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Morphological identification and biological observations of *Lopheucoila mexicana* (Hymenoptera, Figitidae, Eucoilinae), a parasitoid of *Neosilba batesi* (Diptera, Lonchaeidae) in avocado

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Abstract

The lance fly *Neosilba batesi* (Curran, 1932) (Diptera: Lonchaeidae) has traditionally been regarded as a secondary colonizer of damaged fruits, yet recent observations suggest it may infest developing avocado (*Persea americana* Miller, 1768) fruits and contribute to premature fruit drop. Despite its potential economic importance, little is known about its natural enemies. In May 2025, fallen avocados were collected in Michoacán, Mexico, and puparia of *N. batesi* were reared under laboratory conditions to investigate associated parasitoids. A figitid parasitoid was recovered and morphologically identified. Morphological characters of females corresponded to *Lopheucoila mexicana* Weld, 1951 (Hymenoptera: Figitidae: Eucoilinae). Parasitism in field-collected puparia reached 4.7%. The duration of the egg-to-adult developmental

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period of this parasitoid could not be determined directly because the timing of oviposition by parasitoid females on the host larvae was unknown. A total of 1,933 *N. batesi* puparia were obtained from 125 avocado fruits collected in the field. Of these, 42 parasitoid adults emerged between 37 and 43 days after the infested avocado fruits were collected. The highest number of parasitoids emerged on day 44 (n = 20). After this day, the number of parasitoids emerging was 27 between 45 and 49 d. Other two parasitoids were recovered through dissection of the puparia. The sex ratio was female-biased (63.73%). The present study provides the first confirmed host record for *L. mexicana* and the first documentation of this parasitoid-host association in avocado. These findings expand current knowledge of Eucoilinae biology and highlight the potential role of native parasitoids in regulating *N. batesi* populations in avocado agroecosystems. They provide the basis for further work on its ecological role and applicability in biological control.

Keywords
Avocado, biological control, *COI* barcoding, parasitoid-host association

Introduction

Lonchaeidae, commonly known as lance flies, is a globally distributed family currently comprising 10 genera and approximately 611 described species (MacGowan 2023). Most species are saprophagous, with larvae developing in decomposing organic substrates such as rotting fruits (McAlpine and Steyskal 1982). However, several taxa have transitioned to exploit living plant tissues, becoming economically important pests of horticultural crops. For example, *Silba adipata* McAlpine (1956) is considered a major pest limiting fig production worldwide (Paniagua-Jasso et al. 2024), whereas species of *Dasiops* Rondani, 1856, and *Neosilba* Waddill & Weems, 1978, have been reported to cause damage to passion fruit, yellow pitaya, cassava, and pepper (Peñaranda et al. 1986; Imbachi et al. 2012; Gisloti and do Prado 2013; Cardozo and Jiménez 2014). These cases suggest repeated evolutionary shifts within Lonchaeidae from saprophagy to facultative or obligate phytophagy, raising questions about host use, ecological plasticity, and pest emergence within the family.

Neosilba batesi (Curran, 1932) is a widespread Neotropical species whose biology remains poorly resolved despite its increasing association with cultivated hosts (McAlpine and Steyskal 1982; MacGowan 2023). In Colombia, it has been reported as a potential pest of avocado (*Persea americana* Miller, 1768; Lauraceae) (Campos-Rivera 2014). More recently, it has been suggested that this species may account for up to 30% of avocado crop losses in Michoacán, Mexico (Gómez 2024), a region of major global importance for avocado production (SADER 2024). However, this estimate was reported without a rigorous evaluation of the insect's actual phytosanitary status (Lasa et al. 2025). Infestation by *N. batesi* is manifested by a reddish ring-shaped discoloration surrounding the peduncle or by localized reddish patches on the fruit surface, symptoms that are associated with accelerated ripening and premature fruit abscission (Lasa et al. 2025). Although not formally recognized as a key pest in Mexico, current management recommendations aim at reducing the impact of *N. batesi* in avocado production (APEAM 2024).

