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# Exploring the searching efficacy of *Macrolophus pygmaeus* and *Nesidiocoris tenuis* (Hemiptera, Miridae) on different *Tuta absoluta* (Lepidoptera, Gelechiidae) egg densities and distribution patterns

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## Abstract

*Tuta absoluta* is a notorious pest causing serious economic damages in tomato crops, worldwide. *Macrolophus pygmaeus* (*Mp*) and *Nesidiocoris tenuis* (*Nt*) are the most important natural enemies of this pest. However, their predation rates have been studied only in Petri dishes when *T. absoluta* eggs were placed randomly on a tomato leaflet. Our study aimed to compare *Mp* and *Nt* efficacy in locating and consuming *T. absoluta* eggs when offered at three densities (3, 5 and 8 eggs/dish) and four distribution patterns: i) the natural oviposition pattern (the one most frequently) followed by *T. absoluta* females ovipositing the respective egg number on a leaflet, ii) the linear pattern, by placing the eggs on the central vein, iii) the clumped pattern, placing them in a group and iv) the peripheral, placing them close to the leaflet edge. After 15´, 30´ and 60´ the number of consumed eggs was recorded. Results showed that both predators had similar prey searching efficiency when the eggs were positioned following the natural egg distribution pattern. However, when the eggs had been placed following the clumped pattern (at 3 and 5 egg density), *Mp* consumed more eggs than *Nt* 15´ and 30´ after their releasing. In addition, *Mp* consumed more eggs than *Nt* when placed following the linear egg distribution, 15´ after predator releasing. Consequently, *Mp* showed higher adaptability in prey searching than *Nt*. These results indicate that *Mp* may be more efficient than *Nt* to locate and consume *T. absoluta* eggs when laid following different distribution patterns.

## Key Words

natural enemy, omnivorous, oviposition behaviour, prey, predation, tomato, tomato pinworm

## Introduction

The generalist predators *Macrolophus pygmaeus* (Rambur) (*Mp*) and *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) (*Nt*) are important biological agents against serious agricultural pests of tomato crops including the tomato leafminer *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae). Following the appearance of this pest in Europe, the predation capacity of these two predators against *T. absoluta* was one of their first traits to be assessed as directly associated with their efficacy in the pest control (De Backer et al. 2014; Biondi et al. 2018; Ferracini et al. 2019). Both predatory species have been proved mostly efficient preying on *T. absoluta* eggs and their predation capacity has been found to reach similar levels (Arnó et al. 2009; Mollá et al. 2009, 2014; Urbaneja et al. 2009). For this reason, they are considered of similar efficacy, because both species share also similar identities such as polyphagy and plant feeding ability (Perdikis and Lykouressis 2000; Castañé et al. 2011; Pérez-Hedo et al. 2020). In addition, *Nt* may activate the plant defense through its feeding behaviour reducing egg oviposition of *T. absoluta* (Sarmah et al. 2022). However, *Nt* may cause damage to tomato plants by plant feeding (Perdikis et al. 2009; Castañé et al. 2011; Moerkens et al. 2020; Souto et al. 2022) whereas *Mp* damage is considered as exceptional (Castañé et al. 2011; Sanchez et al. 2018). This difference in their plant feeding behaviour may be associated with their success rate in prey searching i.e. more phytophagous species may be less efficient (Gillespie and Mcgregor 2000; Li et al. 2016). In this context, a previous study showed that the two predatory species had a different success rate in locating *T. absoluta* eggs when placed on tomato plants following the different egg distribution patterns of *T. absoluta* females (Dervisoglou et al. 2022). These differences indicate that *Mp* and *Nt* may differ in their prey searching behavior, however this potential has not been studied explicitly.

