The rate of decrement of light intensity rather than an absolute threshold may inhibit flight or attack. Such a mechanism could explain the lack of immediate responses to cloud cover (a weather condition which can change very rapidly), yet would result in ending activity with the steady decrease of light intensity in late afternoon.

The vector potential of *Symphoromyia*

The tendency of a fly to resume feeding after an interruption increases its potential as a mechanical vector. The tenacity of the *Symphoromyia* attacking deer has been noted above, together with the impression that *S. sackeni* was more readily discouraged in mid-meal than were species of the *S. pachyceras* complex.

The spectrum of hosts acceptable to a given species is also related to the vector potential. An insect species with a narrow host spectrum would be an efficient vector of parasites with a high degree of host specificity; a species with a wide host spectrum simultaneously serves as a dead end for highly specific parasites and as an efficient vector of those that are less specific. Judged in these terms, the *S. pachyceras* complex appears to be a more likely vector of deer parasites whereas *S. sackeni* would be a more efficient vector of parasites with broader host spectrums.

The volume of blood taken by an insect influences the probability of picking up a parasite (or a minimal number of parasites) just as does the number of meals taken. All of the *Symphoromyia* species which attack deer could be expected to take about as much blood per meal as *S. sackeni*, i.e., 5 or 6 mg, inasmuch as they are nearly all the same size. That volume, much more than a typical nematoceran takes, would be conducive to acquisition of blood parasites that circulate in limited numbers.

All flies feeding during the second half of the season are parous. Considering the estimated imaginal life span, the time required for utilization of a bloodmeal, and the estimated survivorship curve for imagines, some *S. sackeni* females may take three or four bloodmeals each. Since *S. sackeni* females are relatively abundant, take large volumes of blood, and feed several times during their lives, they may serve as vectors of deer parasites and perhaps even of zoonoses.

In light of concurrent studies on the filarial worms of a variety of vertebrate hosts at the H.F.S., preliminary investigations of the possible insect vectors of deer filariae were included in this study. Although many of the 359 flies examined may have been taking a third blood meal when collected, all proved negative for helminths. The vectors of the three filarial worm parasites of deer, *Setaria yehi* Desset, *Elaeophora schneideri* Wehr and Dikmans, and *Onchocerca cervipedis* Wehr and Dikmans were recently reported (Anderson and Weinmann, 1972; Weinmann, *et al.*, 1973) to have the following respective vectors: a mosquito, *Aedes sierrensis* (Ludlow); two tabanids, *Hybomitra procyon* (Osten Sacken) and *Tabanus monoensis* Hine; and a black fly, *Prosimulium imposter* Peterson.

At the H.F.S. and surrounding areas, 92 percent of the adult deer are infected with *Anaplasma marginale* (Howarth *et al.*, 1969). This parasite produces no clinical symptoms in deer, but it causes a severe disease in older cattle infected for the first time. Hence, infected deer represent the major obstacle to the control of anaplasmosis in cattle (Boynton and Woods, 1933; Howarth *et al.*, 1969). Since various species

of horse and deer flies have been incriminated as mechanical vectors (Anthony, 1962), the density of the closely related, pool-feeding *Symphoromyia* species attacking deer at the H.F.S. makes them serious potential vectors of *A. marginale* among deer and from deer to cattle.

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