Despite its potential economic relevance, *N. batesi* remains insufficiently studied from both ecological and evolutionary perspectives. Existing work has focused primarily on morphological descriptions of immature and adult stages (Illescas 2012), host associations in avocado and fig agroecosystems (Aluja et al. 2004; Lasa et al. 2025), and preliminary life-history observations (Hipólito-López, S., unpublished data). In contrast, its natural enemies are largely undocumented. To date, *Lopheucoila anastrephae* (Rohwer, 1919) (Hymenoptera: Figitidae: Eucoilinae) is the only parasitoid reported from *N. batesi*, based on records from Costa Rica (Wharton et al. 1998). However, the parasitoid-host complex of *L. anastrephae-N. batesi*, associated with avocado plants, has not been reported. This limited knowledge constrains our understanding of the role of parasitoids in regulating populations of *N. batesi* and, more broadly, the ecological networks linking saprophagous Diptera and hymenopteran parasitoids.

Given the importance of parasitoid diversity and host associations for both biological control and hymenopteran systematics, the discovery of previously unrecorded parasitoids associated with *N. batesi* offers an opportunity to address key biological questions. Therefore, determining whether this host supports a more diverse parasitoid assemblage than currently recognized is essential for improving our understanding of its associated natural-enemy community. Here, we report an eucoiline parasitoid species, *Lopheucoila mexicana* Weld, 1951, reared from field-collected *N. batesi* in Michoacán, Mexico, and characterize its basic biological attributes, including parasitism rate, developmental parameters, and sex ratio. These data provide new insights into host-parasitoid associations in Figitidae and Lonchaeidae and contribute to the evaluation of their potential applied significance in the management of lonchaeid pests.

Materials and methods

Insect collection and rearing

On 14 May 2025, 125 avocado fruits were collected from an orchard in San Francisco Peribán (19°33'06.8"N, 102°26'25.1"W; 1,446 m a.s.l.), municipality of Peribán de Ramos, Michoacán, Mexico. The samples were collected directly from the ground while systematically walking through the orchard, as in Lemus-Soriano et al. (2025), who reported that fallen avocado fruits are infested with dipteran larvae. After collection, fruits were placed in ventilated plastic containers (50 × 30 × 15 cm) and transported to the laboratory.

In the laboratory, each fruit was individually placed in a 500-ml plastic cup, covered with a perforated lid for aeration, containing a 3–5-mm layer of vermiculite to provide a standardized pupation substrate. From these fruits, a total of 1933 puparia were recovered and preliminarily identified as *N. batesi* based on the diagnostic characters of the puparium (Illescas 2012). At 24 h after pupation, the puparia were individually transferred into 2-cm^2 cylindrical wells of 24-well Castor tissue culture plates containing vermiculite. This procedure allowed for an unambiguous association of host

and potentially emerging wasp. Puparia were maintained under laboratory conditions (~23.5 °C, 50% RH, 12:12 h L:D photoperiod) and monitored at 24-h intervals until the emergence of either adult flies or parasitoids.

Species identification

Species identity of *N. batesi* was confirmed on 100 adult males, randomly selected, based on genitalia morphology using McAlpine and Steyskal (1982). Molecular identification was also conducted using the *COI* gene. For this, sequences were obtained from three individual adults (two females [IIAF25/1F, IIAF25/2F] and one male [IIAF25/3M]) and compared with sequences retrieved from GenBank that correspond to the *N. batesi* species collected in Mexico.

