BioControl (2025) 70:747–757
https://doi.org/10.1007/s10526-025-10339-9

Influence of refuge availability on the oviposition strategy of anachoretic and non-anachoretic aphidophagous ladybirds

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Received: 18 February 2025 / Accepted: 18 July 2025 / Published online: 28 July 2025

Abstract *Scymnus nubilus* Mulsant and *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) are two generalist aphidophagous predators abundant in herbaceous habitats. *C. undecimpuctata*, a larger species, lays its eggs in uncovered clusters, whereas *S. nubilus*, a tiny species, lays its eggs singly and, possibly, in concealed sites. Reproductive strategies in ladybirds seem to be adaptive, allowing the co-occurrence of both predators, apparently without interfering with each other. The aim of this study was to characterize the following oviposition strategies in *S. nubilus* and *C. undecimpunctata*: daily fecundity, effect of available sites on females' fecundity, and circadian rhythmicity of oviposition. We hypothesize that the single-egg-laying strategist (1) is more dependent on the availability of concealed sites to oviposit and (2) lays eggs closer to aphid colonies. We found that different levels of site concealability allows *S. nubilus* to increase fecundity. Contrary to *C. undecimpunctata*, in the absence of a suitable substrate to conceal its eggs, *S. nubilus* females refrain ovipositing. *S. nubilus* prefers to hide their eggs beneath prey carcasses while *C. undecimpunctata* is less selective concerning the oviposition sites. *S. nubilus* dilutes its fecundity effort through more oviposition sites and events, while *C. undecimpunctata* requires one event to lay its clusters. Our results showed that the smaller ladybird is more dependent than the larger one on habitat structural complexity to maximize its fitness and that laying a single hidden egg mainly during the scotophase confers a potential adaptive advantage to increase fitness.

Keywords Oviposition strategy · Single egg-laying · Cluster egg-laying · Circadian rhythmicity of oviposition · Coleoptera · Coccinellidae

Introduction

Ladybird females are able to select the most suitable oviposition sites to ensure development of eggs and larvae. Relying on their sensorial orientation, based on visual and olfactory cues, Coccinellidae females have to balance between several environmental factors

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Handling editor: Marta Montserrat.

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that could sometimes be conflicting: host finding, host suitability, proximity of prey, predation risk, and microclimate conditions (Obata 1986; Merlin et al. 1996; Seagraves 2009). Ladybird females usually lay their eggs in the area where they feed (Seagraves 2009). *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae) lay near large aphids colonies (Sloggett and Majerus 2000), whereas *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) oviposit far from colonies (Michaud and Jyoti 2007). Here arises a trade-off: if the eggs are laid too close to aphid colonies the predation risk increases since the aphid colonies attract intraguild predators and if the eggs are laid too far the progeny could not find the prey (Sloggett and Majerus 2000; Michaud and Jyoti 2007).

In nature, insects display different oviposition strategies that evolved in order to increase the reproductive success of species (e.g., Kindlman and Dixon 1993; Peckarsky et al. 2000; Holland et al. 2004; Almohamad et al. 2008; Almohamad et al. 2010; Azimizadeh et al. 2012; Gonzalez et al. 2023). Usually, insect females lay their eggs in clusters, on the surface of the host plants (Seymour 1974; Stamp 1980; Porter 1982; Tabashnik 1983; Davies and Gilbert 1985; Agarwala and Dixon 1993; Dixon and Guo 1993; Clark and Faeth 1998; Hemptinne and Dixon 2000; Agarwala and Yasuda 2001; Timms and Leather 2007). However, other insect species, including ladybirds, lay their eggs singly (e.g., Coccidophagous ladybirds) or concealed in the habitat on the underside of leaves, in crevices of the substrate or beneath undigested remnants of eaten preys (e.g., Aleyrodidae ladybirds) (Arakaki 1988; Agarwala and Dixon 1993; Völkl 1995; Hemptinne and Dixon 2000; Agarwala and Yasuda 2001; Brown et al. 2004).

Apparently, most of the ladybird species can be roughly divided into anachoretic (concealed—single egg laying) and non-anachoretic (exposed—cluster egg laying) strategists. Their fecundity and the ability to hide the eggs could be related to body size and thus can be adaptive. Indeed, Courtney (1984) showed that egg clustering reproductive tactics, in some insect groups such as Lepidoptera, Diptera, Hemiptera and Hymenoptera, is not only a response to the characteristics of the host plant, e.g., its structure and ecology, but also a response to increase fecundity.