The predatory behavior of an insect predator depends on its prey density and distribution (Yasuda and Ishikawa 2001; Gontijo et al. 2010; Higginson and Ruxton 2015). Nevertheless, the prey searching efficiency of *Nt* and *Mp* has been searched only in dishes with a tomato leaflet on which *T. absoluta* eggs were offered to the predators randomly (e.g. Arnó et al. 2009; Urbaneja et al. 2009; Michaelides et al. 2017). In fact, the females of Lepidoptera and other insects make decisions in their egg laying behavior and may oviposit their eggs following certain oviposition patterns. This strategy is aiming to ensure food availability for their offspring and to increase their fitness (Fretwell and Lucas 1970; Thompson and Pellmyr 1991) as well as may aim to reduce exposure of their offspring to natural enemies (Plath et al. 2012; Castagneyrol et al. 2013). Studies on the egg laying behavior of *T. absoluta* on tomato plants proved that females showed preferences in their egg laying among the plant parts (i.e. lower, middle and upper plant strata) (Torres et al. 2001; Leite et al. 2004; Cherif et al. 2013; Galdino et al. 2015). Even more, in a more detailed study, Dervisoglou et al. (2022) showed that when the density of *T. absoluta* females was increased the females followed an adaptive behavior spreading their eggs to a larger part of the plant canopy. Therefore, variability in density and the respective spatial distribution of *T. absoluta* eggs on tomato leaves due to the active decisions of *T. absoluta* females may differentially affect the efficacy of *Mp* and *Nt*.

The effect of different prey densities (i.e. eggs of the mite *Tetranychus pacificus* McGregor) when offered following different distribution patterns (i.e. uniform, random, clumped) was searched on the searching efficiency and predation capacity of the mite predators *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius degenerans* Berlese (Acari: Phytoseiidae). *Phytoseiulus persimilis* found faster the eggs when placed following the clumped oviposition pattern while *A. degenerans* detected the eggs faster when the eggs were uniformly distributed (Eveleigh and Chant 1982). Similarly, in the case of the predator *Franklinothrips orizabensis* Johansen (Thysanoptera: Aelothripidae) more eggs of its prey were consumed when the eggs had been distributed in a circle than in more complicated patterns (i.e. snowflake or triangle) (Hoddle 2003). These results reveal that changes in the complexity of prey distribution and its density may significantly affect efficacy of a predator species in pest control. However, an aspect that has been largely ignored in studying predation rates is that prey species such as *T. absoluta* may deposit their eggs selecting certain oviposition patterns. For this reason, results of studies assessing predation by randomly or intentionally distributing prey items may not show the potential of a predator species to locate its prey under more field-realistic conditions.

The aim of this study was to investigate the foraging behavior of the two predators, *Mp* and *Nt* when *T. absoluta* eggs deposited in typical patterns used by Lepidoptera vs the exact pattern followed by *T. absoluta* females (i.e. natural ovipositional pattern), at three egg densities. This information will offer valuable insights into assessing the predators' comparative efficacy in regulating *T. absoluta* populations.

# Materials and methods

## Plant material

Tomato plants (Elpida F1, Spirou S.A., Athens) developed from seeds in an air conditioned glasshouse of the Laboratory of Agricultural Zoology and Entomology under natural lighting. The plants were inspected daily and any pest found on them was removed. Tomato plants were fertilized at 15 d intervals (Chemical Nutri-Leaf 20-20-20 Miller Chemical & Fertilizer Corporation Hanover, Pennsylvania 17331 USA) (3 gr/Lt).

## Insect rearing

A colony of *T. absoluta* was established by larvae collected from tomato fields located in Marathonas region (23°58.050'N, 38°06.683'E), 42 Km North of Athens. The *T. absoluta* rearing was kept on tomato plants placed in entomological cages (35 × 35 × 60 cm) (BioQuip, Compton CA, USA) by adding 10% honey solution. The cages were kept at 25 ± 1 °C, 65 ± 5% RH, 16:8 L:D. The rearings of *Mp* and *Nt* were maintained on potted tomato plants in the glasshouse as reported above. Adults and nymphs of *Mp* were collected from a tomato field in Co. Boeotia (23°18.29'N, 38°35.28'E), 108 km NW of Athens. *Nt* were purchased by Koppert Biological Systems, The Netherlands (Nesibug™). Eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) mixed with *Artemia* sp. cysts (Entofood™, Koppert Biological Systems, Rotterdam) were added on plant leaves *ad libitum* as prey for the predators.

