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Pest Profiles

Flighted spongy moths (Lepidoptera: Erebidae), defoliating invasive forest pests

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Flighted spongy moth, *Lymantria dispar asiatica* Vnukovskij and *Lymantria dispar japonica* Motschulsky, is a highly destructive defoliator that threatens forest and urban trees in both its native Asian range and where introduced. This moth goes through outbreak periods with very high population numbers resulting in defoliation of almost all deciduous and coniferous trees and potentially severe human allergic reactions to the insect hairs and scales. Adult females are capable of strong ascending flight and at night are attracted to lights where they lay their egg masses on surrounding surfaces. This has resulted in flighted spongy moth hitchhiking multiple times to new areas as egg masses, or occasionally as pupae, on ships and their cargo. Flighted spongy moths have a broad host range that includes several hundred tree species, both broadleaf and conifer. Identification of stages and species, life history, and ecology are reviewed here. There are few biological differences between the 2 subspecies, but *L. dispar japonica* tends to be larger and flies at a slightly different time of day than *L. dispar asiatica*. Both eradication (in introduced areas) and management require detection which is primarily accomplished using male pheromone traps and egg mass surveys. Populations are controlled by various natural and managed methods including parasitoids, predators, pathogens, microbial pesticides registered for aerial and ground application, mating disruption (applying pheromone in various formulations), and aerially spraying insect growth regulators. Synthetic insecticides are rarely used due to public concerns regarding unintended nontarget impacts.

Keywords: Lymantria dispar, invasive species, defoliator, Asia

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Graphical Abstract

Regulatory groups use the name flighted spongy moth complex (FSMC) to refer to a group of 5 taxa: 2 subspecies of *Lymantria dispar* L. (Lepidoptera: Erebidae), *L. dispar asiatica* Vnukovskij and *L. dispar japonica* Motschulsky, and 3 other species in the same genus, *L. albescens* Hori and Umeno, *L. umbrosa* (Butler), and *L. postalba* Inoue. The criteria for considering this group of 5 taxa as FSMC were originally suggested by Pogue and Schaefer (2007). The only other subspecies of *L. dispar*, *L. dispar dispar*, is also invasive but is not considered to be as much of a threat since the females are not capable of flight (Srivastava et al. 2020). All the taxa in the spongy moth species complex are highly destructive defoliators that attack several hundred species of forest and urban trees, mostly hardwood species but also some conifers. Eradication efforts targeting these 2 subspecies in the United States have cost millions of dollars (Mastro et al. 2021) and the costs of management and damage caused by larval feeding in the native countries has not been estimated.

Taxonomy

Lymantria dispar, the spongy moth, was formerly known as the gypsy moth. Spongy moths belong to the superfamily Noctuoidea which is the largest superfamily within Lepidoptera with about 72,000 described species (Kitching and Rawlins 1998). In the most recent classification, 6 families, including Erebidae, have been placed within this superfamily (Zahiri et al. 2011). Based on molecular studies, family Erebidae contains 18 subfamilies (Zahiri et al. 2012). Spongy moths belong to the subfamily Lymantriinae and are described as small to medium-sized moths with bipectinated antennae in both sexes (weakly pectinate in the females, Fig. 1). They also have strongly reduced proboscises, and the larvae have conspicuous dorsal glands on their sixth and seventh abdominal segments (Zahiri et al. 2012). More than 2,900 species have been described in nearly 360 genera within this subfamily (Kitching and Rawlins 1998). The genus *Lymantria* includes about 170 species, some globally recognized as destructive forest pests (Schintlmeister 2004, Pogue and Schaefer 2007). The greatest diversity is found in Asia, with 4 species found in Europe. Only *L. dispar dispar* has been established in the western hemisphere (Schintlmeister 2004).

The FSMC refers to a group of 5 taxa, 3 species, and 2 subspecies of *Lymantria*, all of which have flight-capable females. This includes *Lymantria dispar asiatica*, *L. dispar japonica*, *L. albescens* (ivory spongy moth), *L. umbrosa* (shadow spongy moth), and *L. postalba* (white-winged spongy moth) (Pogue and Schaefer 2007). Recently, it has been shown that *L. albescens* and *L. postalba* are simply morphs of a single species (Djoumad et al. 2020). There is little literature on the 3 species (*L. umbrosa*, *L. albescens*, *L. postalba*) so they will not be covered in this review. However, the 2 subspecies *L. dispar japonica* and *L. dispar asiatica* have been studied extensively and have a wide native distribution. Therefore, while this review will focus only on these 2 subspecies of spongy moths, the management strategies mentioned may be applicable to controlling populations of any of the taxa in the FSMC.

Lymantria dispar japonica was first described in 1860 by Motschulsky, and in the most recent investigations it has been separated into 2 subspecies: *L. dispar hokkaidoensis* from central and eastern Hokkaido and *L. dispar japonica* from western Hokkaido, Honshu, and northern Kyushu (Kishida 2011, Arimoto and Iwaizumi 2014). The new subspecies (*L. dispar hokkaidoensis*) that is proposed is likely valid as cross-mating between the 2 groups results in male death, but hybrid females are fertile and produce normal progeny (Higashiura et al. 2011). *Lymantria dispar japonica* male forewing ground color changes from light brown to brown (Fig. 2), while the female ground color is brownish white (Fig. 3). Despite the similarity of males, both sexes in *L. dispar japonica* have longer forewings compared to *L. dispar dispar* which occurs across Europe and was introduced into North America. The Entomological Society of America's official common name for *L. dispar* is spongy moth and it is applied to all subspecies. The most common name for *L. dispar japonica* is spongy moth, but in Japanese it is also called "*Maimaiga*" or "*Shiroshita-maimai*" (Pogue and Schaefer 2007).

Lymantria dispar asiatica was first described by Vnukovskij in Russia in 1926 and occurs throughout Asia east of the Ural Mountains (Pogue and Schaefer 2007). The males exhibit variations in the ground color of their forewings, ranging from darker to lighter brown (Fig. 2), compared to the grayish cast in the light brown ground color of the forewings in males of *L. dispar dispar*. Although Pogue and Schaefer (2007) state that the female forewings of *L. dispar asiatica* have a more prominent postmedial band than those of *L. dispar dispar*, this is inaccurate, as the Asian spongy moth females may or may not have this band (Fig. 3).

Spongy moth is the most popular common name for *L. dispar asiatica*. However, in different parts of Asia, it is called by various common names. In Korea, the species is called "*Maemi-Nabang*" or "*Gypsy-Nabam*." In China, the moth is known as "*Wu du E*" or "*Shi Mao Chong*" (persimmon caterpillar). "*Shelkopryad neparnyy*" (unpaired silk moth) is used in Russia, while "*Neparniy shovkopryad*" and "*Uruusgul hur erveehei*" are Ukrainian and Mongolian names, respectively (Pogue and Schaefer 2007).

Description of Life Stages

Adults

Adults of flighted spongy moth (*L. dispar asiatica* and *L. dispar japonica*) are sexually dimorphic. Females tend to be larger than males and can be distinguished by their lighter-colored

Fig. 1. Mating couple of *Lymantria dispar asiatica*. Female (left) is the larger white moth, and the male (right) is the smaller dark brown moth. Photo by Melody Keena.

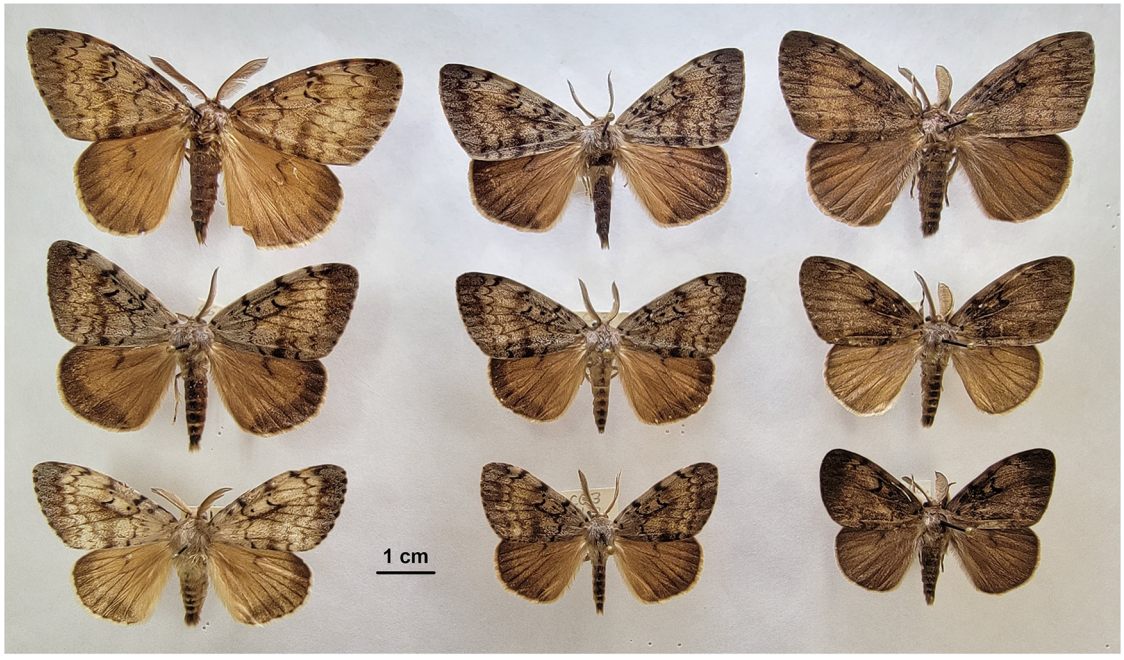

Fig. 2. Male moths of both subspecies showing variation in wing coloration. *Lymantria dispar asiatica* (Russian and Chinese origins) left 2 columns and *L. dispar japonica* (Japanese origin) rightmost column. Photo by Melody Keena.

wings compared to the brown wings of males. The forewings of *L. dispar asiatica* females are white and 28 to 41 mm in length, while those of *L. dispar japonica* are brownish-white and 34 to 41 mm in length, and both subspecies have dark zig-zag markings on this lighter background (Pogue and Schaefer 2007) (Fig. 3). The hindwings of females have a white (*L. dispar asiatica*) to brownish-white (*L. dispar japonica*) background color, and both the fore- and hindwings have darker spots near the outer edge of the wing. The females of both subspecies also have longer fore- and hindwings when compared to *L. dispar dispar* of the same body size (Shi et al. 2015). The average body length of a female *L. dispar japonica* is around 2.5 cm (Sasaki et al. 2016). Males' wings are light to dark brown, some are almost black, and *L. dispar asiatica* wings are 23 to 28 mm long, while *L. dispar japonica* wings are 25 to 32 mm. The forewings of both subspecies have darker zig-zag patterns on them, and the hindwings are light to dark brown with a darker brown outer margin in *L. dispar asiatica* but not in *L. dispar japonica* (Fig. 2).

Females' heads are white to brownish white, while the males' heads are golden brown. The antennae of both sexes are bipectinate (comb-like) but differ in color and the length of the side branches. In females, the antennae are dark brown and the side branches are only a little wider than the width of the antenna, while male antennae are brown with side branches approximately 5 times the width of the antenna. The female thorax is covered with a mass of white hairs, while the male thorax is dark brown. The dense hairs on the female's abdomen are light brown and gradually darken to a dark brown at the tail end. The male abdomen is light brown with dark brown patches along the middle of the back (Pogue and Schaefer 2007).

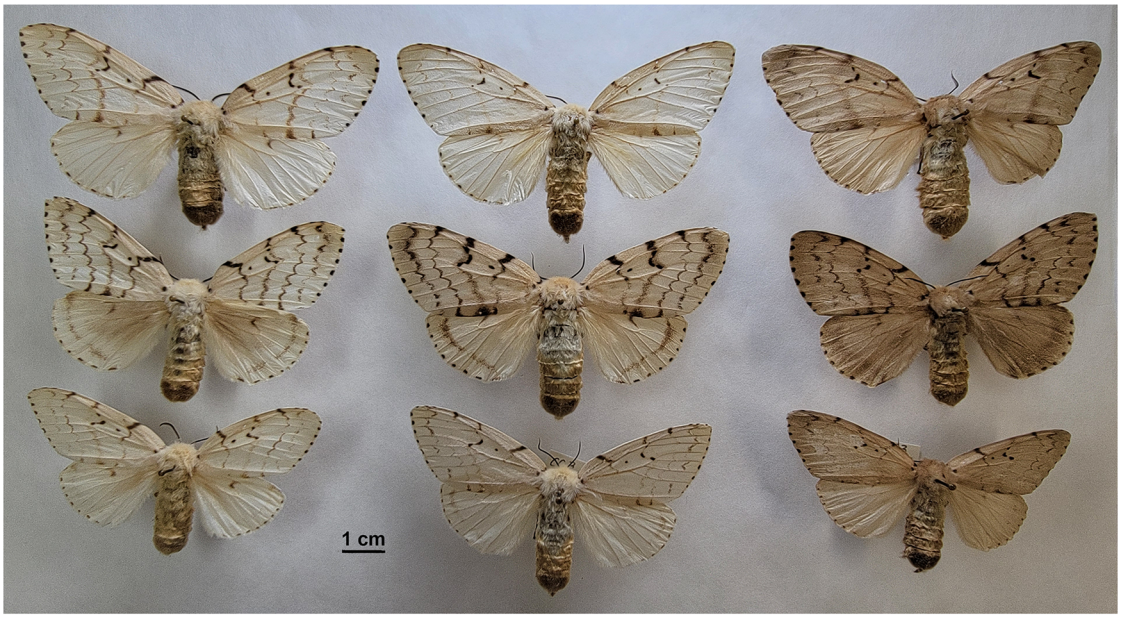

Fig. 3. Female moths of both subspecies showing variation in wing coloration. *Lymantria dispar asiatica* (Russian and Chinese origins) left 2 columns and *L. dispar japonica* (Japanese origin) rightmost column. Photo by Melody Keena.

Fig. 4. Color variation in egg masses of *Lymantria dispar asiatica*. Photo by Melody Keena.

Eggs

Females of both subspecies lay their eggs as a single teardrop-shaped mass and cover them with a thick layer of abdominal hairs that are buff yellowish to dark brown (Fig. 4). Occasionally a female will be disturbed during oviposition and will start laying in a new location, resulting in more than 1 "egg mass." The egg masses can be small enough to fit into a 1.5 cm diameter circle, but average 3.8 cm in length and 1.9 cm in width (USDA APHIS 2016). The number of eggs a female lays varies from fewer than 100 to over 1,000; where conditions are optimum, egg clusters average around 750, but on poor hosts or at the end of outbreaks, 300 or fewer eggs are found in the mass (Keena and Richards 2020, Mastro et al. 2021). Spongy moths from Siberia (Tuva) have lower relative fecundity and higher average egg weights than those from North America (Michigan): 165 ± 6 and 270 ± 9 eggs/g pupal weight and average egg weights of 0.65 ± 0.03 mg (0.3 to 1.1 range) and 0.50 ± 0.02 mg (0.1 to 0.7 range) for Tuva and Michigan populations, respectively (Vshivkova and Baranchikov 2010).

Eggs are initially yellow to tan but turn dark brown as they embryonate. The embryo develops into a fully formed first instar size larva in the egg before entering diapause for the winter (Leonard 1968, Keena and Richards 2020).

Fig. 5. Fifth-instar *Lymantria dispar asiatica* shed head capsule showing the false eye spots. Photo by Melody Keena.

Larvae

Newly hatched *L. dispar* larvae are black and hairy, between 2 and 3 mm long (Parkinson 2023). Fully grown larvae, on average, are 50 to 55 mm with a hairy body, characteristic of Lymantriinae larvae. Larval body weight increases over a 1,000-fold as they grow from the first to final instar. The number of instars can be variable (Table 1). The head is creamy with light brown spots. A pair of black bands on the face resemble eyes, but only after the larva has shed its skin 2 to 3 times (Fig. 5). The prolegs are pale, and the thoracic legs are yellowish brown (Pogue and Schaefer 2007). The larvae have 2 rows of hairy warts on their backs; the first 4 pairs are blue, and the remaining 6 to 7 pairs are red. The larvae also have hair-covered warts along the side of the body that are lighter in color on the third to eighth segments of the abdomen but darker on the thorax and the first 2 abdominal segments (Pogue and Schaefer 2007, Sugiura and Yamazaki 2014). The color of the inflexible hairs in the warts can be tan, reddish, or almost black and the areas between the warts on the larval back can be a range of colors, from bright yellow to gray to black (Fig. 6). Five color forms have been described for spongy moth larvae (Keena 1994).