The aim of this study was to characterize the following components of the oviposition strategies of the anachoretic *Symnus nubilus* Mulsant (Coleoptera: Coccinellidae) and the non-anachoretic *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae), corresponding to single egg laying strategist *vs* a clustering egg laying strategist, respectively: (1) daily fecundity, (2) effect of refuge availability on females' fecundity (hide/not hide; far/close to aphid colonies) and (3) circadian rhythmicity of oviposition. We hypothesize that: (1) the anachoretic single egg laying strategist will be more dependent on the availability of oviposition refuge sites, which is not the case for the non-anachoretic species with the cluster strategy, (2) the anachoretic species should lay eggs closer to the aphid colony (since numerous suitable oviposition sites are present there) whereas the cluster strategist should lay eggs far from the colony.

Material and methods

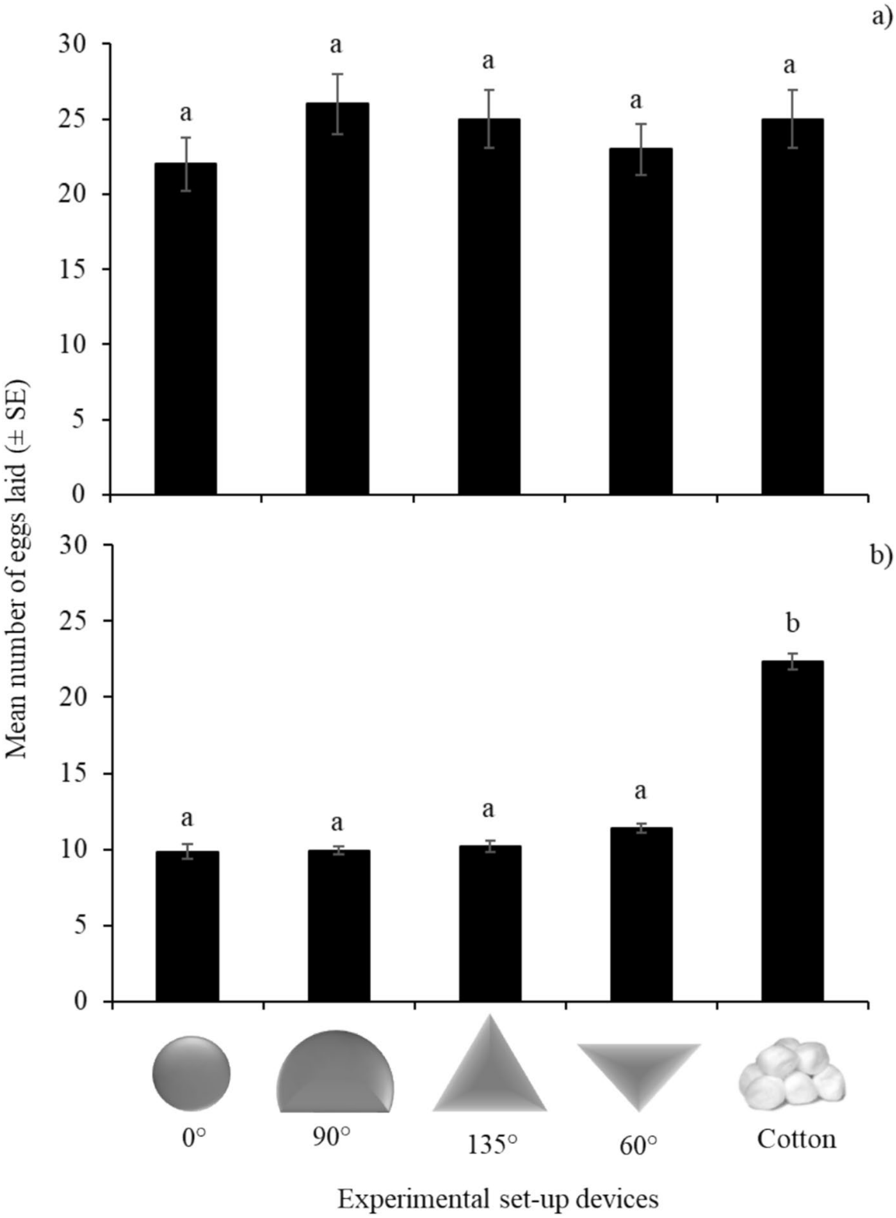
Biological material

Adults of *S. nubilus* and *C. undecimpunctata* were collected in São Miguel and Santa Maria islands (Azores, Portugal), respectively, where they are commonly observed (Soares et al. 2017, 2021). Ladybirds were reared in the laboratory at 25 ± 1ºC, 75 ± 5% RH, under a L:D 16:8 photoperiod using fluorescent lamps (Philips ref. TDL 36W/54). To maintain laboratory populations, optimal prey was used: *Aphis fabae* Scopoli for *S. nubilus* (Borges et al. 2024) and *Myzus persicae* Sulzer, for *C. undecimpunctata* (Cabral et al. 2006).

Availability of refuge sites on fecundity of *S. nubilus* and *C. undecimpunctata* females

This experiment comprises five treatments in which five different experimental set-up devices were offered to ovipositing females of *S. nubilus* and *C. undecimpunctata*. Each device has (or not) specific angles, corresponding to different hiding-places for eggs. Inside of a Petri dish (10 cm diameter) one of the following devices (made using white cardboard paper) was added: no corner (sphere), 90 degree corner (hemisphere), 135 degree corner, 60 degree corner, and a dish with a small piece of cotton (see pictorial representation on x-axis of Fig. 1). One 15-day old ovipositing female was released in the Petri dish

Fig. 1 Mean number of eggs laid (± SE) by *C. undecimpunctata* (**a**) and *S. nubilus* (**b**) females in the experimental set-up devices used to test the effect the availability of refuge sites on fecundity. Different letters indicate significant differences (One-way ANOVA or Kruskal–Wallis tests, followed by a Bonferroni post-hoc test; $p < 0.05$)



for 24 h and the number of eggs laid was counted after this period. The number of replicates per treatment was 20.

The effect of the availability of refuge (concealed sites) on females' fecundity