## Experimental setup

The experiments were conducted in Petri dishes (9 cm diameter and 1.5 cm high). The top cover of each dish had a round hole (3 cm diameter), covered with fine muslin to avoid excessive humidity inside the dish. A layer of moistened cotton was put on the base of the dish and a tomato leaflet was placed upside down by adding the prey (*T. absoluta* eggs, <24 h old). Three densities of *T. absoluta* eggs were offered to the predators (3, 5 and 8 eggs). Those eggs densities were used because according to our previous observations the females may lay up to 8 eggs in a single leaflet even when used at high densities (10 females per young plant) (Dervisoglou et al. 2022). In that study in a screened cage a tomato plant was placed and *T. absoluta* adults (<24 h old) were released at the following ratios: 1♀:2♂, 2♀:2♂, 3♀:3♂ and 10♀:10♂. The number of eggs laid and their position (i.e., leaf, leaflet per leaf) on the tomato plant was recorded, 24 h later. Then, the most frequent oviposition pattern followed by the females when ovipositing 3, 5 or 8 eggs on a single leaflet was selected to be used as the natural oviposition pattern in the experiments of the current study (Table 1, Fig. 1). In each combination of female and egg density 15 leaflets had been examined (n = 15).

**Table 1.** Frequency (%) of the most common oviposition pattern followed by *T. absoluta* females when ovipositing 3, 5 or 8 eggs on a single leaflet when 1, 2, 3 or 10 females had been released in a cage with a tomato plant.

| Egg density | 1♀:2♂ | 2♀:2♂ | 3♀:3♂ | 10♀:10♂ |
|---|---|---|---|---|
| 3 | 86% | 86% | 80% | 73% |
| 5 | 73% | 80% | 80% | 80% |
| 8 | NA | NA | 73% | 86% |