Adult parasitoids emerging from *N. batesi* puparia were initially identified to genus using the keys of Buffington (2009) and Buffington and Ronquist (2006), based on female morphological characters. Species identity was subsequently identified by FEG using Gallardo and Díaz (1999) and Gallardo et al. (2009), and on comparisons with two female reference specimens stored in the Entomological Collection of the Museo de La Plata (MLP), Argentina, that had been previously compared with the female holotype deposited at Texas A&M University. Morphological terminology follows Gallardo and Díaz (1999), Gallardo et al. (2009), and Buffington (2009), with terms standardized for consistency throughout the present study. Voucher specimens are deposited in the Colección de Plagas Agrícolas (Instituto de Investigaciones Agropecuarias y Forestales, Universidad Michoacana de San Nicolás de Hidalgo, Tarímbaro, Mexico) and in the Entomological Collection of the MLP, Argentina.

The photographs were obtained using a Canon EOS Rebel T7 camera fitted with a 10× microscope objective. Focus stacking of the photographs was performed in Helicon Focus 8.2.2 Pro, and each of them was adjusted using GIMP 2.10.34.

Parasitism-rate, development, and sex ratio

To assess parasitoid performance and its potential role in host regulation, all *N. batesi* puparia were monitored until adult emergence. After 60 days, any puparia without emergence holes were dissected under a stereomicroscope to determine whether they contained dead flies or parasitoids. Puparia containing parasitoid remains were classified as parasitized. Parasitoid percentage was calculated as the quotient between the number of parasitoids (emerged + dead [those seen via dissection]) × 100 and the total number of puparia recovered from the avocados collected in the field.

The development time of the parasitoid was approximated by counting the time lapsed between day of field collection of infested fruits (containing larval stages) and the day of adult parasitoid emergence. Finally, the sex ratio was calculated as the proportion of females in the emerged population [females / (females + males) × 100].

Results

Species identities

Emerging flies were identified as *N. batesi* (Suppl. material 1). In addition, the *COI* sequences of IIAF25/1F, IIAF25/2F, and IIAF25/3M showed 100% similarity to *N. batesi* sequences on GenBank. This analysis confirmed the identity of this species with 99.78%, 99.35%, and 99.78% identity to three sequences of this insect collected from Veracruz, Mexico (PV504763, PV504763, and PV504763, respectively; Lasa et al. 2025).

Of the 1,933 *N. batesi* puparia had developed from larvae that exited avocado fruits; 1,521 adults emerged, of which 762 were females and 759 were males. Of the 412 remaining puparia of this insect, a total of 91 parasitoid adults emerged (58 females and 33 males), 86 of them successfully emerged, while the other 2 parasitoids were recovered through dissection of the puparia. All parasitoid adults belong to the genus *Lopheucoila*. The specimens were identified based on the following diagnostic characters.

Generic diagnosis. *Lopheucoila*. Antenna with 13 segments (Fig. 1A), flagellomeres glabrous, dorsoventrally flattened, and subelliptical in cross section. Mesoscutal keel present, complete, broadened anteriorly. Dorsal surface of the scutellum bears large, radially arranged areolae, posterior margin of the scutellar disc emarginate, with distinct lateral and posterior projections. Scutellar plate small, strongly elevated above the scutellar disc; prominent conical protuberance present anterior to midpit, slightly overhanging midpit. Forewing glabrous, R1 not reaching anterior margin of wing, all wing veins lightly pigmented (Fig. 1B). Lateral syntergum posterior to setal band, with or without strigose dorsoventral impression; micropunctures on posterior third of syntergum and remaining terga.

After genus identification, the parasitoid specimens were identified as *L. mexicana* based on female (Fig. 1C) morphological characters.

Species diagnosis

Lopheucoila mexicana can be distinguished from *L. anastrephae* by the combination of the following characters: mesonotum arcuate; mesoscutal keel conspicuous and complete throughout its length (Fig. 1D); syntergum posterior to setal band without strigose dorsoventral impression (Fig. 1E). In *L. anastrephae*: mesonotum more strongly arcuate; mesoscutal keel inconspicuous in distal third; lateral syntergum posterior to setal band with strigose dorsoventral impression (Gallardo and Díaz 1999; Gallardo et al. 2009).

