Chapter 7
Behavior

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Abstract Adult life span of gall-inducing cecidomyiids is very short, usually one, sometimes two to three days although they live longer under humid laboratory conditions if they do not swarm or lay eggs. In this chapter, various patterns of adult activity including emergence, swarming, mating, and oviposition are demonstrated and compared between diurnal and nocturnal species and between species with different life history strategies. We refer to the results of comparison in the flight ability between a host-alternating and multivoltine *Asphondylia yushimai* and a monophagous and univoltine *A. aucubae*. It is remarkable that *A. yushimai* females carry the potential strong flight ability, i.e. continuously 13.7 km within 10 h. Some aspects of larval behavior are also referred to in this chapter.

Keywords Daily activity · Emergence · Fecundity · Flight ability · Mating · Oviposition · Sex ratio

7.1 Emergence Time of Day

Barnes (1930) first intensively studied the emergence of gall midges from various behavioral and ecological aspects such as danger at the time of emergence, emergence time of day and year, daily fluctuations, and factors governing the emergence. In this chapter, we refer mainly to the emergence time of day, and in Chap. 8 the emergence time of year will be treated together with temperature conditions.

Patterns of daily activity are divided into diurnal and nocturnal, and daily emergence patterns are into unimodal and bimodal (Fig. 7.1). The unimodal

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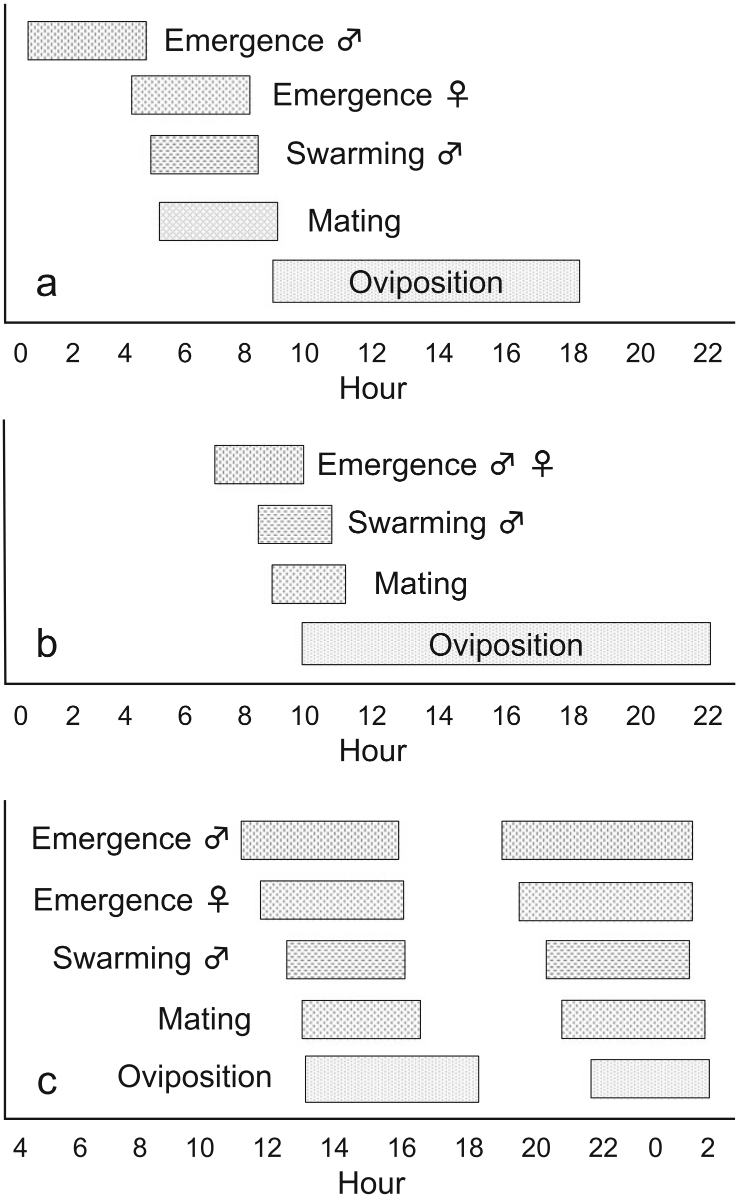