Pupae

The pupae of *L. dispar asiatica* and *L. dispar japonica* are teardrop shaped, and reddish-brown in color. Female pupae (25 mm) are larger than male pupae (20 mm) (Table 1) and less tapered toward the tail end (Nakamura 1976) (Fig. 7). Pupae of both sexes have short hairs emerging from small bumps, and the antennal and wing pads, which will become the actual appendages, are visible.

Molecular Diagnostic Tools for Distinguishing Asian Spongy Moth from Other Insects

A taxonomic revision of the family Erebidae was completed by Zahiri et al. (2012) using DNA sequence data for 1

Table 1. Average weight (mg ± SE) at the beginning of each instar (stage between molts) for both sexes from 4 different populations reared individually on artificial diet. The North American population is *Lymantria dispar dispar*, the Japanese population is *L. dispar japonica*, and the Russian populations are *L. dispar asiatica*

		Population source			
Instar	**Sex**	**North America**	**Honshu, Japan**	**Siberia, Russia**	**Russian Far East**
First	Female	0.54 ± 0.004	0.67 ± 0.008	0.79 ± 0.006	0.61 ± 0.007
	Male	0.53 ± 0.005	0.68 ± 0.006	0.79 ± 0.007	0.61 ± 0.006
Second	Female	6.5 ± 1.4	6.6 ± 0.4	10.4 ± 0.8	6.3 ± 0.4
	Male	5.0 ± 0.3	6.3 ± 0.3	9.3 ± 0.7	5.2 ± 0.2
Third	Female	41.5 ± 3.1	33.0 ± 1.0	43.0 ± 1.8	44.0 ± 4.5
	Male	35.6 ± 3.0	32.6 ± 1.6	40.9 ± 2.3	37.0 ± 3.4
Fourth	Female	147.4 ± 7.6	183.7 ± 8.1	208.6 ± 10.5	192.1 ± 12.0
	Male	101.2 ± 7.0	186.5 ± 10.0	151.9 ± 10.4	144.5 ± 7.5
Fifth	Female	606.3 ± 27.4	674.8 ± 30.1	1096.3 ± 36.0	859.8 ± 61.0
	Male	369.9 ± 12.3	532.9 ± 24.8	539.9 ± 19.2	573.9 ± 18.4
Sixth	Female	1,458.1 ± 101.1	1,685.5 ± 64.7	NA	1,654.4 ± 206.7
	Male	NA	746.1 ± 36.2	NA	NA
Pupae	Female	2,907.5 ± 140.1	3,968.2 ± 186.3	2,854.1 ± 72.5	3,273.5 ± 118.6
	Male	776.1 ± 21.7	1,496.1 ± 36.3	869.7 ± 25.4	1,035.1 ± 36.8

Fig. 6. Larvae of both subspecies showing the color variation that may be present both within and between populations. These larvae are fourth to sixth instars that have been reared on artificial diet. Each circle contains larvae from a single female parent. Photo by Melody Keena.

mitochondrial gene (mtDNA) and 7 nuclear genes and specimens representing a total of 237 taxa. In total, 18 major lineages were revealed, each representing a subfamily (Zahiri et al. 2012). The subfamily Lymantriinae contains more than 2,500 species in approximately 360 genera. A more recent study using 2 mitochondrial genes and 6 nuclear genes confirmed there were 7 tribes, including Lymantriini, in the subfamily Lymantriinae (Wang et al. 2015). To identify various species in the family Erebidae, mtDNA "barcodes" have been used (a mitochondrial cytochrome oxidase subunit I [COI] gene-based identification system) along with morphological keys (deWaard et al. 2010).

A polymerase chain reaction restriction fragment length polymorphism (PCR-RFLP) based method using the second internal transcribed spacer (ITS2) region of nuclear ribosomal DNA can be used to identify 8 *Lymantria* species that occur in Japan: *L. dispar japonica*, *L. umbrosa* (Butler), *L. albescens* Hori and Umeno, *L. postalba* Inoue, *L. xylina* Swinhoe, *L. mathura* Moore, *L. monacha* (Linnaeus), and *L. lucescens* (Butler) (Arimoto and Iwaizumi 2016). There were 2 pairs of species that could not be correctly identified using this method (*L. dispar japonica* and *L. umbrosa*; *L. albescens* and *L. postalba*). More recently, molecular analyses using additional genes have suggested that *L. albescens* and *L. postalba* are a single species with different wing coloration (Djoumad et al. 2020). The 9 Korean *Lymantria* (*L. dispar*, *L. xylina*, *L. monacha*, *L. lucescens*, *L. fumida* Butler, *L. mathura*, *L. bantaizana* Matsumura, *L. minomonis* Matsumura, and *L. sugii* Kishida) have been successfully distinguished to the species level by mtDNA successfully but not to the subspecies level (Kang et al. 2015).

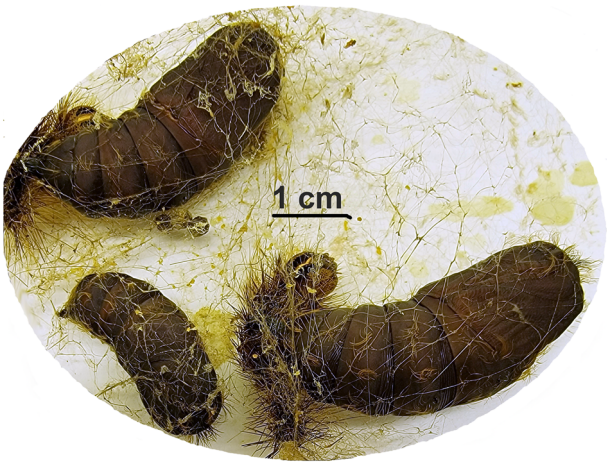

Fig. 7. Pupae of *Lymantria dispar asiatica* held in place by silk the larva spins before pupating. These pupae have been reared on artificial diet, so they are larger than foliage-reared pupae. Male lower left and the other 2 are females. Lower right shows the shed larval skin that is usually retained under the silk at the tail end of the pupa. Photo by Melody Keena.

A total of 36 *Lymantria* species can be distinguished by barcodes (deWaard et al. 2010). In China, a recent study successfully distinguished the FSMC from other morphologically similar species (*L. xylina*, *L. monacha*, *L. apicebrunnea*, *L. fumida*, *L. similis*, *L. mathura*, *L. nebulosa, L. marginata*) based on species specific COI (Ji et al. 2023).

Various molecular tools have been developed to separate European (*L. dispar dispar*) and Asian subspecies (*L. dispar asiatica* and *L. dispar japonica*) based on different molecular methods and genes—including mtDNA, microsatellite markers, RFLPs, and single nuclear genes—but many can distinguish only general geographic origin of specimens (Garner and Slavicek 1996, Bogdanowicz et al. 1997, Keena et al. 2008, Djoumad et al. 2017, Stewart et al. 2019, Zahiri et al. 2019). A suite of TaqMan assays (real-time PCR process) has provided a significant improvement in distinguishing among all 3 *L. dispar* subspecies as well as the other 3 *Lymantria* species within the FSMC and the other 5 *Lymantria* species that may threaten the forests of North America (Stewart et al. 2019). Knowing if an *L. dispar* moth that is introduced came from a population where females are capable of flight is critical to survey and eradication/suppression efforts. Further research has been completed to further identify geographic origins and to search for flight gene markers.

More precise origins of *L. dispar* have been possible using larger numbers of genes and more recently developed molecular methods. Using a diagnostic panel of 60 DNA loci, including 55 nuclear and 5 mitochondrial, 5 geographic groups were described: (i) North America; (ii) Europe, North Africa, and the Middle East; (iii) the Urals, Central Asia, and Russian Siberia; (iv) continental East Asia; and (v) the Japanese islands (Wu et al., 2020). *Lymantria umbrosa* was placed in the same group as *L. dispar japonica* in this study. Finer scale separation of origins was possible for all geographic groups except North America, so it was also possible to infer the source of Asian spongy moth introductions into North America as originating from the coastal area of continental East Asia or Japan during 2014–2015 (Wu et al. 2020). Some mitochondrial DNA assessments have shown that some Chinese populations of spongy moth have haplotypes that are common in both Asian and European populations, indicating that the Ural Mountains may not be a good geographic barrier for separating the subspecies or that human-aided transport may have created populations of mixed ancestry (Chen et al. 2016a, Zhao et al. 2019, Zuo et al. 2019). With recent advances in molecular techniques, thousands of single nucleotide polymorphisms have been derived using genotyping-by-sequencing that have improved our understanding of the evolutionary origins of the species and further defined distinctions between regions (Picq et al. 2018). These data confirmed the restriction of *L. dispar japonica* to Japan and suggested that due to how genetically distinct the populations present in North America and the Caucasus/Middle East are, they could be considered separate subspecies from other populations of *L. dispar*.

A recent study comparing the gene expressions of flighted (*L. dispar asiatica* and *L. dispar japonica*) versus flightless (*L. dispar dispar*) female spongy moth populations using RNA (ribonucleaic acid) identified some genes that code for aspects of flight activity, such as flight muscle function and energy production, weight and fat content, and power output of flight machinery (Wang et al. 2022). A suite of potential flight-associated genes (435 total, with 27 that have gene expression confirmed in the literature) has now been identified using a wide array of methods (Blackburn et al. 2024). Further work to assess the candidate genes is needed to determine what flight-related traits they code for and whether they definitively distinguish between flight-capable and flightless moths.

Biology

Life History

Eggs

The spongy moth (all sub species) spends 8 to 9 mo as an egg and overwinters in this stage (Ananko and Kolosov 2021). Eggs begin to embryonate soon after being laid in the early to mid-summer, and fully formed larvae develop in the eggs in about a month (16 d at 25 °C and 48 d at 15 °C; Gray et al. 1991). Development then ceases, and most eggs enter a period of arrested development known as diapause while a small percentage of eggs in some egg masses continue to develop and hatch. This trait is controlled by a single dominant gene, which could result in the development of a nondiapausing strain if conditions are right for these larvae to complete development to adulthood and subsequently mate (Keena 2016). Eggs in diapause require a period of low temperature to deplete an inhibitory chemical that prevents hatch during winter warm-ups (Gray et al. 2001). Once enough time at cool temperatures has accumulated, the inhibitory chemical is depleted, and the eggs respond to warming temperatures by completing their development and proceeding to hatch (Ponomarev et al. 2023). Populations of spongy moths vary in the amount of chill required for this to occur (Keena 2016, Gray and Keena 2019). However, spongy moth egg masses exposed to >200 d at ≤10 °C temperatures (Keena 1996, Wei et al. 2014) or temperatures <-29 °C for short periods (Ananko and Kolosov 2021) will die and fail to hatch. Spongy moth egg hatch generally occurs in the spring when trees of the preferred host are just leafing out (Higashiura 1989b, Ponomarev et al. 2023)

Larvae

Newly hatched larvae of all subspecies of *L. dispar* remain on or near the egg mass until their exoskeleton hardens and they turn black but will stay longer if it is rainy or if the temperature is <7 °C (McManus 1973). The larvae are positively phototrophic and negatively geotropic, so they climb up the host or inanimate object the egg mass was laid on. When they reach the top, they will spin some silk and use it as a balloon to disperse on the wind to a suitable host if they do not find new leaves to feed on (Pogue and Schaefer 2007). Larvae first feed on the leaf hairs, then on the leaf epidermis, cutting small holes, and will rest on the underside of leaves on a silk mat they spin (Fig. 8A). As the larvae grow, they begin feeding on the leaf margins and consume all but the petiole and more prominent leaf veins (Fig. 8B). Larvae are estimated to consume about 1 m^2 of foliage as they develop (Doane and McManus 1981). Unlike populations of European spongy moth (*L. dispar dispar*) established in North America that have diurnal feeding patterns, all instars of Asian spongy moth larvae (*L. dispar asiatica* and *L. dispar japonica*) remain in the tree/shrub crowns and feed, only leaving following defoliation in search of more food. Larval developmental rate increases with temperature between 10 and 29 °C, but at temperatures above and below that, the larvae face difficulty shedding their skins to change instars (Limbu et al. 2017). The number of larval instars and the time it takes to complete each varies from 4 to 8 depending on temperature, sex, population, and larval food source (Pogue and Schaefer 2007, Keena and Richards 2020). For example, the time it takes to complete the first instar differs by population of *L. dispar asiatica*: 51 to 78 d at 10 °C, 14 to 17 d at

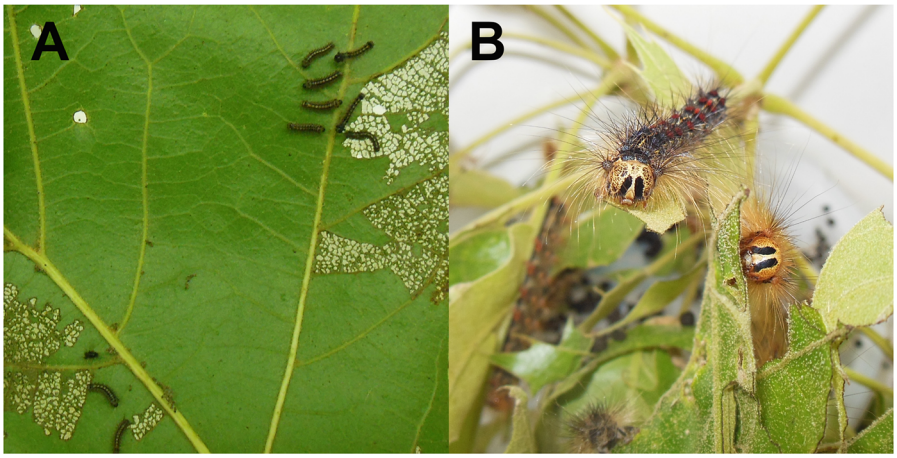

Fig. 8. Small larvae of *Lymantria dispar asiatica* feeding on underside of an oak leaf causing small holes (A) and larger larvae of *Lymantria dispar asiatica* feeding on oak leaves, starting at the margin and consuming all but the main rib and petiole (B). Photo by Melody Keena.

15 °C, 7 to 10 d at 20 °C, 5 to 7 d at 25 °C, and 4 to 6 d at 30 °C (Limbu et al. 2017). In most populations, male and female larvae go through 5 and 6 instars, respectively. Seventh and eighth larval instars are rarely observed and only occur when environmental conditions are unfavorable for larval development (Limbu et al. 2017). In areas with a very short growing season and cooler climate, like Siberian Russia, males may have only 4 instars (Limbu et al. 2017). In the ultimate instar, the larvae stop feeding, spin a sparse silk net around themselves, and shrink in length before they pupate. Larvae often seek protected sites such as cracks in tree bark and underneath loose moss for pupation (Parkinson 2023), but in Siberia they pupate in the crown where they spin leaf nets together which may then fall to the ground (Ponomarev et al 2012).

Pupae

The pupal stage (all subspecies) takes about 2 wk at 25 °C, but males take slightly longer than females (Furuno 1964, Humble and Stewart 1994, Limbu et al. 2017). Pupae survive better when reared at temperatures below 30 °C. At 15 and 30 °C, pupae generally weigh less than those that develop at 20 and 25 °C, have difficulty completing development, and may emerge as deformed adults (Limbu et al. 2017). Pupae are also smaller when populations reach outbreak levels, especially just before the populations collapse; the average weight of live pupae in the outbreak phase, regardless of sex, has been reported to be 720 mg (Kurenshchikov et al. 2020). Lower pupal weights result in lower adult weights, ultimately resulting in lower female fecundity and overall fitness.

Adults

Males of all subspecies usually complete development a few days earlier than females (Limbu et al. 2017), and there is only 1 generation per year throughout the native range (Pogue and Schaefer 2007, Petrovskii and McKay 2010). The upper and lower developmental thresholds for populations vary and are estimated to be 30 to 31 and 7 to 9 °C, respectively (Limbu et al. 2017).

