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## OVIPOSITION PATTERNS IN THE MYRMECOPHILOUS BUTTERFLY *MACULINEA ALCON* DENIS & SCHIFFERMÜLLER (LEPIDOPTERA: LYCAENIDAE) IN RELATION TO CHARACTERISTICS OF FOODPLANTS AND PRESENCE OF ANT HOSTS

**ABSTRACT:** To test the hypothesis of random oviposition by *Maculinea* butterflies we investigated the oviposition patterns of *M. alcon* Denis & Schiffermüller in wet meadows in the Vistula valley, southern Poland, in relation to the stem length and flower number of *Gentiana pneumonanthe* Linnaeus foodplants as well as to their spatial distribution, the height of the surrounding vegetation and the presence of potential ant hosts. Analysis conducted for 403 gentians recorded within the 0.96 ha study plot indicated that plants with *M. alcon* eggs present were significantly higher and had more flowers. On the other hand, neither the local density of gentians nor the presence of ant hosts had any apparent effect on oviposition preferences of *M. alcon*. Our conclusion is that females of the butterfly select visually conspicuous plants as the oviposition sites regardless of their clumping or ant presence. As a consequence, the two factors do not need to be included in computer models developed to study the population dynamics of the species and its trophic interactions with foodplants and ant hosts.

**KEY WORDS:** *Maculinea alcon*, oviposition patterns, *Gentiana pneumonanthe*, foodplant distribution, *Myrmica* ants

### 1. INTRODUCTION

All five species in the genus *Maculinea* van Eecke existing in Europe are highly endangered and listed in the European Red List (Munguira and Martin 1999, Van Swaay and Warren 1999). They are also unique because of their specialised life-styles. The larvae feed for a short time on specific foodplants and they are then adopted by *Myrmica* Latreille ants. In ant colonies they either prey on ant brood, in the case of 'predatory species' (*M. arion* Linnaeus, *M. nausithous* Bergsträsser, and *M. teleius* Bergsträsser) or are fed by nurse ants, in the case of the 'cuckoo species' (*M. alcon* Denis & Schiffermüller, and *M. rebeli* Hirschke) (Elmes *et al.* 1991a, b, Thomas and Wardlaw 1992). The availability of both specific foodplants and specific *Myrmica* ant hosts is essential for the survival of *Maculinea* butterflies. Hence trophic relations between the butterflies, their foodplants and ant hosts have attracted considerable interest among entomologists. Recently, computer simulation models (Hochberg *et al.* 1992, 1994, Elmes *et al.* 1996,

Clarke *et al.* 1997, 1998, Thomas *et al.* 1998) have been developed to study the population dynamics and interactions between the *M. rebeli*, its foodplant *Gentiana cruciata* Linnaeus, and its host *Myrmica schencki* Emery as well as other competing *Myrmica* species. Their results, confirmed empirically during field experiments, have proved that a too high density of foodplants ( $> 1500$  genets  $\text{ha}^{-1}$ ) leads to the overexploitation of host ant colonies by *M. rebeli* and thus to reduced population of the butterfly. All the models, however, were based on the assumptions that the butterflies lay their eggs on foodplants at random, and this does not necessarily have to be the case. Although some authors (Thomas 1977, 1984, Thomas *et al.* 1989) found that *Maculinea* butterflies oviposit regardless of the presence of colonies of the host ants or any other *Myrmica* species in the vicinity of foodplants, others (Figurny-Puchalska 1998, Wynhoff 2001) argued that they tend to select plants growing near host ant colonies. Furthermore, it is possible that the oviposition patterns are affected by the spatial distribution of plants, as found in some butterfly species (review in: Chew and Robbins 1984, Thompson and Pellmyr 1991). Both factors might have serious implications for the conservation of *Maculinea*. The negative impact of the butterflies on the host ant populations would be stronger than expected from the aforementioned models if they preferred to deposit eggs on isolated plants or near ant colonies, because few colonies would avoid parasitism. On the other hand, it would be weaker if the butterflies selected mainly plants within patches, as in such case the area between patches would remain a refuge for ants.

