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Using the Pungent Seed Flesh of the Durian Fruit, *Durio zibethinus*, to Synchronize the Second Ovarian Cycle of *Phormia regina* (Diptera: Calliphoridae)

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Chih-Ming Yin, Bai-Xiang Zou, Mei-Fang Li and John G. Stoffolano Jr. (1997) Using the pungent seed flesh of the durian fruit, *Durio zibethinus*, to synchronize the second ovarian cycle of *Phormia regina* (Diptera: Calliphoridae). *Zoological Studies* **36**(4): 353-359. Because it is very difficult to synchronize subsequent egg cycles among individuals to allow correlation of various endocrine events with vitellogenic events, most research on the dietary-regulated endocrine control of oogenesis in higher Diptera has been focused on the 1st gonotrophic cycle. This difficulty stems from the fact that flies usually feed to varying degree on the oviposition substrate either while laying eggs, or immediately after laying eggs. This lack of control over both meal size and timing of feeding in egg-laying females results in asynchrony in the next ovarian cycle. We report here that a female *Phormia regina* (Meigen) readily lays her eggs on the odorous seed flesh of the tropical fruit durian, *Durio zibethinus* Murr. Further, the amount of durian flesh ingested while egg laying appears insufficient in terms of protein content to initiate/support the 2nd ovarian cycle. Thus, after egg deposition on durain seed flesh, the 2nd ovarian cycle of a cohort of flies can be initiated and supported synchronously by a 2nd replete liver (protein) meal.

Key words: Durian aril, Blow fly, Oogenesis, Anautogeny, Egg cycle.

It is well documented that dietary protein is essential for all ovarian cycles of anautogenous blow flies and is important for all but the 1st cycle of autogenous blow fly species. The dietary-controlled endocrine regulation of oogenesis has been reviewed recently by Yin and Stoffolano (1990 1994 1997). Except for Strangways-Dixon (1961), most researchers on higher Diptera have addressed endocrine control for the 1st gonotrophic cycle only. It is well known that blow flies are attracted to odoriferous resources such as carrion, decaying offal, animal feces, and slimy plant secretions (Stoffolano et al. 1989 1990 1995b) for feeding and/or egg laying. At the time of egg laying, females usually simultaneously feed on the oviposition substrate. This is specially true for the primary screwworm, *Cochliomyia hominivorax* (Hammack 1990). Belzer (1979) notes that *Phormia regina* females have a post-oviposition rebound in protein feeding at the oviposition site which may occur either immediately after egg laying or even before all the eggs are deposited. This behavior of feeding while egg laying results in females ingesting varying quantities of protein. The size of the meal depends partly on the status of egg laying (i.e., the more eggs already laid the more room in the abdomen for the crop to store proteinaceous food) (Stoffolano et al. 1995a). We have observed that any variance in protein ingestion while ovipositing results in asynchrony of endocrine phenomena and in variability of oogenic stages among members of a given cohort. Such asynchrony makes it difficult, if not impossible, to correlate endocrine events with oogenesis for a cohort.

One way to circumvent the above problem is to introduce a physical barrier so that ovipositors can reach the substrate but mouthparts can not. We found that the ovipositor and the proboscis of *P. regina* are similar in both length [3.06 ± 0.22 (mean ±

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SD) vs. 2.59 ± 0.18 mm for ovipositor and proboscis, n = 25 each] and circumference (1.03 ± 0.08 vs. 1.14 ± 0.08 mm in width, respectively, n = 25 each), therefore unless machined precisely, a physical barrier allowing oviposition would also permit feeding. Practically, we must turn to other approaches to solve this problem for *P. regina*. An alternative strategy is to develop an artificial egg-laying substrate whose nutritive value will not support egg development, such as the substrate moistened with ammonium chloride for egg laying of the house fly, *Musca domestica* (Adams and Gerst 1993). A 3rd possibility is to induce egg laying onto a natural substance that is attractive for oviposition but nutritionally insufficient to provide either for the next ovarian cycle or to trigger the involved endocrine cascade. To facilitate routine research work, a large supply of this natural substance should be readily available throughout the year.