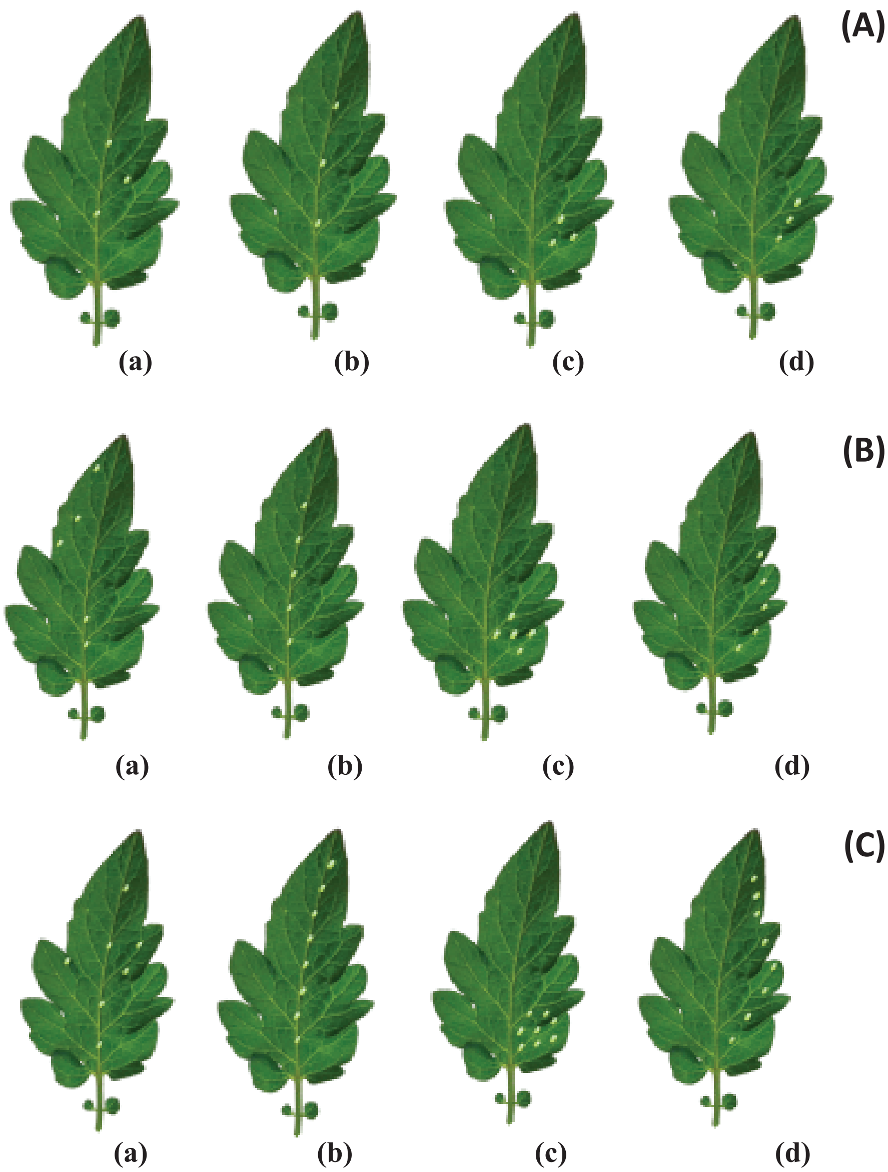


**Figure 1.** Schematic diagram representing the position of *Tuta absoluta* eggs placed on a tomato leaflet following different distribution patterns ((a) natural oviposition, (b) linear, (c) clumped and (d) peripheral) when 3 (**A**), 5 (**B**) or 8 (**C**) eggs were used per leaflet.

In each replicate (i.e. a dish with a leaflet with eggs placed on it a single nymph of *Mp* or *Nt* (5th instar), which had been previously starved of prey for 24 h, was released in the center of the arena and its predation rates were recorded in three time periods (15´, 30´ and 60´ after its release). The number of consumed *T. absoluta* eggs during the three periods was recorded without removing the dishes from the climatic chamber to avoid predator's disturbance. In each egg density tested and based on our previous results, *T. absoluta* eggs were distributed on the tomato leaflet according to the natural oviposition pattern. In addition, eggs were distributed on the leaflet following three patterns resembling those commonly followed by Lepidoptera (i.e. clumped, linear and peripheral pattern followed by *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) (Busck 1917), *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Rahman et al. 2019) and *Drepana arcuata* Francis Walker (Lepidoptera: Drepanidae) (Yadav and Yack 2018), respectively. In the clumped pattern the eggs were positioned close to each other, in the linear pattern the eggs were positioned along the central vein of the leaflet and in the peripheral pattern the eggs were positioned in the margin of the leaflet (Fig. 1). Experimental arenas were kept under controlled conditions (25 ± 1 °C, 65 ± 5% RH and 16:8 h (L:D)). Ten replicates (dishes) were used per treatment (i.e. egg density and distribution pattern).

## Statistical analysis

The data on the total number of eggs consumed by the predators *Mp* and *Nt* in each period (15´, 30´ and 60´) were analyzed by Generalized Linear Mixed Models (GLMM) with a normal distribution and a identity link function. The factors were the "predator species", "prey density" and "prey distribution pattern" and their interactions, followed by a Student t- test to separate means. Analyses of data did not show significant differences at 60´ (almost all prey items were consumed, results not presented). Analyses were conducted with the statistical package JMP 18.0 (SAS Institute 2018).

# Results

The number of *T. absoluta* eggs consumed 15´ after the initiation of the experiments was significantly affected by the factor "predator species", "oviposition pattern" and the interaction of "oviposition pattern" and "predator species" (the factor "density" was not significant and excluded from the analysis) (F = 4.10, df = 1,231, P < 0.044, F = 3.23, df = 3, 231, P < 0.021, F = 3.0, df = 3, 231, P < 0.03, respectively). At the density of 3 *T. absoluta* eggs, *Mp* consumed significantly more eggs than *Nt* when the eggs were offered following the clumped or the linear pattern (Fig. 2A). At the egg density of 5 eggs per leaflet again *Mp* consumed more eggs than *Nt* when eggs had been placed following the clumped distribution pattern (Fig. 2B).