Adults of *L. dispar asiatica* and *L. dispar japonica* emerge during the day between late June and early September, depending on the climate (impacted by both latitude and elevation), population, and available hosts (Higashiura 1989b, Koshio 1996, Trotter et al. 2020). When moths first emerge, they are fully formed, although the wings must be expanded and it takes a couple of hours for adult exoskeletons and wings to harden enough to fly. Adults do not feed and are ready to mate as soon as they can fly. Females usually start calling males on the day of eclosion by emitting the sex pheromone (7R, 8S-cis-7, 8-epoxy-2methyloctadecane [(+) disparlure]) which is the same for all subspecies (Iwaizumi et al. 2010) (Fig. 9). Males are diurnally active with peak activity in the afternoon (2 to 6 PM) and a second small peak at the beginning of night (11 PM to 2 AM) (Cardé et al. 1996). Mating occurs during afternoon hours (Schaefer and Strothkamp 2014). At dusk, the females begin preflight behaviors, walking and wing fanning to raise thoracic temperature, before taking flight toward a light source such as the moon or a light-colored surface like birch bark (Keena et al. 2008). This preoviposition flight allows them to find a suitable oviposition site over a broad area (Koshio 1996). Females of *L. dispar japonica* fly at a slightly lower light intensity than do those of *L. dispar asicatica* suggesting they fly at a slightly later timeframe in nature (Chen et al. 2016b). The majority of females that fly (94%) are already mated, so once they land they start laying eggs. If oviposition is not completed by morning, females will cease ovipositing until the evening (Iwaizumi et al. 2010, Schaefer and Strothkamp 2014). Unmated females will resume calling and may fly again before laying eggs. Female flight capability dramatically declines with age and varies within and between populations (Keena et al. 2008, Srivastava et al. 2021, Akram et al. 2022). Males mate between 4 and 5 times (Pogue and Schaefer 2007), while females usually mate only once (Iwaizumi et al. 2010). Matings must last at least 10 min to be successful (Pogue and Schaefer 2007) but generally last 30 to 60 min and may continue for over 2 h (Iwaizumi et al. 2010).

Females of all subspecies lay eggs in a single clump, covering them with a thick layer of abdominal hair (Koshio 1996). The average life span of the female moths is about 7 d, but oviposition only occurs in the first 5 d (Koshio 1996, Iwaizumi et al. 2010). In forests, females lay their egg masses in different locations across the native range. In the midlatitudes (cooler climates) where there is no moderating effect of water bodies or wind, females lay on stones and rock outcroppings outside forests, and in warmer regions on tree trunks, under surfaces of

Fig. 9. Asian spongy moth (*Lymantria dispar asiatica*) female calling (releasing pheromone to attract a mate). Photo by Melody Keena.

lower branches, or on leaves (Gninenko and Orlinskii 2003, Pogue and Schaefer 2007, Sasaki et al. 2016) (Fig. 10). Concentrations of egg masses are also found near outdoor light sources on vertical surfaces, including vehicles and cargo, which has resulted in the transport and introduction of this insect into new areas (Wallner et al. 1995, Charlton et al. 1999, Schaefer and Strothkamp 2014) (Fig. 11). In Japan, the number of egg masses found in urban areas within 1 meter of forests was 10-fold higher than in adjacent forested areas, demonstrating the strong attraction of females to lights (Liebhold et al. 2008).

Distribution

The native range of the 2 subspecies covers a vast area, including a significant part of the Holarctic region between 20 and 60° north latitude (Ananko and Kolosov 2021, Ponomarev et al., 2023). *Lymantria dispar asiatica* is found east of the Ural Mountains up to the Russian Far East in Russia, throughout China between 20 and 58° north latitude in 20 provinces, throughout Korea except in the southwest region, and parts of Japan, whereas *L. dispar japonica* is restricted to small areas on all main islands in Japan and also in the Kuril Islands of Russia (Pogue and Schaefer 2007, Bi et al. 2008, Keena et al. 2008, Song et al. 2022). Recent population genomics work has shown that there is no sharp geographic boundary between *L. dispar dispar* and *L. dispar asiatica* distributions in Eurasia, but this paper will focus on the populations in which the majority of the females have full flight capability, which extends as far west as the coast of Lithuania in the northern latitudes (21°E) but only as far west as about 60°E in the southern part of Russia (Keena et al. 2008, Picq et al. 2023).

Since the 1990s, multiple introductions of spongy moths from Asia into North America have occurred (Mastro et al. 2021). The first infestation of an Asian subspecies was found in British Columbia in 1991 (Bogdanowicz et al. 1993, Savotikov et al. 1995). This led to increased monitoring for flighted spongy moth within ports and nearby forested areas in both the native range—initially just the Russian Far East and subsequently expanded to China, Japan, and South Korea—and North American ports (Mastro et al. 2021). This involves both pheromone-baited traps and light traps to monitor population levels in ports, early warning of female flights in port areas, and development of a predeparture ship inspection program by regulatory officials in the native range to ensure ships were inspected and egg masses removed (Savotikov et al. 1995). In 2009, the North American Plant Protection Organization adopted these preventive measures as the Regional Standard for Phytosanitary Measures 33 guidelines. However, infested vessels are still found despite these regulatory and monitoring programs. A total of 62 flighted spongy moth infestations were found and successfully eradicated in the United States from 1991 to 2019, at a cost of millions of dollars (Mastro et al. 2021). Other countries, such as New Zealand, Australia, and Chile also utilize the monitoring data and inspect ships entering their ports to prevent introductions.

Fig. 10. Adult female *Lymantria dispar asiatica* ovipositing on an oak leaf. Photo by Yuri Baranchikov.

Ecological niche models predict that the potential invasive distribution of flighted spongy moth (*L. dispar asiatica* and *L. dispar japonica*) could include the entire temperate zone of both the Northern and Southern hemispheres, excluding desert and mountainous areas (Peterson et al. 2007). Both Maximum Entropy and Genetic Algorithm for Rule-set Prediction models predict that the potential distribution areas of flighted spongy moth in Canada include the provinces of British Columbia, Ontario, Quebec, Nova Scotia, and New Brunswick (Srivastava et al. 2020). Under different climate change scenarios, the northern border of flighted spongy moth climatic range could reach the 64th parallel in Eurasia by the end of the 2030s (Bogdanovich et al. 2023). Flighted spongy moth has yet to be established in Australia or New Zealand, but egg masses have frequently been discovered on cargo from Asia. Based on climate conditions, it has been predicted that northern and southeastern New Zealand and southeastern and southwestern Australia are at a high risk of population establishment (Matsuki et al. 2001).

Ecology

Flighted spongy moth (*L. dispar asiatica* and *L. dispar japonica*) eggs do not tolerate freezing but do build stress proteins in response to cool temperatures that help them resist freezing at temperatures near −20 °C in the winter (Denlinger et al. 1992). However, in some parts of their native range, the temperature repeatedly falls below −30 °C during winter, which is lower than their physiological limit to survive. To deal with these lower temperatures, the female has different ovipositional behaviors in various geographical regions to save her progeny

Fig. 11. Female *Lymantria dispar asiatica* ovipositing on a ship near a light in the Russian Far East. Photo by Steven Munson.

(Ananko and Kolosov 2021). In Russia, Mongolia, northeastern China, and eastern and southern Siberia, eggs are placed in rock cracks or under rock outcroppings near the soil even if suitable trees are nearby (Pogue and Schaefer 2007, Ananko and Kolosov 2021) (Fig. 12). The rock microhabitat surface is about 2 to 5 °C higher than the average air temperature, which serves both to attract flying females and enables the egg masses to withstand temperatures below their physiological limits (Baranchikov et al. 2008). Another important feature of rocky microhabitats is their role as natural thermostats, reducing the fluctuations in temperatures the eggs are exposed to and preventing early hatch in spring which can lead to asynchrony between host plant and defoliator (Baranchikov and Montgomery 2009, Vshivkova and Baranchikov 2010, Martemyanov et al. 2015). The rocks are also often on hills that are exposed to wind so the hatchlings can disperse back to the trees in the valleys (Fig. 12, Ananko and Kolosov 2021). In China and Korea, the females lay their eggs under pine tree branches (*Pinus tabulaeformis* Carrière) that help to shelter them. In the Russian Far East, females oviposit underneath deciduous tree leaves, which fall to the ground and are covered by snow, ensuring the survival of the eggs (Pogue and Schaefer 2007). In a population of West Siberia, females lay their eggs on tree trunks only 6 to 7 cm above ground level so that they are covered by snow from November to March, providing thermal insulation that helps the eggs survive (Madrid and Stewart 1981, Ponomarev et al. 2023). In Japan, egg masses are often laid below the snow level, increasing survival over those laid higher on the trees. In Hokkaido, females fly to white birch trees to lay, likely attracted to the light-colored bark (Schaefer 1978).

The spongy moth (*L. dispar*) goes through cyclic population outbreaks; they may be hard to find for years, build up to huge numbers over a few years, remain high for a few years, and then drop back to low numbers again. Several outbreaks have been recorded for *Lymantria dispar asiatica* in Russia, the largest of which covered 750,800 ha in Siberia in 1996 and 1.2 million ha in the far east Primor'e territory in 1991 (Gninenko and Orlinskii 2003). In Russia, many outbreaks last 7 to 9 yr, but in the Far East region, they last only 1 to 4 yr (Ilyinykh et al. 2011). The shorter duration of outbreaks in the Russian Far East has been attributed to increased exposure of egg masses to pathogens because females lay on leaves that fall to the ground and come into contact with the soil (Ilyinykh et al. 2011). Outbreaks of *L. dispar japonica* have been reported mainly from Hokkaido and eastern Honshu in Japan (Inoue et al. 2019). Historical records indicate that outbreaks in Hokkaido occur at 11-yr intervals (Inoue et al. 2019), but forest defoliation data for Japan from 1951 to 1997 show a periodic outbreak of spongy moths every 5.84 yr (Johnson et al. 2005). Outbreaks in Japan usually start in larch (*Larix kaempferi* (Lamb.) Carr.) plantations, then spread to nearby natural hardwood forests and are known to be terminated by *Entomophaga maimaiga* Humber, Shimazu, and R.S. Soper (Entomophthorales: Entomophthoraceae) epizootics (Kamata and Kamata 2002). In China, *L. dispar asiatica* has never caused widespread severe outbreaks but has caused more localized defoliation of both hardwoods and conifers grown in plantations (*Larix* and *Pinus*) that have required management (Schaefer et al. 1984a). These smaller outbreaks have occurred mainly in the northeastern provinces and occur on about a 10-yr cycle. However, in Northern Mongolia spongy moth outbreaks may last several years when in *Larix sibirica* forests in hilly landscapes (Yanovskyi 1980, Zhantsantomboo 2003, Namkhaidorzh et al. 2006).

Hosts

Lymantria dispar asiatica and *L. dispar japonica* are polyphagous and can feed on many of the same host plant genera and species as *L. dispar dispar*. There are observations of feeding on 529 species (466 wood hosts and 63 herbaceous hosts) from 76 plant families in the literature for flighted spongy moths in their native range (Table S1). Many of these hosts are native species unique to Eurasia but also include introduced plant species from other regions. Table 2 summarizes the 144 woody plant genera and provides an average utilization code for each genus. Flighted spongy moths are known to reach outbreak levels on various tree species throughout its range, including *Quercus*, *Betula*, or *Larix*-dominated and mixed broadleaf forests. *L. dispar asiatica* populations in the Russian Far East prefer to feed on Mongolian oak (*Quercus mongolica*) and aspen (*Populus tremula*); however, Siberian populations opt for birch (*Betula* sp.), aspen (*Populus tremula*), and Siberian larch

Fig. 12. Females *Lymantria dispar asiatica* laying on rock outcropping in Siberian Russia (left). Newly hatched larvae of *Lymantria dispar asiatica* from egg masses laid on rocks in Mongolia that are "ballooning" back to the valley to find hosts. Photo by Yuri Baranchikov.

Table 2. Woody hosts of flighted spongy moth (*Lymantria dispar asiatica* and *L. dispar japonica*), arranged by plant family and genus. List is based on observations of feeding found in the literature for the Asian native range. An average suitability code is provided for each genus based on feeding studies

Family	Genus	Common name	Number of species feeding reported	Average suitability code[a]	Countries where feeding was observed	References for feeding observations in native range[b]
Altingiaceae	*Liquidambar*	sweetgum	3	5	China, East Asia, Russia	30, 50, 63
Anacardiaceae	*Cotinus*	smokebush	1	5	China	36
	Pistacia	pistachio	2	5	Central Asia, Russia, Kyrgyzstan	3, 4, 28, 31, 50, 51
	Rhus	sumac	5	5	Korea, Russia, Japan	30, 53, 57
	Toxicodendron	Poison ivy, poison oak	5	F	Japan, Korea	26, 53, 64
Aquifoliaceae	*Ilex*	holly	4	F	Japan, China	25, 61, 64, 79
Araliaceae	*Aralia*	spikenard	1	0	Japan	64
	Artemisia	wormwood	1	2	Japan	64
	Chengiopanax	chengiopanax	1	F	Japan	64
	Dendropanax	dendropanax	1	F	Japan	61
	Fatsia	fatsia	1	2	Japan	64
	Kalpanax	castor aralia	1	0	Japan	64
Arecaceae	*Livistona*	fan palm	1	F	Japan	64
Berberidaceae	*Berberis*	barberry	2	3	Central Asia, China, Russia	30
Betulaceae	*Alnus*	alder	6	5	East Asia, Japan, Korea, China, Russia	4, 22, 26, 29, 30, 50, 57, 63, 64, 66, 67, 73
	Betula	birch	15	5	China, East and Central Asia, Japan, Kazakhstan, Korea, Mongolia, Russia, Siberia	2, 4, 10, 12, 21, 22, 26, 29, 30, 31, 32, 40, 48, 50, 53, 55, 57, 58, 62, 63, 64, 65, 68, 69, 71
	Carpinus	hornbeam	8	4	Japan, East Asia, Korea, China, Russia	30, 33, 50, 57, 63, 64, 76
	Corylus	filbert, hazel, hazelnut	4	4	China, Japan, Korea, Russia	4, 26, 30, 32, 53, 57, 63, 64
	Ostrya	hop-hornbeam	2	F	Russia	30
Buxaceae	*Buxus*	boxwood	1	F	China	56
Cannabaceae	*Cannabis*	hemp	1	F	Japan	64
	Celtis	hackberry	4	4	East Asia, Japan, Russia	30, 50, 57, 64
Celastraceae	*Euonymus*	burning bush, spindletree	2	F	Japan, Korea	26, 64
Cercidiphyllaceae	*Cercidiphyllum*	katsura tree	1	3	Japan	64
Clethraceae	*Clethra*	clethra	1	2	Japan	25, 64
Coriariaceae	*Coriaria*	coriaria	1	F	China	34
Cornaceae	*Alangium*	alangium	1	F	China	79
	Cornus	dogwood	5	3	Chian, Japan, Korea, Russia	26, 30, 33, 39, 64
Cupressaceae	*Chamaecyparis*	cypress, false cypress	1	5	Japan, Korea	29, 64
	Cryptomeria	cryptomeria, Japanese cedar	1	5	Japan, Korea	29, 57, 64, 66
	Cupressus	cypress	2	F	Russia, China	30, 79
	Juniperus	juniper	3	2	Russia	30
	Metasequoia	dawn redwood	1	2	China	34, 84
	Platycladus	Chinese thuja, Chinese arborvitae	1	F	Japan	64
	Thuja	arborvitae	1	2	Russia	30
	Thujopis	hiba arborvitae	1	1	Japan	72
Ebenaceae	*Diospyros*	ebony, persimmon	2	2	China, East Asia, Japan, Korea	17, 29, 34, 36, 37, 50, 57, 59, 63, 64
Elaeagnaceae	*Elaeagnus*	silverberry, oleaster	3	F	Japan, Kazakhstan, Korea	4, 26, 64
	Hippophae	sallowthorn	1	5	China	34, 36
Ericaceae	*Calluna*	heather	1	F	Russia	30
	Erica	black-eyed heath	1	F	Russia	30
	Pieris	andromeda, fetterbush	1	F	Japan	64
	Rhododendron	azalea, rhododendron	7	F	Japan, Korea, Russia	1, 26, 29, 30, 53, 57, 64
	Vaccinium	blueberry	6	4	China, Japan, Russia	19, 20, 30, 61, 64