Fig. 7.1 Schematic representation of three types of daily activity exhibited by gall-inducing cecidomyiids. (**a**), unimodal emergence type in which males emerge earlier than females; (**b**), unimodal emergence type in which males and females emerge almost simultaneously; (**c**), bimodal emergence type that is mainly exhibited by nocturnal species

emergence pattern can be seen in various diurnal gall midges. Usually males emerge earlier than females (Fig. 7.1a) as has been noted for *Contarinia merceri* Barnes, *Contarinia tritici* Kirby, *Dasineura alopecuri* Reuter, *Dasineura pyri* Bouché*,* *Rabdophaga terminalis* Loew, *Stenodiplosis geniculate* Reuter (Barnes 1930), *Stenodiplosis sorghicola* (Coquillett) (Summers 1975), *Haplodiplosis marginata* (Roser) (Skuhravý et al. 1993), and *Dasineura mali* Kieffer (Harris et al. 1999). In *Masakimyia pustulae* Yukawa & Sunose, males emerge in midnight between 11:00 pm and 2:00 am, and female emergence reaches a crest 7 h or so later (Sunose 1983). In the laboratory, the males of *Illiciomyia yukawai* Tokuda start emergence from 9:00 pm. The emergence reaches a peak between 0:00 am and 1:00 am and continue intermittently until 11:00 am, while the females emerge from 5:00 am until 5:00 pm, with a peak between 5:00 am and 6:00 am (Yukawa et al. 2013).

Both males and females of *Pseudasphondylia neolitseae* Yukawa emerge at the same time between 7:30 am and 10:00 am (Yukawa et al. 1976) (Fig. 7.1b). The emergence of males and females occurs between 9:00 am and 11:00 am in *Macrodiplosis selenis* Kim & Yukawa (Kim et al. 2014, 2015). It is remarkable that females emerge before males in the Douglas-fir cone gall midge *Contarinia oregonensis* Foote (Miller and Borden 1984).

In some species, an hourly emergence pattern is more or less bimodal (the first peak usually in the morning and the second one after sunset) and extends over several hours (Fig. 7.1c). In *Asphondylia aucubae* Yukawa & Ohsaki, the hourly emergence of individuals extended over 16 hours, but there were two peaks for both sexes, respectively. At 10:00 am to 11:00 am, the males reached the first peak of emergence about 4 h before the females. The emergence of both the sexes attained the second peak almost simultaneously around 9:00 pm to 11:00 pm. This pattern is frequently seen in nocturnal species of *Asphondylia* (Yukawa and Miyamoto 1979; Yukawa and Ohsaki 1988b), but the bimodality sometimes becomes unclear because of the influence of light intensity and daytime temperature.

7.2 Time Required for Emergence

As pointed out by Barnes (1930), the emergence of insects from the pupal stage is a delicate process attended by many dangers, and dependent upon various external influences. Actual emergence takes 5–15 min in *Lasioptera rubi* (Schrank) (Barnes 1930), 20–45 min in *P. neolitseae* (Yukawa et al. 1976), about 105 min in *M. pustulae* (Yukawa and Sunose 1976), about 80 min in *M. selenis* (Kim et al. 2015). In the case of *Asphondylia sarothamni* (Loew), females take 24 min to emerge and males 30 min (Barnes 1930). Laboulbéne (1873) observed that males of *Monarthropalpus buxi* (Laboulbéne) required longer time for emergence than females probably because of the difference in the length of the antennae.

7.3 Mortality at the Time of Emergence

During the time of emergence, insects are in a helpless condition. Their enemies take advantage of this. For example, the common flowerbug *Anthocoris nemorum* Linnaeus (Hemiptera: Anthocoridae) greedily seizes emerging *R. terminalis* and *D. pyri* (Barnes 1930). Spiders have been observed sucking *D. alopecuri* in the act of emergence (Barnes 1930). Eleven species of spiders have been known as predators of *P. neolitseae* at the time of emergence or oviposition (Yukawa 1983). Heavily galled leaves of its host plant *Neolitsea sericea* (Blume) Koidzumi (Lauraceae) are frequently folded outward in various degrees, providing favorable webbing conditions to the spiders. Because *P. neolitseae* emerges from galls on under surface of the host leaves, adult gall midges are killed by the direct predation and are also caught in the webs. More than 50% of galled leaves are folded under high gall midge population density (Yukawa 1983).

7.4 Emergence Projections Induced by Fig Gall Midges

Gall induction and leaf mining are major examples in the manipulation of plant development, including morphological and physiological changes of host plant tissues. Giron et al. (2016) demonstrated various examples of host plant manipulation by gall-inducing organisms and leaf-mining insects, including other herbivorous insects that share the plant manipulation with inducers.

