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Female Foundresses Egg Parasitoids Deprived of Host: Do Age and Mating Status Affect Reproductive Attributes of Three Egg Parasitoids (Hymenoptera: Scelionidae)?

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ABSTRACT

Egg parasitoids forage for hosts in a dynamic ecosystem. The short longevity of the adult stage forces them to access a host in a short time. The current study examined optimal reproductive attributes of three egg parasitoids: *Trissolcus agriope* (Kozlov and Le), *Trissolcus delucchii* Kozlov and *Trissolcus niceppe* (Kozlov and Le) (Hymenoptera: Scelionidae). The characteristics used were fecundity, immature survival rate, daily reproduction, and sex ratio that emerged from host eggs, *Acrosternum arabicum* Wagner (Hemipteran: Pentatomidae). Experiments were conducted separately in the first day of emergence, 20, 40, 60 and 80% of the mean longevity of naïve foundresses, influenced by mating status and under host deprivation conditions. The results revealed that the immature survival rate of foundresses of *T. agriope* on the first day of emergence, and at 20 and 40% of longevity were higher than other progeny produced by the three parasitoids, whether mated or unmated. All foundresses produced maximum progeny in the first oviposition experience, although the oviposition period was continuous. Regardless of mating status, the progeny production of *T. agriope* and *T. niceppe* declined in the last two stages (60 and 80% of female longevity). The proportion of male progeny increased with foundress age from 40% of their longevity. The species-specific performance of female parasitoids is discussed with regards to oogenesis, oosorption and survival of male gametes in female spermatheca. The results provided information about suitable female age for mass rearing and mass release programs, whether in inundation method or for determination of inoculation rhythms.

Keywords: Delay oviposition, Host deprivation, Oosorption, Oviposition trend, Scelionidae.

INTRODUCTION

The performance of natural enemies is estimated by their fitness gain via successful reproduction and the number of regenerating female progeny (Boivin, 2010; Price *et al.*, 2011). Ecological aspects that influence reproduction attributes of natural enemies include host suitability, temperature, humidity, and the innate status of foundress females such as age, mating status and egg load (Chidawanyika *et al.*, 2019; Jervis *et al.*, 2008; Oku *et al.*, 2019; Vinson, 2010).

Non-availability of a host for foundress females due to the early emergence of parasitoids and low density of suitable hosts are the main factors affecting the reproduction potential of parasitoids (Jervis *et al.*, 2008; Price *et al.*, 2011; Quinn *et al.*, 2018; Tillman, 2019; Wajnberg *et al.*, 2016).

Hymenopteran egg parasitoids forage in a dynamic ecosystem to parasitize the hosts' eggs that may either be exposed or remain concealed in plant matrices (Hilker and Fatouros, 2015; Wajnberg *et al.*, 2008; Wajnberg and Colazza, 2013). The short longevity of the adult stage forces them to

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access a host in a short time, so, access to a host for parasitoids that live in a complex ecosystem is an important aspect of fitness gain by optimal foragers (Bannerman *et al.*, 2011; Fischbein *et al.*, 2019; Henri *et al.*, 2012; Louâpre *et al.*, 2019; Romo and Tylianakis, 2013).

Among the two ovigeny sterategies (pro-ovigeny and synovigeny) that exist in parasitoids, those with pro-ovigenic attributes have to oviposit in time considering their oosorption potential (Irvin and Hoddle, 2009; Jervis *et al.*, 2001). Host deprivation to parasitoids causes the death of mature eggs in their ovarioles, and this is reflected in egg load reduction (Asplen and Byrne, 2006; Leather, 2018). Hence, parasitoids not having this ovigeny strategy should have the ability to reach the host immediately after emergence. Another endogenous aspect affecting successful reproduction in parasitoids is the mating of foundress females (Li *et al.*, 1993; Shera and Karmakar, 2018).

Scelionid females produce a sex pheromone from the end of the pupa stage to two days after emergence (Schwartz and Gerling, 1974; Waage, 1982). Therefore, the males that emerged before them fertilize females immediately after female emergence and before females' dispersion (Gaudon *et al.*, 2018; Loch and Walter, 2002; Martel *et al.*, 2016; Wajnberg *et al.*, 2008). On mating, it is possible that mated foundresses save received spermatozoa in their spermatheca during their life span (Heimpel and de Boer, 2008). Haplodiploid wasps usually have the ability to determine their progeny sex; diploid females were produced from fertilized oocytes and haploid males developed from unfertilized oocytes (Harpur *et al.*, 2013; Heimpel and de Boer, 2008).

