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Ovipositional Rhythmicity in Ladybirds (Coleoptera: Coccinellidae): A Laboratory Study

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Abstract

Complete and diel ovipositional rhythms have been observed in three aphidophagous ladybirds (Coleoptera: Coccinellidae): *Coccinella septempunctata* Linnaeus, *Coccinella transversalis* Fabricius and *Propylea dissecta* (Mulsant) for the first time. The complete ovipositional rhythm could be described in terms of a polynomial curve and daily fluctuations in all three species. In the diel cycle, all three ladybird species oviposited significantly in the scotophase. *C. septempunctata* females preferred to oviposit at the end of scotophase in the early morning hours (0300–0700), *P. dissecta* laid most eggs in the middle of scotophase during the night (2100–2300), and *C. transversalis* laid most at the beginning of the scotophase at dusk (1700–1900). While the diel ovipositional rhythm of *C. septempunctata* and *P. dissecta* did not differ between days, that of *C. transversalis* changed dramatically; there was a single peak on the first and second day of observation, and four oviposition peaks on the fifth day with the peaks being situated in the two hours preceding and succeeding the onset and end of the scotophase. Diel rhythms of *C. septempunctata* and *P. dissecta* appear to be endogenous in nature while that of *C. transversalis* is partly modified by exogenous factors.

Keywords: Coccinellidae, *Coccinella septempunctata*, *Coccinella transversalis*, *Propylea dissecta*, complete ovipositional rhythm, diel ovipositional rhythm.

Introduction

Rhythms in insects, including ovipositional ones, have been well documented and reviewed (Saunders, 1982). The two major components of an ovipositional rhythm in insects that oviposit on a daily basis are: the complete ovipositional rhythm and the diel cycle, which includes fluctuations in oviposition within a 24-hour period. The complete ovipositional rhythm in *Sitona lineatus* (Linnaeus) was statistically defined

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as consisting of three levels: (1) day-to-day fluctuations (daily oscillations), (2) lunar fluctuations (ca. 28-day cycle), and (3) a second-degree polynomial curve (Schotzko & O'Keeffe, 1986). The polynomial equation explained the long-term trend and the other two components explained variations within this. The diel ovipositional cycle in insects that lay eggs in clusters can be divided into the preferred and non-preferred times of oviposition, which may occur once (diurnal) or twice (crepuscular) every 24 hours. Diel and a few complete ovipositional cycles have been described for a number of insects, viz. *Aedes aegypti* (Linnaeus) (Haddow et al., 1961), *Oncopeltus fasciatus* (Dallas) (Rankin et al., 1972), *Laspeyresia pomonella* (Linnaeus) (Riedl & Loher, 1980), *Drosophila melanogaster* Linnaeus (Fluegel, 1978; Allemand & David, 1984), *S. lineatus* (Schotzko & O'Keeffe, 1986), *Delia antiqua* (Meigen) (Havukkala & Miller, 1987) and *Thyanta pallidovirens* (Stal) (Schotzko & O'Keeffe, 1990). However, there has been no account so far of such rhythms in ladybirds, although foraging rhythms have been described (Hull et al., 1977; Mack & Smilowitz, 1978; Miura & Nishimura, 1980; Nakamuta, 1987).

Oviposition in ladybirds (Coleoptera: Coccinellidae), which are potential biocontrol agents, has been widely studied and is a vital part of their life cycle (Dixon, 1959; Iperti, 1966; Radwan & Lovei, 1982; Iperti & Quilici, 1986; Ferran et al., 1989; Omkar & Srivastava, 2002; Omkar & Mishra, 2003). Aphidophagous ladybirds oviposit in clusters, are highly fecund (Hodek & Honek, 1996; Dixon, 2000), and synchronize their reproduction with prey populations (Dixon, 2000). Oviposition is reduced by intra- and inter-specific interactions (Agarwala et al., 2003; Omkar & Mishra, unpubl. data). However, except for a few studies on the age-specific fecundity of ladybirds, which revealed the daily course of oviposition (complete ovipositional rhythm) and termed it as triangular fecundity function (Dixon, 2000; Omkar & Pervez, 2002; Dixon & Agarwala, 2002), no attempts have been made to observe any component of rhythmicity — either the complete ovipositional cycle or the diel pattern of oviposition.