There are morphologically distinct examples of host plant manipulation by fig gall midges. Yafuso et al. (2013) found that species-specific projections developed before emergence from female flower galls induced by three unidentified cecidomyiid species in the syconia of *Ficus microcarpa* Linnaeus (Moraceae) on Okinawa and Amami Islands, Japan (Fig. 7.2). The projection was derived from

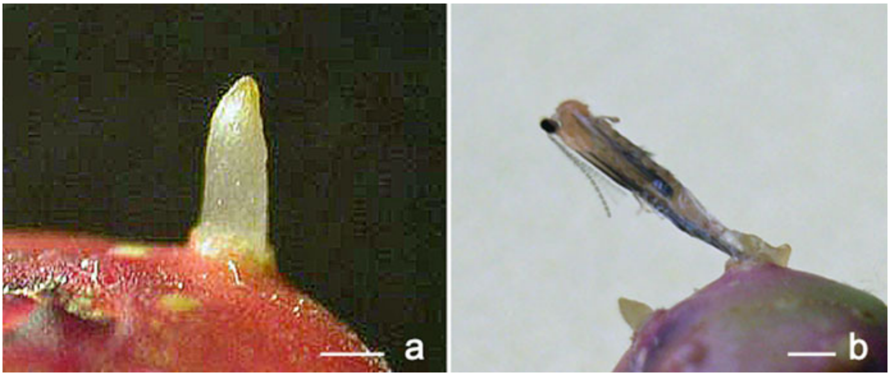

Fig. 7.2 Emergence projections of fig gall midges. (**a**), horn-like projection of sp. 1 of Yafuso et al. (2013); (**b**), female emergence of sp. 1. Scale bars, 2 mm

plant tissues consisting of a mass of small square cells in the basal and distal portions and regularly arranged long cells in the middle portion. Yafuso et al. (2013) considered that the gall midges manipulate the fig plant to develop the projection before emergence, so that the pupa can easily pass through the sticky epidermis of the syconium.

A similar way of cecidomyiid departure from fig fruit galls has been observed for *Ficiomyia perarticulata* Felt on *Ficus citriflora* Miller in Florida, USA (Roskam and Nadel 1990) and unidentified gall midges on *Ficus benjamina* Linnaeus in Xishuangbanna, southwestern China (Bai et al. 2008; Miao et al. 2011). In 2013, N Wachi (University of the Ryukyus, Japan) informed us that he found similar projections on fruit galls of *Ficus sundaica* Blume in Cambodia. Such a way of departure from fig fruit galls seems to be common in tropical and subtropical areas and to be an adaptive habit for fig gall midges to reduce risks under helpless conditions at the time of emergence.

7.5 Sex Ratio

The sex ratio is usually 1:1 (Barnes 1931) but is frequently biased in favor of females. For example, the sex ratio is approximately 1:2 in *P. neolitseae* (Yukawa et al. 1976), *Asphondylia sphaera* Monzen (Yukawa and Miyamoto 1979), *A. aucubae* (Yukawa and Ohsaki 1988b), *I. yukawai* (Yukawa et al. 2013), and 70% in *M. selenis* (Kim et al. 2015) although the ratio varies with locality and from year to year (Yukawa and Sunose 1976; Yukawa et al. 1976) and with season and host plant quality (Dorchin and Fredberg 2004). In *C. oregonensis*, females constitute 53–58% of the total number emerged (Miller and Borden 1984).

In addition, 'unisexual' families exist, in which female offspring of all-female families can produce all males, all females, or both males and females (Barnes 1931). Elimination of paternally derived chromosomes during spermatogenesis explains the incidence of unisexual families for the Hessian fly *Mayetiola destructor* (Say) (Gallum and Hatchett 1969). Dorchin and Fredberg (2004) demonstrated that *Izeniola obesula* Dorchin exhibited strict monogeny, resulting in galls that contain either all female or all male progeny and that the skewed sex ratio among galls, ranging from 1:1 to 1:4, possibly caused by higher mortality occurred among male galls. Both *Dasineura folliculi* Felt and *Dasineura carbonaria* Felt exhibit monogeny, and gall sex ratios differed between generations of *D. folliculi* on *Solidago rugosa* Miller (Asteraceae) but not on *Solidago gigantean* Aiton (Dorchin et al. 2007).

