EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **119**: 227–231, 2022
doi: 10.14411/eje.2022.024
ORIGINAL ARTICLE

Egg maturation in an invasive gall wasp, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae): An experimental test of the pro-ovigenic and facultatively synovigenic hypotheses

Yajiao WU[1] and Yoshihisa ABE[2,*]

[1] Graduate School of Integrated Sciences for Global Society, Kyushu University, Fukuoka, Japan; e-mail: yajiao.wu.728@s.kyushu-u.ac.jp

[2] Faculty of Social and Cultural Studies, Kyushu University, Fukuoka, Japan; e-mail: y_abe@scs.kyushu-u.ac.jp

Key words. Adult age, body size, egg load, egg size

Abstract. There are two hypotheses on egg maturation in the invasive chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae). That it is pro-ovigenic (most or all of its potential lifetime egg complement is mature upon emergence) or facultatively synovigenic (not all eggs are fully developed upon emergence and may be resorbed when suitable hosts are absent). These hypotheses were tested by determining the effects of adult age and food (honey) on egg maturation in *D. kuriphilus* wasps with no access to host plants. Egg load (the number of mature eggs per female) neither increased nor decreased with adult age in the presence or absence of honey when deprived of host plants. These findings support the pro-ovigenic hypothesis. Some eggs mature during the adult lifetime of cynipoid parasitoids even without hosts, but the cynipoid gall inducer, *D. kuriphilus*, is pro-ovigenic, probably due to the abundance of chestnut buds available for oviposition under natural conditions. In addition to no competition for oviposition resources, thelytokous reproduction, unintentional introduction of infested chestnut trees and escape from host-specific parasitoids in introduced countries, pro-ovigeny with a high egg load has presumably resulted in *D. kuriphilus* becoming a global pest of chestnuts. In addition, body length, mesosomal and metasomal lengths and widths, hind femoral length, hind tibial length, and egg load as well as egg width of this wasp were also measured. There was no variation in egg width, but all the other measurements were positively correlated with egg load. Large females of *D. kuriphilus* had higher egg loads than small females.

INTRODUCTION

The invasive chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), a destructive pest of chestnuts in Japan (Yasumatsu, 1951), originated from China (Murakami, 1980) and has become a global pest of chestnuts in Asia, the USA and Europe (Aebi et al., 2006 and references therein). In addition to updating the biology and invasion history of *D. kuriphilus*, the parasitoids of *D. kuriphilus* and other oak gall wasps in Asia are reviewed by Abe et al. (2007). Oak gall wasps (tribe Cynipini) induce galls on Fagaceae plants and mainly have one sexual and one asexual generation each year (Askew, 1984; Ronquist et al., 2015; Ide & Abe, 2021), whereas *D. kuriphilus* is univoltine and thelytokous (Moriya et al., 1990). Polyploidy is associated with thelytoky in animals including some insects (Suomalainen et al., 1987), whereas *D. kuriphilus* is diploid (Abe, 1994). In Cynipidae, *Wolbachia*-induced thelytoky is wide-spread in "Aylacini", herb gall wasps, and "Rhoditini", rose gall wasps (Plantard et al., 1999) and in Hymenoptera other than the above two tribes (Stouthamer, 1997). Currently, the correct name for "Rhoditini" is Diplolepidini (Ronquist et al., 2015). To clarify the possible role of *Wolbachia* in the unisexuality of Cynipini, *Wolbachia* infection was studied in the *Andricus mukaigawae* complex, which consists of closely related bivoltine heterogonic and univoltine thelytokous species, but *Wolbachia* is not responsible for unisexuality in these oak gall wasps (Abe & Miura, 2002). Similarly, in *D. kuriphilus*, another thelytokous species in the Cynipini, four out of six Chinese populations were *Wolbachia*-free (Zhu et al., 2007). The mechanism of thelytokous reproduction in *D. kuriphilus* remains an open question.