The objective of this paper was to observe and determine the complete and diel ovipositional rhythmicity in three aphidophagous ladybirds, *Coccinella septempunctata* Linnaeus, *Coccinella transversalis* (Fabricius) and *Propylea dissecta* (Mulsant), common to India including areas adjoining the city of Lucknow (Omkar & Bind, 1993; Omkar & Pervez, 2004). These are native predators of aphids in the Oriental and Palearctic regions (Hussein, 1991; Omkar & Pervez, 2004), and can be easily reared in the laboratory due to their high fecundity (Parker & Singh, 1973; Agarwala & Bardhanroy, 1997; Omkar & Srivastava, 2002; Pervez, 2002). Knowledge of the ovipositional rhythm of a biological control agent can be useful in evaluating its efficacy and developing management strategies (Idoine & Ferro, 1990).

Material and Methods

Stock culture

Adults of three ladybird species, viz. *C. septempunctata*, *C. transversalis*, and *P. dissecta*, were collected from agricultural fields adjoining the city of Lucknow (India)

in 2002, and a stock culture was established in the laboratory at $25 \pm 2^\circ\text{C}$, $65 \pm 5\%$ R.H and LD 10:14. The adults were reared in the laboratory using locally and seasonally abundant aphid species as prey. Male and female adults were paired and allowed to mate in Petri dishes (9.0×1.5 cm). Eggs were collected daily and the hatched instars reared in glass beakers (11.0×9.0 cm) until pupation with daily replenishment of *ad libitum* prey. Newly emerged (NE) adults were immediately isolated and fed in Petri dishes (as above). *C. septempunctata* and *C. transversalis* were sexed by their size, as they show marked sexual dimorphism (male smaller than the female). *P. dissecta* adults were categorized on the basis of pronotal patterns; a crown-shaped black mark on the male pronotum and a triangular black mark on the female (Omkar & Pervez, 2000).

Experimental setup

Newly eclosed ladybirds were taken from stock and used in the experiments. The experimental ladybirds were provided with their most suitable prey, viz. *Aphis craccivora* Koch (on *Dolichos lablab* Linnaeus) for *C. transversalis* and *P. dissecta* and *Lipaphis erysimi* (Kaltenbach) (on *Brassica campestris* Linnaeus) for *C. septempunctata*. They were kept at 10L:14D (white light); this photoperiod was chosen to reflect the natural prevailing field conditions when the experiments were conducted in the winter months. The lights were on between 0700 and 1700 hours (photophase) and switched off between 1700 and 0700 hours (scotophase). A temperature of $25 \pm 2^\circ\text{C}$ during light phase and that of $15 \pm 2^\circ\text{C}$ during dark phase was provided in an attempt to simulate field conditions.

Complete ovipositional rhythm

Newly eclosed adults of ladybirds, viz. *C. septempunctata*, *C. transversalis* and *P. dissecta* were sexed and paired in transparent Petri dishes with an *ad libitum* supply of mixed instars of their preferred aphids (see above). Individual pairs were checked for eggs, and food replenished in excess every 24 hours. The pairs were transferred daily to a new Petri dish. Observations were taken daily at approximately the same time (between 0900 and 1100 hours) to minimize variation due to diel cycle fluctuations. The complete ovipositional rhythm, the oviposition and inter-oviposition periods were observed and interpreted by eye. The experiment was conducted in 10 replicates, with a reproducing pair constituting a replicate.

Diel ovipositional rhythm

To record the diel cycle of oviposition, mating pairs of each ladybird species were observed after every two hours from the 10 to 14th day of the ovipositional period of the ladybirds. The pairs were provided with an *ad libitum* supply of suitable aphids. There were 10 replicates of *C. septempunctata* and *P. dissecta*, and five replicates of *C. transversalis*, with a mating pair constituting a replicate.

Data analysis

Data on complete ovipositional cycle were subjected to second-order polynomial analysis. Schotzko and O'Keefe (1986) described this polynomial as an important statistical component of insect ovipositional rhythms. The daily oscillations and lunar fluctuations, if any, were deduced by observation of the plots of oviposition rate against time.