Challenges for the foundress female are the limited opportunity to mate and the short survival period of the spermatozoa in the spermatheca. This necessitates the foundress forager to orient quickly to its host, have an optimal number of regenerating female progeny (Chirault *et al.*, 2019; Gotoh and Furukawa, 2018; Orr and Brennan, 2015).

With the backdrop described above, we aimed to determine the effect of two endogenous factors of foragers (age and mating status) on the reproduction attributes of three egg parasitoids of the pistachio green stink bug, *Acrosternum arabicum* Wagner (Hem.: Pentatomidae), namely, *Trissolcus agriope* (Kozlov and Le, 1976), *T. delucchii* (Kozlov), 1968, and *T. niceppe* (Kozlov) and Le, 1976, (Hym.: Seclionidae), which occurred in pistachio orchards in Rafsanjan, Kerman Province, Iran (Mohammadpour *et al.*, 2016). We also planned to determine the impact of mating status and delayed oviposition (or host deprivation conditions) on fecundity, immature survival rate, daily reproduction and sex ratio.

MATERIALS AND METHODS

Insects

Pistachio green stink bug, *A. arabicum* Wagner (Hemiptera: Pentatomidae) was used as a host for all experiments. *Acrosternum arabicum* colony was initiated from sample manually collected from pistachio orchards in Rafsanjan, southeastern Iran (30° 42' 2" N and 55° 53' 51" E). In the laboratory, the bugs reared in plastic boxes (20.0×30.0×10.0 cm) covered with mesh (0.5 mm aperture) in a climate-controlled room (27.0±1.0°C, 60±10% RH and 16 L:8 D hours photoperiod). *A. arabicum* was reared on composite diet (the combination of the green beans (*Phaseolus vulgaris* L.), sunflower seeds (*Helianthus annuus* L.) and wild rue capsules (*Peganum harmala* L.)) as described by Pourkhatoon *et al*. (2016). The diet was changed twice a week and water was provided through a cotton wick. The bugs were provided with paper towel as an oviposition substrate. The eggs were collected daily and used for rearing parasitoids and for perpetuation of host culture. Also, some of egg masses were collected daily and stapled to the yellow cards (7.0×7.0 cm) as card traps

(Mohammadpour *et al.*, 2016). The parasitoids, *T. agriope*, *T. delucchii* and *T. niceppe* were collected by sentinel egg masses (Card traps) placed in the above-mentioned pistachio orchard. Card traps were collected every two days and parasitized eggs were held in an incubator (27.0±1.0°C, 65±5% RH, and 16 L:8 D hours photoperiod) until the parasitoid's emergence. The parasitoids were identified using systematic key (Mohammadpour *et al.*, 2016), confirmed by Prof. Norman Johnson and using voucher specimens deposited in the insect collection of the Department of Plant Protection, Faculty of Agriculture, Vali-e-Asr University of Rafsanjan.

For culturing, the parasitoids individuals were exposed on host eggs (80±10 eggs with < 24 hours old) housed in 15 mL tubes for 24 hours and were fed with diluted honey (10%). Parasitized hosts were incubated in controlled condition described above until adult emergence. The parasitoids emerging from F3–F5 generation were used for biological bioassays.

Longevity of Female Parasitoids

Two groups of newly emerged females (mated and virgin) were selected from progeny produced by 10 separate foundresses of *T. agriope*, *T. delucchii* and *T. niceppe*. Experimental egg masses were prepared by fastening a group of 20 *A. arabicum* eggs (< 24 hours old) and then exposing them to each of these foundresses in a test tube (Falcon 15 mL, 120.0×17.0 mm). Parasitized patches were incubated in controlled conditions (27.0±1.0°C, 65±5% RH, and 16 L: 8 D hours photoperiod) and were observed daily until the wasps emerged.

Male and female parasitoids were paired for mating within 24 hours of adult emergence. The males that emerged one day prior to females (unpublished data) were removed from patches to prepare cohorts of virgin foundresses. From each tube, 5 females were selected, so, cohorts were provided with 25 mated females and 25 virgin females per species. The longevity of *T. agriope*, *T. delucchii* and *T. niceppe* females was recorded from eclosion to death.