In a study to ascertain the reproductive capacity of *D. kuriphilus*, Nohara (1956) reports the egg load (number of mature eggs per female) of newly emerged adults. The mean egg load is estimated to be 308 and the lifespan 2–2.5 days, Nohara (1956) therefore hypothesized that *D. kuriphilus* is a pro-ovigenic species in which most or all potential

* Corresponding author; e-mail: y_abe@scs.kyushu-u.ac.jp

lifetime egg complement is mature upon emergence (Flanders, 1950). In a study on the female adult fecundity of *D. kuriphilus* in which female wasps immediately after emergence from the galls were individually released in polyethylene bags that covered cut branches of chestnut with fresh buds under laboratory conditions, Tokuhisa (1981) reports the number of eggs laid in the fresh buds and remaining in the body of wasps immediately after death. The results indicate that the mean number of eggs deposited in the buds was 55.5 during the lifespan (1.9 days) of a wasp. Moreover, the mean total number of eggs deposited in the buds and remaining in the wasp body was 287.6 (Tokuhisa, 1981). These results support Nohara's hypothesis, whereas Graziosi & Rieske (2014) report that the egg load in *D. kuriphilus* decreased with adult age when offered water, but not honey and a host plant. Since egg resorption is common in females of synovigenic species, in which egg maturation continues throughout the adult stage (Flanders, 1950), when suitable hosts are rare or absent (Rosenheim et al., 2000; Jervis et al., 2001), Graziosi & Rieske (2014) suggest that *D. kuriphilus* is facultatively synovigenic. The absence of food for the female wasps in their experiments indicate that there should be additional work on the effects of food on egg load (Graziosi & Rieske, 2014).

Female body size positively correlates with egg load in most parasitoid wasps (Jervis et al., 2005). Therefore, it is considered to be a primary proxy of fitness (Roitberg et al., 2001). A study on the relationship between body size and egg load in *D. kuriphilus* in which body weight, body length, mesosomal and metasomal lengths and widths, hind femoral length and egg load were recorded indicates that egg load is positively correlated with both body weight and metasomal width (Graziosi & Rieske, 2014).

In this study, the effects of adult age and food on egg load were recorded for *D. kuriphilus* in order to test the two hypotheses on the mode of egg maturation. Moreover, body metrics were also measured in order to detect features that are correlated with egg load in this gall wasp.

MATERIALS AND METHODS

Experimental design

Galls induced by *D. kuriphilus* were collected from a tree of *Castanea crenata* Sieb. et Zucc. in Itoshima City, Fukuoka Prefecture, Japan on June 13 and June 15, 2020. These galls were placed in a plastic box ($17.5 \times 10.5 \times 12.5$ cm^3) at 22°C under constant-dark conditions and checked daily for the emergence of female wasps of *D. kuriphilus*. In a preliminary study, 6 of 10 female wasps of *D. kuriphilus* died on day 6 when offered water and honey at 20°C under a 15L : 9D photoperiod. In order to determine the effects of adult age and food on egg load, 0-, 2- and 4-day-old female wasps that emerged between 18th and 23rd of June, 2020, were prepared as follows. Forty wasps were captured within 24 h of emergence and grouped into the following four categories: (1) 0-day-old wasps, (2) 4-day-old wasps without food, (3) 2-day-old wasps with food and (4) 4-day-old wasps with food. Each category consisted of 10 females. Thirty wasps in categories (2), (3) and (4) were kept individually in 30 10-ml glass vials containing a water-soaked cotton ball, without host plant material for 2 or 4 days at 20°C under a 15L : 9D photoperiod. In addition, the inside of the vials of categories (3) and (4) was streaked with honey as food for the wasp.