Data on diel ovipositional cycle were subjected to one-way ANOVA followed by Tukey's test of significance to determine the most favoured time for oviposition. Also, oviposition in the photophase (0700–1700) and scotophase (1700–0700) were analysed in the same way. To assess whether the diel rhythm changed significantly within the five days of observation, a two-way ANOVA was performed with the factors *n* day number and time of day. All statistical analyses were performed on PC using software MINITAB.

Results

Complete ovipositional rhythm

The complete oviposition cycle consisted of two components, the days when oviposition took place and the days between oviposition (the inter-oviposition periods). The total oviposition period (days of oviposition + inter-oviposition period) was 34.60 ± 1.48 days in *C. septempunctata*, of which there were 15.70 ± 2.90 days of oviposition and 18.90 ± 1.66 days of inter-oviposition periods. The inter-oviposition periods spanned 1.93 ± 0.18 days (range 1–6 days) and occurred 10.00 ± 0.59 times (range 6–12 times) in the entire oviposition cycle. The total number of eggs laid was 612.10 ± 45.20 . The trend of complete ovipositional cycle was Gaussian (inverted 'U'), with the peak in oviposition occurring on the 10th day of the oviposition cycle (Fig. 1a). The cycle was erratic with prominent peaks and troughs. The second-order polynomial equation describing the complete ovipositional cycle of *C. septempunctata* ($Y = -0.0271X^2 + 0.8389X + 13.047$; $r^2 = 0.2482$; $P < 0.01$) was significant. Visual inspection did not reveal the presence of a lunar rhythm. The total oviposition cycle in *C. transversalis* lasted for 50.80 ± 1.44 days, of which oviposition totalled 28.40 ± 1.46 days and the inter-oviposition period, 22.40 ± 1.27 days. The inter-oviposition periods spanned 3.47 ± 0.37 days (range 1–14 days) and occurred 6.90 ± 0.57 times (4–10 times) in the entire oviposition cycle. A total of 877.30 ± 39.90 eggs were laid during the entire ovipositional cycle. The peak in oviposition occurred on the 20th day of the oviposition period. The second-order polynomial regression equation describing the complete ovipositional cycle of *C. transversalis* ($Y = -0.0162X^2 + 0.5531X + 17.219$; $r^2 = 0.4808$; $P < 0.01$) was significant. There was no visual evidence for a lunar rhythm (Fig. 1b).

The oviposition cycle in *P. dissecta* extended to 40.70 ± 0.26 days while the fecundity was 945.80 ± 23.90 eggs. Oviposition attained its peak on the 19th day from the day of start of oviposition. The complete ovipositional cycle was suitably described by a second-order polynomial equation ($Y = -0.1001X^2 + 4.1609X - 5.9911$;