In our study we concentrated on the oviposition preferences of *M. alcon*, which resembles *M. rebeli* in many aspects of its ecology to the extent that for a long time both species were considered conspecific (Kaaber 1964, Wells *et al.* 1983). The aim of the study was to investigate habitat factors affecting the oviposition, with a special focus on the spatial distribution of the host plant *Gentiana pneumonanthe* as well as the presence of *Myrmica* ants.

## 2. MATERIAL AND METHODS

The study was conducted on the wet meadow complex of Królówki Wielkie located in southern Poland (50°01'N; 19°53'E), 6 km south-west of Cracow city centre. The meadows occupy the flat bed of the Vistula river valley, at an altitude of 207 metres above sea-level. A small population of *M. alcon* exists there sympatrically with two other species of the genus: *M. nausithous* and *M. telexus*. The site where *G. pneumonanthe* grows covers 3.92 ha (Pępkowska 2002). In recent years it has been partly mown in late spring, i.e. before the flowering season. For the data collection a 120 × 80 metre (i.e. 0.96 ha) plot was delimited within the site occupied by *G. pneumonanthe*. Excluding the mown strips its total area comprised 0.68 ha.

All genets of *G. pneumonanthe* found within the plot were marked with consecutively numbered brightly-coloured marks at the end of August 2001, i.e. directly after the end of the *M. alcon* flying season. The relative position of the genets within the plot was estimated to within 10-centimetre precision by measuring distances along established grid with measuring tapes. Subsequently, based on the position measurements, the local density of *G. pneumonanthe* – assumed to be a good measure of its clumping – was calculated for each genet. An area comprising a circle 10-metres in diameter with the genet in the centre was used each time for density calculations. We also measured stem length and the number of genet flower buds, as well as the height of the surrounding vegetation. Finally, the number of conspicuous white eggs of *M. alcon* on the genets was counted.

In order to reject the null hypothesis of random distribution of eggs, their observed distribution was compared to a fitted Poisson distribution using a goodness of fit Chi-square test. Subsequently the relationships between the number of eggs and the characteristics of genets were tested by stepwise multiple regression. The  $\log(n+1)$  ( $n$  being the number of eggs) was used as dependent variable in the model, while four independent variables included local density of gentians, their stem length, the number of flower buds and the height of surrounding vegetation. One-way ANOVA followed by the Tukey test were also

conducted. Four categories were defined in the analysis: (1) genets with no eggs; (2) genets with one egg; (3) genets with two to three eggs; (4) genets with four or more eggs. This classification was based on the assumption that females of *Maculinea* butterflies generally lay a single egg, but occasionally up to three eggs at one time (Thomas 1984, Thomas *et al.* 1991, Figurny and Woyciechowski 1998). Our own observations also confirmed this assumption, as most eggs we found were single and there was no case of a batch larger than three adjacent eggs. Therefore the four categories represented plants differently utilised by ovipositing females of *M. alcon*, from those completely avoided (category 1) to those accepted at least twice (category 4).

The presence of ants was investigated at the beginning of October, i.e. shortly after *M. alcon* larvae left flowers, fell to the ground and were adopted by *Myrmica* foragers. Ants were baited with sugar baits, placed on the ground directly under investigated gentians. Only isolated genets, situated at least 3 meters from all others (i.e. twice the average foraging range of a *Myrmica* colony according to Elmes *et al.* 1991a), were chosen for the analysis so as to avoid the spatially autocorrelated data. Ants were collected three times on 2nd October (at 8.30 a.m., 12.30 p.m. and 5.00 p.m.) and later classified to the species. Since only five nests of *M. scabrinodis* (the host ant of *M. alcon* in Poland – (Sielezniew and Stankiewicz 2001, authors' unpublished data)) were found, to make the analysis powerful all three species of *Myrmica* known to be hosts of the butterfly in other European locations, i.e. *M. ruginodis*, *M. rubra* and *M. scabrinodis* (Thomas *et al.* 1989, Elmes *et al.* 1994) were considered as the potential hosts. The presence of eggs of *M. alcon* on gentians and the presence of host ants under them (during at least one of the three occasions) were compared with Fisher's exact test. To compare average number of eggs on gentians in the proximity of *Myrmica* nests and in the absence of the ants, the Kolgomorov-Smirnov test was used.