7.6 Swarming and Mating

Swarming mass has been observed for various non-gall inducing cecidomyiids of Micromyinae such as *Micromya lucorum* Rondani, *Ansifera gombakensis* Jaschhof, and *Campylomyza flavipes* Meigen and Lestremiinae such as *Conarete calcuttaensis* Nayar. Swarming of *Anarete pritchardi* Kim and *Anarete* sp. (Lestremiinae) was most intensively studied by Chiang and his group (see Kanmiya and Yukawa 2020 for the references as to Micromyinae and Lestremiinae).

Some other non-gall inducing cecidomyiids mate by hanging on abandoned spider-webs or other substrates in a face-to-face position. This way of mating has been seen in predacious or flower-visiting cecidomyiids, such as *Aphidoletes aphidimyza* (Rondani) (Yukawa et al. 2008), an aphidophagous species, and *Resseliella kadsurae* Yukawa, Sato & Xu, a pollinator of *Kadsura longipedunculata* Finet & Gagnepain (Schisandraceae) (Yukawa et al. 2011).

Gall-inducing cecidomyiids with type IA or IB life history strategy overwinter as mature larvae on the ground (Yukawa 1987; see also Chap. 6). Therefore, males usually fly over the ground under the host plants in search for females that locate on fallen leaves or short grasses after emergence (e.g. Yukawa and Tsuda 1987 for *Celticecis japonica* Yukawa & Tsuda; Kim et al. 2015 for *M. selenis*). However, some females of *Hartigiola faggalli* (Monzen) fly from the fallen leaves and alight on fresh leaves or old twigs of the host tree, *Fagus crenata* Blume (Fagaceae), and mating takes place there as well as on the ground (Mishima et al. 2014).

Kim et al. (2015) observed emergence (Fig. 7.3a, b), swarming and mating of *M. selenis* under natural conditions. The males started swarming from 9:00 am over the ground under the host trees *Quercus serrata* Thunberg ex Murray (Fagaceae). The swarming consisted of two to ten males and continued until noon. Some males were walking on the ground in search for females. Females rested on the fallen leaves or grasses after emergence, waiting for males to locate them. To call males, females protruded the ovipositor until males arrived. Females seemed to emit sex pheromones during this time because some males, sensing the presence of females, left the swarm and flew to the females. Mating took place without ceremony and lasted for about 40 seconds. After mating, the males returned to the swarm. Mating was observed mainly between 9:00 am and 10:00 am soon after the emergence of females. Males disappeared after swarming and mating. This pattern of hourly activity of *M. selenis* varied to some extent depending on weather conditions of the day, as has been noted for other gall midges (e.g. Barnes 1930; Yukawa et al. 1976; Skuhravá et al. 1998; Yukawa et al. 2013).

Gall-inducing cecidomyiids with type IIA or IIB life history strategy overwinter in the galls on evergreen host plants (Yukawa 1987; see also Chap. 6). Males exhibit swarming around the host plant from which they emerged because females are expected to emerge from galls on the same plant. After emergence, the females locate on the galls from which they emerged and wait for the males to come. Some of swarming males fly towards females in response to pheromonal calling. Such mating behavior has been observed for *P. neolitseae* (Yukawa et al. 1976), *Asphondylia*