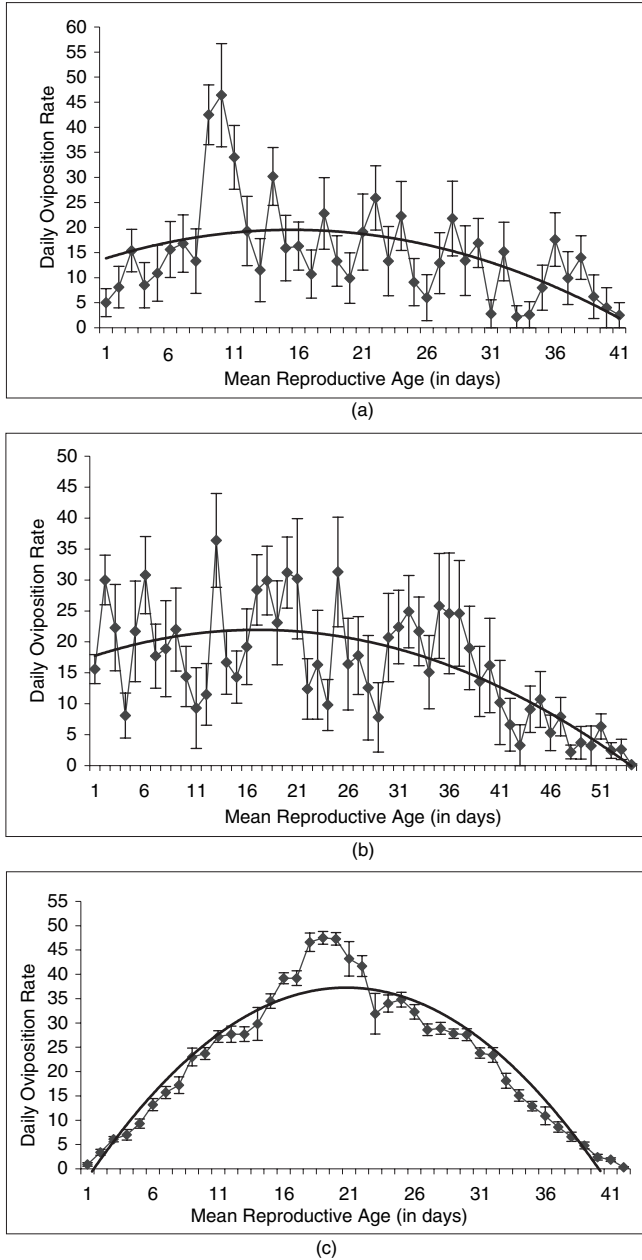


Figure 1. Complete ovipositional rhythms of (a) *C. septempunctata*, (b) *C. transversalis*, and (c) *P. dissecta*; Thin line denotes daily oscillations and bold line denotes second-order polynomial equation.

$r^2 = 0.9089$; $P < 0.001$). Daily egg laying was less erratic than in the other two species, and an inter-oviposition period of 0.17–1.17 days was recorded. In addition, the complete oviposition cycle was far more symmetrical than in the other two species (Fig. 1c).

Diel ovipositional rhythm

The differences in frequency of oviposition measured in 2-hourly intervals over the course of 24 hours in *C. septempunctata* were statistically significant ($F = 5.91$; $P < 0.001$; $df = 11, 108$), indicating a prominent diel rhythm (Fig. 2a). Maximum percent oviposition took place during 0500–0700 hours. The difference in oviposition between 0500–0700 and 0300–0500 hours was not statistically significant, thus revealing 0300–0700 hours (end of the scotophase) to be the preferred time for oviposition in this species. About $60.60 \pm 9.01\%$ of total oviposition took place in this timespan.

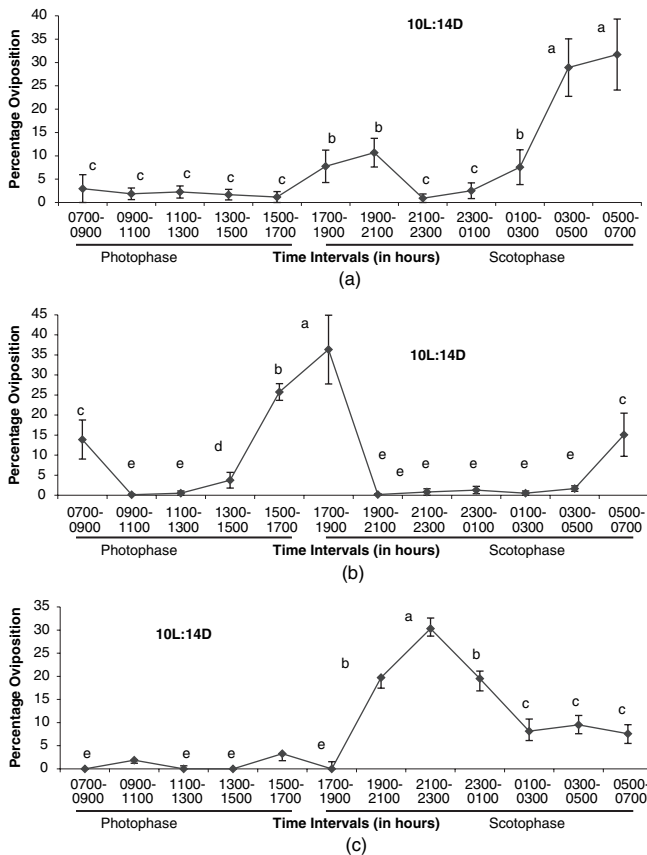


Figure 2. Diel ovipositional rhythms of (a) *C. septempunctata*, (b) *C. transversalis*, and (c) *P. dissecta* under 10L:14D (0700–1700 hrs photophase and 1700–0700 hrs scotophase); Values are Mean \pm SE.