Family	Genus	Common name	Number of species feeding reported	Average suitability code[a]	Countries where feeding was observed	References for feeding observations in native range[b]
Eucommiaceae	*Eucommia*	Chinese rubber tree	1	F	China	34
Euphorbiaceae	*Mallotus*	mallotus	1	5	China, Japan	64, 79
	Vernicia	vernicia	1	F	China	79
Fabaceae	*Caragana*	pea shrub	3	F	China, Kazakhstan, Mongolia	4, 42, 66
	Dalbergia	dalbergia	1	F	China	59, 76
	Lespedeza	lespedeza	4	5	China, East Asia, Japan, Korea, Japan, Russia	12, 29, 32, 50, 63, 64
	Maackia	maackia	1	F	Russia	32
	Robinia	locust	2	4	China, East Asia, Japan, Korea	26, 32, 37, 50, 53, 55, 57, 60, 64
	Styphnolobium	necklacepod	1	F	Japan	64
	Wisteria	wisteria	3	5	China, East Asia, Japan	50, 57, 60, 64
Fagaceae	*Castanea*	chestnut	5	5	Russia, Korea, China, East Asia	17, 26, 29, 30, 34, 50, 53, 55, 57, 59, 63, 64, 67, 83
	Castanopsis	chinquapin	2	5	China, East Asia, Japan, Korea, Russia	50, 57, 61, 64
	Fagus	beech	6	4	China, East Asia, Japan, Russia	30, 50, 57, 59, 61, 64, 73, 76
	Lithocarpus	stone oak	1	F	China	44
	Quercus	oak	29	5	China, East and central Asia, Japan, Kazakhstan, Korea, Russia	2, 4, 12, 17, 18, 22, 25, 26, 27, 29, 30, 31, 32, 33, 34, 35, 36, 40, 41, 45, 46, 50, 53, 54, 55, 57, 61, 63, 64, 66, 69, 73, 76, 79, 81, 82
Ginkgoaceae	*Ginkgo*	ginkgo	1	F	China	38
Grossulariacea	*Ribes*	currant, gooseberry	7	3	Russia, Japan	4, 30, 64
Hamamelidaceae	*Distylium*	winter hazel	1	F	Japan	78
	Hamamelis	witch hazel	3	4	East Asia, Japan, Russia	30, 50, 57
Hydrangeaceae	*Deutzia*	deutzia	1	F	Japan	64
	Hydrangea	hydrangea	3	F	Japan, Korea	26, 64
Juglandaceae	*Juglans*	walnut	6	4	China, East and Central Asia, Korea, Kyrgyzstan, Russia	3, 4, 17, 24, 26, 28, 30, 31, 34, 41, 50, 51, 59, 63, 75, 76
	Pterocarya	wingnut	1	F	Japan	64
Lamiaceae	*Callicarpa*	beautyberry	1	2	Korea	26
	Vitex	chastetree	1	F	China	79
Lardizabalaceae	*Akebia*	akebia	1	F	Japan	64
Lauraceae	*Cinnamomum*	cinnamon	1	5	China, Japan, Korea	29, 64, 80
	Laurus	sweet bay	1	F	Korea	29
	Lindra	spice bush	1	2	Korea	26
	Persea	avocado	1	F	Japan	47
	Phoebe	phoebe	1	F	China	79
Lythraceae	*Lagerstroemia*	crape-myrtle	1	F	Japan	64
	Punica	pomegranate	1	F	China	43
Magnoliaceae	*Liriodendron*	tuliptree	1	2	Russia	30
	Magnolia	magnolia	1	2	Japan	64
Malvaceae	*Hibiscus*	hibiscus	1	F	Korea	1
	Malva	mallow	1	F	Japan	64
	Tilia	basswood, lime, linden	7	5	China, East Asia, Japan, Russia	12, 30, 31, 40, 50, 57, 63, 64, 82
Moraceae	*Broussonetia*	broussonetia	1	F	Japan	64
	Morus	mulberry	5	2	China, East Asia, Japan, Korea, Russia	17, 26, 29, 30, 50, 57, 59, 63, 64, 86
Myricaceae	*Morella*	bayberry	2	F	Russia, Japan	30, 61, 64
	Myrica	sweetgale	1	F	Russia	30
Oleaceae	*Fraxinus*	ash	8	2	China, East Asia, Japan, Korea, Kyrgyzstan, Russia	4, 26, 30, 50, 57, 63, 64
	Ligustrum	privet	3	F	Japan, Korea, Russia	26, 30, 61

Family	Genus	Common name	Number of species feeding reported	Average suitability code[a]	Countries where feeding was observed	References for feeding observations in native range[b]
	Olea	olive	1	F	Russia	30
	Syringa	lilac	2	2	China, Russia	30, 35
Paulowniaceae	*Paulownia*	princesstree	1	2	Japan, Korea	53, 64
Pentaphylacaceae	*Cleyera*	cleyera	1	F	Japan	61, 64
	Eurya	eurya	2	F	Japan, Korea, China, East Asia	29, 50, 64, 79
Phyllanthaceae	*Flueggea*	bushweed	1	2	Korea	26
Pinaceae	*Abies*	fir	3	3	East and Central Asia, Japan, Korea, Siberia	4, 26, 29, 50, 64
	Keteleeria	keteleeria	1	F	China	17
	Larix	larch	8	5	China, East and Central Asia, Japan, Korea, Mongolia, Russia, Siberia,	4, 7, 8, 10, 11, 12, 16, 17, 26, 27, 29, 30, 31, 34, 40, 41, 50, 57, 59, 62, 63, 64, 65, 67, 69, 71
	Picea	spruce	5	4	China, Japan, Russia, Siberia	4, 6, 11, 17, 30, 34, 37, 42, 57, 59, 63
	Pinus	pine	21	5	China, Central Asia, Japan, Korea, Mongolia, Russia, Siberia	4, 5, 10, 12, 26, 29, 30, 33, 34, 41, 42, 53, 55, 57, 59, 63, 64, 66, 77, 79
	Tsuga	hemlock	1	F	Russia	30
Pittosporaceae	*Pittosporum*	pittosporum, cheesewood	1	F	China	79
Plantaginaceae	*Plantago*	plantain	1	3	Japan	64
Platanaceae	*Platanus*	sycamore	2	2	Korea, Russia	26, 30
Poaceae	*Saccharum*	sugarcane	1	F	China	59
	Sasa	bamboo	2	F	Japan	64
Rhamnaceae	*Rhamnella*	rhamnella	1	F	China	79
	Sageretia	mock buckthorn, sageretia	1	F	China	13
Rosaceae	*Amelanchier*	serviceberry	1	4	Russia	30
	Chaenomeles	flowering quince	2	F	China, Japan	60, 64
	Crataegus	hawthorn	4	5	China, Central Asia, Kyrgyzstan, Russia	3, 4, 28, 30, 34, 36, 37, 41, 50, 59, 60, 76, 84
	Cydonia	quince	1	4	East Asia, Japan	50, 57, 64
	Malus	apple, crab apple	6	5	China, East and Central Asia, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia	3, 4, 14, 17, 22, 23, 28, 29, 30, 34, 36, 37, 41, 50, 51, 57, 59, 60, 63, 64, 66, 77
	Neilla	lace shrub	1	2	Korea	26
	Photinia	photinia, Christmas berry	1	4	Japan	61
	Prunus	almond, cherry, plum	25	4	China, East and Central Asia, Japan, Kazakhstan, Korea, Kyrgyzstan, Mongolia, Russia	1, 3, 4, 17, 26, 28, 29, 30, 34, 36, 37, 41, 50, 53, 56, 57, 59, 60, 63, 64, 71, 79, 85
	Pyracantha	firethorn	2	4	China, Russia	30, 34
	Pyrus	pear	5	4	China, Central Asia, Japan, Korea, Russia	4, 30, 32, 53, 57, 63, 64, 84
	Rhaphiolepis	loquat	2	4	East Asia, Japan	50, 57, 64
	Rosa	rose	9	4	China, East and Central Asia, Japan, Kazakhstan, Korea, Russia	4, 29, 30, 34, 35, 50, 57, 60, 64
	Rubus	blackberry, bramble, raspberry	4	F	East and Central Asia, Japan, Kazakhstan, Korea, Mongolia	4, 26, 50, 53, 57, 64, 66
	Sorbus	mountain ash	6	5	Japan, Kazakhstan, Korea, Russia	4, 26, 30, 40, 64
	Spiraea	spirea	4	3	China, Central Asia, Japan, Kazakhstan, Russia	4, 6, 30, 50, 64

Family	Genus	Common name	Number of species feeding reported	Average suitability code[a]	Countries where feeding was observed	References for feeding observations in native range[b]
Rutaceae	*Citrus*	lemon, lime, orange	3	4	China, Japan	17, 59, 64
	Phellodendron	corktree	1	2	Russia	30
	Zanthoxylum	pricklyash	2	4	Japan	64
Salicaceae	*Populus*	aspen, cottonwood, poplar	19	5	China, East and Central Asia, Japan, Kazakhstan, Korea, Kyrgyzstan, Mongolia, Russia, Siberia, Tajikistan	3, 4, 6, 7, 12, 18, 26, 28, 29, 30, 31, 32, 36, 42, 50, 53, 55, 57, 58, 59, 63, 64, 65, 68, 76, 84, 85
	Salix	willow	16	5	China, East and Central Asia, Japan, Kazakhstan, Korea, Kyrgyzstan, Mongolia, Russia, Siberia, Uzbekistan	2, 4, 6, 29, 30, 32, 50, 55, 57, 63, 64, 65, 66, 70, 78, 84, 85
	Xylosma	brush holly, xylosma, logwood	2	F	China, East Asia	44, 50, 63
Sapindaceae	*Acer*	maple	22	4	China, East and Central Asia, Japan, Korea, Kyrgyzstan, Russia, Tajikistan	1, 4, 15, 26, 28, 30, 33, 34, 36, 40, 41, 50, 53, 55, 57, 59, 63, 64, 76, 82, 84
	Aesculus	buckeye, horse-chestnut	1	2	Russia	30
Simaroubaceae	*Brucea*	brucea	1	5	Japan	64
Smilacaceae	*Smilax*	greenbrier	1	F	Japan	64
Styraceaceae	*Pterostyrax*	epaulette tree	1	2	Korea	26
	Styrax	snowbell, storax	2	F	Japan, Korea	53, 64
Symplocaceae	*Symplocos*	sweetleaf	1	F	Japan, Korea	26, 64
Tamaricaceae	*Myricaria*	myricaria	1	F	Tajikistan	4
Taxaceae	*Taxus*	yew	2	F	Russia	26, 30
	Torreya	nutmeg-yew	1	F	Japan, Korea	64
Theaceae	*Camellia*	camellia	3	F	China, Japan	34, 64
Ulmaceae	*Ulmus*	elm	11	4	China, East and Central Asia, Japan, Kazakhstan, Korea, Kyrgyzstan, Mongolia, Russia	4, 9, 13, 17, 18, 26, 29, 30, 34, 35, 36, 37, 41, 42, 57, 59, 60, 63, 64, 82, 85
	Zelkova	zelkova	2	5	East Asia, Japan	1, 26, 50, 57, 64
Viburnaceae	*Sambucus*	elder	1	1	Russia	30
	Viburnum	viburnum	3	1	China, Japan, Korea, Russia	30, 33, 53, 64, 80
Vitaceae	*Vitis*	grape	1	1	Russia	30

[a]Suitability codes: (F) feeding no details, (1) feeding no molting <50% survival at 15 d, (2) early instar molting <50% survival, (3) early instar molting ≥50% survival, (4) pupation <50% survival, (5) pupation ≥50% survival, and (6) outbreak/preferred species. Based on all available information from laboratory (information available in Table S1) and field studies, using Asian populations, but using the ratings in Liebhold et al. (1998) if no specific information was available.

[b]References: (1) Ahn et al. 2022, (2) Andreeva 2002, (3) Bakhvalov et al. 2010, (4) Baranchikov et al. 1998, (5) Bi et al. 2008, (6) Cui 2010, (7) Duan et al. 2012, (8) Dulamsuren et al. 2008, (9) Dulamsuren et al. 2009, (10) Dulamsuren et al. 2010, (11) Eichhorn and Kanamitsu 1965, (12) Gninenko and Orlinskii 2003, (13) Gu et al. 2000, (14) Gui 2006, (15) Han et al. 2013, (16) Hauck et al. 2008, (17) He et al. 2009, (18) Higashiura 1987, (19) Hu et al. 2009, (20) Huang et al. 2010, (21) Il'inykh 2005, (22) Inoue et al 2019, (23) Jashenko and Tanabekova 2019, (24) Ji et al. 2001, (25) Jikumaru and Sano 2007, (26) Jung et al. 2020, (27) Jung et al. 2024, (28) Khodyrev et al. 2010, (29) Kim et al. 1982, (30) Kozhanchikov 1950, (31) Kurenshchikov et al. 2020, (32) Lee and Pemberton 2010, (33) Lee et al. 2002, (34) Li 2001, (35) Li 2003, (36) Li 2012a, (37) Li 2012b, (38) Li and Yin 2007, (39) Liang et al. 2007, (40) Liebhold et al. 1998, (41) Lin 2000, (42) Liu et al. 2000, (43) Ma and Bai 2004, (44) McFadden et al. 1981, (45) Nakajima 2015, (46) Nakajima 2018, (47) Nishi et al. 2019, (48) Ohno et al. 2008, (49) Orlinski 1993, (50) Orozumbekov et al. 2009a, (51) Orozumbekov et al. 2009b, (52) Park et al. 1978, (53) Pemberton and Lee 1996, (54) Pemberton and Lee 1996, (55) Pemberton et al. 1993, (56) Peng 2010, (57) Pogue and Schaefer 2007, (58) Ponomarev et al. 2009, (59) Pu et al. 2008, (60) Qi 2003, (61) Sasaki et al. 2016, (62) Schaefer 1978, (63) Schaefer et al. 1984a, (64) Schaefer et al. 1988a, (65) Schaefer et al. 2004, (66) Schedl 1936, (67) Shimazu and Takatsuka 2010, (68) Soukhovolsky et al. 2016, (69) Sun 1989, (70) Sun and Liu 2002, (71) Tiralla et al. 2012, (72) Togashi and Nakano 1979, (73) Wada et al. 2000, (74) Wang et al. 2008, (75) Winter et al. 2009, (76) Xie et al. 2007, (77) Xu et al. 2007, (78) Yamazaki and Sugiura 2004, (79) Yan et al. 1994, (80) Yang et al. 2008, (81) Yoshida 1985, (82) Zhang et al. 2010, (83) Zheng and Wang 2010, (84) Zhu et al. 2013, (85) Zhu and Lin 2009.

(*Larix sibirica*) (Gninenko and Orlinskii 2003). Some populations in central Asia prefer the pistachio tree (*Pistacia* sp.) and common walnut (*Juglans regia*). The primary host plants of *L. dispar japonica* come from the following tree families: Fagaceae (eg *Quercus acutissima, Q. dentata, Q. crispula*, and *Q. glauca*), Betulaceae (eg *Betula platyphylla* and *Alnus japonica*), Pinaceae (*Larix kaempferi*), and Rosaceae (eg *Malus baccata*) (Schaefer et al. 1984a, Sasaki et al. 2016, Inoue et al. 2019). During outbreaks, both *L. dispar asiatica* and *L. dispar japonica* defoliate a wide range of trees and will even defoliate some herbaceous plants (Table S1). An outbreak of *L. dispar japonica* was reported to defoliate rice paddies in Honshu, Japan in 1941, when larvae moved out of nearby forests after defoliating them first (Kato and Okazaki 1941). Several laboratory studies

of host suitability have been conducted using various Asian populations of spongy moths to assess the risk to North American, Australian, and New Zealand hosts and to compare host utilization between *L. dispar dispar*, *L. dispar asiatica*, and *L. dispar japonica* populations (Baranchikov 1987 and 1989, Matsuki et al. 2001, Withers and Keena 2001, Kay et al. 2002, Baranchikov and Montgomery 2009, Onodera and Hara 2011, Matsuki et al. 2011, McCormick et al. 2019, Keena and Richards 2020) (Table S2). In laboratory tests, *L. dispar asiatica* was able to feed and successfully complete its life cycle on some *Eucalyptus* species (*Eucalyptus gunnii*, *E. ornigera*, and *E. risdoni*) as well as *Corymbia maculata* and *Callistemon brachiandrus* which are native to Australia and some *Nothofagus* species (*Nothofagus alpina*, *N. betuloides*, *N. cunninghamii, N. obliqua*, and *N. pumilio*) which are native to Australia or South America (Kay et al. 2002, Matsuki et al. 2011). Laboratory studies comparing populations from different world areas showed that some Asian populations developed faster and survived better on hosts considered marginal for *L. dispar dispar*. However, utilization of conifers, which was previously thought to be a flighted spongy moth trait, was not consistent within subspecies and seemed to be driven more by populations being preadapted to utilize different hosts based on hosts present in their area of origin (Keena and Richards 2020).