This experiment was carried out in a 2 l acrylic box, inside of which there was a host plant of *Vicia faba* L. with 15 cm height infested with fresh prey, in an amount sufficient to fulfil the needs of the reproducing females for 24 h. Three different treatments were set, corresponding to different simulated conditions that females may find in nature: (1) plant infested with fresh prey (IP), (2) plant infested with fresh prey and prey carcasses (IPC), (3) plant infested with fresh prey and three pieces of bark with 5 cm length (IPB). The prey carcasses and pieces of bark were placed next to the aphid colonies. A 15-day old ovipositing female was released inside of the acrylic box. After

24 h, eggs and their location were noted (far from aphid colonies in the wall of the box) or close to aphid's colonies, including the carcasses or pieces of bark. The number of replicates per treatment was 22.

Circadian rhythmicity of oviposition of *S. nubilus vs C. undecimpunctata* females

To assess circadian rhythmicity of oviposition of each ladybird species female, we provided the preferred set-up device for their oviposition (tested in the experiment 1), that is, devices where the highest number of eggs were laid (cotton for *S. nubilus* and hemisphere to *C. undecimpunctata*). The devices were placed inside a Petri dish (10 cm diameter). A 15-day old ovipositing female was released in the corresponding Petri dish, again provided with *ad libitum* suitable aphids. The laid eggs were counted hourly, from 7 am to 6 pm, and an additional count at 10 pm. Egg counts carried out between 8 am and 6 pm were labeled "early" and the remaining as "late" (mostly after the climate chamber light has been turned off). After each daily observation, females were transferred into a new Petri dish with the same experimental device. This experiment was conducted for three days. The number of replicates was 21.

Statistical analysis

Kolmogorov–Smirnov and Levene's tests were used to assess normal distribution and homogeneity of variances of data, respectively. When data meets requirements to run parametric tests, t-tests or ANOVA were used, otherwise a Kruskal–Wallis test (χ^2) was performed. Mean values were considered significantly different when $p < 0.05$.

Differences in *S. nubilus* and *C. undecimpunctata* daily fecundity depending on the availability of refuge sites (factors tested were the experimental set-up devices) were analyzed using one-way ANOVA, followed by a Bonferroni post-hoc test. However, we first ran a two-way ANOVA to contrast the independent factors species and experimental set-up devices. A Kruskal–Wallis (χ^2) test was performed to analyze the effect of available concealed refuge sites on females' fecundity, followed by a Bonferroni post-hoc test, and a t-test to contrast circadian rhythmicity of oviposition between ladybird species. The proportion of eggs laid (far from aphid colonies in the wall of the box) or close to aphid's colonies, including the carcasses or pieces of bark and earlier and later, was compared with a χ^2 test. All statistical analyses were done using SPSS v. 27 (IBM Corp 2020).