### 3. RESULTS

We recorded 403 genets of *G. pneumonanthe* within the studied plot, which corre-

sponded to a mean density of 593 genets per hectare. Overall, 745 eggs of *M. alcon* were found on 158 genets, i.e. the mean number of eggs equalled 1.8 per genet, and 4.7 per genet with eggs. More than 60% of genets lacked eggs and more than 10% had merely a single egg present, while the maximum number of eggs found on a genet reached 26 (Fig. 1). The distribution of eggs was therefore skewed and clearly differed from the Poisson distribution ( $\chi^2 = 1132.6$ ,  $df = 5$ ,  $P < 0.0001$ ).

Stem length of genets and their numbers of flower buds (positively) as well as the height of surrounding vegetation (negatively) significantly affected the number of oviposited *M. alcon* eggs, together explaining almost 15% of its variation in the stepwise multiple regression (Table 1). On the other hand the effect of local density of gentians could not be detected, despite the considerable range of densities recorded (127–2930 per ha). This variable remained insignificant even when we tried to change the diameter of the circle used for calculations of the gentian density. The findings were confirmed by the ANOVA results (Fig. 2), which revealed that the genets with *M. alcon* eggs had significantly more flowers (mean > 10 in all three categories) than those lacking eggs (mean = 6.5). A similar pattern was found in the case of genet stem length – ovipositing butterflies tended to select higher plants, while rejecting shorter ones. The relationship between the number of eggs and the height of vegetation was also significant though less obvious, with the highest vegetation surrounding gentians with a single egg (mean = 57.6 cm), and the lowest recorded around those with more than three eggs (mean = 51.2 cm), whereas in the case of the local density of gentians once again there was no evident pattern.

Forty isolated (i.e. > 3 m distant from the nearest neighbour) gentians were found, and 20 of them had *M. alcon* eggs present. Ants collected under 17 gentians included all three species of potential hosts of the butterfly, i.e. *Myrmica ruginodis*, *M. rubra* and *M. scabrinodis*. There was no relationship between the presence of *M. alcon* eggs and the presence of potential ant hosts as proved by Fisher's exact test ( $P = 1.00$  for the total numbers from the Table 2). Similarly, the number of