In addition, we here describe the males of *L. mexicana* for the first time (Fig. 1F). Similar to female. Antennae 15-segmented; F1 modified, longer than F2, outwardly curved, and laterally excavated. Metasoma as in female, but with terga posterior to syntergum abruptly angled ventrally, forming a 90° angle between syntergum and remaining terga.

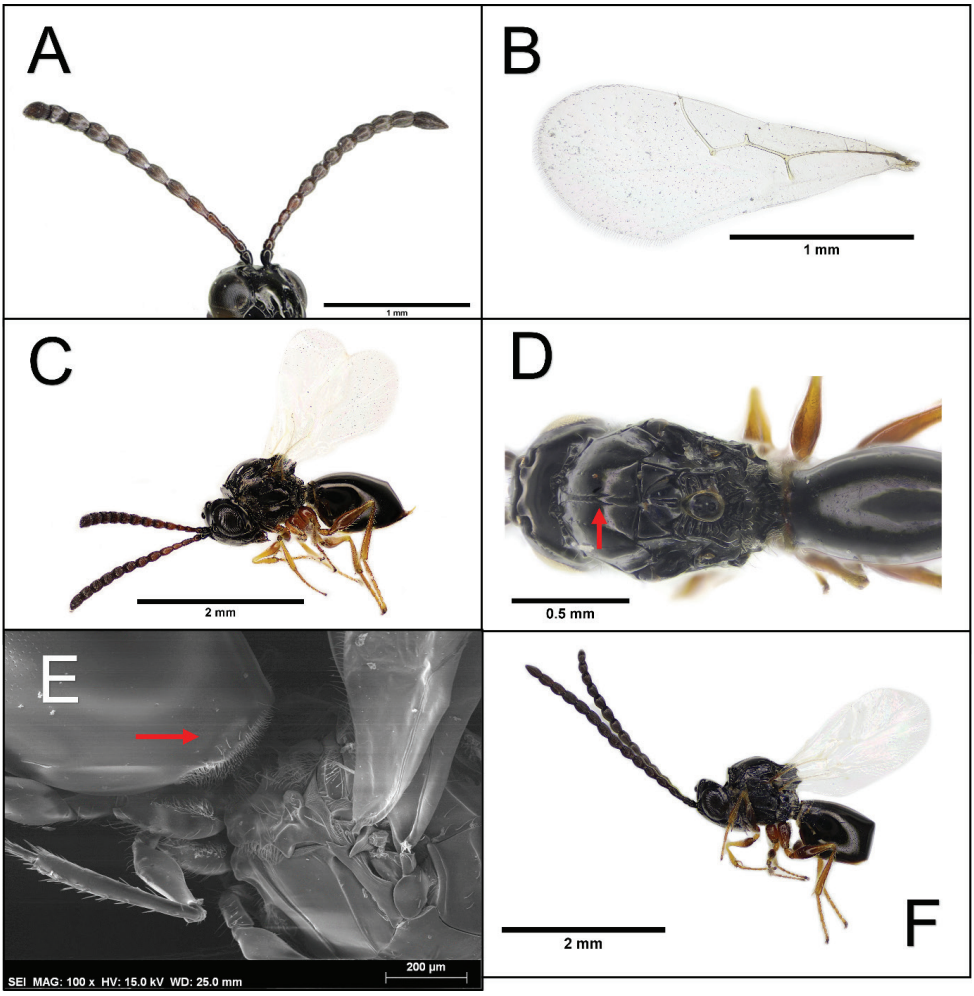

Figure 1. *Lopheucoila mexicana*. **A** female antennae **B** forewing **C** Female habitus in lateral view **D** mesosoma and anterior part of metasoma in dorsal view, arrow indicates mesoscutal keel **E** mesopectus, metapectal-propodeal complex, and base of syntergum in lateral view, arrow indicates syntergum posterior to setal band, without strigose dorsoventral impression **F** male habitus in lateral view.