2300–0100 hours was least frequent time for oviposition ($0.92 \pm 0.92\%$). When ovipositional data were divided into the number of eggs laid in the photophase and scotophase, ANOVA revealed a significantly higher percentage oviposition in the scotophase ($90.04 \pm 3.88\%$) ($F = 41.42$; $P < 0.001$). The diel ovipositional rhythm did not vary significantly between days when subjected to two-way ANOVA ($F = 0.57$; $P > 0.05$; $df = 4,540$).

Statistically significant differences over the course of 24 hours were found in mean two-hourly oviposition by *C. transversalis*, indicating a prominent diel ovipositional rhythm ($F = 19.47$; $P < 0.001$; $df = 11,108$; Fig. 2b). The time of maximum oviposition ($36.27 \pm 3.32\%$ of the total) occurred at 1700–1900 hours. The differences in oviposition in the scotophase and photophase were significant ($F = 20.01$; $P < 0.001$), with greater oviposition in the scotophase ($59.77 \pm 2.99\%$).

Unlike *C. septempunctata*, the diel rhythmicity pattern of *C. transversalis* varied significantly between days ($F = 4.49$; $P < 0.01$; $df = 4,240$; Fig. 3). An interesting observation of this variation in the diel ovipositional rhythmicity of *C. transversalis* was that on the first day there was a single peak of oviposition (1700–1900 hours) immediately after the start of scotophase. On the second day, peak oviposition was obtained at the same period as the prior day but oviposition in the two hours just previous to the peak (1500–1700 hours) increased significantly in comparison to the first day ($F = 19.98$; $P < 0.001$). On the third day, a second peak in oviposition was observed during the two hours before (0500–0700 hours) and after (0700–0900 hours) the commencement of the photophase. On the fourth and fifth days, the two peaks, at the LD and DL transitions, were equally marked (Fig. 3). The two morning peaks, viz. 0500–0700 ($F = 10.06$; $P < 0.01$) and 0700–0900 ($F = 9.14$; $P < 0.01$) differed more significantly than the two evening peaks, viz. 1500–1700 ($F = 5.81$; $P < 0.05$) and 1700–1900 ($F = 6.65$; $P < 0.05$) over the period of five days. A prominent diel rhythm was observed in *P. dissecta* ($F = 25.38$; $P < 0.001$; Fig. 2c) with maximum oviposition ($30.32 \pm 1.63\%$) in the middle of the scotophase, viz. 2100–2300 hours. Very few eggs were laid in the period 0700–1900 hours. *P. dissecta* oviposited a significantly higher percentage of eggs ($94.81 \pm 2.12\%$) during the scotophase ($F = 190.84$; $P < 0.001$). This pattern did not vary significantly between days ($F = 1.10$; $P > 0.05$).

Discussion

Our results show that the ovipositional rhythm in the three ladybird species studied here had both a complete ovipositional cycle and a prominent diel ovipositional cycle.

The complete ovipositional cycle of all three species had an ‘inverted U’ function, though, in the cases of *C. septempunctata* and *C. transversalis*, daily oscillations were also very prominent, probably owing to the presence of the inter-oviposition periods. *P. dissecta* on the other hand showed a very prominent and symmetrical ‘inverted U’ complete ovipositional cycle owing to daily oviposition with very little variation. The r^2 values of *C. transversalis* and *C. septempunctata* were lower than that of *P. dissecta*, probably owing to the inter-oviposition periods in the former two species.