Damage and Impacts

Lymantria dispar, which is listed among the most dangerous forest pests in many countries in the Holarctic, can cause extensive defoliation of forest (Fig. 13) and urban trees and horticultural crops, resulting in severe economic and ecological impacts (Dominiak et al. 2013). Recently, in northern and eastern China, *L. dispar asiatica* larvae have defoliated an average of 800,000 ha of forest annually, and in the Russian Far East, there have been outbreaks that defoliate 1.2 million ha in a single year (Gninenko and Orlinskii 2003, Sun et al. 2014). In addition to these direct impacts, there are the indirect costs of quarantine services in harbor cities to prevent the spread of Asian subspecies that are estimated to be in the millions of dollars. Despite these efforts, significant direct losses have been imposed on transport companies in cases where the flighted spongy moth has passed through quarantine filters (Kovalev et al. 2023). These costs of prevention and exclusion are warranted since, in Australia alone, it is estimated that there are 973,000 ha of forest plantations that are at risk of defoliation by flighted spongy moth should it become established, with a value between $900 million to $1.2 billion annually (Dominiak et al. 2013, Blackburn and Hajek 2018).

Spongy moths cause damage when developing larvae consume the leaves or needles of their hosts. A single male and single female larva of *L. dispar japonica* can consume an estimated total leaf area of 700 to 1,100 cm^2 and 1,100 to 1,800 cm^2, respectively, as they complete development (Furuno 1964). During outbreaks, susceptible trees or shrubs may be completely defoliated. Deciduous trees can usually refoliate, but at a cost to the tree's stored reserves, making them more susceptible to attack by pathogens and other insects (Coleman et al. 2020), and tree mortality can result after repeated bouts of severe defoliation. Conifers, which cannot refoliate, are less tolerant of defoliation, especially since larvae may eat both new and old foliage, and trees can be killed by a single year of defoliation (Coleman et al. 2020). Losses to the forest canopy can have additional impacts on understory vegetation, forest composition, food and habitat availability for wildlife, forest floor microclimate, and water quality due to leaching of nutrients from leaves and frass (insect excrement) (Nakajima 2015, Coleman et al. 2020).

Spongy moths also disrupt everyday human activities when larvae or adults congregate on or in buildings and frass from larval feeding accumulates on vehicles or other surfaces, especially during outbreaks. Direct contact with larval hairs or

Fig. 13. Widespread *Lymantria dispar asiatica* defoliation in Mongolia on larch (bottom) and Siberia on pine (top). Photos on right show larvae feeding on larch (bottom) and spruce (top). Photo by Yuri Baranchikov.

adult wing scales or hairs can cause dermatitis and respiratory problems (Gooderham et al. 2021). The hairs have been found to contain histamine, so an allergic response can occur even if a person is not allergic to the proteins present in the hairs (Beaucher and Farnham 1982).

Dispersal

Natural spongy moth dispersal (*L. dispar asiatica* and *L. dispar japonica*) occurs both in the early instars by wind and again as adults through active flight. Young larvae disperse passively in the wind by spinning silken threads on which they suspend themselves from the surface on which the egg mass was laid to catch a wind current and disperse to a new location. In laboratory studies, up to 28% of young *L. dispar asiatica* larvae dispersed in a wind tunnel. They had a mean settling velocity of 0.96 m/s, and peak dispersal occurred in the afternoon (4 PM) (Zlotina et al. 1999). This would allow for dispersal distances of up to 1 km in nonmountainous and up to 3 km in mountainous terrain based on modeling developed for *L. dispar dispar* larval wind dispersal (Mason and McManus 1981).

Adults of both sexes of flighted spongy moth (*L. dispar asiatica* and *L. dispar japonica*) are capable of ascending sustained flight. All males are strong fliers, but female flight diminishes from east to west across Eurasia and is not completely fixed at either end of the cline, ie some females in east Asia do not exhibit strong directed flight (Keena et al. 2008). Female flight ability also declines with age, and virgin females fly less frequently than mated females (Keena et al. 2001). Eastern Siberian female *L. dispar asiatica* have been reported to fly over mountain ranges for distances up to 100 km (Rozhkov 1982). In caged studies, mated females from Japanese populations flew an average of 269 m and a maximum of 746 m in 1 night (Iwaizumi et al. 2010). Estimates of how far from a forest females fly before laying eggs on human structures near lights in Kanazawa, Japan suggest females fly ≤1 km but could travel further if no suitable landing site is within that distance (Liebhold et al. 2008). The average flight distance for 1-d-old Chinese *L. dispar asiatica* females in a single night on a flight mill ranges from 4 to 8 km, varying by population (Yang et al. 2017). The minimal flight distance between forested areas and ports where egg masses have been laid near lights was estimated to be 1.7 km in the Republic of Korea, 3.1 km in Japanese ports, and 0.5 km in the Russian Far East (Srivastava et al. 2021). In southern Siberia females have been documented to fly 3 km toward lights at a speed of 47 m per minute (Baranchikov et al. 2019). It is difficult to estimate the actual maximum distance that females will fly since there are many factors that can influence when and where they will land after departing from a given location, and there is considerable variation both between and within populations in capability.

Spongy moths are also dispersed by human-aided means. Females of *L. dispar asiatica* and *L. dispar japonica* are attracted to bright lights, which draws females to well-lit shipping and transportation terminals where they can lay their eggs on vessels, cargo, or vehicles, which are then transferred to new sites throughout the world (Wallner et al. 1995, Mastro et al. 2021). Once these egg masses begin hatching at the new locations, the young larvae will disperse by wind and, if suitable hosts are found, start feeding and potentially establishing. Large larvae also wander before pupating, and pupae can be moved with cargo or in vehicles. For example, during a spongy moth outbreak in Germany, flight-capable females pupated on military equipment and once the infested equipment reached the United States the moths had emerged, and females flew out when the ship hold was opened (Wallner 1996).

Sampling and Scouting Procedures

It is difficult to sample spongy moths (all subspecies) accurately for several reasons: the variety of host trees they utilize, larval activity patterns, and rapid fluctuations between low and high

Fig. 14. Inspecting a ship for *Lymantria dispar asiatica* eggs while in port in China. Photo by Juan Shi.

Fig. 15. Adult *Lymantria dispar asiatica* of both sexes that have been attracted in large numbers to lights at night. Photo by Yuri Baranchikov.

populations (Nealis and Erb 1993). Spongy moth larvae and pupae can be trapped relatively inexpensively and easily by placing a band of dark fabric such as burlap around tree trunks. Later the instar larvae will shelter under these fabric bands during the day and pupate beneath them. Many factors can affect the number of larvae using the bands, so this method is unreliable for population assessment. Sampling larvae from the tree foliage is another method used to determine the presence or absence of larvae (Lallemand Inc./BioForest 2020). The most accurate method to determine larval density is to deploy containers on the ground under the tree to collect frass, but this is too time-consuming for general use (Liebhold and Elkinton 1988).

Egg masses can be counted easily if laid on bark, especially after leaf fall when they are more visible, and they are available during a long period from early summer to midspring the following year (Lallemand Inc./BioForest 2020). In the Urals and in western Siberia, spongy moth population density is monitored by counting egg masses located near the base of tree trunks below the future snow level in the fall but there are no methods to assess population density where eggs are laid on rock outcroppings in southern and eastern Siberia (Ponomarev et al. 2012). In addition, egg mass size is a good predictor of the stage in the outbreak cycle the population is in. During the outbreak decline phase, egg masses are small, <20 mm, but when an outbreak is imminent and population size is increasing, the egg masses are larger, ≥30 mm in length (Nealis and Erb 1993). However, to monitor for flighted spongy moth egg masses, it must be determined where the females prefer to lay their eggs; for example, spongy moth eggs in warm-temperate evergreen broad-leaved forests in Japan and the Russian Far East are found primarily on the underside of large leaves (Yurchenko and Turova 2007, Sasaki et al. 2016). Egg mass counts to determine the presence of breeding populations and general density trends can be as simple as counting all the egg masses observed in a timed walk, but for more precise estimates and efficacy assessments of management options, fixed-area plots must be used (Fleischer et al. 1991). The most cost-efficient and accurate protocol was found to be sampling 5.4-m radius (0.01 ha) plots where all egg masses are counted, including those laid high up in trees and only visible using binoculars (Kolodny-Hirsch 1986).

Adult males (all subspecies) can be trapped using synthetic mimics of the pheromones that females release to attract mates. There are several different trap designs, varying from canisters made of plastic with insect kill strips to paper traps with a sticky interior surface (see Nealis and Erb 1993 for a list of types and sources). Pheromone traps are very sensitive and can be used to detect sparse populations or new infestations and to assess the effectiveness of treatments or eradication programs but are not very accurate for estimating population size or predicting population trends when spongy moth density is high because the traps get overwhelmed with males. Pheromone traps have been used yearly in the southern, central, and western United States to detect early introductions of flighted spongy moth since 1991 (Hajek and Tobin 2009). Moreover, traps were deployed in Russian port areas to monitor for population increases in forest areas within 20 km to prevent accidental transportation of *L. dispar asiatica* on vessels or cargo (Mastro et al. 2021). Similar programs are being conducted at ports in China, South Korea, and Japan to prevent accidental movement of flighted spongy moth worldwide. Light traps are also mounted in the port areas to detect female flight that may result in egg masses being laid near lights on vessels or cargo (Mastro et al. 2021).

Management Options

Quarantine and Eradication Efforts

Lymantria dispar asiatica was first discovered in pheromone traps in the northwestern United States in 1991 and identified by analyzing mitochondrial DNA (Bogdanowicz et al. 1993). This introduction to North America was due to the attraction of gravid females to lights in Russian Far East ports (Wallner

et al. 1995). Each new find of flighted spongy moth in North America has led to an eradication effort, sometimes in the same year of introduction, while the population is still small and confined to a restricted geographic area (Hajek and Tobin 2009). However, even when populations are small, eradication programs are very costly (Mastro et al. 2021).

To reduce the spread of flighted spongy moth to new areas, ships that depart from Russia, China, South Korea, and Japan during the period when females are flying are inspected by quarantine personnel and cleaned if there are egg masses or other life stages present before ship departure (Fig. 14). At the last Asian port of call, these inspected ships receive a phytosanitary certificate which allows them to enter ports in other countries. After arriving at their destination, local officials will inspect the ships for a second time (Mastro et al. 2021). High-risk vessels are those that visit specific regulated ports in high-risk areas in Japan, China, Korea, and Russia during port-specific date ranges between May 15 and October 15 (https://www.aphis.usda.gov/sites/default/files/joint-fsmc-bulletin-usda-cfia.pdf) and arrive at destination ports in North America during the high-risk periods, which are location specific based on foliage availability and hatch timing (see Gray 2017 for details). In addition to the United States and Canada, Australia, New Zealand, Chile, and Argentina also inspect ships and traps for flighted spongy moth to prevent introductions or locate introductions while populations are still small so they can be eradicated quickly (Hajek and Tobin 2009, Dominiak et al. 2013, Areces-Berazain 2022). In the Pacific states in the United States, eradication is pursued for any spongy moth population, even *L. dispar dispar*, which is not yet established there (Dreistadt and Dahlsten 1989).

The United States Department of Agriculture (USDA) Animal Plant Inspection Service (APHIS) has developed survey and response guidelines for dealing with flighted spongy moth (USDA 2014), including the use of pheromone traps to both detect and delimit new introductions. When eradication is the management strategy, the HD-1 strain of *Bacillus thuringiensis* var. *kurstaki* (BtK) has been widely used. A range between 59 and 94 BIU/ha or higher of BtK is used in multiple applications applied at 5- to 10-d intervals. For optimal results, BtK must be applied to second- and third-instar larvae. In some areas where an endangered lepidopteran species is present, the more

Table 3. Pathogens of spongy moth reported from Asian countries and notes on establishment in North America

Type	Class and order	Scientific name	Stage attacked[a]	Location	Reference(s)[b]	Established in North America
Bacterium	Bacilli: Bacillales	*Bacillus thuringiensis* Berliner, 1915 (8 subspecies)	L, P	Broad distribution	12	Yes
Bacterium	Bacilli: Bacillales	*Bacillus disparis* Hori and Bokura	L	Japan	3, 26	No
Bacterium	Bacilli: Bacillales	*Bacillus thuringiensis* Berliner, 1915 (8 subspecies)	L, P	Broad distribution	15	Yes
Bacterium	Gammaproteobacteria: Enterobacterales	*Serratia marcescens* Bizio, 1823 (=*Bacillus prodigiosus*)	L	Japan	3, 26	Yes
Bacterium	Mollicutes: Mycoplasmatales	*Spiroplasma* sp.	L?	Japan	9	Yes
Bacterium	Bacilli: Lactobacillales	*Streptococcus disparis* Glaser	L	Japan	4	Yes
Fungus	Dothideomycetes: Pleosporales	*Alternaria alternata* (Fr.) Keissl. (=*tenuis* Nees)	L?	Siberia	12	Yes
Fungus	Dothideomycetes: Pleosporales	*Alternaria* sp.	L?	Kyrgyzstan	16	Yes
Fungus	Dothideomycetes: Pleosporales	*Alternaria tenuissima* (Kunze) Wiltshire	L	Siberia	12	Yes
Fungus	Eurotiomycetes: Eurotiales	*Aspergillus flavus* Link	L	Japan	26	Yes
Fungus	Eurotiomycetes: Eurotiales	*Aspergillus* sp.	L	Kyrgyzstan	15	Yes
Fungus	Sordariomycetes: Hypocreales	*Beauveria bassiana* (Bals.-Criv.) Vuill., 1912	L	China, Korea, Kyrgyzstan, Russia, Siberia	2, 12, 15, 19, 25, 30	Yes
Fungus	Sordariomycetes: Hypocreales	*Beauveria brongniartii* (Sacc.) Petch (=*tenella* (Sacc.) Siemaszko)	L	Siberia	12	Yes
Fungus	Sordariomycetes: Hypocreales	*Beauveria* sp.	L, P	Korea, Russia	17, 18	Yes
Fungus	Dothideomycetes: Capnodiales	*Cladosporium brevicompactum* Pidopl. & Deniak, 1938	L	Siberia	12	Yes
Fungus	Dothideomycetes: Capnodiales	*Cladosporium gossypiicola* Pidopl. & Deniak, 1935	L	Siberia	12	No
Fungus	Sordariomycetes: Hypocreales	*Cordyceps (=Isaria) javanica* (Bally) Kepler, B. Shrestha & Spatafora, 2017 (=*Paecilomyces javanicus* (Bally) A.H.S. Br. & G. Sm., 1957)	L	Japan	27	Yes
Fungus	Sodariomycetes: Hypocreales	*Cordyceps (=Spicaria) farinosa* (Holmsk.) Kepler, B. Shrestha & Spatafora	L	Siberia	12	Yes

Type	Class and order	Scientific name	Stage attacked[a]	Location	Reference(s)[b]	Established in North America
Fungus	Sodariomycetes: Hypocreales	*Cordyceps fumosorosea* (Wize) Kepler, B. Shrestha & Spatafora (=*Paecilomyces fumosoroseus* (Wize) A.H.S. Br. & G. Sm., 1957)	L	China	28	Yes
Fungus	Saccharomycetes: Saccharomycetales	*Dipodascus albidus* Lagerh. (=*Geotrichum albidum* (Lagerh.))	L?	Siberia	12	Yes
Fungus	Entomophthoromycetes: Entomophthorales	*Entomophaga* (=*Entomophthora) aulicae* (E. Reichardt) Humber, 1984	L	China, Japan	1, 29	Yes
Fungus	Entomophthoromycetes: Entomophthorales	*Entomophaga maimaiga* Humber, Shimazu, & Soper, 1988	L	China, Georgia, Japan, Korea, Russian	6, 7, 8, 11, 13, 14, 18, 21, 22, 24, 27, 29, 31	Yes
Fungus	Sordariomycetes: Hypocreales	*Fusarium incarnatum* (Desm.) Sacc., 1886 (=*semitectum* Berk. & Ravenel, 1875)	L	Karakhstan, Russia, Siberia	12	Yes
Fungus	Sordariomycetes: Hypocreales	*Fusarium oxysporum* Schltdl. (=*oxysporum var. orthoceras* (Appel & Wollenw.) Bilaĭ)	L	Siberia	12	Yes
Fungus	Sordariomycetes: Hypocreales	*Fusarium poae* (Peck) Wollenw. (=*sporotrichiella var. poae* (Peck) Bilaĭ)	L	Siberia	12	Yes
Fungus	Sordariomycetes: Hypocreales	*Fusarium* sp.	L	Kyrgyzstan	15	Yes
Fungus	Sordariomycetes: Hypocreales	*Fusarium sporotrichiella* Bilaĭ	L	Karakhstan, Russia	12	No
Fungus	Sordariomycetes: Hypocreales	*Isaria* sp.	L	Kyrgyzstan	15	No
Fungus	Dothideomycetes: Pleosporales	*Macrosporium* sp.	L	Kyrgyzstan	15	No
Fungus	Sodariomycetes: Amphisphaeriales	*Microdochium (=Fusarium) nivale* (Fr.) Samuels & I.C. Hallett	L?	Siberia	12	Yes
Fungus	Eurotiomycetes: Eurotiales	*Paecilomyces canadensis* (Vuill.) A.H.S. Br. & G. Sm., 1957	L	Japan	1	Yes
Fungus	Eurotiomycetes: Eurotiales	*Penicillium albicans* Bainier	E	Siberia	12	Yes
Fungus	Eurotiomycetes: Eurotiales	*Penicillium brevicaulis*	E	Russia	2	Yes
Fungus	Eurotiomycetes: Eurotiales	*Penicillium* sp.	E	Kyrgyzstan	15	Yes
Fungus	Dothideomycetes: Pleosporales	*Phoma* sp.	L?	Siberia	12	Yes?
Fungus	Sordariomycetes: Microascales	*Scopulariopsis* sp.	L	Kyrgyzstan	15	Yes?
Microsporidium	Microsporea: Glugeida	*Endoreticulatus* (=*Pleistophora*) *schubergi* (Zwölfer) A. Cali & M. El Garhy, 1991	L	Russia	2, 8	No
Virus	Naldaviricetes: Lefavirales	*Alphabaculovirus lydisparis* (= *Borrelinavirus reprimens* Holmes, 1948) *(Lymantria dispar* nuclear polyhedrosis virus (LdNPV))	L, P	China, Japan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia	2, 5, 7, 9, 15, 17, 18, 19, 20, 22, 23, 24, 27, 31	Yes
Virus	Resentoviricetes: Reovirales	*Dendrolimus punctatus cypovirus* 1 (DpCPV-1)	L	Siberia	23	No
Virus	Resentoviricetes: Ortervirales	*Hubei lepidoptera* virus 3 (proposed as *Lymantria dispar* cypovirus 4)	L	Siberia	23	No
Virus	Resentoviricetes: Reovirales	*Lymantria dispar* cypovirus 1 (LdCPV-1)	L	Japan	26	No
Virus	Pisoniviricetes: Picornavirales	*Lymantria dispar* iflavirus 1 (LdIV1)	L	Siberia	23	Yes