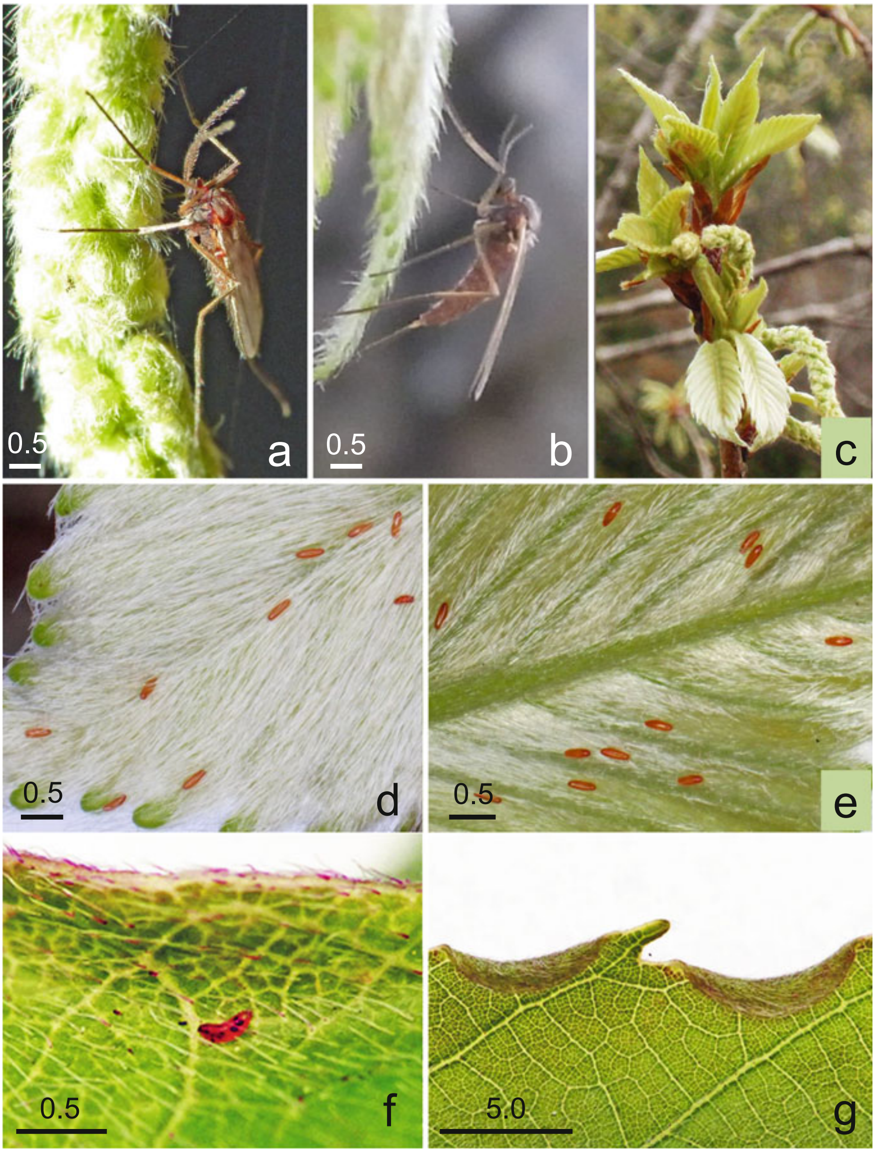

Fig. 7.3 *Macrodiplosis selenis* and its galls on the host plant *Quercus serrata*. (**a**), male; (**b**), female (reproduced with permission from Kim et al. 2015); (**c**), newly extending shoot of *Q. serrata*; (**d**), eggs deposited on the upper surface of a host leaf; (**e**), eggs deposited on the under surface of a host leaf; (**f**), first instar crawling toward leaf margin on the upper surface of a host leaf; (**g**), leaf margin folded galls. Scale bars, mm

yushimai Yukawa & Uechi (Yukawa et al. 1983) and *I. yukawai* (Yukawa et al. 2013).

The followings are detailed observation records for swarming and mating behavior of *P. neolitseae* (Yukawa et al. 1976). Under favorable conditions, the males started swarming around the host plant *N. sericea*, from which they had emerged, at 8:30 am and continued until 11:00 am. The females were usually resting on the undersurface of the host leaves and waiting for males to locate them. One or more males, sensing the presence of the females, left the swarm and flew to the leaves to mate. Mating took place without ceremony and lasted for 99 ± 8 s (average ± s.d.). Under favorable weather conditions, at least 75 % of females mated on each census data. After mating the males returned to the warm.

According to Yukawa et al. (1976), mating failures were caused by: (1) too many males attempting to mate with one female, which made the female flying far away from both the host plant and swarming site (in this case the female could not be recognized again by any of swarming males); (2) the contrary case where females were not located by any of the males during the swarming period. The first case occurred when the male swarm size was large and the second when it was too small or there was no available swarm near the females. The second situation was caused mainly by the small number of daily emergences, which was frequently observed during several days before and after main emergence period of the year. The large sized swarm was naturally observed during the main period of emergence.

When the temperature was over 6.5 °C at the time of emergence, the daily emergence normally occurred, otherwise it did not occur even during the main emergence period of the year. The adults that had postponed their emergence were then added to those that were to emerge on the next favorable morning. If the temperature was not warm enough (below 16 °C) at swarming time, the emerged males could not fly off and were compelled to stay on the under surface of the leaves and were unable to mate. Thus, mating was seriously impaired by unfavorable temperature when it might be warm enough for emerging, but not for swarming. Once the females mated, they could fly and oviposit even if the temperature was considerably lower than 16 °C in the afternoon.