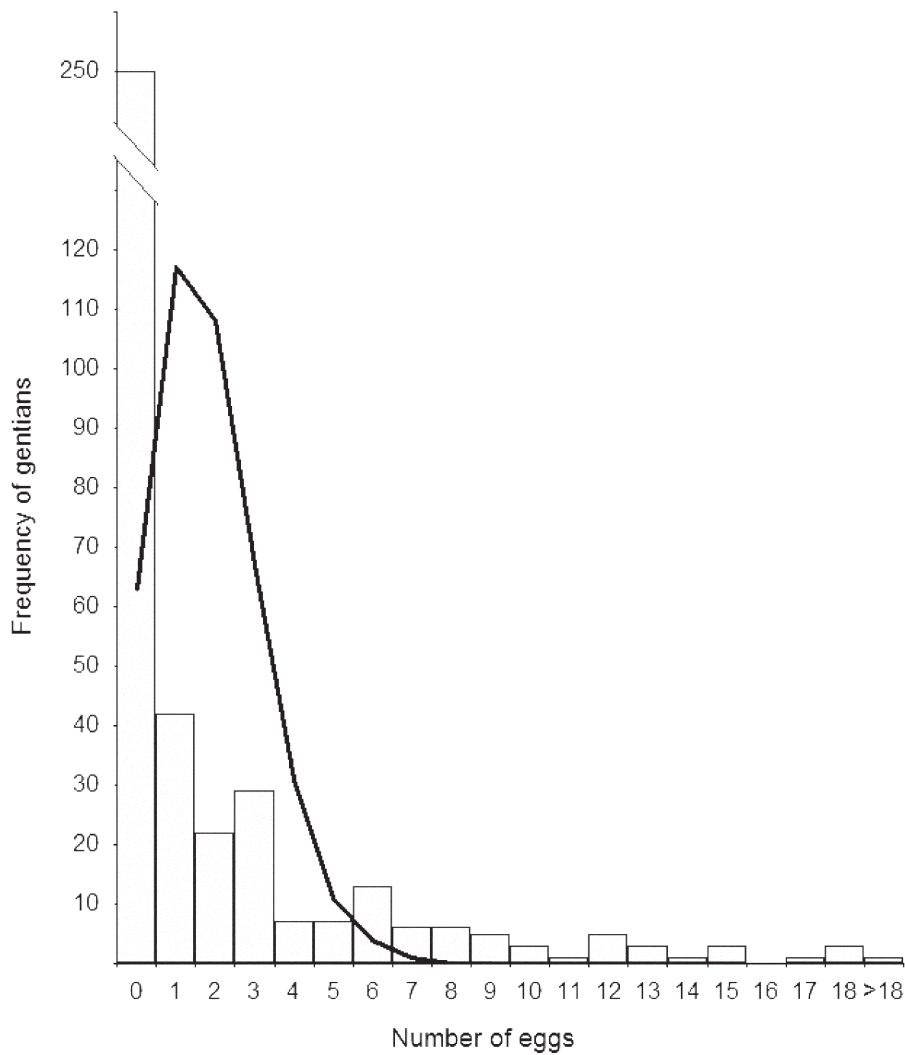


Fig. 1. Distribution of *Maculinea alcon* eggs recorded on 403 genets of *Gentiana pneumonanthe*. Solid line represents fitted Poisson distribution presented for comparison.

Table 1. The influence of four investigated parameters of *Gentiana pneumonanthe* on the number of eggs oviposited by *Maculinea alcon* (expressed as  $\log(n+1)$ , where  $n$  is the number of eggs) tested by stepwise multiple regression.

Independent variable	Partial r	R <sup>2</sup>	t	df	P
Number of flower buds	0.256	0.1104	5.28	401	<0.0001
Height of surrounding vegetation	-0.165	0.0219	-3.35	400	0.0009
Stem length	0.118	0.0139	2.36	399	0.0186
Local density	-0.068	0.0039	-1.35	398	0.1773
Constant			1.49	398	0.1380