[a]Stage attacked codes: (E) egg, (L) larva, (P) pupa. When a "?" follows a letter it is because there is uncertainty about that stage.
[b]References: (1) Aoki 1974, (2) Baranchikov et al. 1998, (3) Bokura 1922, (4) Glaser 1918, (5) Gulii 1971, (6) Hajek 1999, (7) Hajek 2007, (8) Hajek et al. 2016, (9) Ilinsky et al. 2017, (10) Il'yinykh 2005, (11) Jikumaru and Sano 2007, (12) Kal'vish 1969, (13) Kenis and Lopez Vaamonde 1998, (14) Kereselidze et al. 2011, (15) Khodyrev et al. 2010, (16) Kurenshchikov et al. 2020, (17) Lee and Pemberton 2009, (18) Lee and Pemberton 2010, (19) Lee et al. 2002, (20) Lewis et al. 1984, (21) Nielsen et al. 2005a, (22) Orozumbekov et al. 2009a, (23) Pavlushin et al. 2021, (24) Pemberton et al. 1993, (25) Polovinko et al. 2010, (26) Schaefer et al. 1988a, (27) Shimazu and Takatsuka 2010, (28) Song et al. 2001, (29) Soper et al. 1988, (30) Yan et al. 1993, (31) Yan et al. 1994.

host-specific spongy moth nucleopolyhedrovirus (*L. dispar* multiple nucleopolyhedrovirus [LdMNPV]) may be used (Hajek and Tobin 2009).

Other strategies used in ports of origin to decrease the risk of oviposition on vessels and cargo are reduced port and ship lighting and loading ships during the day when females are not attracted to the ship or port lights (Wallner et al. 1995). The addition of filters to port and ship lighting that block spectral emissions <480 nm can also be used to reduce lamp attractiveness to Lymantriid moths without a reduction of illumination (Wallner et al. 1995).

Physical and Mechanical Control

In small areas, removing egg masses from trees during the winter can help decrease the population the following year. Larvae can also be collected and destroyed by wrapping burlap and sticky bands around tree trunks (Baranchikov et al. 1998). Birds that feed on insects can also help to reduce the larval population, and installing bird-nesting boxes on trees near infested forests has been suggested to attract more birds that feed on larvae (Areces-Berazain 2022). To prevent *L. dispar japonica* larvae from invading rice fields in Japan, ditches have been recommended as a barrier for larger crawling larvae (Areces-Berazain 2022). Observations have shown that in high populations of *L. dispar japonica*, adults are attracted to light traps at night (Fig. 15). Ultraviolet lamps are the most attractive light source for spongy moths and can attract both sexes, which can then be killed before they can reproduce (Iwaizumi et al. 2010).

Biological Control

Pathogens

In the literature, 30 fungi, 1 microsporidium, 5 viruses, and 5 bacteria have been identified that kill *L. dispar asiatica* in natural settings (Table 3). LdMNPV and Btk are pathogens that can be sprayed to effectively control larvae of all spongy moth subspecies. Btk is a commercially available biopesticide and LdMNPV has been registered for use as Gypcheck in the United States but is only available for use on state or federal lands. Additionally, another host-specific entomopathogen native to Japan, northeastern China, and the Russian Far East, the fungus *Entomophaga maimaiga*, has been imported to other world areas for control of spongy moth (Nielsen et al. 2005b).

LdMNPV is a spongy moth-specific virus that infects larvae of all subspecies when they feed on contaminated foliage (Blackburn and Hajek 2018). Three different virus-based products have been developed: Virin-ENSh in the USSR (Harrison et al. 2014), Gypchek in the United States (Reardon et al. 2012), and Disparvirus which was developed from Gypchek in Canada in 1997 (Moreau and Lucarotti 2007). In nature, LdMNPV only becomes epizootic in outbreak populations (Doane and McManus 1981) but its spread is slow, so spraying these virus products can induce an epizootic more quickly to reduce populations levels (Hajek et al. 2015). LdMNPV can cause 75% to 90% mortality, depending on the specific strain of NPV, instars treated, and the general health of the spongy moth population (Reardon et al. 2009, Hwang et al. 2023). The Asian isolates of LdMNPV extracted from *L. dispar asiatica* and *L. dispar japonica* and the European/North American isolates are genetically distinct and may differ in virulence against different populations (Harrison et al. 2014). The residual effectiveness of LdMNPV lasts for 1 d but adding Blankophor BBH as an activity enhancer helps maintain residual activity for up to 35 d(Webb et al. 1998). Larvae that die from LdMNPV have very thin and fragile cuticles, remain on the trees in a typical upside-down V shape and contain a large number of virus particles inside them that can be released to infect additional larvae (Blackburn and Hajek 2018). Due to the limp, V-shaped dead larvae, LdNPV is commonly called "wilt disease" (Petrovskii and McKay 2010).

Bacillus thuringiensis var. *kurstaki* is applied aerially over extended areas for *L. dispar* control and eradication (Reardon et al. 1994). First- and second-instar larvae are the most vulnerable to Btk (Smitley and Davis 1993, Webb et al. 1998) and the optimal time for control lasts about 2 wk between 90% egg hatch and the third instar (Smitley and Davis 1993). The significant activity of Btk lasts for 7 d (Webb et al. 1998) and there is no significant difference in mortality of different *L. dispar asiatica* instars (Webb et al. 1998, Hwang et al. 2023).

Spongy moth larvae that are infected and killed by *E. maimaiga* are either firm with the body coated with the grayish velvet-like conidiophores in humid conditions or very soft and fragile with a similar appearance to the larvae killed with LdMNPV (Shimazu and Soper 1986). The fungus infects larvae older than the second instar with a preference for third- and fourth-instar larvae (Shimazu and Soper 1986). Different strains of *E. maimaiga* vary in the speed with which they kill larvae and the types of spores that they produce (Nielsen et al. 2005a). Mortality caused by both LdMNPV and *E. maimaiga* increases with precipitation during the period of infection (Hajek et al. 2015). *Entomophaga maimaiga* has become established in parts of North America where it has spread through the endemic *L. dispar dispar* populations and often causes high mortality, even interrupting the normal 10-yr outbreak cycle that was seen before *E. maimaiga* became established (Hajek 1999).

Predators

There are 155 different predator species documented as attacking flighted spongy moth: 2 mites, 6 nematodes, 4 spiders, 101 insects from 8 different orders, 33 birds, and 9 mammals (Table 4). Predation can have a substantial influence on flighted spongy moth populations (Petrovskii and McKay 2010); however, predation pressure changes significantly from generation to generation and is unrelated to population density (Higashiura 1989b). The predation rate on spongy moth larvae and pupae can be influenced by the density of other available prey items, such as other foliage-feeding insects or berries (Liebhold et al. 2000). In Hokkaido, Japan, the highest predation (mean 38.8%, range 4% to 71%) of *L. dispar asiatica* by birds usually occurs during February and March when snow is persistently present, and they attack the egg masses on the lower sections of the tree trunk (Higashiura 1989a). Many birds and small mammals feed on insects and predation by small mammals has been considered an important regulating factor for low-density populations of spongy moth in North America (Elkinton et al. 1996, Liebhold et al. 2000, Johnson et al. 2005). In Japan, forest type has been shown to influence predation by small mammals like the small Japanese field mouse, *Apodemus argenteus*, large Japanese field mouse, *Apodemus speciosus ainu*, and *Clethrionomys rufocanus bedfordiae*, with higher

Table 4. Predator genera of spongy moth observed in Asian countries with notes on establishment in North America

Type	Order: family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Established in North America
Invertebrate—Insect	Coleoptera: Cantharidae	*Athemus*	1	L, P	Japan	14	No
Invertebrate—Insect	Coleoptera: Cantharidae	*Cantharis*	1	L	Russia	3	No
Invertebrate—Insect	Coleoptera: Carabidae	*Amara*	2	E, L	Azerbaijan, China	35, 36, 37, 54	No
Invertebrate—Insect	Coleoptera: Carabidae	*Calosoma*	9	L, P	Azerbaijan, Central Asia, China, Georgia, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Siberia, Tajikistan, Uzbekistan	1, 2, 7, 10, 15, 16, 17, 23, 26, 27, 29, 30, 34, 35, 37, 38, 41, 42, 48, 49, 50, 51, 54	Yes
Invertebrate—Insect	Coleoptera: Carabidae	*Carabus*	6	L, P	China, Japan, Russia	29, 47, 48, 53	No
Invertebrate—Insect	Coleoptera: Carabidae	*Dolichus*	1	L	China, Uzbekistan	30, 54	No
Invertebrate—Insect	Coleoptera: Carabidae	*Harpalus*	2	L	China, Russia	2, 54	Yes
Invertebrate—Insect	Coleoptera: Carabidae	*Pterostichus*	1	L	Uzbekistan	30	No
Invertebrate—Insect	Coleoptera: Coccinellidae	*Harmonia*	1	E, L?	China	10	Yes
Invertebrate—Insect	Coleoptera: Dermestidae	*Anthrenus*	4	E	Japan, Korea, Russia	2, 4, 7, 23, 44, 45	Yes
Invertebrate—Insect	Coleoptera: Dermestidae	*Attagenus*	6	E	Japan, Kyrgyzstan, Russia, Uzbekistan	2, 4, 14, 15, 30, 45	Yes
Invertebrate—Insect	Coleoptera: Dermestidae	*Dermestes*	8	E, L	Azerbaijan, Chian, Japan, Russia, Russian Far East, Siberia, Uzbekistan	2, 3, 4, 15, 16, 19, 23, 25, 26, 30, 35, 37, 43, 45, 47, 49, 54	Yes
Invertebrate—Insect	Coleoptera: Dermestidae	*Globicornis*	1	E	Russia	2, 23	No
Invertebrate—Insect	Coleoptera: Dermestidae	*Megatoma*	2	E, P	Russia, Russian Far East, Siberia, Uzbekistan	2, 25, 30	No
Invertebrate—Insect	Coleoptera: Dermestidae	*Orphinus*	2	E	Japan	44, 45	No
Invertebrate—Insect	Coleoptera: Dermestidae	*Thaumaglossa*	1	E	Japan	44	No
Invertebrate—Insect	Coleoptera: Dermestidae	*Trogoderma*	4	E	China, Japan, Russia, Uzbekistan	23, 30, 44, 45, 53	Yes
Invertebrate—Insect	Coleoptera: Melyridae	*Cordylepherus*	1	L	Russia	2, 23, 26	No
Invertebrate—Insect	Coleoptera: Melyridae	*Malachius*	2	E	Kyrgyzstan, Uzbekistan	15, 30	No
Invertebrate—Insect	Coleoptera: Ptinidae	*Ptinus*	1	E	Japan, Russia	4	No
Invertebrate—Insect	Coleoptera: Staphylinidae	*Dendroxena*	2	L	Azerbaijan, China, Japan, Russia	2, 7, 23, 26, 30, 48, 49	No
Invertebrate—Insect	Coleoptera: Staphylinidae	*Uniden-tified* sp.	1	L	Japan	47	Yes
Invertebrate—Insect	Coleoptera: Tenebrionidae	*Tribolium*	1	L	Uzbekistan	30	Yes
Invertebrate—Insect	Coleoptera: Trogossitidae	*Tenebroides*	1	L	Russia	59	Yes
Invertebrate—Insect	Dermaptera: Anisolabididae	*Anisolabididae*	1	L	Japan	47	Yes
Invertebrate—Insect	Hemip-tera: Nabidae	*Himacerus*	1	L	China, Kazakhstan	1, 54	Yes
Invertebrate—Insect	Hemiptera: Pentatomidae	*Arma*	2	L	Azerbaijan, China, Japan, Russia	10, 26, 49, 54, 55	No

Type	Order: family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Established in North America
Invertebrate—Insect	Hemiptera: Pentatomidae	*Dinorhynchus*	2	L, P, A	China, Japan, Korea, Russia	7, 27, 42, 46, 48	Imported
Invertebrate—Insect	Hemiptera: Pentatomidae	*Picromerus*	2	L	China, Japan, Korea	42, 48, 54	Yes
Invertebrate—Insect	Hemiptera: Pentatomidae	*Pinthaeus*	1	L	China	48, 60	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Agriosphodrus*	1	L	China	55, 57	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Ectomocoris*	1	L	China	55	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Epidaus*	1	L	China	48	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Harpactor*	1	L	China	55	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Isyndus*	1	L	China	53, 55, 56	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Rhynocoris*	4	L	China, Japan, Russia	2, 48, 53, 54	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Sphedanolestes*	1	L	China	54, 55	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Sycanus*	1	L	China	55	No
Invertebrate—Insect	Hemiptera: Reduviidae	*Velinus*	1	L	China	55	No
Invertebrate—Insect	Hymenoptera: Eumenidae	*Polistes*	1	L	Japan	13	No
Invertebrate—Insect	Hymenoptera: Formicidae	*Camponotus*	1	L	China	10, 53	No
Invertebrate—Insect	Hymenoptera: Formicidae	*Formica*	5	L, A	Japan, Russia	2, 26, 47	Yes
Invertebrate—Insect	Hymenoptera: Formicidae	*Lasius*	1	L	China	53	Yes
Invertebrate—Insect	Mantodea: Mantidae	*Hierodula*	1	L	China	54	Yes
Invertebrate—Insect	Mantodea: Mantidae	*Mantis*	1	L	Russia	2, 30	No
Invertebrate—Insect	Mantodea: Mantidae	*Tenodera*	1	L	China	54	Yes
Invertebrate—Insect	Neuroptera: Chrysopidae	*Chrysoperla*	1	L	Azerbaijan	35, 37	No
Invertebrate—Insect	Orthoptera: Tettigoniidae	*Atlanticus*	1	L, P	China	53, 54	No
Invertebrate—Insect	Orthoptera: Tettigoniidae	*Gampsocleis*	1	L	China	54	No
Invertebrate—Insect	Orthoptera: Tettigoniidae	*Metrioptera*	1	L	China	54	No
Invertebrate—Insect	Orthoptera: Tettigoniidae	*Tettigonia*	1	L	Siberia	5	No
Invertebrate—Insect	Raphidioptera	*Raphidioptera* sp.	1	E, L	Russia	38	No
Invertebrate—Insect	Raphidioptera: Raphidiidae	*Mongoloraphidia*	1	E, L	Kyrgyzstan	15	No
Invertebrate—Insect	Raphidioptera: Raphidiidae	*Raphidia*	1	E	Russia	59	No
Invertebrate—Mite	Trombidiformes: Erythraeidae	*Leptus*	1	L	Korea	42	No
Invertebrate—Mite	Trombidiformes: Trombidiidae	*Trombidium*	1	L	Russia	2	Yes
Invertebrate—Nematode	Mermithida: Mermithidae	*Amphimermis*	2	L	Azerbaijan, Russia	2, 49	No
Invertebrate—Nematode	Mermithida: Mermithidae	*Hexamermis*	2	L, P	China, India, Japan, Korea, Kyrgyzstan, Russia	2, 7, 15, 18, 29, 31, 32, 48, 55	Imported
Invertebrate—Nematode	Mermithida: Mermithidae	*Isomermis*	1	L	Georgia	2	No