Reproductive Attributes

The effects of mating status and delay in oviposition (under host deprivation conditions) on the reproductive attributes of three egg parasitoids, namely, *T. agriope*, *T. delucchii* and *T. niceppe* were examined. The characteristics used to estimate were fecundity, immature survival rate, daily reproduction, and sex ratio that emerged from host eggs, *A. arabicum*. The experiments were conducted by separate assay in five stages of their longevity according to the biology of each species (first day of female emergence and 20, 40, 60, and 80% of the mean longevity of naïve foundresses). The parasitoids had no oviposition experience until the bioassays. Based on preliminary studies, the experiments were conducted in 1, 9, 18, 27, 36 days-old for *T. agriope*; 1, 6, 12, 18, 24 days-old for *T. delucchii*, and 1, 7, 14, 21, 28 days-old for *T. niceppe*. Replication ranging from 16–20 were maintained due to varying oviposition period of parasitoids. Mated and virgin females of *T. agriope*, *T. delucchii* and *T. niceppe* were selected randomly from offspring that were produced by 20–25 separate foundresses of each species. The foundresses were released on host patches as described in the previous section. Host patches with 120 eggs were offered for single female parasitoids in the first week to oviposit. Subsequently, the parasitoids were offered patches having 60 eggs on a daily basis until death. The parasitized hosts were separated daily and incubated in controlled conditions until adults emerged and were frozen at -20°C for 24 hours, numbered, and sexed. Immature mortality of the parasitoids was determined by unhatched host eggs with changes in color and distinctive scar on the

Table 1. Mean naïve female longevity (days±SE) of *Trissolcus agriope*, *Trissolcus niceppe* and *Trissolcus delucchii*, related to mating status.[a]

Species	Virgin foundress (Mean±SE)	Mated foundress (Mean±SE)	t-Test analyze (df= 48)
Trissolcus agriope	49.08 ± 1.33	46.88 ± 1.15	t= 1.253, P= 0.216
Trissolcus delucchii	33.48 ± 0.76	31.16 ± 0.87	t= 2.010, P= 0.050
Trissolcus niceppe	43.12 ± 1.42	37.52 ± 1.42	t= 2.720, P= 0.009
Analysis details	$F_{2,74}$= 42.69	$F_{2,74}$= 43.66	
	P< 0.0001	P< 0.0001	

[a] Comparisons of longevity within mating status were made by GLM (Tukey) (α= 0.05) and between mating status was made by t-test.

chorion. When the host egg color and scar on the chorion did not provide correct information, eggs were dissected to ensure parasitoid mortality.

Statistical Analysis

Data on fecundity was measured as the total number of hosts' eggs parasitized and number of progeny per day. Immature survival rate that was number of emerged parasitoids divided by total number of parasitized hosts. Sex ratio was the proportion of male progeny in total emerged wasps and female longevity. All data was analyzed using SAS 9.1.3 *via* the Generalized Linear Model (GLM) procedure. Tukey's range test was used to explore any differences between means of significant effects. Ryan-Joiner test were run before analysis for normality distribution by Minitab® software. The data not fitting a normal distribution were transformed to the normal scores for normalization. Biological attributes were compared between mated and virgin wasps by t-test and for unequal variances by Welch-test, using MedCalc software.

RESULTS

Longevity of Female Parasitoids

Results on naïve female longevity revealed that *T. agriope* had the longest (46-49 days) and *T. niceppe* had the shortest (37-43 days) longevity. Neither *T. agriope* nor *T. delucchii* exhibited significant difference between longevity of mated and virgin foundresses. Moreover, unmated foundresses of *T. niceppe* exhibited a higher longevity than mated ones (Table 1).

Reproductive Attributes

Total fecundity refers to the total number of host eggs parasitized and number of progeny per day. Regardless of mating status, the progeny production of *T. agriope* and *T. niceppe* declined in the last two stages (60 and 80% of female longevity). In respect to mated and unmated status, *T. agriope* fecundity declined from 207.19±3.41 and 203.81±8.89 on the first day of emergence, to 27.41±4.42 and 14.25±2.59 at 80% of their longevity (Mated: $F_{4, 86}$= 318.28, P< 0.0001; Virgin: $F_{4, 88}$= 180.86, P< 0.0001). The means of fecundity on the first day for mated and unmated foundresses of *T. niceppe* were 212.65±7.53 and 212.18±10.92, respectively. These means declined at 80% longevity to 97.8 ±6.39 and 71.00±4.02 ($F_{4, 90}$= 50.29, P< 0.0001 and $F_{4, 90}$= 49.16, P< 0.0001). Overall, the mated foundresses of *T. agriope* and *T. niceppe*, produced a greater number of progeny (Figure 1). Overall, the survival rate of immature stages for virgin foundresses of *T. delucchii* was less than that of those produced by mated ones, although this factor exhibited an age-dependent decline for both mated ($F_{4, 90}$= 11.90, P< 0.0001) and unmated ($F_{4, 90}$= 6.19, P< 0.0001) (Figure 2) foundresses. No