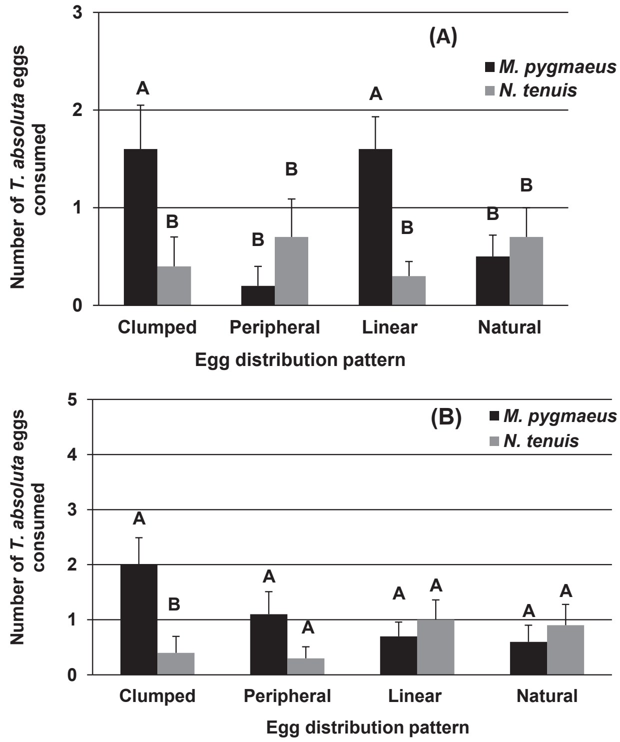


**Figure 2.** Total number (mean ± SE) of *T. absoluta* eggs consumed when 3 eggs (**A**) or 5 eggs (**B**) offered in four distribution patterns (clumped, peripheral, linear and natural), 15´ after releasing *Mp* and *Nt*. Columns followed by a different capital letter differ significantly between the two predator species within each egg distribution pattern.

The predation rates of *Mp* and *Nt* recorded 30´ after the initiation of the experiments were affected by the interaction of "oviposition pattern" and "predator species", and the main effects of the "prey density" and the "oviposition pattern" (F = 4.46, df = 3,224, P < 0.0046, F = 19.4, df = 1,2242, P < 0.0001, F = 3.12, df = 3,224, P < 0.026, respectively). At the density of 3 *T. absoluta* eggs *Mp* consumed significantly more eggs than *Nt* when the eggs were offered following the clumped pattern (Fig. 3A). Similar results recorded in the case of the 5 eggs where again *Mp* consumed more eggs than *Nt* (Fig. 3B).

In the density of 8 *T. absoluta* eggs offered no statistically significant differences were recorded for both predators in all tested oviposition patterns.

# Discussion

According to our results, *Mp* was able to detect and consume the eggs much faster than *Nt* when the eggs were offered following either the clumped or the linear distribution pattern 15 min after their release in the dish. *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) was proposed as a better biological agent for the aphid control in comparison to *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae) since its adults consumed more aphids 4 h after their releasing in a Petri dish (Sarmad et al. 2015).

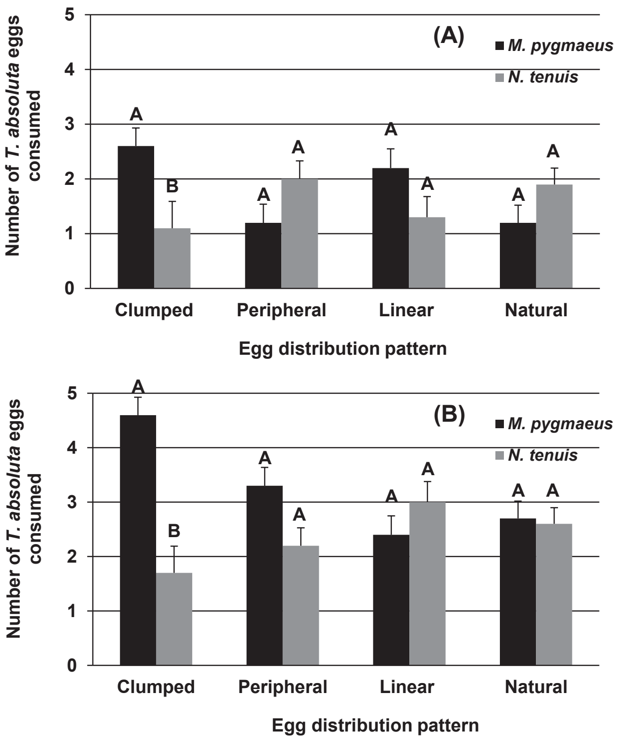


**Figure 3.** Total number (mean ± SE) of *T. absoluta* eggs consumed when 3 eggs (**A**) or 5 eggs (**B**) offered in four distribution patterns (clumped, peripheral, linear and natural), 30´after releasing *Mp* and *Nt*. Columns followed by a different capital letter differ significantly between the two predator species within each egg distribution pattern.

