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Influence of courtship feeding on fecundity of *Conocephalus maculatus* (Le Guillou, 1841) (Orthoptera: Tettigoniidae: Conocephalinae)

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Abstract
Investigation on the influence of courtship feeding on fecundity of *Conocephalus maculatus* was studied during November, 2016 to April 2018. The spermatophylax produced by the male is eaten by the female over the following 4 hours after copulation and this had an influence on the number of eggs produced by *C. maculatus*. However, there was no significant difference in the weight and length of the eggs produced. Feeding on an extra spermatophylax resulted in more number of eggs, increased weight and length of eggs being produced per day. Females preferred to oviposit their eggs in the leaf sheaths of *Panicum maximum* and the incubation period ranged between 14-39 days. Most of the eggs hatched within two hours after midnight although the eggs began to hatch from 18hrs and ended by 12 hrs in the afternoon of the next day.

Keywords: Nuptial feeding, spermatophore, katydid and bushcricket

1. Introduction
Males of many Tettigoniidae species produce a spermatophore during copulation consisting of a sperm ampulla containing the ejaculates and spermatophylax, a product of the male's accessory glands, which is a protein acetous food being eaten by the female following mating [1]. It was shown that females preferentially mate with males that are able to supply larger spermatophores [2]. Courtship feeding in insects represents the mating effort that evolved to ensure successful insemination. Females feeding on spermatophylax gain nutrients, which may probably increase the egg size, thereby increase the fitness of offspring's [3]. The protein rich diet is one of the important factors for the reproductive success of katydids: the spermatophylax plays both a nutritional as well as a protective role [4]. The present study aims at providing information on the effect of courtship feeding on the fecundity of *C. maculatus* (Le Guillou) (Orthoptera: Tettigoniidae) along with the notes on mating, ovipositional behaviours and ovipositional preference.

2. Materials and methods
2.1 Animal - *C. maculatus*
Adults of *C. maculatus* collected from a grassland in Coimbatore, Tamilnadu, (India) during November, 2016 to April 2018. It is situated between 10°57'57.6" latitude and 76°57'48.96" longitude. Insects were reared in insect cages (30x30x30cm-wooden framed with fine iron mesh of 0.5mm diameter and with glass front) at laboratory room temperature ranging from 20-30 °C (Mean 28.6 ± 1.7 °C) with 60-90 % relative humidity and a photoperiod of 12.34: 11.26 (L:D) hours. Cut stalks of *Panicum maximum* (Jacq.) immersed in Knop's [Potassium nitrate, 1gm; Magnesium sulphate, 1gm; Calcium nitrate, 4gm; Acidopotassium sulphate, 1gm; Ferric chloride solution, trace; and Distilled water - 1000ml] solution was provided in the cage as an oviposition site. *C. maculatus* had shown preference to *P. maximum* in a pilot experiment. The leaf sheaths with eggs were transferred to an incubation chamber containing a damp filter paper in a muslin-topped 0.5 liter capacity plastic jar. The eggs were incubated at room temperature and under normal lighting conditions as stated above. Water was added to the filter paper in the incubation chamber daily to maintain the required moisture. Newly hatched nymphs were reared singly in muslin-topped 0.5 litre capacity plastic jars, at a mean temperature of 28.6±1.7°C with a relative humidity of 60%. The early nymphs were fed with small pieces of baby corn (an immature flowering part of *Zea mays* Linn.).

A wet cotton wad was placed in the cage to maintain high humidity. Fresh food was provided every day and care was taken to remove all excreta and unfed food regularly to maintain a healthy culture as well as to prevent fungal infection. For the later developmental stages (third nymphal stage onwards), a single full corn was dipped in a small bottle containing water and placed inside the rearing cage. Food was replenished every day. Cut stalks of *P. maximum* immersed in Knop's solution were provided in the cage for oviposition as pilot experiments have shown them to be the best for oviposition. From the third nymphal stage onwards they were reared in a larger cage (30x30x30cm) in order to provide more moving space and to prevent the incidence of malformations and wing deformities, since such malformations were prevalent among the older nymphs reared in smaller and crowded jars. Since all stages ate their own exuvia soon after moulting, the nymphs were carefully marked with red nail polish (Lakme) on the dorsal pronotum. The disappearance of the marking, accompanied by detectable increase in body size, confirmed moulting and this facilitated the recording of the nymphal development duration. Insects (both adults and nymphs) were drawn from this stock culture for all experimental analysis.