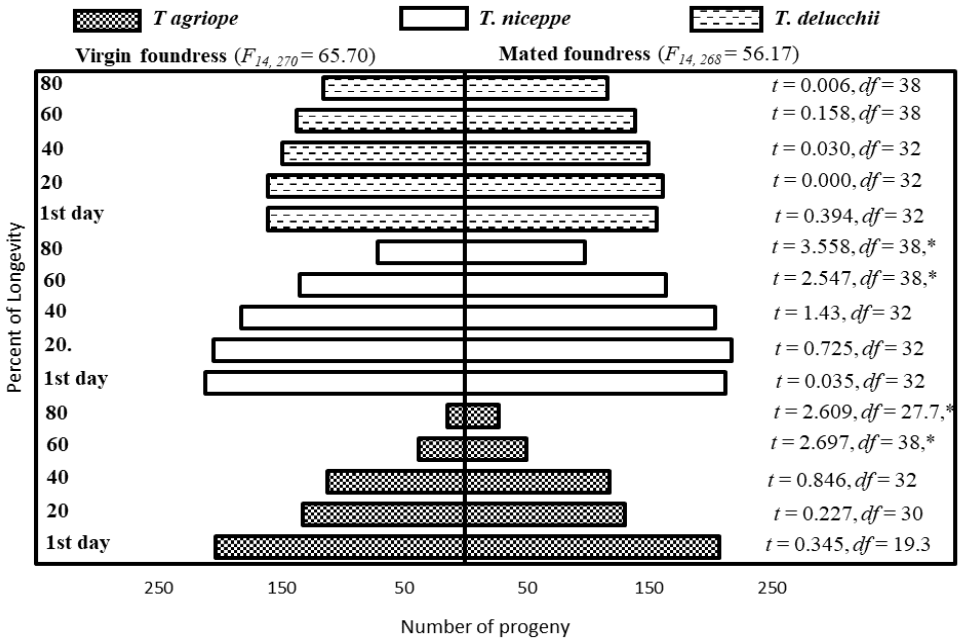

Figure 1. Fecundity of *Trissolcus agriope*, *Trissolcus niceppe* and *Trissolcus delucchii*, related to female age (different percent of their longevity) and mating status. Comparisons of fecundity were made by GLM (Tukey) (α= 0.05) and comparisons of mating status in the given age were made by t-test stage (α= 0.05).