We report our finding that the smelly seed flesh of the tropical fruit, *Durio zibethinus* Murr., commonly called durian, stimulates oviposition but lacks the nutrients (i.e., presumably proteinaceous substances) to support oogenesis even after *P. regina* females are allowed to feed, ad libitum, during the oviposition bout of 2 h. Durian is a very large prickly fruit widely eaten in the southeast Asian region. Durian fruit develops on trees, which can reach 20 to 40 m high. Fruits are elongated or irregularly round-shaped, weigh up to 3 kg, contain 6 to 18 seeds, and are densely covered with stiff, short, and sharp thorns. Ripened fruit emits a pungent (foul) scent which smells like a mixture of rotten onions or eggs, sharp blue cheese, and turpentine. It is an odor unpleasant to the novice. The yellowish-white flesh (i.e., aril) surrounding each seed is less odoriferous and has a creamy consistency and a sweet taste that has been likened to a mixture of banana and fried figs, with an aftertaste reminiscent of vanilla. Durian is available worldwide either fresh or frozen in specialty fruit stores year round and thus could adequately support research needs.

MATERIALS AND METHODS

Fly colony maintenance and age of feeding

Phormia regina was reared and maintained as previously described (Stoffolano 1974, Zou et al. 1988, Yin et al. 1994). Mature larvae were allowed to crawl out of the diet into sand to pupate. Pupae were collected daily and adults were allowed to emerge in screened cages. Flies emerging within a 12 h period were sexed and each sex was placed in the same age group or cohort (hour 0) of the same sex. Unless otherwise indicated, a 4.3% sucrose solution was provided to all flies, ad libitum, and again following the feeding bout on beef liver which was provided at 72 h of adult age for 2 h, ad libitum. All flies were kept at 28 ± 2 °C under a 16 h light, 8 h dark photoregime.

Failure of NH_4Cl to induce egg laying

Cotton soaked with a saturated NH_4Cl solution in a Petri dish was placed into a screened cage (150 × 150 × 150 mm^3) together with 5 pairs of male and female *P. regina* that were liver-fed 2 d previously for 2 h following a previously published procedure (Yin et al. 1994). Daily observations for egg-laying were made for the ensuing 3 d. Four replicates were performed.

Egg laying on liver or durian seed flesh

Five pairs of male and female *P. regina*, liver-fed 2 d previously for 2 h were transferred into a screened cage and given both beef liver and durian seed flesh (both purchased frozen, and thawed prior to use). Each of these egg-laying substrates was placed randomly on the cage floor in 4 separate Petri dishes to allow the flies a free choice of egg-laying substrates, which were offered for 2 h on each of the 3 successive days. The experiment was replicated 5 times.

Failure of durian seed flesh to support oogenesis after a 2 h feeding bout

Female black blow flies were removed from the sucrose solution 12 h (i.e., at 60 h of age) prior to the durian feeding to allow emptying of the crop (Yin et al. 1994). At 72 h of age, durian seed flesh instead of liver was provided, ad libitum, for 2 h. Ovaries of these durian-fed flies were checked 48 h later for the developmental status of the synchronously maturing primary follicles. Egg development in the primary follicles was scored using a 10-stage system (Adams and Reinecke 1979) with stages 1 to 3 representing pre-vitellogenic follicles (oocytes), stages 4 to 9 vitellogenic follicles, and stage 10 follicles containing fully developed and chorionated eggs.

Determination of meal weight

Meal weight was determined as the difference

in total body weight immediately before and after a meal.

Oogenesis occurred after continuous exposure to durian seed flesh for 3 or more days

In contrast to the above experimental design, this experiment permitted flies continuous exposure to durian seed flesh from 1 to 5 full days. For each feeding duration, ovaries were checked for their status of follicular (oocyte) development 2 d after the final removal of durian seed flesh.

Protein content of durian seed flesh

Protein content of beef liver, gleba [i.e., a slimy secretion of the stinkhorn fungus, *Mutinus caninus* (Pers.)], and the yellowish durian seed flesh was compared. Protein quantity was measured with Bradford's method (1976) using bovine serum albumin as the standard for both wet and dry weight determinations.