Parasitism-rate, development, and sex ratio

Of the 125 avocado fruits collected in the field, 1,933 *N. batesi* puparia were recovered, and the parasitism rate of *L. mexicana* was 4.7% (n = 91). A total of 42 parasitoid adults emerged between 37 and 43 days after the puparia were placed on vermiculite in the cylindrical wells of 24-well Castor tissue-culture plates (Fig. 2). The numbers of parasitoids emerging on days 37–43 were 4, 2, 5, 3, 7, 10, and 11, respectively. On day 44, the highest number of parasitoids emerged (n = 20). Thereafter, emergence declined, with 7, 10, 4, 5, and 1 parasitoids emerging on days 45, 46, 47, 48, and 49, respectively.

The sex ratio of *L. mexicana* emerging from *N. batesi* puparia was female-biased, with females comprising 63.73% of the population.

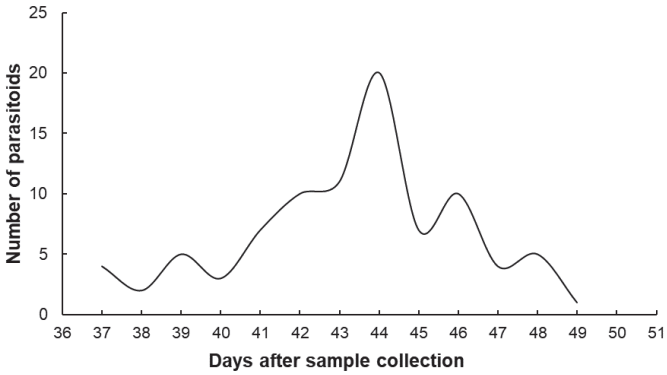

Figure 2. Number of adult *Lopheucoila mexicana* emerging from *Neosilba batesi* puparia under laboratory conditions following field collection of infested avocado.

Discussion

From a systematic and biogeographic perspective, the present record of *L. mexicana* is notable as this parasitoid has been reported only from Córdoba (Veracruz, Mexico; Weld 1951) and La Gran Piedra (Cuba; Gallardo et al. 2009), each based on a single female specimen without host association (Weld 1951). Within the genus *Lopheucoila* Weld, 1951, only one additional species is currently recognized, *L. anastrephae* (Weld 1951; Gallardo et al. 2009). Therefore, this study represents the second confirmed record of *L. mexicana* in Mexico, which was collected in San Francisco Peribán, Michoacán (~600 km apart from Córdoba, Veracruz). This study also represents the first to establish a host association, linking this parasitoid with *N. batesi* in avocado agroecosystems. This finding addresses a major gap in the biology of *L. mexicana* and its late discovery shows that host associations within Eucoilinae remain significantly under-documented, particularly in cyclorraphous flies (Buffington et al. 2020). In addition, our study here represents the first report of males for this parasitoid. Only a few females were known since its original description (Weld 1951; Gallardo et al. 2009). This finding has important implications for understanding the reproductive biology of the species.

Lopheucoila anastrephae is more widely documented and exhibits a broader host range than *L. mexicana*, including lonchaeids such as *Lonchaea* spp. (Weld 1951; Wharton et al. 1998; Schliserman et al. 2010) and *Neosilba* spp. (Uchôa-Frenandes et al. 2003), as well as tephritids of the genus *Anastrepha* Schiner, 1868, in multiple regions (Rhower 1919; Guimarães et al. 1999). The apparent difference in host range between *L. mexicana* and *L. anastrephae* raises important ecological questions. The record of *L. mexicana* parasitizing *N. batesi* is remarkable because the species of the tribe Zaeucoilini (to which *L. mexicana* belongs) are known to primarily parasitize leafminer flies of Agromyzidae (Buffington et al. 2020). This might indicate that the general host of *Lopheucoila*, following the rule that there is one host family for each genus of Eucoilinae (Buffington et al. 2020), might be Lonchaeidae, as both species share this host family. The tephritids of the genus *Anastrepha* would then be an exception to the rule. Therefore, the present record suggests that the diversity and host associations of *Lopheucoila* species should be studied across the Neotropics.