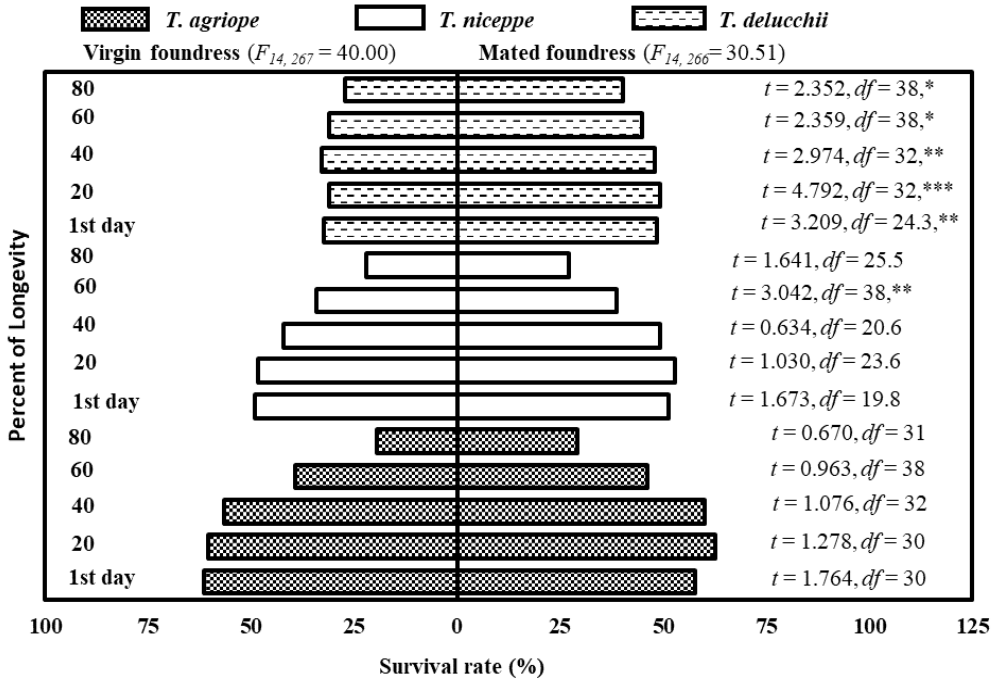

Figure 2. Immature survival rate of *Trissolcus agriope*, *Trissolcus niceppe* and *Trissolcus delucchii* related to female age (different percent of their longevity) and mating status. Comparisons of fecundity were made by GLM (Tukey) (α= 0.05) and comparisons of mating status in the given age were made by t-test or Welch-test t(d) stage (* P< 0.05; ** P< 0.01, and *** P< 0.0001).

significant difference in immature survival rate was observed between mated and unmated foundresses of *T. agriope* and *T. niceppe*, except at 20% longevity of *T. agriope* and 40% longevity of *T. niceppe.* The immature progeny produced by mated ones survived longer than virgin-produced progeny. The comparison of species revealed that the immature survival rates of foundresses of *T. agriope* on the first day of emergence, and at 20 and 40% of longevity, were higher than those of other progeny produced by the three studied parasitoids, whether mated or unmated (Figure 2). Species-specific analysis revealed that the survival of immature stages of *T. niceppe* declined while longevity of the naïve increased (Mated: $F_{4, 84}$= 24.65, P< 0.0001; Virgin: $F_{4, 85}$= 29.80, P< 0.0001). While their mothers aged, the immature individuals of *T. niceppe* significantly declined (Mated: $F_{4, 90}$= 37.57, P< 0.0001 and Virgin: $F_{4, 90}$= 49.99, P< 0.0001). The proportion of male progeny increased with foundress age from 40% of their longevity for *T. agriope* ($F_{4, 80}$= 9.37, P< 0.0001), *T. delucchii* ($F_{4, 90}$= 47.79, P< 0.0001), and *T. niceppe* ($F_{4, 90}$ = 3.75, P= 0.0074). Moreover, offspring sex ratio for *T. delucchi* was low in level, even at 60 and 80% of longevity (Figure 3). All foundresses produced maximum progeny in the first oviposition experience, although oviposition period was continuous (Figure 4).

DISCUSSION

This study revealed that species-specific reproduction of three scelionid egg parasitoids, namely, *T. agriope*, *T. delucchii*, and *T. niceppe* was influenced by mating status and host deprivation condition. Host deprivation led to the aging of naïve females affecting progeny production of all the three species tested, whether mated or unmated females. The highest reproduction rate (the number of egg progeny) of all females was observed in the first oviposition experience. The first event to define pro-ovigenic wasps was the emergence of adult females with high egg load, leading to better reproduction potential due to their matured oocytes (Jervis *et al.*, 2008). Clearly, parasitoid species that are pro-ovigeny have better attributes and are qualitatively better (Asplen and Byrne, 2006; Jervis *et al.*, 2001). The long-term oviposition period producing fewer progeny than the offered hosts on the first day (= 120 host eggs), and the agility of female wasps to exploit a host patch (unpublished data), indicate that