Results

Availability of refuge sites on fecundity of *S. nubilus* and *C. undecimpunctata* females

There was significant interaction between the independent variables: set-up devices and ladybird species on daily fecundity of ladybirds ($F_{4,590} = 11.668$, $p < 0.0001$). For this reason, we analyzed independent factors separately. We found that the average number of eggs laid by *C. undecimpunctata* females ranged from 21 to 26 and did not significantly differ according to the experimental set-up devices ($F_{4, 295} = 1.226$, $p = 0.3$) (Fig. 1a). For *S. nubilus* females, daily fecundity ranged from 10 to 22 and only differed when the experimental set-up device was cotton ($\chi^2 = 134.278$, df = 4, $p < 0.001$) (Fig. 1b).

The effect of the availability of refuge (concealed site) on females' fecundity

The number of eggs laid by *C. undecimpunctata* females was significantly lower (5.67 ± 1.34) than that of *S. nubilus* females (8.05 ± 0.74) ($\chi^2 = 25.189$, df = 1, $p < 0.001$). *S. nubilus* females laid significantly more eggs (6.59 ± 1.16 *vs* 1.18 ± 0.91) ($\chi^2 = 17.065$, df = 1, $p < 0.001$) in the treatments with a plant infested with fresh prey (IP) and the plant infested with fresh prey and prey carcasses (IPC) (10.77 ± 1.52 *vs* 5.35 ± 2.39) ($\chi^2 = 12.474$, df = 1, $p < 0.001$). For the treatment with plants infested with fresh prey and three pieces of bark with 5 cm length (IPB), no significant differences were found 10.5 ± 2.82 *vs* 6.77 ± 0.96) ($\chi^2 = 0.71$, df = 1, $p = 0.4$).

Mean number of eggs laid by *C. undecimpunctata* females significantly differed between treatments ($\chi^2 = 8.125$, df = 2, $p = 0.017$), being lower when the set-up device included only a plant infested with fresh prey (IP) and was higher when comprised of a plant infested with fresh prey and three pieces of bark (IPB) (Fig. 2a). For *S. nubilus* females, no significant differences between the mean number of eggs laid was found ($\chi^2 = 4.522$, df = 2, $p = 0.104$) (Fig. 2b).