Synchronization and potential fecundity of the 2nd ovarian cycle

Standard timing and procedures regularly used in our laboratories (Yin et al. 1994) were followed to obtain mated and gravid females during the 1st cycle. After the eggs of the 1st cycle were laid on durian aril during a 2-h oviposition period, females were allowed to rest for 3 d. During these 3 d, females were provided with 4.3% sucrose solution for 2.5 d only. In the last 12 h, the sugar solution was taken away to facilitate emptying of the crop before a 2nd liver meal was offered. Status of oogenesis was checked at each 12-h interval for a total of 36 h after the 2nd liver meal. The rate of oogenesis of the 2nd ovarian cycle was compared to that of the 1st ovarian cycle, which was checked at 12-h intervals for a total of 48 h after the 1st liver meal. Potential fecundity was estimated by counting the number of maturing eggs in the ovary of flies during the 1st and 2nd ovarian cycles.

RESULTS

NH_4Cl failed to induce egg laying

In all 4 replications, no eggs were laid during the 5-d observation period indicating that cotton soaked with a saturated NH_4Cl solution was not accepted as an egg-laying substrate for mated, liver-fed, and gravid *P. regina*.

Egg laying on liver and durian

No eggs (Table 1) were laid on either beef liver or durian seed flesh on the 2nd day after the onset of liver feeding. On day 3, however, a total of 6194 or 1640 eggs was laid by 25 females, while on day 4, a total of 1005 and 3825 eggs was laid by the same cohort on beef liver or durian, respectively. When offered side by side, beef liver was preferred to durian at a ratio of ca. 7.2:5.5 (56.7% vs. 43.3%), if the 2-d results were totaled. Durian certainly was also highly acceptable even in the presence of beef liver.

Durian seed flesh failed to initiate/support oogenesis after a 2-h feeding bout

Flies in 3 cohorts of 8 each [all before entering

Table 1. Effect of oviposition substrate on the number of eggs laid by *P. regina*

	Number of eggs laid on different days after liver feeding[b]					
	2nd day		3rd day		4th day	
Replication[a]	Liver	Durian	Liver	Durian	Liver	Durian
1	0	0	1600	0	555	488
2	0	0	1550	0	0	1174
3	0	0	44	1525	438	1078
4	0	0	1500	0	0	1055
5	0	0	1500	115	12	31
Total	0	0	6194	1640	1005	3826

[a]Each replication contained 5 pairs of flies.

[b]Females in their first ovarian cycle were used. A total of 7199 (56.7%) and 5466 (43.3%) eggs was laid on liver and durian seed flesh, respectively.

their 1st ovarian cycle and each weighing 38.1 ± 2.5 mg (mean ± SD) before feeding] had ingested an average of 15.3 ± 4.4 mg of durian aril each during a 2-h feeding bout. This 2-h duration was chosen because in previous experiments, liver-fed flies would have laid all their egg on durian within this time span. When examined at 48 h after the onset of durian feeding, none of the flies contained developing oocytes beyond stage 3. Thus, it appeared that under the circumstances, the protein (or nutritive) contents of the durian aril meal were insufficient to initiate/support the 1st cycle of oogenesis.

Oogenesis occurred after continuous exposure to durian seed flesh for 3 or more days

Data (Table 2) showed that if durian flesh was provided continuously for 24 h, flies still did not ingest enough nutrients (i.e., proteins mainly) to support oogenesis. If durian seed flesh was provided for 2 full days, only 7.1% of the flies contained stage 4 vitellogenic oocytes when examined 48 h after the ending of the durian feeding bout. In contrast, longer exposure to durian at 3, 4, and 5 d supported full oogenesis in 46.6%, 94.8%, and 100% of the flies, respectively. Enough durian seed flesh was cumulatively ingested between days 3 and 4 to provide sufficient nutrients to support oogenesis if flies were exposed to a continuous supply of this fruit material.

Table 2. Effect of durian provided for various durations on follicle (oocyte) development in *P. regina*

Duration (d)	No. of flies	Stage of follicle development (No. of flies)							
		1-3[a]	4	5	6	7	8	9	10
1	58	58							
2	56	52	4						
3	58	5	9	6	7	3	1		27
4	58		3						55
5	45								45

[a]Stages 1 to 3 are pre-vitellogenic; stages 4 to 9 are vitellogenic; stage 10 is post-vitellogenic. Follicle development was examined 48 h after the end of each available feeding duration.