7.7 Flight Ability

Insects with wings fly to find food resources, to locate places to live, to hold territories, to search mating partners, to escape from danger and for other purposes (e.g., Pringle 1957). Therefore, an evaluation of their potential flight ability is essential in predicting their movement and dispersal. Therefore, various sorts of apparatus have been devised to evaluate the flight ability (Cloudsley-Thompson 1955, 1961; Miller 1979; Kanmiya 1994). Among these apparatuses, the thread tethered flight method is relatively simple, convenient and has been used to evaluate the flight ability of various insects (see references in Yukawa et al. 2019). In particular, a flight-mill together with various subordinate devices, (a high-speed video camera, for example), is an effective tool to evaluate the potential flight ability of insects (e.g. Fyodorova and Lapshin 1990; Ribak et al. 2017).

As to gall-inducing cecidomyiids, however, their flight ability had seldom been studied because the flight-mill has difficulties in measuring the flight ability of insects that do not have a strong power to pull the rotor of the flight-mill. Kanmiya (1994) developed a thread tethered flight method using strain gauge transducers to overcome the difficulties and successfully analyzed the flight power, flight direction and temporal progress of *Oraesia* spp. (Lepidoptera: Noctuidae).

Hao et al. (2013) studied the active flight potential of the orange wheat blossom midge *S. mosellana* under various environmental factors using a 26-channel computer-monitored flight-mill system. They demonstrated that the most suitable temperature for flight and mean flight distance was 16–24 °C (438 m in male, 735 in female); mean flight duration peaked at 16 °C (70 min in male, 113 in female) while mean speed peaked at 28 °C (9.0 m/min in male, 10.2 in female). Flight performance gradually declined between 10 and 400 lux light intensity.

Yukawa et al. (2019) compared the flight ability between *A. yushimai* and *A. aucubae* using the thread tethered flight method by modifying devices with a CCD camera and an apparatus for analyzing tethered flight sounds to measure the flight power of tiny gall midges that have a weight of about 2 mg (see Figs. 2 and 3 in Yukawa et al. 2019 for the devices and apparatus). *Asphondylia yushimai* is a host-alternating, multivoltine gall midge and one of the major pests of soybean in Japan and South Korea (e.g., Uechi et al. 2018; Yukawa et al. 2003; see also Chaps. 6 and 12). *Asphondylia aucubae* is a monophagous, univoltine species, and induces fruit galls on *Aucuba japonica* Thunberg (Garryaceae) in Japan (Yukawa and Ohsaki 1988a; Yukawa et al. 2016).

According to Yukawa et al. (2019), the total flying time of females of the two *Asphondylia* species was more than 2 h on average. The maximum continuous flying time was nearly 10 h in *A. yushimai* and 5 h in *A. aucubae*. The speed of wing-beat stroke was higher in males than in females in the two species, being adapted to mobile flight for swarming of the males, while the lower speed of stroke enables the females to fly long distance. In particular, the larger wing size of *A. yushimai* females was considered to support their gentle flight for long-distance. The flying speed of *A. yushimai* was 22.9 m/min. The flying speed and the maximum continuous flying times indicated that the *A. yushimai* females carry the potential strong flight ability, i.e. continuously 13.7 km within 10 h. In addition, *A. yushimai* females have a habit to fly up to the sky after mating hence they are carried by wind for long distance. These results were reflected well in the different life history traits between *A. yushimai* and *A. aucubae*. The long-distance flight ability of *A. yushimai* supports the possibility of its host-searching behavior.

Further data of flying behavior and ability of gall midges should be accumulated to evaluate their dispersal beyond border because tiny gall midges may be able to move for a longer distance than our supposition.

7.8 Chemical Communication

Chemical communication plays an important role in reproductive activities of gall midges. According to Hall et al. (2012), the presence of female-produced sex pheromones has been known in 19 cecidomyiid species and components of the sex pheromones have been identified for 16 species among them (Table 7.1).

The chemical ecology of cecidomyiids was reviewed comprehensively by Harris and Foster (1999), thereafter by Wicker-Thomas (2007). More recently, Hall et al. (2012) reviewed progress on identification of sex pheromones, chemicals involved in location of host plants, the neurophysiology of reception of volatile chemicals, and application of semiochemicals to control pest cecidomyiids that occurred during the last decade. See Hall et al. (2012) for further references as to cecidomyiid chemicals.