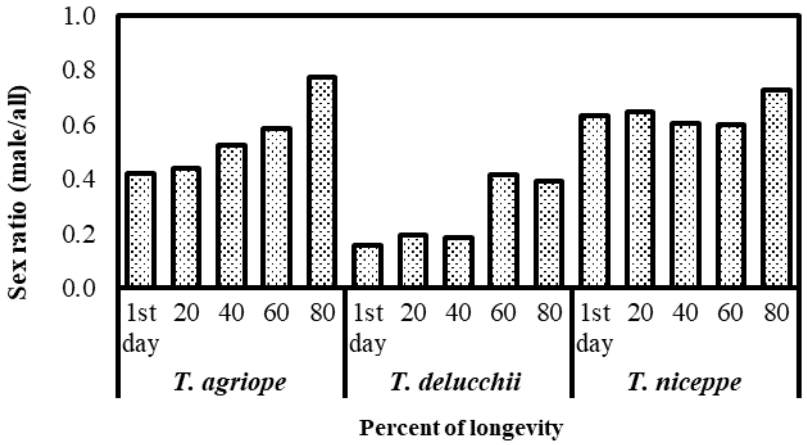

Figure 3. Offspring sex ratio for egg parasitoids, *Trissolcus agriope*, *Trissolcus niceppe*, and *Trissolcus delucchii* depending on different percentages of their longevity. Comparisons were made by GLM (Tukey) (α= 0.05) ($F_{14, 262}$= 40.12, P< 0.0001).