Table 3. Protein contents in different diets provided to *P. regina*

Diet	Protein contents (ug/mg)[a]	
	Wet weight	Dry weight
Liver (beef)	94.1 ± 4.7	274.9 ± 13.8
Gleba	6.6 ± 0.3	22.3 ± 1.1
Durian	3.7 ± 0.1	12.6 ± 0.9

[a]Protein was measured using Bradford's method (1976).

Protein content of durian seed flesh

Analyses (Table 3) revealed that among beef liver, gleba, and durian seed flesh, durian contains the least amount of soluble protein.

Synchronization and potential fecundity of the 2nd ovarian cycle

Follicle development (Table 4) was observed for the liver-meal-induced 2nd ovarian cycle in flies whose 1st cycle eggs were laid on durian seed flesh. This induced 2nd cycle required less time (36 rather than 48 h) to complete.

Potential fecundity remained the same for the first 2 ovarian cycles. An average of 146.5 ± 13.8 and 145.8 ± 17.9 eggs was found in each ovary during the 1st and 2nd cycles, respectively. The difference was not significant (*t*-test, $p < 0.05$, $df = 46$).

DISCUSSION

We report an economical and easy 2-step pro-

Table 4. Comparison of follicle (oocyte) development in the 1st and 2nd ovarian cycles[a] in *P. regina*

Cycle		Follicle development at different times after the 1st or 2nd liver meal (Follicle stage × no. of flies in that stage)			
		12 h	24 h	36 h	48 h
First		3 × 6 4 × 2 5 × 1 6 × 1	4 × 4 5 × 2 6 × 2 7 × 2	5 × 1 6 × 1 7 × 8	10 × 10
	M	3.7	5.2	6.7	10.0
Second		4 × 1 5 × 2 6 × 6 8 × 1	7 × 1 8 × 3 9 × 5 10 × 1	9 × 1 10 × 9	2nd cycle eggs were all laid
	M	5.8	8.6	9.9	

[a]First ovarian cycle was induced by a 2-h liver meal at 72 h of adulthood. To study the 2nd ovarian cycle, flies were permitted to lay their 1st cycle eggs on durian aril at 120 h of age and rest for 2 d (without any access to protein) on a sucrose diet. At 168 h of age, a second 2-h liver meal was provided ad libitum. Follicle development was examined at time intervals indicated in the table.
M = mean.

cedure facilitating the study of the 2nd ovarian cycle of *P. regina*. The 1st step was to induce females in their 1st ovarian cycle to lay eggs onto durian seed flesh, which is readily accepted as an egg-laying substrate by *P. regina*. The post-gravid females were then provided (3 d later) with a sufficient protein meal of beef liver to initiate and support their 2nd ovarian cycle. Ingestion of durian aril both while ovipositing or feeding ad libitum for 2 full days thereafter was insufficient to initiate/support the 2nd ovarian cycle as a liver meal would (i.e., because durian aril is a poor source of proteins). Durian aril contained from 1.26 (present study) to 2.5% (Berry 1980) of soluble protein. The variance may be attributed to differences in durian varieties or degree of fruit ripening. Apparently, the failure of durian aril to support oogenesis when ingested in limited quantity was due to its low protein contents. When it was provided to flies on a continuous basis for 3 or more days, oogenesis proceeded. Another natural substance, gleba from the stinkhorn fungus, *Mutinus caninus*, also fails to support oogenesis when ingested in a limited quantity. Since gleba contains a similar content of protein (2.23%) to durian seed flesh, several days of continuous exposure of female flies to gleba are also required to support fully developed eggs (Stoffolano et al. 1990). Differences between liver and durian in terms of minerals, vitamins, lipids, and carbohydrates, etc. may also contribute to the insufficiency of durian after up to 2 d feeding ad libitum. Minerals and vitamins are important, Pappas and Fraenkel (1977) find that a potassium salt is needed in addition to a purified protein to support oogenesis in *P. regina*. They also find that full oocyte development requires protein, a vitamin, and a mixture of salts in *Sarcophaga bullata*.