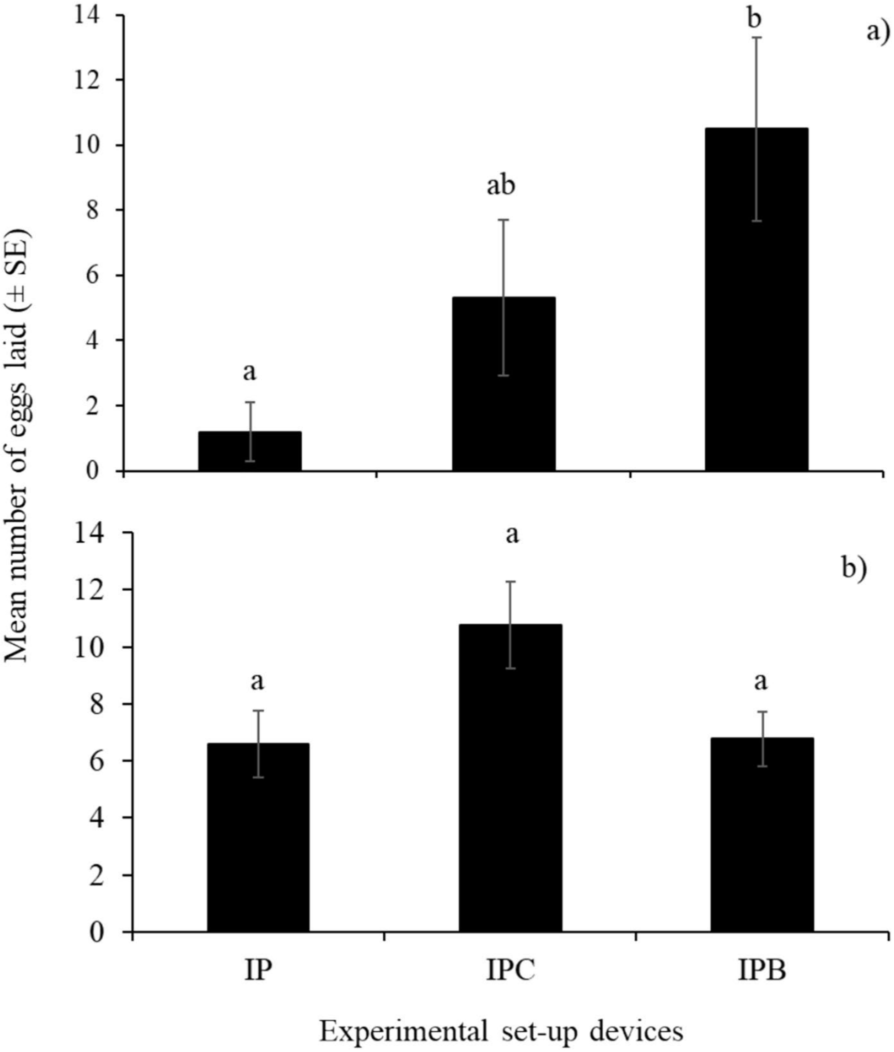


Fig. 2 Mean number of eggs laid (± SE) by *C. undecimpunctata* (**a**) and *S. nubilus* (**b**) on IP: infested plant; IPC: infested plant and prey carcasses; IPB: infested plant and bark. Different letters indicate significant differences (Kruskal–Wallis test, followed by a Bonferroni post-hoc test; $p < 0.05$)

Concerning the proportion of the eggs laid on the available substrate to oviposition *vs* on acrylic box, we found, in general, that *C. undecimpunctata* females (n = 22) laid a higher proportion of eggs far from the aphid colonies (Fig. 3a), whereas *S. nubilus* females (n = 22) laid a higher proportion of eggs close to the aphid colonies (Fig. 3b). Except for IPB set-up device ($\chi^2 = 0.000$, df = 1, $p = 1$), *C. undecimpunctata* females laid a higher proportion of eggs on the sides of the acrylic boxes, away from the aphid colony (IP: $\chi^2 = 53.678$, df = 1, $p < 0.00001$; IPC: $\chi^2 = 21.263$, df = 1, $p < 0.00001$; Fig. 3a). *S. nubilus* females laid a higher proportion of eggs close to or on the devices, near to the aphid colony (IP: $\chi^2 = 5.952$, df = 1, $p = 0.0147$; IPC: $\chi^2 = 27.920$, df = 1, $p < 0.00001$; IPB: $\chi^2 = 27.920$, df = 1, $p < 0.00001$; Fig. 3b).

Circadian rhythmicity of oviposition of *S. nubilus vs C. undecimpunctata* females

During this experiment, *C. undecimpunctata* laid significantly more eggs than *S. nubilus* (t = 5.54, df = 82, $p < 0.001$; Fig. 4). However, from 7 am to 6 pm with hourly observations, we recorded 54 oviposition events for *C. undecimpunctata* and 110 for *S. nubilus.* The mean number of hourly oviposition events differed significantly for both species ($\chi^2 = 14.345$, df = 1, $p < 0.001$). We also found a tendency for oviposition events to occur during

Fig. 3 Proportion of eggs laid (± SE) by *C. undecimpunctata* (**a**) and *S. nubilus* (**b**) on the oviposition substrate or boxes in the treatments IP: infested plant; IPC: infested plant and prey carcasses; IPB: infested plant and bark. * and ns means significant and not statistically significant, respectively (χ^2 test; $p = 0.05$). Asterisks along each single bar contrast the proportion of eggs laid on the oviposition substrate *vs* acrylic boxes