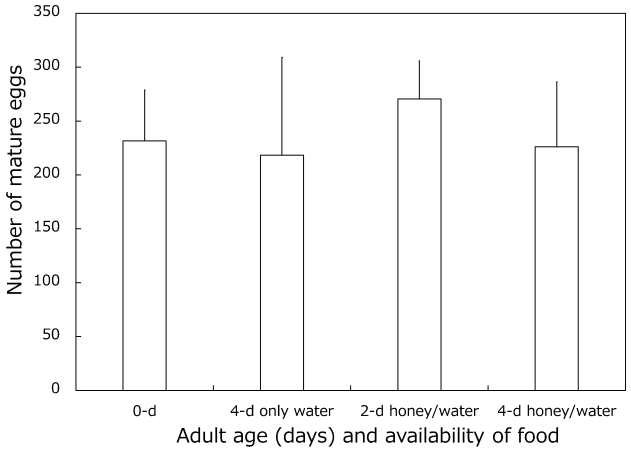

Fig. 1. Effects of adult age and availability of food on the number of mature eggs in *Dryocosmus kuriphilus*. The mean values for the four categories do not differ significantly at P = 0.05 (ANOVA). Bars indicate the standard deviation of the mean. Sample sizes are: (0-d) 10, (4-d only water) 7, (2-d honey/water) 10 and (4-d honey/water) 10.

The 40 wasps in the four categories mentioned above were killed by freezing, but three wasps in category (2) were damaged before they were examined. The remaining 37 wasps were individually transferred to a Petri dish containing distilled water and dissected using forceps and minute pins under a stereomicroscope (Leica WILD M10, Leica Microsystems, Wetzlar, Hesse, Germany) as in Wu & Abe (2020, 2021). Similar to Wang et al. (2018), the mature eggs were characterized by a thin translucent and smooth chorion and a stalk. Moreover, the relationship between egg load and body size was determined by measuring the body length, mesosomal and metasomal lengths and widths, hind femoral length, and hind tibial length of the wasps using an ocular meter. In addition to recording egg load and body size, ten mature eggs were randomly selected from each female wasp and their maximum widths measured and used as an index of egg size. Since the transition between an egg and its stalk is somewhat gradual, the length of the eggs was not measured.

Statistical analysis

One-way analysis of variance (ANOVA) was used to detect differences in the egg load of the four categories of *D. kuriphilus*. Moreover, the effects of body size on the egg load of this species were expressed by regressing the egg loads against indices of body size and calculating the regression coefficients for the 37 wasps. A linear regression for each index was then generated using a least-squares method. The mean and SD of the maximum width of the eggs were also calculated.

RESULTS

The mean (± SD) egg loads of the 4 categories of *D. kuriphilus* were as follows: (1) 231.5 ± 47.3 (n = 10), (2) 218.4 ± 90.9 (n = 7), (3) 270.6 ± 35.1 (n = 10) and (4) 226.0 ± 60.2 (n = 10). There was no significant difference in the mean egg loads of the four categories (ANOVA, F = 1.472, P = 0.24) (Fig. 1). In addition, the egg load was positively correlated with each index of body size: body length, mesosomal and metasomal lengths and widths, hind femoral length, and hind tibial length (Table 1). The mean (± SD) maximum width of an egg was 0.12 ± 0.01 mm (n = 370).

Table 1. Relationship between body size (X) and egg load (Y) in *Dryocosmus kuriphilus*.

Indices of body size	y = ax + b	*F*	*P*	r^2
Body length	y = 268.89x – 450.52	17.42	<0.001	0.33
Mesosomal length	y = 381.19x – 168.35	8.90	0.005	0.20
Mesosomal width	y = 641.11x – 181.44	7.68	0.009	0.18
Metasomal length	y = 523.51x – 410.43	15.87	<0.001	0.31
Metasomal width	y = 580.77x – 248.69	23.00	<0.001	0.40
Hind femoral length	y = 844.42x – 345.53	10.44	0.003	0.23
Hind tibial length	y = 468.17x – 129.34	6.52	0.015	0.16