7.9 Fecundity

From 40 to 400 ovarian eggs have been recorded for many gall-inducing cecidomyiids (Yukawa et al. 1976; Yukawa and Miyamoto 1979; Basedow and Schütte 1982; Sunose 1983; Miller and Borden 1984; Yukawa and Ohsaki 1988b; Harris and Rose 1989; Simbolon and Yukawa 1992; Kolesik 1993; Pivnick and Labbé 1993). Because ovarian eggs are normally mature at the time of emergence, we can easily examine the number of eggs by dissecting the female abdomen. Usually females of most species start ovipositing soon after mating but females of *Sitodiplosis mosellana* (Géhin), for example, do not start oviposition in the first night after mating, and the greatest mean daily fecundity occurs on the third night (Pivnick and Labbé 1993).

Only a few examples of realized fecundity have been recorded: 93% of 254 ovarian eggs were laid by *C. oregonensis* (Miller and Borden 1984), and 189 of 248, on average, by *P. neolitseae* (Yukawa et al. 1976). In addition, the presence of an oviposition deterrent has been suggested for *C. oregonensis* (Miller and Borden 1984).

7.10 Oviposition

Eggs are laid either outside or inside the tender plant tissue depending on the length and morphological characteristics of ovipositor. The outside plant tissue means not only the open surface of plant organs but also inside folded leaves or chinks between plant organs where eggs can be hidden. The gall midges with an aciculate ovipositor, such as species of *Asphondylia*, *Pseudasphondylia* and *Schizomyia*, lay their eggs into plant tissue. Some eggs are laid gregariously and others individually.

Table 7.1 Cecidomyiid species of which female sex pheromones have been found or identified

Species[a]	Host plants (Family)[b]	Reference (see Hall et al. 2012 for the details of literature cited here)
*Aphidoletes aphidimyza**		Choi et al. (2004)
*Contarinia nasturtii**	*Brassica* and other genera (Brassicaceae)	Hillbur et al. (2005), Boddum et al. (2009)
*Contarinia oregonensis**	*Pseudothuga menziesii* (Pinaceae)	Miller and Borden (1984), Gries et al. (2002)
*Contarinia pisi**	*Pisum* spp. (Fabaceae)	Wall et al. (1985), Hillbur et al. (1999, 2000)
*Contarinia pyrivora**	*Pyrus communis* (Rosaceae)	Amarawardana (2009)
*Dasineura gleditchiae**	*Gleditsia triacanthos* (Fabaceae)	Molner et al. (2009)
*Dasineura mali**	*Pyrus malus*, *P. sylvestris* (Rosaceae)	Harris et al. (1996), Heath et al. (1998, 2005), Cross and Hall (2007, 2009)
Dasineura napi	*Brassica napi*, *B. oleracea* (Brassicaceae)	Williams and Martin (1986)
*Dasineura plicatrix**	*Rubus caesius*, *Rubus* spp. (Rosaceae)	Hall et al. unpublished
*Dasineura pyri**	*Pyrus communis* (Rosaceae)	Amarawardana (2009)
*Dasineura tetensi**	*Ribes nigrum* (Saxifragaceae)	Garthwaite et al. (1986), Amarawardana (2009)
*Mayetiola destructor**	*Triticum, Hordeum* and other genera (Poaceae)	McKay and Hatchett (1984), Foster et al. (1991), Anderson et al. (2009)
*Mayetiola thujae**	*Thuja plicata* (Cupressaceae)	Gries et al. (2005)
*Orseolia oryzae**	*Oryza sativa*, *O. perrenis* (Poaceae)	Sain and Kalode (1985), Zao (1982)
*Resseliella theobaldi**	*Rubus* sp., *R. idaeus* (Rosaceae)	Hall et al. (2009)
*Rhopalomyia longicauda**	*Chrysanthemum* spp. (Asteraceae)	Liu et al. (2009)
*Sitodiplosis mosellana**	*Triticum* spp. (Poaceae)	Pivnick (1993), Gries et al. (2000)
Stenodiplosia sorghicola	*Sorghum bicolor*, *Sorghum* spp. (Poaceae)	Sharma and Vidyasagar (1992)
Thecodiplosis japonensis	*Pinus densiflora*, *P. thunbergii* (Pinaceae)	Lee and Lee (1985)

Mainly based on Hall et al. (2012)

[a] Asterisks indicate species of which female sex pheromones have been identified

[b] Based mainly on Gagné and Jaschhof (2017)

According to Kim et al. (2015), the females of *M. selenis* were observed ovipositing between 1:00 pm and 4:00 pm on half or fully opened new leaves of *Q. serrata* (Fig. 7.3c). They required about 30 s to lay one egg. One female laid four eggs successively within 120 s. It is remarkable that females of *M. selenis* lay their eggs both on the upper and under surfaces of the fresh leaves (Fig. 7.3d, e). This indicates that females may have no ability to distinguish chemical and physical signals from different surfaces of the leaf blade.