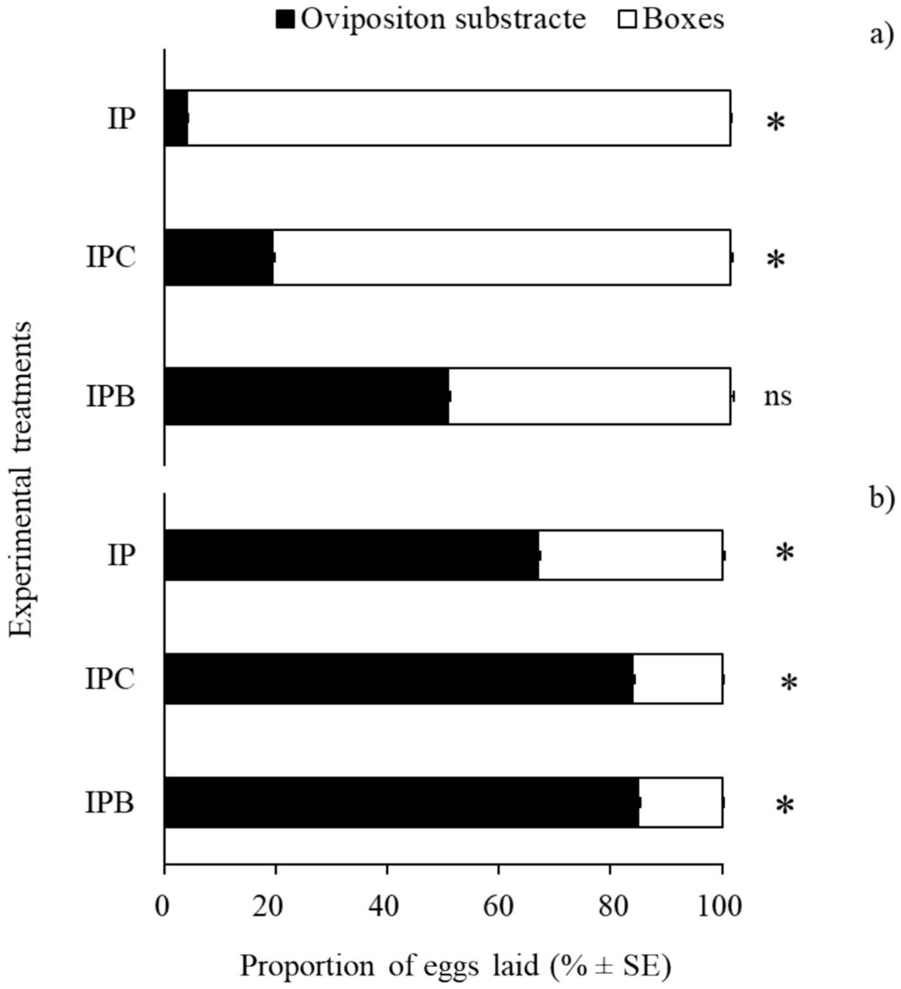
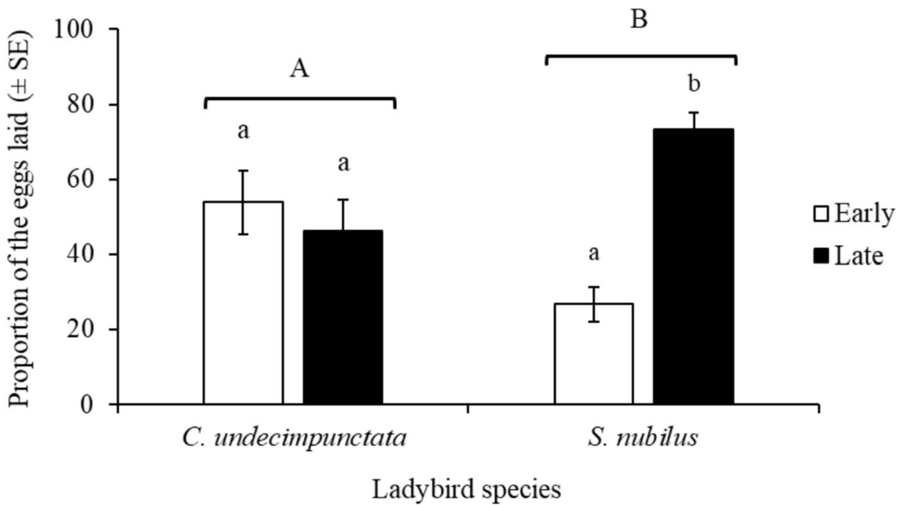


Fig. 4 Proportion of egg number laid (± SE) by *C. undecimpunctata* and *S. nubilus* from 8 am and 6 pm (Early) and from 6 pm 7 am (Late). Different letters indicate significant differences: capital letters refer to statistical significance between ladybird species (t-test; $p = 0.05$) and lowercase letters to the proportion of egg laid earlier and later (χ^2 test; $p = 0.05$)



scotophase, significantly for *S. nubilus* ($\chi^2 = 61.212$, df = 1, $p < 0.00001$), but not for *C. undecimpunctata* ($\chi^2 = 3.354$, df = 1, $p = 0.067$) (Fig. 4).