2.2 Effect of spermatophylax on fecundity

The following groups were established after virgin females were mated

1. Spermatophylax (Sppx.) - removed: Normal matting but insect was not allowed to eat spermatophylax. The spermatophylax was removed (with forceps) from the spermatophore after mating but before the female had grasped it.
2. Normal mating but the insect was allowed to eat the spermatophylax (Sppx.) 4hrs later: the normal mated female was made to crawl into a glass test tube plugged at the mouth with cotton wool and allowed to eat the spermatophylax (Sppx.) 4hrs after mating since the entry of sperm into the spermatheca takes 4 hrs.
3. Normal mating and insect was allowed to eat the spermtophylax (Sppx.).
4. Extra spermatophylax (Sppx.): Normal mating and insect was allowed to eat spermatophylax; additional spermatophylax was also provided after mating.

Females from all mating were reared in separate plastic containers and cut stalks of *P. maximum* were provided for oviposition with ample supply of food. Eggs laid were removed from the leaf sheaths with a fine Camlin hair brush every day. The following data were recorded for each group.

1. Time taken to consume the Spermatophylax (not needed for Sppx. removed females)
2. Number of mature eggs laid per day.
3. Mean egg weight
4. Mean egg length

Single factor analyses of variance, followed by pairwise comparison by Student-Newman-Keuls test, were carried out in all cases.

2.3 Ovipositional site selection

P. maximum Jacq., *Cynodon dactylon* Pers., *Oryza sativa* Linn., *Chloris barbata* Sw., *Coix lachryma* Jobi, Linn., *Cyperus rotundus* Linn., *Pennisetum typhoideum* S & H, filter paper, thermacol, wet cotton wad, and soil (sieved) were tested for the suitability and preference for oviposition by *C. maculatus* using "no choice" and "free choice" experiments. In the "no choice" test only one ovipositional substrate was offered at a time; while in the "free choice" test all the ovipositional substrates were provided simultaneously. Five gravid adult *C. maculatus* females were introduced into five separate cages and observations were made on their oviposition for 30 days. The experiment was replicated five times (25 insects/oviposition site/30days) and the data collected were maintained separately for statistical analysis. In case of "free choice" test all the ovipositional substrates were kept in a cage and a single gravid female was introduced into it. Twenty-five such cages with a gravid female in each cage were observed for their oviposition for 30 days. The patterns of distribution of eggs between different parts of the oviposition site, in both no-choice and free choice tests, were recorded separately. The oviposited leaf sheath was viewed under a dissection microscope to observe the pattern of arrangement of the eggs. Then the eggs were collected from the leaf sheaths with the help of fine Camlin hair brush. The eggs were thoroughly washed in sterile water and placed on damp filter paper in petri dishes and incubated at 23 ± 2 °C in order to assess the percentage hatchability and duration of the incubation period. High humidity was maintained by keeping the filter paper always wet.

3. Results

3.1 Mating behaviour

Males and females of *C. maculatus* resemble each other barring difference in size, the males being smaller than the females. Males, when sexually mature, make a species-specific mild calling song or sound to attract the conspecific females for mating. Males tap their antenna while approaching the female for copulation, moving along the sides of a potential female. If the female is receptive, it also gives a positive signal by touching the calling male with its antennae. The male then grasps the female with its cerci and flip into a peculiar mating position i.e., male engages the female with cerci and rotates to an angle of 180°, just opposite to female's abdominal side, and hangs from the female (the female maintains its foot hold by hanging from the cage or branch of the plant). After 2-5 minutes of copulation, a series of abdominal contractions were initiated by the copulating male so as to release the spermatophore. After 10-15 minutes of copulation, the male produces intense backward and forward abdominal contraction lasting for 9-10 minutes. Subsequently, both the partners remain quiet for about twenty-five to forty minutes. After copulation, prior to disengagement, the female eats more than 80% of the spermatophylax. Subsequently the female enters the refractory period (time interval between two successive matings during which it will resist advances of a male by jumping away). On several occasions, it was noticed that the female tries to pull off the mating males by dragging them against branches. If the male is not sexually mature, it rejects the female by kicking with the hind legs.