In contrast, oviposition site selection is clear for other leaf gall-inducing cecidomyiids. For examples, females of *Daphnephila machilicola* Yukawa, *M. pustulae*, *Lasioptera camelliae* Ohno & Yukawa, *H. faggalli* and its sibling species can discriminate upper or lower leaf surfaces at the time of oviposition (e.g. Yukawa 1974; Yukawa and Sunose 1976; Ohno and Yukawa 1984; Mishima et al. 2014). However, females of *M. pustulae* lay their eggs not only on fresh leaves of *Euonymus japonicus* Thunberg (Celastraceae) but also on 1- or 2-year old host leaves or on leaves of various understory plants, but galls have never developed on these leaves (Yukawa and Sunose 1976) (see Sect. 2.2, Mistaken oviposition).

In the sorghum midge *Stenodiplosis sorghicola* (Coquilett), ovipositional time was significantly greater for females on panicle of a midge-resistant than a midge-susceptible sorghum hybrid, indicating that, at the same gall midge density and time interval, fewer eggs are deposited in flowers of the resistant than the susceptible hybrid (Waquil et al. 1986).

In the case of *P. neolitseae* reported in Yukawa et al. (1976), the mated females remained on the under surface of the leaves for 1 h or so after mating, then, flew off between 10:30 am and 11:30 am to find suitable host buds for oviposition (22–38 mm in length). At 3:00 pm, the females reached a peak of oviposition. Once they found suitable buds on a host plant, they usually stayed at the plant throughout their oviposition period, which ended between 8 pm and 10 pm. In the census field, the females that have found suitable buds were usually fewer in number than those that had left the leaves after mating. The females moving in and out of the census filed, as well as those caught by predators such as spiders or empidid flies (Diptera: Empididae), are involved in a total dispersal loss during the course of the search for the buds.

7.11 Larval Behavior

Larvae that hatched from eggs outside plant tissue move to appropriate feeding sites. Larvae of some species penetrate the plant tissue without the help of a fungus. The first instars of *M. pustulae*, for example, enter the leaf blade of *E. japonicus* (Yukawa and Sunose 1976), and those of *D. machilicola* sink into the plant tissue of *Machilus thunbergii* Siebold & Zuccarini (Lauraceae) just beneath the eggshell (Yukawa 1974). A similar behavior is also evident in *Rabdophaga degeerii* (Bremi) on *Salix*. In contrast, larvae of *Lasioptera arundinis* (Schiner) penetrate the plant tissue of *Phragmites australis* (Cavanilles) Trinius ex Steudel (Poaceae) in association with a fungus (Skuhravá and Skuhravý 1992; Rohfritsch 1997). Such an association is common in ambrosia gall midges such as *Lasioptera* species.

All hatched larvae of *M. selenis*, even those derived from eggs on the under surface, crawl to the upper surface of the leaf margin (Fig. 7.3f), where they settle down (Kim et al. 2015). This means that hatched larvae can recognize appropriate places for settling down and gall induction (Fig. 7.3g). Crawling seems to be more dangerous for larvae from the under surface than those from the upper surface. Nevertheless, females did not develop safer ways of oviposition to benefit their progeny. Otherwise, laying eggs on both surfaces may contribute to spreading risks during the egg stage because various mortality factors, such as predators or rainfall, would operate differently on eggs on different surfaces.

Larvae of type IA species are more active than those of types IB, IIA and IIB. After they exit their galls, they drop to the ground and crawl their way into the soil. Larvae of *Contarinia* species spin cocoons in which they overwinter and pupate. In particular, larvae of *Contarinia* and *Thecodiplosis* can jump. Mature larvae of the Japanese cedar gall midge *Contarinia inouyei* Mani moved 62.8 ± 21.0 mm (mean ± s.d.) per random jump under uniform lighting conditions while moved 81.1 ± 42.5 mm (mean ± s.d.) per jump toward light source under unidirectional lighting conditions (Tokuhisa et al. 1979). This behavior appears to be an adaptation for exiting galls and finding a suitable site on the ground to construct a cocoon (Tokuhisa et al. 1979). In contrast, larvae of types IB, IIA and IIB are usually inactive and do not jump, probably because they do not exit their galls and do not search for cocooning sites on the ground.

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