Type	Order: family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Established in North America
Invertebrate—Nematode	Mermithida: Mermithidae	Unidentified sp.	1	P	Korea	48	No
Invertebrate—Spider	Araneae: Araneidae	*Araneus*	1	L, A	China	48	No
Invertebrate—Spider	Araneae: Oxyopidae	*Oxyopes*	2	L	Japan	12	No
Invertebrate—Spider	Araneae: Theridiidae	*Takayus*	1	L	Japan	12	No
Vertebrate—Bird	Bucerotiformes: Upipidae	*Upupa*	1	L, P	China	33	Yes
Vertebrate—Bird	Cuculiformes: Cuculidae	*Cuculus*	4	L	China, Japan, Russia	2, 9, 22, 33, 47	Yes
Vertebrate—Bird	Passeriformes: Corvidae	*Corvus*	1	L, P, A	Russia	40	No
Vertebrate—Bird	Passeriformes: Corvidae	*Cyanopica*	1	L, P, A	China	33	No
Vertebrate—Bird	Passeriformes: Corvidae	*Garrulus*	2	E	Japan	19, 20	No
Vertebrate—Bird	Passeriformes: Emberizidae	*Emberiza*	1	L	Japan	47	No
Vertebrate—Bird	Passeriformes: Laniidae	*Lanius*	1	L	China	47	Yes
Vertebrate—Bird	Passeriformes: Motacillidae	*Motacilla*	1	L	Japan	47	Yes
Vertebrate—Bird	Passeriformes: Paridae	*Parus*	3	E, L, P, A	China, Japan	8, 19, 20, 27, 33, 47	Yes
Vertebrate—Bird	Passeriformes: Paridae	*Poecile*	3	L, A	Japan	20, 47	No
Vertebrate—Bird	Passeriformes: Passeridae	*Passer*	3	E	Mongolia, Japan	6, 11, 12, 13, 47	No
Vertebrate—Bird	Passeriformes: Sittidae	*Sitta*	2	E	Japan	20, 21	No
Vertebrate—Bird	Passeriformes: Sturnidae	*Agropsar*	2	L, A	Japan	11, 47	No
Vertebrate—Bird	Passeriformes: Sturnidae	*Spodiopsar*	1	L	China	8, 58	Yes
Vertebrate—Bird	Passeriformes: Turdidae	*Turdus*	1	A	China	47	No
Vertebrate—Bird	Piciformes: Picidae	*Dendrocopos*	2	E, L	Chian, Japan	20, 47	Yes
Vertebrate—Bird	Piciformes: Picidae	*Yungipicus*	2	E	Japan	20, 21	No
Vertebrate—Bird	Strigiformes: Strigidae	*Ninox*	1	L, P, A	Japan	39	No
Vertebrate—Bird	Strigiformes: Strigidae	*Otus*	1	L, P, A	China	8	No
Vertebrate—Mammal	Chiroptera: Rhinolophidae	*Rhinolophus*	1	A?	China	24	Yes
Vertebrate—Mammal	Eulipotyphla: Soricidae	*Sorex*	1	L, P?	Japan	34	No
Vertebrate—Mammal	Rodentia: Cricetidae	*Myodes*	1	P	Japan	34	No
Vertebrate—Mammal	Rodentia: Gliridae	*Dryomys*	1	L, P	Siberia	2	No
Vertebrate—Mammal	Rodentia: Muridae	*Apodemus*	5	L, P	East Asia, Japan, Siberia	2, 34, 41	No

[a]Stage attacked codes: (E) egg, (L) larva, (P) pupa, (PP) prepupa, (A) adult. When a "?" follows a letter it is because there is uncertainty about that stage.
[b]References: (1) Agibaev and Alimkulova 2017, (2) Baranchikov et al. 1998, (3) Barayshchuk 2008, (4) Brown and Cameron 1982, (5) Charlton et al. 1999, (6) Cheke 2003, (7) Coulson et al. 1986, (8) Fan 1965, (9) Feng and Liu 2003, (10) Feng et al. 1999, (11) Furuta 1976, (12) Furuta 1977a, (13) Furuta 1977b, (14) Furuta 1982, (15) Gabrid 2003, (16) Gasimov 2008, (17) Hajek 2007, (18) Hajek et al. 2016, (19) Hérard et al. 1979, (20) Higashiura 1980, (21) Higashiura 1989a, (22) Ishizawa and Chiba 1966, (23) Ivantsova and Vostrikova 2015, (24) Jin et al. 2005, (25) Kenis and Lopez Vaamonde 1998, (26) Khitsova and Isaeva 1986, (27) Kim et al. 2017, (28) Kiziroğlu et al. 2002, (29) Kobzar et al. 2013, (30) Kolomiets 1987, (31) Lee and Pemberton 2010, (32) Lee et al. 2002, (33) Li 1981, (34) Liebhold et al. 1998, (35) Mamedov and Muradova 2014, (36) Mammadov 2013, (37) Mammadov and Alieva 2010, (38) Martemyanov et al. 2013, (39) Mizota et al. 2020, (40) Nazarov et al. 2020, (41) Orozumbekov et al. 2009a, (42) Pemberton et al. 1993, (43) Safarova 2018, (44) Sawahata et al. 2021, (45) Schaefer and Beal 1996, (46) Schaefer et al. 1979, (47) Schaefer et al. 1988a, (48) Schaefer et al. 1984b, (49) Shapiro 1956, (50) Stolbov et al. 2018, (51) Sugiura and Yamazaki 2014, (52) Ueda et al. 1981, (53) Yan et al. 1992, (54) Yan et al. 1993, (55) Yan et al. 1994, (56) Yao et al. 1993, (57) Yao et al. 1995, (58) Yao et al. 2006, (59) Zelenev 1976, (60) Zhao et al. 2013.

predation seen in oak forests than in birch or larch plantations (Liebhold et al. 1998).

The layer of dense hairs on lepidopteran larvae appears to be involved in defense against invertebrate predators (Dyer 1995). For example, although the adults of the predatory beetle, *Calosoma maximowiczi* A. Morawitz (Coleoptera: Carabidae), can consume most of the *L. dispar japonica* larvae available in laboratory tests, they require more effort for successful attacks compared to the smooth larvae of other Lepidoptera species (Sugiura and Yamazaki 2014). Larvae can also use the long hairs on the lateral surface to detect *Calosoma* attacks and will drop from plants as an avoidance behavior (Sugiura and Yamazaki 2014).

Parasitoids

A total of 245 parasitoid species that attack spongy moths have been documented: 96 Diptera (3 families, Table S3 for more details) and 149 Hymenoptera (11 families, Table S4 for more details) (Table 5). Three families of parasitoids including Tachinidae (Diptera), Braconidae (Hymenoptera), and Ichneumonidae (Hymenoptera) have been reported to cause up to 99% of parasitoid mortality in *L. dispar asiatica* larvae and pupae in Korea (Pemberton et al. 1993, Lee et al. 2002). Tachinids were more abundant than braconids or ichneumonids over a range of flighted spongy moth densities and were also collected over a longer period of time in the field (Pemberton et al. 1993). The total parasitism rate for *L. dispar asiatica* reported from Korea is 23.8%, which is comparable to that reported in parts of Europe (Pemberton et al. 1993).

The 2 species *Parasetigena silvestris* (Robineau-Desvoidy, 1863) and *Blepharipa* sp. are the most effective tachinid parasitoids in the Asian range of spongy moths (Pemberton et al. 1993). *Parasetigena silvestris* parasitized 27.6% of fifth- and sixth-instar larvae and 36.3% of prepupae while *Blepharipa schineri* killed 37.5% of pupae in Korea. Parasitoid flies from the families Tachinidae and Sarcophagidae actively attack Far Eastern populations of *L. dispar asiatica* and prefer females to males 2 to 1 (Kurenshchikov et al. 2020).

Among the Hymenopteran parasitoids, *Cotesia melanoscelus* (Ratzeburg) (Hym.: Braconidae) caused 24.4% of first- and second-instar larval mortality of *L. dispar asiatica* in South Korea, but this species does not have the same impact in northeastern China or Japan (Lee and Pemberton 2010). *Glyptapanteles liparidis* was the most important parasitoid wasp of *L. dispar asiatica* in Japan with approximately 50% larval parasitism (Schaefer 1981). *Anastatus japonicus* is the dominant egg parasitoid of *L. dispar asiatica* in northern South Korea, the northern part of Japan (Schaefer et al. 1988a), and the Russian Far East (Kolomiets 1987). In the Ichneumonidae, *Phobocampe* spp. were among the most active parasitoids of *L. dispar asiatica*, even more so than tachinids in the Russian Far East (Pemberton et al. 1993, Lee and Pemberton 2009, 2010).

Chemical Controls

In the 1970s, the insect growth regulator diflubenzuron and the broad-spectrum neurotoxin carbaryl were the preferred insecticides for spongy moth eradication in the Pacific Northwest of North America; however, due to public concerns and new label restrictions, carbaryl is no longer available and diflubenzuron is less frequently used (Dreistadt and Dahlsten 1989). The organophosphate Phthalophos was used in central Asia in the 1970s against flighted spongy moth (Kim et al. 1976). Mimic 2LV (tebufenozide) is considered a low risk "biorational" insecticide that has been applied to suppress spongy moth populations by affecting their growth cycle. Tebufenozide triggers a premature molt of spongy moth larva that results in its death (https://www.valentbiosciences.com/forestheath/products/mimic/) and has been used to suppress spongy moth populations in Germany. Studies are underway to find other insect growth regulators and semisynthetic bioinsecticides to treat spongy moth populations. One study of emamectin benzoate, which is a conventional synthetic insecticide widely used in forest settings, has shown some promise (Xu et al. 2021), and there is also work on the insect growth regulator methoxyfenozide for potential registration for use against spongy moth (Wu et al. 2015).

Mating disruption has also been deployed as a suppression tactic for spongy moth of all subspecies by aerially applying pheromone in various formulations when males are flying. This method is most effective when the population density is low and males can be prevented from finding a mate, such as in small, isolated populations in front of the invading front of spongy moth. This suppression strategy is currently employed in the "Slow the Spread" program used in the United States (Lance et al. 2016).

In recent years, botanical insecticides have been developed as an eco-friendly method to control different insect pests in forests, orchards, and many other crops (Sundararaj 2014, Bande-Borujeni et al. 2015, Zandi-Sohani and Ramezani 2015, Janaki et al. 2018, Isman 2020). They have shown low toxicity to mammalian and other nontarget organisms and may provide a practical alternative to synthetic chemical insecticides (Sundararaj 2014). While many products are available to manage *L. dispar* post-emergence, few exist to prevent egg hatch when applied to egg masses. Chase et al. (2023) conducted 3 separate experiments determining the efficacy of preemergent insecticides against *L. dispar* egg hatch. Golden Pest Spray Oil (GPSO; AI: 93% soybean oil) can prevent *L. dispar* larvae from emerging in both field and lab assays. Various mixtures of plant-based insecticides were evaluated against the egg masses of *L. dispar asiatica* in Korea. The potential mixture of botanical insecticide applied to spongy moth egg masses is composed of 5% cinnamon extract, 10% derris extract, 20% neem extract, 10% citronella oil, and 30% citrus oil in addition to 25% penetrating surfactant. This mixture caused 97.6% mortality in *L. dispar asiatica* eggs containing fully grown larvae (Lee et al. 2023). The 1% essential oil concentration from seeds of anise (*Pimpinella anisum*), dill (*Anethum graveolens*), and fennel (*Foeniculum vulgare*) (all from the Apiaceae family) was more toxic to European *L. dispar dispar* larvae than the commercial insecticide NeemAzal T/S (neem) (Kostić et al. 2021). Although spraying botanical insecticides is not feasible in large-scale natural forests, it is considered a necessary component along with other options for forest pest management (Sundararaj 2014).

Due to the significant impacts of these pest subspecies and their propensity to spread with world trade there is a continuing need for research to identify new potential pest management options and refine existing options to improve timing and efficacy. For example, mating disruption has long been used in the "Slow the Spread" program for spongy moth in North America but is only recently being evaluated for use in Asia (Minegishi et al. 2024). The potential to use RNA interference

Table 5: List of spongy moth parasitoid genera found in Asia with notes on occurrence in other world areas

							Other world areas found or established		
Order	Family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Europe	Middle East	North America
Diptera	Polleniidae	*Pollenia*	1	L	Kyrgyzstan	16	Yes	Yes	Yes
Diptera	Sarcophagidae	*Agria*	3	P	Azerbaijan, Kyrgyzstan, Russia, Russian Far East, Siberia, Uzbekistan	6, 7, 16, 17, 22, 24, 26, 28, 39, 43, 55	Yes	No	Yes
Diptera	Sarcophagidae	*Sarcophaga*	14	L, P	Azerbaijan, China, Japan, Kyrgyzstan, Russia, Russian Far East, Siberia	6, 7, 11, 16, 22, 24, 26, 27, 28, 37, 43, 55, 65, 67, 69,	Yes	Yes	Yes
Diptera	Sarcophagidae	Unidentified	1	L, P	Korea, Russia, Russian Far East	7, 30, 31, 32, 45	No	No	No
Diptera	Tachinidae	*Actia*	1	L	Japan	49, 57, 60	No	No	No
Diptera	Tachinidae	*Austrophorocera*	2	L	China, India	11, 50, 60, 69	No	No	Imported
Diptera	Tachinidae	*Bactromyia*	1	L	Russia	24, 26	Yes	No	Yes
Diptera	Tachinidae	*Bampura*	1	L?	Azerbaijan	37	Yes	No	No
Diptera	Tachinidae	*Baumhaueria*	1	L?	China	67	Yes	Yes	No
Diptera	Tachinidae	*Bessa*	1	L?	Japan	40, 60, 67	Yes	No	No
Diptera	Tachinidae	*Blepharipa*	6	L, P	Azerbaijan, China, Japan, Kazakhstan, Korea, Russia, Russian Far East, Siberia	3, 6, 7, 11, 15, 19, 23, 24, 25, 26, 28, 31, 32, 33, 45, 49, 50, 53, 55, 60, 67	Yes	Yes	Yes
Diptera	Tachinidae	*Blondelia*	1	L	China, Russia, Russian Far East	6, 23, 28, 59, 60, 67	Yes	Yes	Imported
Diptera	Tachinidae	*Carcelia*	10	L	Azerbaijan, China, Japan, Kazakhstan, Russia, Russian Far East	6, 12, 24, 26, 28, 50, 55, 60, 66	Yes	Yes	No
Diptera	Tachinidae	*Ceromasia*	1	L	China, Uzbekistan	6, 67	Yes	Yes	No
Diptera	Tachinidae	*Compsilura*	1	L, PP, P	Central Asia, China, Japan, Kazakhstan, Korea, Russia, Siberia, Russian Far East	3, 6, 7, 11, 13, 19, 22, 23, 24, 25, 26, 28, 29,31, 42, 44, 45, 49, 55, 56, 59, 60, 65	Yes	Yes	Yes
Diptera	Tachinidae	*Drino*	4	L, P	Central Asia, Azerbaijan, China, Georgia, India, Russia, Russian Far East, Siberia	6, 11, 13, 23, 24, 26, 28, 42, 55, 60, 66	Yes	Yes	Yes
Diptera	Tachinidae	*Eumea*	1	L	China	67	Yes	No	No
Diptera	Tachinidae	*Eurithia*	2	L	Russian Far East	28	Yes	No	No
Diptera	Tachinidae	*Exorista*	10	L, P	Central Asia, Azerbaijan, China, Georgia, India, Japan, Kyrgyzstan, Korea, Russia, Russian Far East, Siberia, Uzbekistan	6, 11, 13, 15, 16, 16, 17, 19, 22, 23, 24, 25, 26, 28, 29, 31, 34, 37, 40, 42, 44, 45, 48, 49, 50, 53, 54, 55, 58, 60, 64, 65, 66, 67, 69	Yes	Yes	Yes
Diptera	Tachinidae	*Linnaemya*	1	L	Russian Far East	6, 28	Yes	No	No
Diptera	Tachinidae	*Maculosalia*	1	L, P	China	69	No	No	No
Diptera	Tachinidae	*Masicera*	1	L	Russia, Russian Far East, Siberia	6, 28, 60	Yes	Yes	No
Diptera	Tachinidae	*Meigenia*	1	L	China	35, 67	Yes	No	No
Diptera	Tachinidae	*Nemorilla*	1	L	Azerbaijan	36, 37	Yes	No	No
Diptera	Tachinidae	*Pales*	1	L	Japan, Russia, Russian Far East	6, 28, 49, 60	Yes	Yes	No