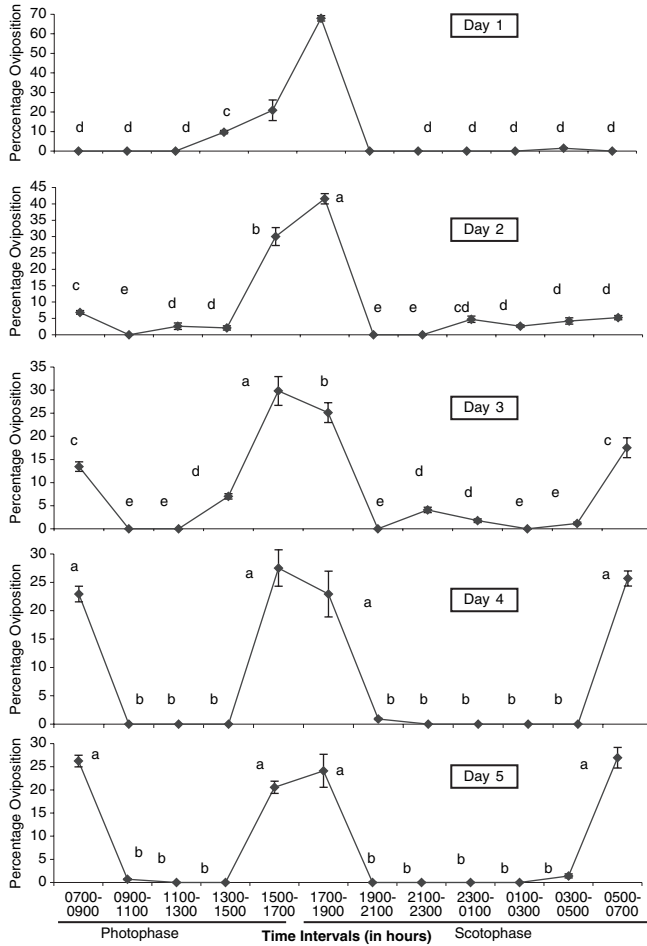


Figure 3. Diel ovipositional rhythms of *C. transversalis* on five days depicting the shifting of peaks under 10L: 14D (0700–1700 hrs photophase and 1700–0700 hrs scotophase); Values are Mean \pm SE.

In other insects (Schotzko & O’Keeffe, 1986; Wright et al., 1983; Strong et al., 1970), a third rhythmic component has been demonstrated — lunar fluctuations. However, this cycle length was not found in the species under consideration in this report.

All the three ladybird species showed prominent diel ovipositional rhythms. While *C. septempunctata* oviposited at the end of scotophase in the early morning, *C. transversalis* laid most eggs during the beginning of scotophase at dusk, and *P. dissecta* oviposited maximally in almost the middle of the scotophase at night. In all three species, significantly higher oviposition was found to take place in the scotophase.

Previously, the rhythms of ladybirds have been studied in terms of foraging activity and their presence in the field. Based on their activity levels, ladybirds are diurnal in nature (Hull et al., 1977; Mack & Smilowitz, 1978; Miura & Nishimura, 1980; Nakamuta, 1987). Ladybeetles, *C. septempunctata*, *Harmonia axyridis*, *Hippodamia convergens*, *Coccinella transversoguttata* and *Coleomegilla maculata* are found mostly in the field from 0900 to 1700 hours (Mack & Smilowitz, 1978; Miura & Nishimura, 1980). Larvae and both sexes of the ladybird *Stethorus punctum* ceased their feeding activity at dusk and resumed it at dawn (Hull et al., 1977). The increased foraging in the photophase could be a reason for the ovipositional peaks in the scotophase, since ladybirds are known to cannibalize and prey on eggs (Hodek & Honek, 1996; Dixon, 2000). Moreover, since oviposition increases the vulnerability of the female to predation and/or injury, its occurrence at a time when foraging and predatory activities are low would greatly enhance the females' chances of survival. Ovipositional peaks in the scotophase thus appear to be a survival strategy and of evolutionary significance.

The rhythms in *C. septempunctata* and *P. dissecta* did not vary during the five days of observation, suggesting it to be endogenous in nature and unaffected by extrinsic factors. The diel rhythm of *C. transversalis*, however, varied significantly; a single peak on day one was transformed to two peaks on the fifth day. The peaks occurred around the times of the onset and end of the scotophase. The variation was especially prominent in the morning peak, though the significance of this is not yet clear. This variation over the span of five days might indicate a role of LD cycle or of other exogenous factors, that is, that the cycle is endogenous and exogenous in origin. It might also possibly reveal conditioning to the photoperiod. The rhythm of *C. transversalis* is probably entrained by the light regime, while no such phenomenon was observed in *C. septempunctata* and *P. dissecta*.

Field studies of oviposition may benefit especially from a knowledge of biological rhythms, as it would help in the identification of the peaks of activity and thus in the conduct and design of experiments. Further, this knowledge may help in the evaluation of performance of a biocontrol agent, such as the ladybird, and in the development of management strategies such as the release of the species at a time when activity levels are low, so preventing immediate dispersion.

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