DISCUSSION

The egg load of *D. kuriphilus* adults did not vary with age in the presence and absence of food when deprived of host plants. Moreover, no increase or decrease in egg size was recorded. These results support the pro-ovigenic but not the facultatively synovigenic hypothesis. This gall wasp was first found in Japan and the USA in the 1940s and the 1970s, respectively (Yasumatsu, 1951; Rieske, 2007). The Japan and USA populations of *D. kuriphilus* induce galls on different species of *Castanea* (Yasumatsu, 1951; Rieske, 2007) and are adversely affected by certain aspects of climate and natural enemies (Abe et al., 2007; Cooper & Rieske, 2007). The differences in host plant and environmental conditions might have caused the discrepancy in the egg maturation in the two populations of *D. kuriphilus*. Nohara (1956), Tokuhisa (1981) and this study examined the Japanese population of *D. kuriphilus*, while Graziosi & Rieske (2014) examined the USA population. Our study cannot exclude completely the possibility that the USA population of *D. kuriphilus* is facultatively synovigenic. Because *D. kuriphilus* originated from China (Murakami, 1980), there is need for a study on egg maturation in the Chinese population of this species.

Furthermore, there is a close relative of *D. kuriphilus*, *Dryocosmus zhuili* Liu and Zhu in China (Zhu et al., 2015). The gall and adult morphology, adult emergence period, and partial sequences of COI gene are similar in these two species, but *D. zhuili* reproduces bisexually (Zhu et al., 2015). Although *D. zhuili* has not yet been reported from outside China, this species might become a serious pest of chestnuts in other countries like *D. kuriphilus* (Zhu et al., 2015). Estimates of the infestation ability of *D. zhuili* is essential for predicting and controlling any future invasion and egg maturation should be compared in *D. kuriphilus* and *D. zhuili*. Such a study might also contribute to the problem of the evolution of sex in terms of evolutionary biology.

Cynipoidea is a diverse lineage of Hymenoptera consisting of gall wasps and parasitoids (Buffington et al., 2020). When female wasps of cynipoid parasitoids are deprived of hosts but fed with carbohydrates, egg load continues to increase throughout adult life in *Ganaspis brasiliensis* Ihering (Hymenoptera: Figitidae) (Wang et al., 2018) or increases with age after emergence up to the midpoint of their adult life and thereafter remains constant in *Ibalia leucospoides* (Hochenwarth) (Hymenoptera: Ibaliidae) (Fischbein et al., 2013), *Leptopilina japonica* Novković et Kimura (Hymenoptera: Figitidae) (Wang et al., 2018) and *Gronotoma micromorpha* (Perkins) (Hymenoptera: Figitidae) (Wu & Abe, 2021). These parasitoids are prosynovigenic: females emerge with many mature eggs and mature additional eggs throughout their lifetime (Wu & Abe, 2021). In Cynipoidea, female wasps do not feed on hosts (Bartlett, 1964; Abe, 2009) and their eggs probably contain little yolk (Vårdal et al., 2003). The increase in egg load in cynipoid parasitoids indicates that when suitable hosts are rare or absent, females enhance their reproductive capacity in anticipation of a future improvement in the availability of hosts by using carbohydrates and nutritional reserves stored during the larval stage (Wu & Abe, 2021). Unlike cynipoid parasitoids, *D. kuriphilus* is pro-ovigenic. When the female wasp emerges from a gall on a chestnut tree, there are usually an abundance of chestnut buds available for oviposition under natural conditions (Graziosi & Rieske, 2014). Pro-ovigeny in *D. kuriphilus* can be attributed to the availability of oviposition sites. A high host availability occurs in other gall-inducing cynipids that do not obligatorily host alternate between species of *Quercus*. Further studies are necessary to determine how many species of gall-inducing cynipids are pro-ovigenic.