3.2 Ovipositional behaviour

Copulation occurred throughout the year, irrespective of seasons, and mostly during midnight. Females oviposited in the leaf sheaths of *P. maximum*. Before oviposition, females tested the site by superficial scarring of the leaf sheath, covering the stem with their mouthparts. Subsequent to this behavioural pattern, the female took a position lengthwise to

the stem, and with the fore leg embraced the stem to have a good hold and then it initiated oviposition. The middle region of the body was arched to form a semicircle, bringing the apex of the abdomen forward beneath the body until the tip of the ovipositor reaches the scar on the stem beneath the thorax. As soon as the tip of the ovipositor established a physical contact with the stem, the female initiated to pull the legs and push the ovipositor, so as to cut and insert it into the stem. The blade like ovipositor is adapted for such unique oviposition behaviour. The egg was released in between the guides of the ovipositor, after which, the ovipositor was withdrawn, leaving the egg with its head-end near the puncture and rest of it extending away from the puncture in a direction opposite to that in which the female was facing. Then, moving forward slightly, the body was again arched, the ovipositor feels for the egg puncture and, if successful in finding it, was sunken through the same aperture but the egg was directed this time in the opposite direction. After the egg was laid and the ovipositor removed, the insect again turns to face in the opposite direction, splits the stem above the earlier puncture and then, advancing slightly, thrust the ovipositor a third time through the original aperture and placed the third egg by the side of the first one. This process of laying eggs directed alternately up and down the stem, and each deposition followed by splitting the stem above the puncture, continues until ten to twelve eggs are laid during a single oviposition. In case of such heavy deposition, the interior of the stem gets packed with eggs. It is believed that the toughness and pliability of the eggshell prevents the ovipositor from breaking the eggs, already laid, by its subsequent thrusts. The ovipositor may also be sensitive to the presence of eggs in the stem and avoid thrusting directly into them.

3.3 Oviposition and incubation period

Eggs were usually light brown in colour and laid in 7-8 clutches during a female's lifetime with about 9-20 eggs per clutch. The number of eggs laid by a female in a single leaf sheath ranged between 1 and 20 (Fig.1). Oviposition period ranged between 57-84 days and a specific zig-zag pattern was observed in the number of eggs laid throughout the life of a single female (Fig.2). The numbers of eggs laid in the first few clutches were high, and this slowly decreased in the later clutches. At specific frequent intervals, lesser number of eggs was laid. The eggs were 5-6 mm long, 0.2-0.3 mm wide, thin and cylindrical. A female after a single mating laid on average 119 ± 16.5 eggs and with multiple mating it laid on average 345 ± 56 eggs (Table.1). The incubation period ranged between 14-39 days and percent of hatchability was observed to be 83.66 ± 9.84 % under laboratory conditions. Most of the eggs hatched within two hours after midnight although the eggs began to hatch from 18 hrs and ended in the next day (Fig. 3).

3.4 Ovipositional preference

The ovipositional preference of *C. maculatus* towards 11 different ovipositional sites viz., *P. maximum, C. dactylon, O. sativa, C. barbata, C. lachryma, C. rotundus, P. typhoideum*, filter paper, thermocol, wet cotton wad, and soil (sieved) were tested through no-choice and choice tests and the results are presented in table 2. The results showed that *P. maximum*, was the most preferred plant for oviposition. Also a comparatively greater number of eggs were laid on *P. maximum* (46.5) than the other sites. 94.8 % of the eggs laid on *P. maximum* were viable whereas in the case of eggs laid on *C. dactylon* only 34.48 % of them hatched. The incubation period was also significantly different between the eggs laid on *P. maximum* (16.6days) and on *C. dactylon* (28.3 days).

3.5 Influence of courtship feeding on fecundity

The egg production rate, egg weight and length of eggs laid by mated females were compared for four groups namely 1) those that received sperms but no spermatophylax (Sppx. removed), 2) those that received sperms and allowed to eat the spermatophylax after four hours of mating, 3) those that received sperms and ate spermatophylax (Normal mating) and 4) those that received sperms and ate at least half of an extra spermatophylax (Extra sppx.) (Table.3). Results from this study revealed that the number of eggs produced by a female per day is not significantly different from those that did not receive spermatophylax and those allowed to eat spermatophylax after four hours of mating. But a significant difference was observed in the number of eggs laid between females of normal mating (5.5 eggs) and those fed with extra spermatophylax (8.3 eggs). Same trends of observation was also made on the weight and length of the eggs produced. Feeding on an extra spermatophylax resulted in more number of eggs, weight and length being produced per day.