In *M. domestica*, egg laying readily occurs onto substrates (e.g., cotton or cheese cloth) impregnated with NH_4Cl (Adams and Gerst 1993), while we found NH_4Cl ineffective here for *P. regina*. Likewise, Cragg (1956) has shown that the sheep blow fly, *Lucilia sericata*, is mainly responsive to ammoniacal attractants while *L. caesar* is responsive to sulfurous compounds. This difference indicates that different stimuli are important in the regulation of ovipositional behavior of these two species. Since durian aril is rich in sulfurous compounds, which give a ripened durian its characteristic odor, it is possible that the ovipositioning behavior of *P. regina* is triggered by these sulfurous compounds including hydrogen sulfide, ethyl hydrodisulfide, and several dialkyl polysulfides (Moser et al. 1980) rather than by an ammoniacal compound such as NH_4Cl. Since oviposition is a complex behavior, other non-sulfurous volatile and non-volatile components may also participate in its regulation in *P. regina*. Cragg (1956) has observed in *L. sericata* and *L. caesar* that the full display of oviposition behavior requires the presence of sheep wool. It will be interesting to test if differential responses also exist in other closely related flies, such as, *M. domestica, Neobellieria vomitoria, Lucilia cuprina*, and *Sarcophaga bullata*, or the more distantly related flies, *Bactrocera dorsalis* and *Ceratitis capitata*, in terms of both chemical and physical identities of the oviposition substrate.

The quantity of protein in a substance is apparently not an important factor used to determine if *P. regina* will accept a substrate for egg laying. Many pungent substances containing equal or higher protein contents than durian seed flesh are not accepted as egg-laying substrates. These substances include gleba, as well as chicken, cat, sheep, and pig feces (Stoffolano et al. 1990). We have not observed egg-laying behavior onto any of these substrates.

Our observation of the same potential fecundity for the first 2 cycles is consistent with that of Vogt and Walker (1987). In the bush fly, *Musca vetustissima*, they find that potential fecundity does not change between successive ovarian cycles. In contrast, Spradbery and Schweizer (1981) find that females of the screw-worm fly, *Chrysomya bezziana*, mature approximately 16% fewer oocytes in the 2nd and subsequent ovarian cycle than in the 1st.

Our result that the 2nd oogenesis cycle required less time than the 1st is consistent with a previous observation of the face fly, *Musca autumnalis*, which shortens cycle duration from 6 to 5 days between the 1st and 2nd cycles (Burkett 1987). An explanation for the shortened 2nd cycle may lie at the molecular level. Study of fat body cells of *Locusta migratoria* has shown that, at the time of egg laying, vitellogenin mRNA is stored in an untranslated form for use in the next cycle of oogenesis (Glinka et al. 1994). If similar mRNA storage also occurs for *P. regina* and *M. autumnalis*, it is conceivable that the presence of this mRNA may save some time for vitellogenin biosynthesis for the 2nd cycle. This hypothesis requires future testing. There is some vitellogenin (1 ug/ul of hemolymph, Zou et al. 1988) remaining in the hemolymph after the completion of the 1st ovarian cycle in *P. regina*, and presence of this protein may also help to shorten the 2nd cycle.

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用榴槤假種皮同步化晚蠅，*Phormia regina*，第二週期卵發育

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過去研究雙翅目非自發性卵發育的生物學家，多將注意力放在第一卵週期。因為各個雌蠅的第二及以後卵週期的卵很不容易同步發育。本文報告利用榴槤有臭味的假種皮能使蠅的卵在第二週期同步發育的方法。雌晚蠅很容易產卵在榴槤假種皮上。但是產卵時所取食的榴槤假種皮在量及蛋白質含量上都不足以啓動下一個（第二）卵週期。因此研究人員可依實驗需要，用高蛋白質的食物餵已下卵的雌蠅來同步啓動第二週期的卵發育。因為有很多蠅類，在第二及以後卵週期所產的卵數比第一卵週期為多，本文報導的方法對於研究瞭解蠅類產卵的全盤調控機制，應有助益。

關鍵詞： 榴槤假種皮，晚蠅，卵發育，自發性卵發育，卵週期 。

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