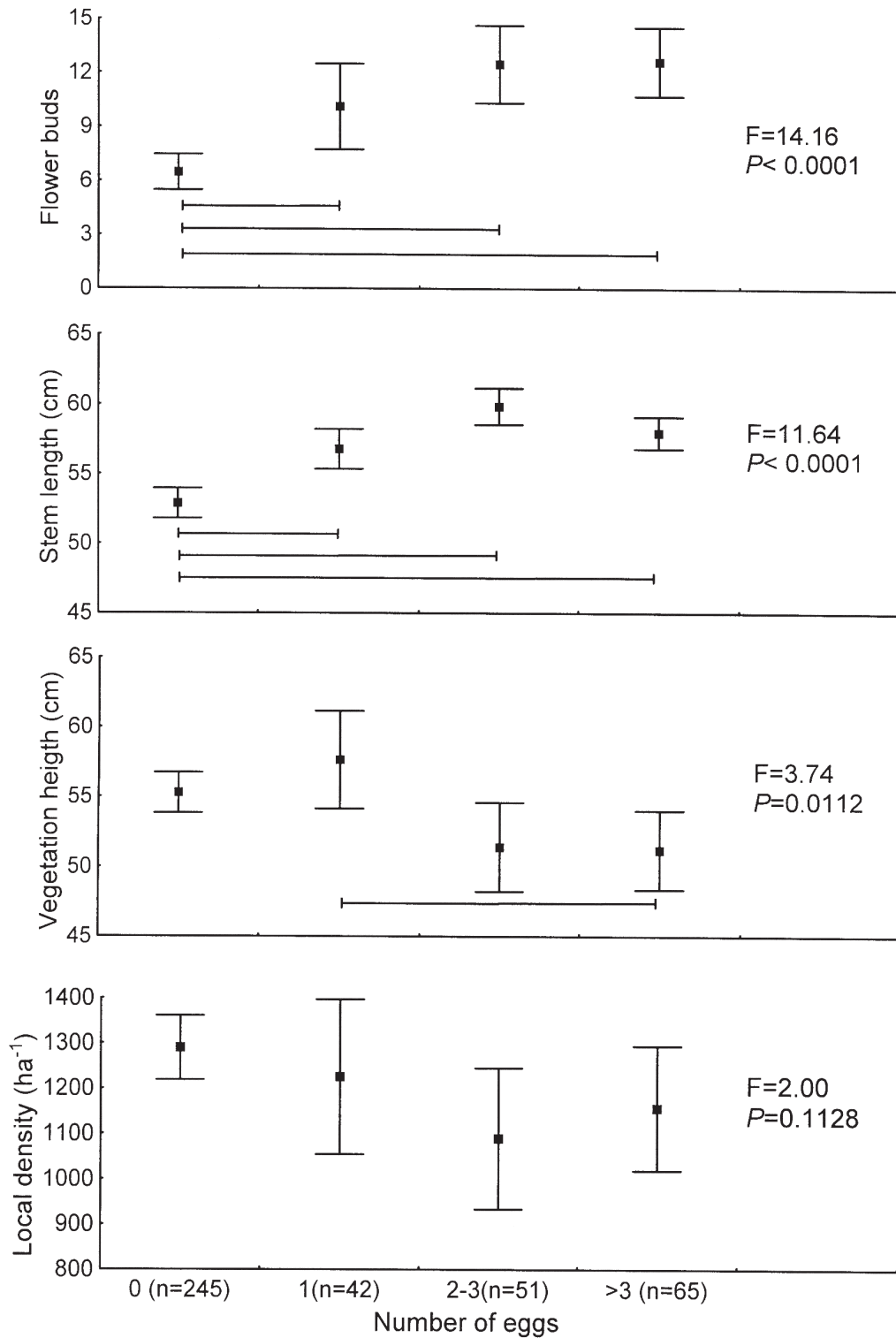


Fig. 2. Differences in the characteristics of *Gentiana pneumonanthe* in relation to the numbers of *Maculinea alcon* eggs found on them (for each category mean values and Tukey HSD intervals are presented; arrows indicate significantly different categories at 0.95 confidence level revealed by ANOVA).

Table 2. Ant species recorded under 40 isolated genets of *Gentiana pneumonanthe* in relation to the presence of *Maculineaalcon* eggs.

Ant species present	Number of gentians	
	with <i>M.alcon</i> eggs	without <i>M.alcon</i> eggs
<i>Myrmica ruginodis</i>	7	4
<i>M. rubra</i>	1	0
<i>M. scabrinodis</i>	0	5
None	12	11
Total: potential ant host	8	9
Total: no potential ant host	12	11

eggs on gentians in the presence of ants did not differ from those laid on gentians where ants were absent (Kolgomorov-Smirnov test,  $D = 0.242$ ,  $P > 0.1$ ).

#### 4. DISCUSSION

Both *Maculineaalcon* and *M. rebeli*, which evolved an efficient 'cuckoo' strategy of feeding within ant nests, are known to lay eggs at high densities (Thomas *et al.* 1991). In the Netherlands Thomas *et al.* (1991) found 9.6 *M.alcon* eggs per genet on average, while egg density in seven out of nine populations of this species investigated by Schep er *et al.* (1995) exceeded 3.5 per genet. Egg density in extensively studied *M. rebeli* colonies in the Pyrenees, the Alps, and the Jura Mountains was even higher, exceeding 15 per genet (Elmes *et al.* 1996, Kery *et al.* 2001). The density of *M.alcon* eggs recorded in our study (1.8 per genet) was considerably lower than the aforementioned figures, which suggests a very small population. Assuming that: (1) a single *M.alcon* female oviposit 150 eggs during a season (since we do not know of any relevant data for the species, we use the value stated for *M. rebeli* by Hochberg *et al.* 1992), (2) the sex ratio in the population is 1:1, and (3) the studied plot comprised approximately one fourth of the area covered with *Gentiana pneumonanthe*, the size of the population in the study area (see Material and Methods) can be estimated at about 40 individuals. Nevertheless, it seems that the population, and therefore also its ovipositing preferences, may be considered representa-

tive of the species, which often occurs in small, but stable isolated colonies supported by a few hectares of suitable habitat (Elmes and Thomas 1992, Elmes *et al.* 1994, Gadeberg and Boomsma 1997).