4. Discussion

4.1 Mating behaviour and courtship feeding

Male acoustical signaling is the predominant form of sexual advertising in Ensifera. The matured male starts the calling song only after noticing females that are matured, active and ready for copulation. Then the females respond to the signal by antennal tapping. In *C. maculatus,* like other Ensifera, copulation is mainly under the control of female. Females bend their abdomen ventrally to allow their genitalia to come in contact with that of males. Lacking an intromittant organ, the male transferred the ejaculate in a simple spermatophore consisting of a bulbous, sperm containing ampulla with an ejaculatory canal connecting it to the female's spermatheca. Spermatophore formation occurred during pair formation. Copulation ended when the male released the sperm ampulla, leaving much of it protruding beyond the female's genital opening. After genital separation, the female dismounted the males, and an ejaculation lasting several minutes to hours occurred as sperm and other components moved into the female genital tract. Prior to complete ejaculate transfer, the female curved its head towards the abdomen and removed the spermatophore using mandibles and consumed it. Female feeding on the spermatophylax in addition to the sperm ampulla is a common feature in Ensifera [5]. The females become refractory towards mating for some period afterward but eventually regained sexual receptivity. Males probably experienced no lengthy refractory period, as the cost of copulation was probably negligible.

During copulation, the male *C. maculatus* produce a spermatophore with a large spermatophylax. The spermatophylax is eaten over the following 5hr after copulation. Investment in the spermatophylax can be regarded as parental as the investment not only enhances the female fecundity but also a cost of one male. A spermatophore represents a weight loss of upto 40% for the male bush cricket [6]. In *C. maculatus* there was a reduction in the size (50%) of the spermatophore produced in a second mating after 24 hours after the first. A cost would be reflected in a decreased ability to invest in further offspring if a

reduction in this food donation to the female reduced the numbers and size of those eggs subsequently by the male. So females prefer to mate with males that are able to supply large spermatophore. Spermatophylax itself had an influence on the fecundity of *R. verticalis* [7]. Results from the present study revealed that the number of eggs produced by a female per day is not significantly different between those that did not receive a spermatophylax and those allowed to eat the spermatophylax four hours after mating. The mean number of eggs produced by a female per day in the experimental schedule of those that received sperm but devoid of spermatophylax was 1.6. Whereas, the eggs produced per female per day in the normal mating was 5.5. But in the case of those that received an extra spermatophylax, more number of eggs (8.3) was produced when compared to other experimental schedule. Similarly there was significant difference in the weight and length of the eggs produced (Table. 3). Feeding on an extra spermatophylax resulted in more number of eggs being produced per day. Similar results were reported on *R. verticalis*. It produced 33 eggs in normal matting and while feeding on extra spermatophylax *R. verticalis* produced 59 and 70 eggs per day when fed with 3 and 7 extra spermatophylax.

4.2 Ovipositional behaviour and preference

The vast majority of destructive insects cause injury by feeding. A relatively small number, injure plants in laying their eggs. *C. maculatus* lays eggs on the leaf sheaths of several monocot plants, thereby causing physical injury. Before oviposition, females test the site by superficial scarring the leaf sheath covering the stem with their mouthparts. A similar behaviour was also observed in *O. vulgare* [8] in Illinois cane plantations in *O. glaberrimum* Burmeister [9].

Eggs are usually light brown in colour and are laid on leaf sheaths of *P. maximum*. Female of *O. vulgare* laid eggs in the twigs of the raspberry cane [8]. *P. furcifera* laid eggs in the veins of young leaves of various plants at night [10]. The oviposition period of *C. maculatus* ranges between 57-84 days while incubation period of egg ranges between 14-39 days and percent of hatchability observed was 83.66 ± 9.84 % under laboratory conditions. Adults of *H. nitidulus vicinus* laid its eggs on the leaf sheaths of various grasses and hatched only after 17-18 days of incubation period [11]. Eggs of the tropical katydid species, *Z. apicalis* developed and hatched within 18 days but it increased with decreasing temperature [12].