In another study held by Delgado-Ramírez et al. (2019), larvae of *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) consumed more aphids than larvae of *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) 30 mins after the initiation of the experiments. For this reason, these authors suggested that the former species may be more effective at locating the prey and thus may contribute more to aphid control than the latter one. *Harmonia axyridis* Pallas and *C. septempunctata* consumed more aphids than other coccinellid species 30 and 60 mins after their release in a Petri dish exhibiting higher efficacy in aphid control according to Bertleff et al. (2021).

The results showed the higher adaptability of *Mp* than *Nt* in prey searching and consuming eggs of *T. absoluta* when laid at variable patterns suggesting a higher efficacy of *Mp* than *Nt* in the control of *T. absoluta*. This is also supported by the fact that the egg distribution patterns under field conditions may be variable although the two predator species showed a similar efficacy in consuming the eggs offered following the oviposition pattern of *T. absoluta* females. This is because several factors may affect the selection of oviposition sites by the *T. absoluta* females such their density (Dervisoglou et al. 2022), the tomato leaf quality (Cherif et al. 2013), the climatic conditions (Martins et al. 2018) or the tomato variety due to i.e. different trichome densities which affect *T. absoluta* infestation (Salem et al. 2016; Sohrabi et al. 2016; Bitew 2018). In relevant experiments conducted in tomato plants, *Mp* fifth instar nymph showed a higher efficacy at intermediate *T. absoluta* egg densities than *Nt* (Dervisoglou et al. 2022). A recent study showed that *Mp* exhibited a better predation efficiency than *Nt* on *T. absoluta* eggs due to its higher attack rate and lower handling time (Yiacoumi et al. 2024). Finally, it is important to note that the differences between *Nt* and *Mp* were found at the lowest prey densities used. Therefore, *Mp* may be more effective in locating and consuming eggs of *T. absoluta* when the pest population is establishing and building up, suggesting again a higher efficacy of this predator against *T. absoluta*.

Our results further showed that *Mp* consumed more eggs when eggs were distributed close to each other (i.e. clumped distribution). The distribution of eggs in clumped pattern may facilitate the hemipteran predators to detect and consume their prey due to their foraging strategy "find and stay". According to the theory, mirids consume all the eggs which are detected in a clutch before moving on, in contrast to anthocorids which follow the strategy of "eat and run" (Björkman et al. 2003).

According to our results at all density treatments in which eggs were placed following the natural oviposition pattern of *T. absoluta* females, both predators effectively found and consumed them. Theory predicts that Lepidoptera may select their oviposition sites aiming to provide their offspring with adequate food sources for their development (Fretwell and Lucas 1970; Jaenike 1978; Thompson and Pellmyr 1991; Bonebrake et al. 2010) whereas experimental evidence has shown that selection of oviposition sites may also aim to reduce exposure of their offspring to natural enemies (Price et al. 1980; Plath et al. 2012; Castagneyrol et al. 2013). However, according to our results oviposition sites may be selected by the females of *T. absoluta* most likely to ensure food resources for their offspring development. Finally, our results seem to support the hypothesis that more phytophagous species may be less efficient in pest control (Gillespie and McGregor 2000; Li et al. 2016).

# Conclusions

Conclusively, although *Mp* and *Nt* have been considered as of similar efficacy in the control of *T. absoluta*, our results indicate that *Mp* may be more efficient showing a better adaptability in locating eggs of *T. absoluta* than *Nt*. Future studies should compare predation efficiencies under more complicated environments (i.e. plants) and further incorporate field-based trials to evaluate whether higher efficacy translates in improved *T. absoluta* control.

# Author Contribution

Conceptualization, D.P. and A.A.; methodology, D.P., A.A. and S.D.; validation, D.P. and A.A.; investigation, S.D.; resources, S.D.; data curation, D.P. and S.D; statistical analysis, D.P. and S.D.; writing-original draft preparation, D.P. and S.D.; writing-review and editing, D.P., A.A. and S.D.; supervision, D.P.; project administration, D.P..

## Data availability statement

The data of this study are available on request from the corresponding author.

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