Discussion

Although having a similar fecundity, the non-anachoretic C. *undecimpunctata* lays its eggs in clusters while the anachoretic *S. nubilus* lays eggs singly, displaying a contrasting circadian rhythmicity of oviposition. So, what are the pros and cons of laying eggs in clusters *vs* singly? Seymour (1974) and Porter (1982) have shown that egg clusters promote thermoregulation efficiency, since each single individual will benefit from the heat loss by siblings. Another advantage of egg clusters is that the hatching success is positively related to the RH. For single eggs and small clusters, the hatching success is lower once the exposed area is larger, and the probability of desiccation is high (Stamp 1980; Clark and Faeth 1998). Laying eggs all together reduces the search for new places to oviposit and, thus, the risk of not being able to find a new site, this consequently allows females to save energy and reduce the risk of mortality (Stamp 1980). Another key factor associated with the clustered strategy is the reduction of predation risk. A group of biological individuals (including eggs and pupae) may generate an encounter effect, dilution effect and selfish herd effect, three passive defensive strategies (Lucas and Brodeur 2001; Dumont et al. 2015; Roberge et al. 2015). In coccinellids, Agarwala and Yasuda (2001) showed that, for *Menochilus sexmaculatus* (Fabricius) and *Coccinella transversalis* (Fabricius) (Coleoptera: Coccinellidae), egg clusters were less attacked by predators than single eggs illustrating that this strategy is an important mechanism of defense against predators. Another remarkable characteristic of egg clusters is their chemical shield. Predators are often deterred from attacking clusters over single eggs due to the presence of alkanes on the egg surface (Agarwala and Dixon 1993; Hemptinne and Dixon 2000). This chemical defense increases from single eggs to pure clusters, so single eggs are more vulnerable to predation (Agarwala and Yasuda 2001).

Larval mobility could play an important role in the oviposition site selection. Hemptinne et al. (2000b) developed the "social feeding" hypothesis to explain the clustering strategy. Neonate larvae are very vulnerable, and their survival depends on how quickly they can obtain their first meal. The capture success of the first young larval instar is low (Fréchette et al. 2008) and a successful capture attracts its siblings, so after a period several larvae may feed on the same aphid individual. So, young lady beetle larvae hatched from clusters improve their survival probabilities to the next stage compared to those hatching from single eggs. Experiments developed by Moore et al. (2012) in *Adalia bipunctata* L. (Coleoptera: Coccinellidae) support this hypothesis. However, *S. nubilus* females seems to balance that disadvantage by protecting the eggs in concealed places, including hiding them inside of and beneath aphid carcasses.

We found that *C. undecimpunctata* (Coleoptera: Coccinellidae) females laid a higher proportion of its eggs in the acrylic box surface, far from the aphid colony, whereas *S. nubilus* females laid close to aphid colonies (beneath aphid carcasses and into bark crevices). Previous studies showed that *A. bipunctata* females tend to lay on the surface of host plants near aphid colonies, which results in higher egg mortality compared with *C. maculata* which oviposit at the bottom of the host plant far from aphid colonies (Schellhorn and Andow 1999). When females are searching for an oviposition site, they must ensure that their larvae will have access to food. However, if they lay eggs far from aphid colonies their offspring may starve, but if they oviposit too close, their progeny will be under higher risk of cannibalism and/or intraguild predation (Michaud and Jyoti 2007). Since the predation risk increases with the proximity of the aphid colonies (shared extraguild resource), eggs of species ovipositing close to colonies will suffer a higher mortality compared to those laying eggs far from prey colonies (Hemptinne and Dixon 2000; Hemptinne et al. 2000a), with the exception of furtive predators whose eggs are protected by the aphid colony (Lucas and Brodeur 2001; Dumont et al. 2015). Oviposition deterring pheromones also mediates the oviposition site choice in Ruzicka (1994). Our results suggest that *C. undecimpunctata* reduces the risk of predation on its eggs by ovipositing freely on the surface of the box, far from prey colonies and benefiting from passive group defensive strategies, whereas that *S. nubilus*, by ovipositing near prey aggregations, mitigates this risk by hiding its eggs in refuge (the underside of the leaves, in the crevices of the substrate or beneath undigested remnants of eaten aphids) and at the same time ensuring that their young larvae would have access to a food resource (Lucas et al. 1998). We found that *C. undecimpunctata* slightly decreased fecundity. A possible explanation could be that the confined experimental set-up does not give females enough oviposition options further away from the aphid colonies and, as such, it reduces its fecundity.