The adult life of *D. kuriphilus* when allowed to oviposit in chestnut buds is 1.9 days (Tokuhisa, 1981), while those of the cynipoid parasitoids provided with an abundance of hosts for oviposition are longer: 6.6 days in *Gronotoma micromorpha* (Abe & Tahara, 2003), 17.7 days in *Ganaspis brasiliensis* (Wang et al., 2018) and 18.7 days in *L. japonica* (Wang et al., 2018). Pro-ovigenic female adult parasitoids are shorter-lived than those of synovigenic species (Jervis et al., 2001). Among Cynipoidea, adult life is short in the pro-ovigenic species *D. kuriphilus* and long in prosynovigenic female parasitoids. Graziosi & Rieske (2014) explain the short adult life and high egg load in *D. kuriphilus* in terms of the energy costs of reproduction (Carey et al., 1998) and host apparency (Price, 1973; Blackburn, 1991). The adult life of *D. kuriphilus* when provided with an abundance of host plant buds for oviposition is 1.9 days (Tokuhisa, 1981), but 4 days or more in the absence of hosts (the present study). These two observations indicate that the decrease in the length of adult life could be due the energy cost of reproduction. Although host apparency is associated with pro-ovigeny, the adult life of the asexual generation females is long in another oak gall wasp. According to Abe (1986), *Andricus mukaigawae* (Mukaigawa) (Hymenoptera: Cynipidae) has a sexual and asexual generation each year, but does not host alternate. The adult life of sexual generation females that emerge from galls is 3–4 days and that of the asexual generation female is 15–40 days (Abe, 1986). Two asexual generation females of this species contained 581 and 609 mature eggs within 24 h after emergence from galls (Abe Y., pers. observ.). Moreover, the short adult life in *D. kuriphilus* is likely to be attributed to the selective pressures inflicted by predation as suggested for female adult parasitoids (Jervis et al., 2001). This is also the case for this gall wasp: the estimated adult percentage mortality of *D. kuriphilus* due

spider predation varies from 8.1 to 100%, depending on the year (Nakamura & Nakamura, 1977). As pointed out by Tokuhisa (1981), energy cost of emerging from galls may also have resulted in the short adult life in *D. kuriphilus*. In contrast, the long adult life in the prosynovigenic female of cynipoid parasitoids appears to be associated with the need to disperse to find suitable hosts.

Pro-ovigeny with a large egg load is probably a major reason why *D. kuriphilus* is a global pest of chestnuts in Asia, the USA and Europe. After it emerges from a gall, female wasps of *D. kuriphilus* oviposit in chestnut buds for a few days. To our knowledge, no other insects lay eggs in chestnut buds worldwide except in China, which might indicate there is no competition for oviposition sites in introduced countries. In addition, thelytoky, which enables a single female wasp to successfully establish a new population and the unintentional introduction by transfer of infested chestnut trees by man in winter before initiation of gall induction contributed to the global expansion in its distribution (Askew, 1984; Rieske, 2007; Csóka et al., 2017). As highlighted for other exotic pest insects (Reitz & Trumble, 2002), *D. kuriphilus* is considered to have escaped from the controlling effects of natural enemies. A Chinese parasitoid *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), which is host-specific and has a life cycle well synchronized with that of *D. kuriphilus*, was imported from China and released in Japan where it succeeded in controlling the chestnut gall wasp in this country (Moriya et al., 1990; Murakami et al., 2001). Similarly, Quacchia et al. (2008, 2014) and Ferracini et al. (2019) report the successful biological control of *D. kuriphilus* using *T. sinensis* in Italy, where this gall wasp heavily damages chestnut production. In the USA, *T. sinensis* has become established and expanded its distribution (Cooper & Rieske, 2007; Rieske, 2007; Labbate & McCullough, 2022).

In most insects, body size is positively correlated with lifetime fecundity (Honek, 1993). Large *D. kuriphilus* females have high egg loads, as suggested by Graziosi & Rieske (2014). Graziosi & Rieske (2014) report the body length, mesosomal length and width, metasomal length and width, and hind femoral length of *D. kuriphilus*. Of these measurements, metasomal width is positively and significantly correlated with egg load (Graziosi & Rieske, 2014). In contrast, other measurements and hind tibial length were also correlated with egg load in the present study. In parasitoids, female body size is linked with their performance in the field, such as host location (Kazmer & Luck, 1995; Bennett & Hoffman, 1998). Since female wasps of *D. kuriphilus* emerge from galls within the host chestnut canopy, where there is an abundance of buds suitable for oviposition (Graziosi & Rieske, 2014), large wasps may oviposit in more host buds during their short lifetime than small wasps.