The ovipositional preference of *C. maculatus* towards 11 different ovipositional sites showed that *P. maximum* was the most preferred plant for oviposition as a comparatively higher number of eggs were laid on *P. maximum* (46.5 eggs) than the other sites. Percentage hatchability was maximum from the eggs laid on *P. maximum* (94.8%) whereas in the case of *C. dactylon* only 34.48% of the eggs hatched. The incubation period was also significantly different for the eggs laid on *P. maximum* (16.6 days) than on *C. dactylon* (28.3 days). The species of the genus *Decticita* laid eggs in the stem of monocotyledons [13]. Eggs of *P. furcifera* were laid at night in the veins of young leaf and required 19 to 24 days to develop [10]. Adults of *H. nitidulus vicinus* laid its eggs on the leaf sheaths of various grasses and hatched only after 17-18 days of incubation period [11]. *Leptophyes punctatissima* (Bosc.) had specific choice of plants to lay their eggs [14]. *R. crassicornis* was found ovipositing into a woody stem [15]. *Typophyllum mortuifolium* Walker laid eggs in a rottery woody vine and fallen decomposing twig species of *Pterochroza*, *Cycloptera* and readily oviposited in the laboratory in basal wood slabs and rotting twigs and no oviposition in soil or leaf tissues [16]. All these work add support to the observation that *C. maculatus* like other tettigoniids have a specific choice of plants for oviposition.

5. Conclusion

The present study concludes that courtship feeding in *Conocephalus maculatus* represents the mating effort that evolved to ensure successful insemination. The protein rich diet is the important factor for reproductive success and the spermatophylax plays both a nutritional as well as a protective role. The number of eggs produced by a female per day is not significantly different from those that did not receive spermatophylax and those allowed to eat spermatophylax after four hours of mating. But a significant difference was observed in the number of eggs laid between females of normal mating and those fed with extra spermatophylax. Feeding on an extra spermatophylax resulted in more number of eggs, weight and length being produced per day.

Table 1: Observations on life history features of *C. maculatus* fed on *Z. mays*

Post embryonic development period	= 43.5 ± 7.4 (39-55 days)
Number of nymphal instars	= 6
Preoviposition period in days	= 15.3 ± 5.3 (9-21 days)
Oviposition period in days	= 70.3 ± 9.98 (57-84 days)
Mean number of eggs laid by female After a single mating	= 119 ± 16.5 (103-136)
Mean number of eggs laid by female After multiple matings	= 345 ± 56 (290-400)
Mean number of eggs laid per day	= 5.46 ± 0.137 (4-7 days)
Number of eggs laid per day per leaf sheath (range)	= 1-20
Incubation Period in days (Embryonic development period)	= 18.3 ± 4.5 (14-39 days)
Egg hatchability	= 83.66 ± 9.84%
Total life span (Both male and female - range)	= 95-175 days

Ranges given in parenthesis values are mean ± SD of 4 replicates of 25 insects

Table 2: Ovipositional preference of *C. maculatus*

Sites	Plant Parts	Eggs laid/female over 30 days		Incubation period	% hatchability
		No choice	Free choice		
Panicum maximum	Leaf sheath	79 ± 1.76a	46.5 ± 22.38a	18.67 ± 3.29a	94.8 ± 1.45a
Cynodon dactylon	Leaf sheath	47 ± 1.73b	8.5 ± 3.45b	28 ± 3.61b	34.48 ± 2.03b
Oryza sativa	Leaf sheath	0	0	0	0
Chloris barbata	Leaf sheath	0	0	0	0
Coix lachryma	Leaf sheath	0	0	0	0
Cyperus rotundus	Leaf sheath	0	0	0	0
Pennisetum typhoideum	Leaf sheath	31.67 ± 1.76c	3 ± 2.58b	30.67 ± 1.25b	33.3 ± 1.45c
Filter paper		0	0	0	0
Thermacol		0	0	0	0
Wet cotton wad		0	0	0	0
Soil (sieved)		0	0	0	0

All values are mean ± SE, values followed by the same alphabets are not significantly different at *P*<0.05 (DMRT)

Table 3: Effect of feeding on the spermatophylax on the reproductive performance of *C. maculatus*