Circadian rhythmicity of oviposition by *C. undecimpunctata* and *S. nubilus* differs. Scattering the eggs in time and space may confer an advantage given it dilutes the risk of natural enemies finding them (Taylor 1977; Inman and Krebs 1987). Many activities of ladybirds take place during the day, whereas they rest during the night (Nedvěd and Honěk 2012). However, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) females preferred to oviposit at the end of the scotophase and in the early photophase hours. *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae) lay 86% of its eggs during the early half of scotophase (Mishra and Omkar 2004). *Coccinella transversalis* (Fabricius) lay most by dusk, i.e., at the beginning of the scotophase (Omkar et al. 2004). In *Cheilomenes sexmaculatus* (Fabricius) (Omkar and Singh 2007), the peak of oviposition (62%) was attained during early scotophase. The oviposition preference during scotophase on the smaller species *S. nubilus* may be seen as a strategy of life cycle desynchronization promoting guild partition, and reducing interactions with other predators, including *C. undecimpunctata*. For instance, interactions between *A. bipunctata* and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Japan may be avoided by desynchronization of their occurrences (Toda and Sakuratani 2006) and temporal guild partition has often been reported (Lövei and Radwan 1988; Brown 2004; Dixon 2007). However, further work is needed to evaluate the adaptive significance of each strategy.

In this study we contrasted the oviposition strategies of the anachoretic *S. nubilus* corresponding to small and single egg laying strategist and the non-anachoretic *C. undecimpunctata*, corresponding to larger and clustered egg laying strategist. Our results suggest that oviposition by females of *S. nubilus* increases with architectural complexity of the habitat, compared to *C. undecimpunctata*. The anachoretic species (1) laid more eggs in more complex experimental-set-ups providing hiding sites for the eggs (e.g., in a piece of cotton), (2) laid eggs closer to aphid colonies, and (3) hided the eggs beneath prey carcasses. Furthermore, *S. nubilus* females (4) diluted oviposition effort through more oviposition sites and events, (5) laid eggs mainly during the scotophase. The complex oviposition behaviour of *S. nubilus* is clearly adaptive. However, the extent to which this behaviour confers an advantage will depend on numerous factors linked to the environment, the aphid populations and the guild considered. Indeed, the oviposition strategy is a complex issue that involves numerous factors and additional experiments are required. For instance, oviposition deterring pheromone present in the tracks of conspecific larvae, prevent *A. bipunctata* to oviposit. This is also adaptive as larval cannibalism is a major threat to egg survival (Hemptinne et al. 2001). Females of *H. axyridis* produce more infertile eggs when starvation risk for offspring is greater. These infertile eggs (i.e., trophic eggs) seem to result from a maternal strategy to feed offspring (Perry and Roitberg 2005). From an evolutionary perspective we may ask to what extent do the oviposition strategies demonstrated in the present study also result from phylogenetic constraints? Indeed, the species under the scope of this study were from Coccinellini (*C. undecimpunctata*) and Scymnini (*S nubilus*) tribes. Further experiments are required to disentangle the role of phylogenetic *vs* ecological constraints in the contrasted strategies.

Author contributions António O. Soares and Isabel Borges: Conceptualization. António O. Soares and E. Lucas: methodology. Marta Vale Isabel Borges: formal analysis. Marta Vale: investigation. António O. Soares, Isabel Borges, Marta Vale and Eric Lucas: writing—Original draft preparation and review António O. Soares: supervision. António O. Soares: project administration. António O. Soares: funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding Open access funding provided by FCT|FCCN (b-on). Fundação para a Ciência e Tecnologia, FCT-UIDB/00329/2020-2024, António Onofre Soares, Agência Regional para o Desenvolvimento da Investigação, Tecnologia e Inovação, UID/00329/2025, António Onofre Soares.

Data availability Not applicable.

Declarations

Conflict of interest All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Ethical approval This research does not involve humans or animals.

Informed consent All authors agreed with the content and that all gave explicit consent to submit and that they obtained consent from the responsible authorities at the institute/organization where the work has been carried out, before the work is submitted.

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