ACKNOWLEDGEMENTS. This work was supported by JST SPRING, Grant Number JPMJSP2136.

REFERENCES

Abe Y. 1986: Taxonomic status of the *Andricus mukaigawae* complex and its speciation with geographic parthenogenesis. — *Appl. Entomol. Zool.* **21**: 436–447.

Abe Y. 1994: The karyotype in the chestnut gall wasp *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae). — *Appl. Entomol. Zool.* **29**: 299–300.

Abe Y. 2009: The effect of the age of the serpentine leafminer *Liriomyza trifolii* (Diptera: Agromyzidae) on parasitism by the parasitoid wasp *Gronotoma micromorpha* (Hymenoptera: Figitidae: Eucoilinae). — *Eur. J. Entomol.* **106**: 595–598.

Abe Y. & Miura K. 2002: Does *Wolbachia* induce unisexuality in oak gall wasps (Hymenoptera: Cynipidae)? — *Ann. Entomol. Soc. Am.* **95**: 583–586.

Abe Y. & Tahara M. 2003: Daily progeny production and thermal influence on development and adult longevity of the leafminer parasitoid, *Gronotoma micromorpha* (Hym., Eucoilidae). — *J. Appl. Entomol.* **127**: 477–480.

Abe Y., Melika G. & Stone G.N. 2007: The diversity and phylogeography of cynipid gallwasps (Hymenoptera: Cynipidae) of the Oriental and eastern Palearctic regions, and their associated communities. — *Orient. Insects* **41**: 169–212.

Aebi A., Schönrogge K., Melika G., Alma A., Bosio G., Quacchia A., Picciau L., Abe Y., Moriya S., Yara K., Seljak G. & Stone G.N. 2006: Parasitoid recruitment to the globally invasive chestnut gall wasp *Dryocosmus kuriphilus*. In Ozaki K., Yukawa J., Ohgushi T. & Price P.W. (eds): *Galling Arthropods and Their Associates*. Springer, Tokyo, pp. 103–121.

Askew R.R. 1984: The biology of gall wasps. In Ananthakrishnan T.N. (ed.): *Biology of Gall Insects*. Oxford & IBH Publishing Co, New Delhi, pp. 223–271.

Bartlett B.R. 1964: Patterns in the host-feeding habit of adult parasitic Hymenoptera. — *Ann. Entomol. Soc. Am.* **57**: 344–350.

Bennett D.M. & Hoffmann A.A. 1998: Effects of size and fluctuating asymmetry on field fitness of the parasitoid *Trichogramma carverae* (Hymenoptera: Trichogrammatidae). — *J. Anim. Ecol.* **67**: 580–591.

Blackburn T.M. 1991: A comparative examination of life-span and fecundity in parasitoid Hymenoptera. — *J. Anim. Ecol.* **60**: 151–164.

Buffington M.L., Forshage M., Liljeblad J., Tang C.-T. & van Noort S. 2020: World Cynipoidea (Hymenoptera): a key to higher-level groups. — *Insect Syst. Divers.* **4**(4): 1–69.

Carey J.R., Liedo P., Müller H.-G., Wang J.-L. & Chiou J.-M. 1998: Relationship of age patterns of fecundity to mortality, longevity, and lifetime reproduction in a large cohort of Mediterranean fruit fly females. — *J. Georontol.* (*A, Biol.)* **53**: 245–251.

Cooper W.R. & Rieske L.K. 2007: Community associates of an exotic gallmaker, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae), in eastern north America. — *Ann. Entomol. Soc. Am.* **100**: 236–244.

Csóka G., Stone G.N. & Melika G. 2017: Non-native gall-inducing insects on forest trees: a global review. — *Biol. Invas.* **19**: 3161–3181.