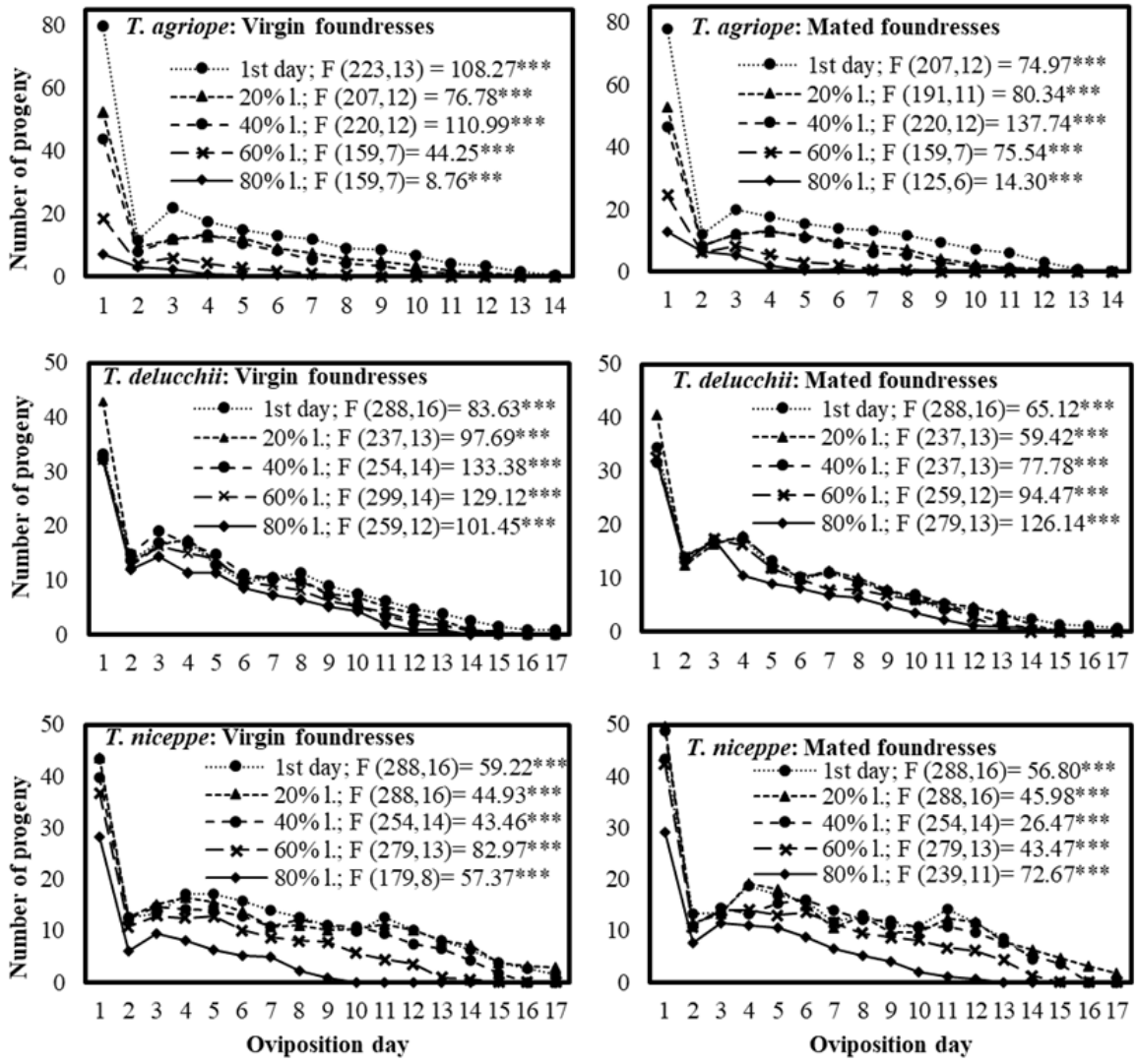

Figure 4. Oviposition trends of *Trissolcus agriope*, *Trissolcus delucchii* and *Trissolcus niceppe* females at five stages of their life (different percent of their longevity), depending on mating status [F (df: Total, model)]. Comparisons of fecundity were made by GLM (Tukey) (*** $\alpha > 0.05$).

oocyte maturation continued until the end of the oviposition period. Such reproduction pattern provides information about the synovigeny of species (Mark A Jervis *et al.*, 2001; Leather, 2018). However, based on the oviposition-induced oogenesis, a time-depended decline in the number of total progeny is predictable for parasitoids (Guo *et al.*, 2011; Kant *et al.*, 2013; Richard and Casas, 2009; Sabbatini Peverieri *et al.*, 2012). Although such decrease in reproduction did not occur for *T. delucchii* females, with the statistical difference, this result may be due to the very short-term longevity of naïve females that provides short intervals in biological bioassays (6 days), without an opportunity for difference exhibition (Pan *et al.*, 2017; Uçkan and Gülel, 2002). Fitness gain by low reproduction decline with aging could compensate for the short-term longevity of females. Therefore, with a conservative judgment, this species may survive in nature, such as other species rewarded with

reverse prosperities (Boivin, 2010; Roitberg *et al.*, 2001). Moreover, this study revealed that mated foundresses produced more total progeny than virgin foundresses at any given age. If total progeny production was produced by virgin wasps (Mills and Kuhlmann, 2000), mating may trigger oocyte maturation or even oogenesis in female wasps. This increase, however, was not observed for low aged females, and this triggering effect was demonstrated in long-term experiments. Such mating-triggered reproduction was revealed for other parasitoids (James, 1988; Kasamatsu and Abe, 2015; Navasero and Elzen, 1992; Ridley, 1988), although for some species it was not a determined effect of mating on the reproduction of females. In such studies, only a limited duration of the female life span was examined (Silva *et al.*, 2018; Sousa and Spence, 2000; Túler *et al.*, 2017). Certainly, for any physiological operation in the insect body such as oogenesis and oocyte maturation, many inducers and enzymatic pathways will be activated that are species-specific (Leather, 2018). Although no information is available regarding all pathways induced by female mating leading to more reproduction, differential expression analysis between virgin and mated spermathecae suggest that antioxidant function is enhanced in mated females (Gotoh *et al.*, 2017). Moreover, mating can even challenge a female's immune system, as mating (up) down-regulates female immune responses and life span (Oku *et al.*, 2019; Reumer *et al.*, 2014). Applied experiments such as this study could provide information on increasing reproduction in mated females (Jia and Liu, 2018; Kant *et al.*, 2013; Pan *et al.*, 2017); therefore, the mentioned spermathecal antioxidant function may depend on enhanced oogenesis or oocyte maturation in mated females. It has been described that female aging causes a decline in progeny production. From a physiological viewpoint, two hormones i.e. ecdyson and juvenile hormone, are essential for oogenesis and oocyte maturation, though their concentrations decline as age increases. Therefore, a decrease in reproduction is predictable for female parasitoids (Leather, 2018). Low quality of oocytes may also affect low survival rate of progeny for high-aged females. *Trissolcus delucchii* exhibited a lower survival rate for male progeny in biological bioassays of virgin mothers; therefore, the low offspring sex ratio for *T. delucchii* could be related to the lower survival rate of male progeny, due to their susceptibility (Herlin *et al.*, 2019). Moreover, total sex ratio may be similar or increase obviously with increases in female age, meaning that the number of female progeny developed from fertilized eggs may decline (Abe, 2019). In regards to the once-mating strategy of the examined species, females received a given number of male gametes, which presumably were stored in spermatheca, which comprises a spermathecal reservoir and a (pair) of spermathecal glands (Pascini and Martins, 2017). Produce back to Secretions that nourish the sperm in spermathecal reservoir may Secretions throughout the life span of the females (Alves *et al.*, 2015; Leather, 2018; Orr and Brennan, 2015; Pascini and Martins, 2017). Recent studies have revealed the importance of the nourishing role of semen liquid produced by male accessory glands and transferred with spermatozoids to the spermathecal reservoir of females (Gotoh and Furukawa, 2018; Liberti *et al.*, 2018). Therefore, limited mating joined with female aging could lead to sperm death in the spermatheca and a low number of female progeny. Moreover, another assumption should consider gamete maintenance, such that aged females use a low number of male gametes to fertilize their eggs (Baer *et al.*, 2016).