							Other world areas found or established		
Order	Family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Europe	Middle East	North America
Diptera	Tachinidae	*Parasetigena*	2	L, P	Central Asia, Azerbaijan, China, Japan, Kazakhstan, Korea, Russia, Russian Far East, Siberia	3, 6, 7, 11, 13, 15, 19, 23, 24, 25, 26, 28, 31, 32, 33, 37, 39, 42, 43, 44, 45, 49, 50, 55, 60, 65	Yes	No	Yes
Diptera	Tachinidae	*Peleteria*	1	L?	Russian Far East	6	Yes	Yes	Yes
Diptera	Tachinidae	*Phorocera*	2	L	China, Japan, Kyrgyzstan, Russia, Russian Far East	6, 11, 28, 50, 67	Yes	No	Imported
Diptera	Tachinidae	*Phryxe*	2	L	Russia, Russian Far East	6, 28, 60	Yes	Yes	Yes
Diptera	Tachinidae	*Phytomyptera*	1	L	Siberia	28	Yes	No	No
Diptera	Tachinidae	*Senometopia*	3	L	Azerbaijan, China, Georgia, Japan, Russia, Russian Far East, Siberia	6, 23, 24, 26, 28, 49, 50, 60	Yes	Yes	Imported
Diptera	Tachinidae	*Sturmia*	2	L	Kyrgyzstan, Russia	6	Yes	Yes	No
Diptera	Tachinidae	*Tachina*	8	L	Azerbaijan, Russia, Russian Far East, Siberia	6, 28, 36, 55, 60	Yes	Yes	Yes
Diptera	Tachinidae	Unidentified *Siphonini* spp.	1	L	Korea	45	No	No	No
Diptera	Tachinidae	Unidentified *Tachinidae* sp.	1	L, P	Japan, Korea, Russia	11, 30, 31, 60	No	Yes	No
Diptera	Tachinidae	*Winthemia*	4	L	Japan, Kazakhstan, Russia, Russian Far East	24, 26, 28, 55, 60	Yes	No	Yes
Diptera	Tachinidae	*Zenillia*	1	P	Azerbaijan, Russia	6, 28, 60	Yes	Yes	No
Hymenoptera	Braconidae	*Agathis*	1	L	Azerbaijan	17	Yes	Yes	Yes
Hymenoptera	Braconidae	*Aleiodes*	4	L	China, India, Japan, Korea, Kyrgyzstan, Russia, Russian Far East	6, 11, 15, 16, 19, 32, 38, 40, 45, 50, 59, 65	Yes	Yes	Yes
Hymenoptera	Braconidae	*Apanteles*	6	L	Azerbaijan, Central Asia, China, Georgia, India, Kazakhstan, Russia	2, 6, 11, 13, 22, 24, 28, 36, 37, 38, 42, 48, 50, 55, 64, 65, 66	Yes	Yes	Yes
Hymenoptera	Braconidae	*Bassus*	1	L	Azerbaijan	17	Yes	Yes	Yes
Hymenoptera	Braconidae	*Cotesia*	14	L	Azerbaijan, Central Asia, China, Georgia, India, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia, Tajikistan	2, 6, 11, 13, 16, 19, 22, 23, 24, 25, 26, 28, 31, 32, 34, 38, 40, 42, 44, 45, 48, 50, 59, 64, 65, 66	Yes	Yes	Yes
Hymenoptera	Braconidae	*Eubazus*	1	L	Azerbaijan	55	Yes	No	No
Hymenoptera	Braconidae	*Glyptapanteles*	1	L	Russia	6, 22	Yes	No	No
Hymenoptera	Braconidae	*Meteorus*	5	L	Azerbaijan, China, Georgia, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia	6, 11, 13, 16, 17, 22, 23, 25, 28, 32, 33, 36, 37, 38, 39, 40, 45, 47, 48, 50, 53, 55, 64, 65, 66	Yes	Yes	Yes
Hymenoptera	Braconidae	*Microgaster*	2	L	Russia	6, 22	Yes	Yes	Yes
Hymenoptera	Braconidae	*Microplitis*	1	L	Russia	22	Yes	Yes	No
Hymenoptera	Braconidae	*Orgilus*	1	L	Azerbaijan	17, 36, 37	Yes	Yes	Yes
Hymenoptera	Braconidae	*Phanerotoma*	2	L	Azerbaijan, Kazakhstan, Korea, Russia	1, 6	Yes	Yes	Imported

							Other world areas found or established		
Order	Family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Europe	Middle East	North America
Hymenoptera	Braconidae	*Protapanteles*	7	L	Azerbaijan, Central Asia, China, Georgia, India, Japan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia	2, 6, 7, 11, 13, 14, 15, 16, 22, 23, 24, 25, 26, 28, 31, 33, 34, 37, 38, 40, 42, 44, 45, 47, 50, 55, 65, 66	Yes	Yes	Yes
Hymenoptera	Braconidae	*Rhysipolis*	1	L	Georgia	28	Yes	Yes	No
Hymenoptera	Braconidae	*Sathon*	1	L	Russia	24	Yes	No	No
Hymenoptera	Chalcididae	*Brachymeria*	7	L, P	Azerbaijan, Central Asia, China, India, Japan, Korea, Kyrgyzstan, Russia, Uzbekistan	6, 11, 13, 16, 17, 19, 23, 24, 25, 28, 31, 34, 36, 37, 42, 45, 48, 53, 55, 59, 64, 65, 66	Yes	Yes	Yes
Hymenoptera	Encyrtidae	*Ooencyrtus*	2	E	Central Asia, China, Japan, Korea, Russia, Russian Far East, Uzbekistan	6, 13, 19, 23, 25, 26, 28, 34, 42, 45, 46, 47, 52, 53, 65, 66, 68	Yes	Yes	Yes
Hymenoptera	Encyrtidae	*Tyndarichus*	1	E	China	64, 65	Yes	No	Imported
Hymenoptera	Eulophidae	*Baryscapus*	1	L	Azerbaijan, Georgia	17, 28, 36, 37	Yes	Yes	Yes
Hymenoptera	Eulophidae	*Elachertus*	2	L	China, Japan, Korea, Russian, Russian Far East	15, 32, 44, 45, 50, 71	Yes	Yes	No
Hymenoptera	Eulophidae	*Eulophus*	1	L	Russia	22	Yes	No	No
Hymenoptera	Eulophidae	*Euplectrus*	1	L	China, Japan, Korea	70	Yes	Yes	Yes
Hymenoptera	Eulophidae	*Miotropis*	1	L	Azerbaijan	55	No	No	No
Hymenoptera	Eulophidae	*Platyplectrus*	1	L	China	66	No	No	No
Hymenoptera	Eupelmidae	*Anastatus*	4	E	Azerbaijan, Central Asia, China, Georgia, India, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia, Tajikistan, Uzbekistan	3, 6, 7, 11, 13, 16, 19, 20, 21, 22, 23, 25, 26, 28, 32, 33, 34, 41, 42, 45, 47, 50, 51, 52, 53, 55, 59, 66, 68	Yes	Yes	Yes
Hymenoptera	Eupelmidae	*Mesocomys*	1	E	Japan, Korea	25, 51	No	No	No
Hymenoptera	Eurytomidae	*Eurytoma*	2	L	China	69	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Alcima*	1	L	Siberia	28	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Amblyteles*	1	L	Japan	18	Yes	No	No
Hymenoptera	Ichneumonidae	*Apechthis*	3	L, P	China, Georgia, Japan, Korea, Russia, Russian Far East	6, 10, 18, 22, 25, 28, 47, 50	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Caenocryptus*	1	L	Central Asia, Kyrgyzstan	16, 42	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Callajoppa*	1	L	Russia	6	Yes	No	No
Hymenoptera	Ichneumonidae	*Campoletis*	1	L	China	50	No	No	No
Hymenoptera	Ichneumonidae	*Campoplex*	1	L	Japan	63	No	No	No
Hymenoptera	Ichneumonidae	*Casinaria*	5	L	Armenia, Azerbaijan, China, India, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia	6, 11, 13, 16, 24, 25, 26, 28, 32, 34, 44, 45, 50, 55, 63, 65, 66	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Coelichneumon*	1	L	Korea	25	Yes	No	No
Hymenoptera	Ichneumonidae	*Diadegma*	1	L	Russia	6	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Diphyus*	1	L	Russia	18	Yes	No	No
Hymenoptera	Ichneumonidae	*Dusona*	1	P?	Korea	9, 25	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Gelis*	3	L	Kazakhstan, Kyrgyzstan, Russia	6, 16, 28	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Gregopimpla*	2	L	China, Japan, Korea	11, 25, 45, 47	No	No	No
Hymenoptera	Ichneumonidae	*Hemiteles*	1	L	Azerbaijan, Japan	51, 55	Yes	No	Yes

							Other world areas found or established		
Order	Family	Genus	Number of species	Stage attacked[a]	Asian countries reported in	Reference(s)[b]	Europe	Middle East	North America
Hymenoptera	Ichneumonidae	*Heterischnus*	1	P	Russia	22	Yes	No	No
Hymenoptera	Ichneumonidae	*Hyposoter*	5	L	China, India, Japan, Korea, Russian Far East	6, 11, 25, 40, 50, 63, 66	Yes	Yes	Imported
Hymenoptera	Ichneumonidae	*Ichneumon*	1	L	Azerbaijan, Russia	18, 48	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Ischnus*	1	L	Azerbaijan, Russia	6, 22	Yes	No	Yes
Hymenoptera	Ichneumonidae	*Itoplectis*	5	L, PP, P	Azerbaijan, China, Georgia, Japan, Kyrgyzstan, Russia	5, 6, 16, 17, 24, 28, 36, 37, 47, 48, 51, 53, 55	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Lymantrichneumon*	2	L, P	Azerbaijan, Korea, Russia, Russian Far East, Siberia	4, 6, 25, 28, 31, 33, 45	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Melalophacharops*	1	L	Japan	51	No	No	No
Hymenoptera	Ichneumonidae	*Mesoleptus*	1	L	Russia	24, 55	Yes	Yes	No
Hymenoptera	Ichneumonidae	*Ophion*	1	L	Siberia	28	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Phobocampe*	4	L	Azerbaijan, Central Asia, China, Japan, Korea, Kyrgyzstan, Russia, Russian Far East, Siberia	6, 11, 13, 16, 19, 23, 24, 25, 26, 28, 32, 42, 45, 50, 55, 63, 65	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Pimpla*	8	L, PP, P	Central Asia, Azerbaijan, China, Georgia, India, Japan, Kazakhstan, Korea, Kyrgyzstan, Russia, Uzbekistan	5, 6, 10, 11, 13, 16, 17, 19, 21, 22, 23, 24, 25, 26, 28, 31, 34, 36, 37, 42, 45, 47, 48, 53, 55, 66,	Yes	Yes	Yes
Hymenoptera	Ichneumonidae	*Theronia*	3	P	Azerbaijan, China, Georgia, Japan, Korea, Kyrgyzstan, Russia, Russian Far East, Uzbekistan	6, 13, 17, 24, 25, 26, 28, 34, 36 ,37, 45, 47, 53, 55, 66	Yes	Yes	Yes
Hymenoptera	Pteromalidae	*Dibrachys*	1	L, P	China, Georgia, Kyrgyzstan, Russia, Russian Far East	6, 16, 24, 28, 55, 69	Yes	Yes	Yes
Hymenoptera	Pteromalidae	*Mesopolobus*	1	L	Russia	6	Yes	No	Yes
Hymenoptera	Pteromalidae	*Mokrzeckia*	1	L	Russian Far East	61	Yes	No	No
Hymenoptera	Pteromalidae	*Pachyneuron*	1	E	Japan	8	Yes	Yes	Yes
Hymenoptera	Pteromalidae	*Roptrocerus*	1	L	Russia	62	Yes	No	No
Hymenoptera	Scelionidae	*Gryon*	3	E	Central Asia, Russian Far East, Uzbekistan	6, 28	Yes	Yes	No
Hymenoptera	Scelionidae	*Telenomus*	6	E	Central Asia, Japan, Korea, Kyrgyzstan, Russia, Uzbekistan	6, 16, 28, 51	Yes	Yes	Yes
Hymenoptera	Torymidae	*Monodontomerus*	3	P	Azerbaijan, Central Asia, Georgia, India, Korea, Kyrgyzstan, Russia, Russian Far East	6, 11, 19, 23, 25, 28, 37, 48, 59	Yes	Yes	Yes
Hymenoptera	Trichogrammatidae	*Trichogramma*	3	E	Azerbaijan, Japan, Korea, Russia	6, 17, 25, 28, 36, 37, 51	Yes	Yes	Yes

[a]Stage attacked codes: (E) egg, (L) larva, (P) pupa. When a "?" follows a letter it is because there is uncertainty about that stage.
[b]References: (1) Abdinbekova et al. 2015, (2) Abdinbekova et al. 2017, (3) Agibaev and Alimkulova 2017, (4) Aliyev 1999, (5) Aliyev and Maharramova 2009, (6) Baranchikov et al. 1998, (7) Barayshchuk 2008, (8) Brown and Cameron 1982, (9) Choi et al. 2012, (10) Choi et al. 2015, (11) Coulson et al. 1986, (12) Doane and McManus 1981, (13) Feng et al. 1999, (14) Furuta 1977b, (15) Furuta 1982, (16) Gabrid 2003, (17) Gasimov 2008, (18) Gupta 1983, (19) Hajek 2007, (20) Hayat 1975, (21) Howard and Fiske 1911, (22) Ivantsova and Vostrikova 2015, (23) Kenis and Lopez Vaamonde 1998, (24) Khitsova and Isaeva 1986, (25) Kim et al. 2017, (26) Kobzar et al. 2013, (27) Kokubo and Kano 1961, (28) Kolomiets 1987, (29) Kolomiets 1996, (30) Kurenshchikov et al. 2020, (31) Lee and Pemberton 2009, (32) Lee and Pemberton 2010, (33) Lee et al. 2002, (34) Li et al. 2001, (35) Liu et al. 2006, (36) Mamedov and Muradova 2014, (37) Mammadov and Alieva 2010, (38) Marsh 1979, (39) Martemyanov et al. 2013, (40) Minami et al. 1999, (41) Narendran 2009, (42) Orozumbekov et al. 2009a, (43) Panina and Belov 2012, (44) Pemberton and Lee 1996, (45) Pemberton et al. 1993, (46) Rasplus et al. 2010, (47) Ren et al. 2002, (48) Safarova 2018, (49) Schaefer and Shima 1981, (50) Schaefer et al. 1984b, (51) Schaefer et al. 1988a, (52) Schaefer et al. 1988b, (53) Schedl 1936, (54) Seo et al. 2019, (55) Shapiro 1956, (56) Shima 1984, (57) Tachi and Shima 1998, (58) Tachi and Shima 2008, (59) Tobias 2004, (60) Tschorsnig 2017, (61) Tselikh 2012, (62) Tselikh 2013, (63) Watanabe 2015, (64) Yan et al. 1992, (65) Yan et al. 1993, (66) Yan et al. 1994, (67) Yang and Ren 2003, (68) Yao and Yan 1994,(69) Zhou 2012, (70) Zhu and Huang 2002b, (71) Zhu and Huang 2002a.

to silence genes the insect needs to survive is also being explored (Zhang et al. 2023, Xie et al. 2025).

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Melody A. Keena (Conceptualization [lead], Data curation [lead], Methodology [lead], Project administration [lead], Resources [equal], Supervision [lead], Visualization [lead], Writing—original draft [equal], Writing—review & editing [equal]), Nooshin Zandi-Sohani (Methodology [equal], Writing—original draft [equal], Writing—review & editing [equal]), Jessica Y. Richards (Data curation [equal], Methodology [equal], Writing—review & editing [equal]), Juan Shi (Data curation [equal], Visualization [equal], Writing—review & editing [equal]), and Yuri Baranchikov (Visualization [equal], Writing—review & editing [equal])

Supplementary Material

Supplementary material is available at *Journal of Integrated Pest Management* online.

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Conflicts of interest

None declared.

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