Feeding schedule	Time (min) for spermatophylax consumption	No. of eggs produced /female/ day	Oviposition period (days)	Wt. of egg (mg) (mean of 100 eggs)	Length of egg (mm) (mean of 100 eggs)
Sppx. Removed	-	1.6 ± 0.75a	54.6 ± 2.07a	0.72 ± 0.05a	4.178 ± 0.86a
Sppx. provided at 4 hrs.	254±32.4a	2.8 ± 0.75a	61.2 ±1.48b	0.76 ± 0.05a	4.287 ± 0.08a
Normal	315 ± 34.4b	5.46 ± 0.14b	74.6 ±1.67c	0.83 ± 0.05b	4.740 ± 0.19b
Extra sppx.	444 ± 34.2c	8.3 ± 0.75c	83.4 ±1.95d	0.94 ± 0.04c	4.982 ± 0.26b

All values are mean ± SE , values followed by thesamealphabets are not significantly different at *P*<0.05 (Students - Newman - Keuls test)
Sppx. - Spermatophylax

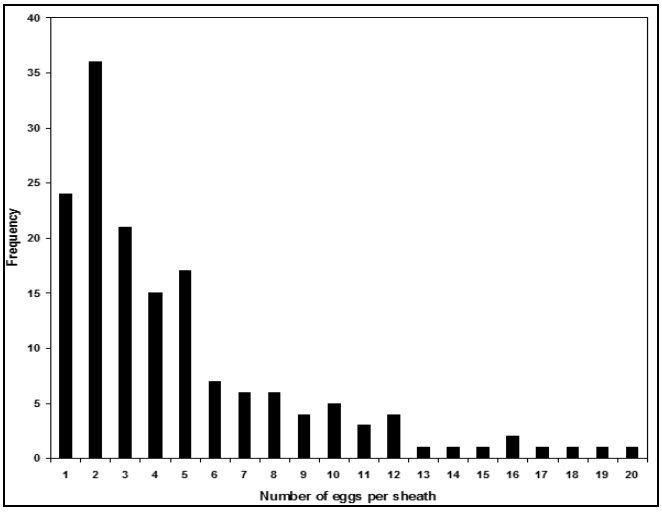

Fig 1: Frequency distribution of the number of eggs oviposited per leaf sheath

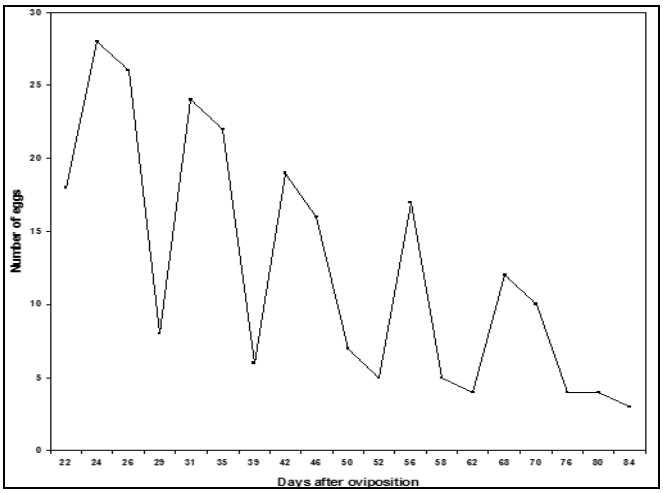

Fig 2: Egg laying pattern of female *C. maculatus* (25 females were observed to plot this figure)

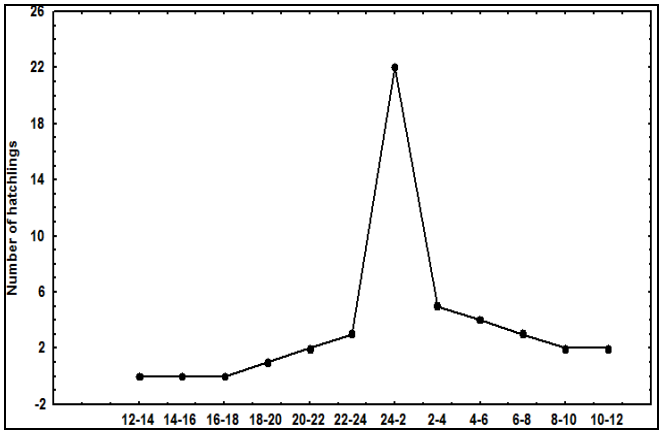

Fig. 3 Pattern in the hatching of *C. maculatus* eggs in a single day (5 batches with 100 eggs each)

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