In conclusion, the current results revealed the long-term effects of mating on progeny production of female parasitoids, although host deprivation leading to female parasitoid aging could down-regulate progeny production. On the survival of male gametes in the female spermatheca, the offspring sex ratio declined with increases in female aging; therefore, female parasitoids

exhibited species-specific performances under host deprivation conditions. Moreover, if the foraging of female parasitoids stopped, depending on dynamic ecological conditions, species-specific optimal performance of the studied parasitoids would be attained before 60, 80 and 100% of the life span of naïve mated foundresses of, respectively, *T. agriope*, *T. niceppe* and *T. delucchii*. The results also provide information about the suitable female age for mass rearing and mass release programs, whether in inundation method or for determination of inoculation rhythms of the three parasitoid species.

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ماده‌های مولد زنبورهای پارازیتویید تخم در شرایط عدم دسترسی به میزبان: آیا سن و وضعیت جفت‌گیری روی ویژگی‌های تولیدمثلی سه گونه زنبور (Hymenoptera: Scelionidae) موثر است؟

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چکیده

پارازیتوییدهای تخم در یک اکوسیستم پویا در جستجوی میزبان هستند و به دلیل عمر کوتاه در مرحله بالغ، مجبور هستند تا در مدتی کوتاه به میزبان دسترسی یابند. در این مطالعه میزان ویژگی‌های تولیدمثلی سه زنبور پارازیتویید تخم *Trissolcus agriope* (Kozlov and Le)، *Trissolcus delucchii* Kozlov و *Trissolcus niceppe* (Kozlov and Le) (Hymenoptera: Scelionidae) مورد بررسی قرار گرفت. میزان بارآوری، بقای نتاج تولید شده، تولیدمثل روزانه و نسبت جنسی نتاج از میزبان *Acrosternum arabicum* Wagner (Hemiptera: Pentatomidae) تعیین گردید. همه‌ی ویژگی‌های تولیدمثلی در شرایط عدم دسترسی به میزبان و وضعیت جفت‌گیری و در اولین روز بالغ شدن افراد ماده و 20٪، 40٪، 60٪ و 80٪ از میانگین طول عمر ماده‌های مولدی که هیچ تجربه‌ی تخم‌گذاری نداشتند، اندازه‌گیری شده است. نتایج مشخص نمود که نرخ بقای نتاج مولدهای گونه‌ی *T. agriope* در اولین روز بلوغ و در زمان‌های 20٪ و 40٪ از میانگین طول عمر ماده‌های مولد، بیشتر از بقای سایر نتاجی که توسط هر سه گونه تولید شد، بوده است و این ویژگی تحت تاثیر وضعیت جفت‌گیری حشرات کامل نبوده است. در پارازیتوییدهای مولد، با وجود این‌که دوره‌ی تخم‌گذاری مداوم بوده است، بیشترین میزان بارآوری، در اولین روز بلوغ مشاهده شد. صرف نظر از وضعیت جفت‌گیری، تولید نتاج پارازیتوییدهای ماده *T. delucchii* و *T. niceppe* در زمان‌های 60٪ و 80٪ از میانگین طول عمر افراد بالغ، کاهش یافته است. درصد نتاج نر با رسیدن سن افراد مولد به 40٪ از میانگین طول عمر افراد بالغ، افزایش داشته است. کارایی ویژه‌ی گونه، با در نظر گرفتن افراد ماده پارازیتوییدها بر مبنای تولید و بقای تخمک‌ها و بقای گامت‌های افراد نر در اسپرماتیکای افراد ماده مورد بحث قرار گرفته است. نتایج اطلاعات مفیدی را در مورد سن مناسب ماده‌ی بالغ پارازیتوییدها برای برنامه‌های پرورش انبوه و رهاسازی انبوه در روش‌های افزون‌سازی و یا تعیین دوره‌های افزون‌سازی تلقیحی ارائه می‌دهد.