Ferracini C., Ferrari E., Pontini M., Saladini M.A. & Alma A. 2019: Effectiveness of *Torymus sinensis*: a successful long-term control of the Asian chestnut gall wasp in Italy. — *J. Pest Sci.* **92**: 353–359.

Fischbein D., Bernstein C. & Corley J.C. 2013: Linking reproductive and feeding strategies in the parasitoid *Ibalia leucospoides*: does feeding always imply profit? — *Evol. Ecol.* **27**: 619–634.

Flanders S.E. 1950: Regulation of ovulation and egg disposal in the parasitic Hymenoptera. — *Can. Entomol.* **82**: 134–140.

Graziosi I. & Rieske L.K. 2014: Potential fecundity of a highly invasive gall maker, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae). — *Environ. Entomol.* **43**: 1053–1058.

Honek A. 1993: Intraspecific variation in body size and fecundity in insects: a general relationship. — *Oikos* **66**: 483–492.

Ide T. & Abe Y. 2021: The heterogonic life cycles of oak gall wasps need to be closed: A lesson from two species of *Dryophanta* (Hymenoptera: Cynipidae: Cynipini). — *Ann. Entomol. Soc. Am.* **114**: 489–500.

Jervis M.A., Heimpel G.E., Ferns P.N., Harvey J.A. & Kidd N.A.C. 2001: Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. — *J. Anim. Ecol.* **70**: 442–458.

Jervis M.A., Copland M.J.W. & Harvey J.A. 2005: The life-cycle. In Jervis M.A. (ed.): *Insects as Natural Enemies – A Practical Perspective*. Springer, Dordrecht, Berlin, Heidelberg, New York, pp. 73–165.

Kazmer D.J. & Luck R.F. 1995: Field tests of the size-fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. — *Ecology* **76**: 412–425.

Labbate L. & McCullough D.G. 2022: Phenology, density and parasitism of Asian chestnut gall wasp (*Dryocosmus kuriphilus*) (Hymenoptera: Cynipidae) in recently invaded chestnut (*Castanea* spp.) orchards in Michigan. — *Environ. Entomol.* [in press].

Moriya S., Inoue K. & Mabuchi M. 1990: The use of *Torymus sinensis* to control chestnut gall wasp, *Dryocosmus kuriphilus*, in Japan. In Mochida O., Kiritani K. & Bay-Petersen J. (eds): *The Use of Natural Enemies to Control Agricultural Pests*. Food and Fertilizer Technology Center (FFTC), Taipei, pp. 94–105.

Murakami Y. 1980: Current topics on the chestnut gall wasp – experience in China. — *Nogyo oyobi Engei* (*Agriculture and Horticulture*). **55**: 249–253.

Murakami Y., Toda S. & Gyoutoku Y. 2001: Colonization by imported *Torymus* (*Syntomaspis*) *sinensis* Kamijo (Hymenoptera: Torymidae) of the chestnut gall wasp (Hymenoptera: Cynipidae). (7) Success in the eighteenth year after release in Kumamoto. — *Kyushu Pl. Prot. Res.* **47**: 132–134.

Nakamura M. & Nakamura K. 1977: Population dynamics of the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) V. Estimation of the effect of predation by spiders on the mortality of imaginal wasps based on the precipitin test. — *Oecologia* **27**: 97–116.

Nohara K. 1956: Considerations on the reproductive capacity of *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae). — *Sci. Bull. Fac. Agr. Kyushu Univ.* **15**: 441–446.

Plantard O., Rasplus J.-Y., Mondor G., Le Clainche I. & Solignac M. 1999: Distribution and phylogeny of *Wolbachia* inducing thelytoky in Rhoditini and 'Aylacini' (Hymenoptera: Cynipidae). — *Insect Mol. Biol.* **8**: 185–191.

Price P.W. 1973: Reproductive strategies in parasitoid wasps. — *Am. Nat.* **107**: 684–693.