Our results indicate that the number of flower buds and their stem length are among the factors affecting the number of *M.alcon* eggs laid on gentians. Kery *et al.* (2001) noted that the number of *M. rebeli* eggs was also positively correlated with the stem length of *G. cruciata*. Selection of high plants with a large number of blooming flowers for oviposition is a pattern commonly found in butterflies (Thompson and Price 1977, Thompson 1978, Myers *et al.* 1981, Courtney 1982). The most probable explanation is that ovipositing females choose visually conspicuous plants as their primary targets. The larger egg numbers that we found on gentians surrounded by lower vegetation are also consistent with this explanation.

On the other hand, we failed to demonstrate any effect of the local density of foodplants on the oviposition patterns of *M.alcon*. In fact, few studies have managed to prove that butterflies accept or reject certain plants as oviposition sites with regard to their relative position within a community (Singer 1984, Thompson and Pellmyr 1991). Furthermore, in many such cases the preference for clumped or isolated plants actually resulted from their greater size and better visibility (Cromartie 1975, Thompson and Price 1977, Thompson 1978, Forsberg 1987) or was a side-effect of regular female

movements between nectar and oviposition sites (Courtney 1981, Murphy 1983).

As for *Maculinea*, whose larval survival strictly depends on the likelihood of adoption by *Myrmica* ants, much controversy arose around the question whether the presence of ants is a determinant for oviposition patterns of the genus. The conclusion of early studies (Thomas 1977, Thomas 1984, Thomas *et al.* 1989) was that *Maculinea* lay their eggs on phenologically suitable foodplants regardless of the presence of *Myrmica* ants, let alone the correct host species. Recently, however, Wynhoff (2001) suggested that ant-mediated oviposition occurs in *M. nausithous* and to some extent also in *M. teleius*. The evidence for the existence of the same phenomenon in *M. alcon* was provided by Van Dyck *et al.* (2000), though it was criticised by Thomas and Elmes (2001). Our results suggests that egg-laying females of this species do not select foodplants visited by host ant foragers. There may be two possible explanations for the presented conflicting findings. First, the ability to detect ant presence is beneficial if foodplants are far more abundant than ant colonies and consequently many of them are sinks for larvae. Therefore, it is likely to have evolved in *M. nausithous* and *M. teleius*, whose foodplant *Sanguisorba officinalis* usually grows at extremely high densities. On the other hand, *M. alcon* and *M. rebeli* may do well without similar adaptation as their *Gentiana* foodplants are rare and unevenly distributed. Second, as noted by Wynhoff (2001), ant-mediated oviposition may presumably be noticed only if field investigations are conducted at the beginning of the flying season. Later in the season, selecting plants lacking conspecific eggs seems to be much more important, since *Maculinea* larvae experience high density-dependent mortality during the period of feeding on foodplants (Elmes and Thomas 1987, Hochberg *et al.* 1992, Thomas *et al.* 1998).

To summarise, present research demonstrated that the visibility of foodplants, determined by their height (especially in relation to the height of surrounding vegetation) and the number of flowers, has the decisive impact on the oviposition preferences of

*M. alcon*. On the other hand, we did not record any effect of neither the spatial distribution of foodplants nor the presence of ants, and thus both main hypotheses of our study could not be confirmed. This seemingly negative conclusion has a major constructive aspect for the conservation of *Maculinea*. It indicates that, as far as the species using gentians as their foodplants are concerned, the spatial models of the butterfly population dynamics (e.g. Hochberg *et al.* 1994, Clarke *et al.* 1997, 1998) may yield reliable results without the incorporation of the additional factor concerning the oviposition patterns, which would otherwise substantially complicate these models.

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