Quacchia A., Moriya S., Bosio G., Scapin I. & Alma A. 2008: Rearing, release and settlement prospect in Italy of *Torymus sinensis*, the biological control agent of the chestnut gall wasp *Dryocosmus kuriphilus*. — *BioControl* **53**: 829–839.

Quacchia A., Moriya S. & Bosio G. 2014: Effectiveness of *Torymus sinensis* in the biological control of *Dryocosmus kuriphilus* in Italy. — *Acta Hort.* **1043**: 199–204.

Reitz S.R. & Trumble J.T. 2002: Competitive displacement among insects and arachnids. — *Annu. Rev. Entomol.* **47**: 435–465.

Rieske L.K. 2007: Success of an exotic gallmaker, *Dryocosmus kuriphilus*, on chestnut in the USA: a historical account. — *Eppo Bull.* **37**: 172–174.

Roitberg B.D., Boivin G. & Vet L. 2001: Fitness, parasitoids, and biological control: an opinion. — *Can. Entomol.* **133**: 429–438.

Ronquist F., Nieves-Aldrey J.-L., Buffington M.L., Liu Z., Liljeblad J. & Nylander J.A.A. 2015: Phylogeny, evolution and classification of gall wasps: the plot thickens. — *PLoS ONE* **10**(5): e0123301, 40 pp.

Rosenheim J.A., Heimpel G.E. & Mangel M. 2000: Egg maturation, egg resorption and the costliness of transient egg limitation in insects. — *Proc. R. Soc. Lond. (B)* **267**: 1565–1573.

Stouthamer R. 1997: *Wolbachia*-induced parthenogenesis. In O'Neill S.L., Hoffmann A.A. & Werren J.H. (eds): *Influential Passengers*. Oxford University Press, Oxford, pp. 102–124.

Suomalainen E., Saura A. & Lokki J. 1987: *Cytology and Evolution in Parthenogenesis*. CRC Press, Boca Raton, FL, 216 pp.

Tokuhisa E. 1981: Number of eggs deposited by the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Cynipidae). — *Proc. Assoc. Pl. Prot. Kyushu* **27**: 154–156.

Vårdal H., Sahlén G. & Ronquist F. 2003: Morphology and evolution of the cynipoid egg (Hymenoptera). — *Zool. J. Linn. Soc.* **139**: 247–260.

Wang X.-G., Nance A.H., Jones J.M.L., Hoelmer K.A. & Daane K.M. 2018: Aspects of the biology and reproductive strategy of two Asian larval parasitoids evaluated for classical biological control of *Drosophila suzukii*. — *Biol. Contr.* **121**: 58–65.

Wu Y. & Abe Y. 2020: Egg maturation and daily progeny production in the parasitoid, *Gronotoma micromorpha* (Hymenoptera: Figitidae: Eucoilinae). — *J. Econ. Entomol.* **113**: 2546–2548.

Wu Y. & Abe Y. 2021: Effects of adult age and body size on egg maturation in the parasitoid *Gronotoma micromorpha* (Hymenoptera: Figitidae). — *Eur. J. Entomol.* **118**: 364–367.

Yasumatsu K. 1951: A new *Dryocosmus* injurious to chestnut trees in Japan (Hym., Cynipidae). — *Mushi* **22**: 89–92, 1 pl.

Zhu D.-H., He Y.-Y., Fan Y.-S., Ma M.-Y. & Peng D.-L. 2007: Negative evidence of parthenogenesis induction by *Wolbachia* in a gallwasp species, *Dryocosmus kuriphilus*. — *Entomol. Exp. Appl.* **124**: 279–284.

Zhu D.-H., Liu Z., Lu P.-F., Yang X.-H., Su C.-Y. & Liu P. 2015: New gall wasp species attacking chestnut trees: *Dryocosmus zhuili* n. sp. (Hymenoptera: Cynipidae) on *Castanea henryi* from southeastern China. — *J. Insect Sci.* **15**: 156, 7 pp.

Received February 1, 2022; revised and accepted May 20, 2022
Published online July 8, 2022