The parasitism rate observed for *L. mexicana* collected in the field was modest (4.7%). However, this value provides the first quantitative measurement of parasitism for this parasitoid and establishes a baseline for future ecological studies. Based on our observations, we can also report that this parasitoid is a solitary larval-pupal koinobiont endoparasitoid, which is consistent with all Eucoilinae species where the biology is sufficiently documented (Díaz and Gallardo 2014).

When compared with other eucoilines that are considered or used as biological control agents, the parasitism rate of *L. mexicana* is comparatively low. For instance, *Aganaspis daci* (Weld, 1951) has been reported to parasitize *Ceratitis capitata* (Wiedemann, 1824) (Diptera: Tephritidae) at rates ranging from 14–23% under laboratory conditions (De Pedro et al. 2018) to as high as 71% in field-collected fruits (Ali et al. 2016). In addition, *Leptopilina japonica* Novković & Kimura, 2011, reached 44–48% of parasitism on *Drosophila suzukii* (Matsumura, 1931) larvae in summer (Martin et al. 2026), whereas parasitism caused by *Gronotoma melanagromyzae* Beardsley, 1988, on larvae of the agromyzid *Melanagromyza tomaterae* Steyskal, 1972, was 3% in spring and 11–31% in summer (Palacios-Torres and Bautista-Martínez 2004). However, such variation is strongly influenced by the environmental context, including host density, fruit type, and season (Ali et al. 2016). The relatively low parasitism-rate observed in this study may therefore reflect specific ecological conditions rather than intrinsic limitations of the parasitoid, though conclusions on this require more targeted studies.

From an applied perspective, even moderate parasitism rates of *L. mexicana* can contribute to natural suppression of *N. batesi* populations, particularly when combined with other mortality factors. However, the effectiveness of this parasitoid as a biological control agent will depend on its capacity to establish and maintain populations in agroecosystems, as well as its response to environmental variability.

In the present study, the duration from egg to adult of *L. mexicana* could not be determined directly because the timing of oviposition by parasitoid females on the host larvae was unknown. However, an approximate developmental duration can be inferred from the available observations. Based on the emergence pattern of parasitoid adults from *N. batesi* puparia after the infested avocado fruits were collected, an egg-to-adult duration of approximately 45–49 days was inferred. This estimate should be interpreted with caution because it is based on a relatively small sample size (n = 91) and does not represent a directly measured developmental period. Further rearing studies with controlled parasitoid exposure and known oviposition times will be necessary to determine the egg-to-adult developmental duration of *L. mexicana* more precisely.

Comparative data from related species highlights the influence of environmental conditions on developmental rates. For example, *A. daci*, *Leptopilina boulardi* Barbotin (Carton & Kelner-Pillault, 1979) and *Zaeucoila unicarinata* Ashmead, 1903, completed their development in 33, 20, and 21 d, respectively, under slightly higher temperatures (25 °C) (Tormos et al. 2013; Kopelman and Chabora 1984; Melo 2021). These differences can be attributed to various factors, including differences among the parasitoid species studied, host quality (developmental stage and nutritional quality) (Farahani et al. 2016; Harvey 2005), as well as temperature (Gonçalves et al. 2014; Martin et al. 2026).

Sex allocation in parasitoids is often influenced by host size, quality, and environmental conditions. In *A. daci*, for example, female proportions vary widely depending on fruit type and season, ranging from 13.3% to 55.71% (Ali et al. 2016). Similarly, in *Ganaspis pelleranoi* (Brèthes, 1924) (originally described as *Aganaspis pelleranoi* (Brèthes, 1924)) female proportions differ depending on host species and diet (Agostini et al. 2019). The female-biased ratio observed in *L. mexicana* could reflect favorable host conditions or adaptive sex allocation strategies, as predicted by local mate competition theory.

Despite the advances provided by the present study, two important limitations should be acknowledged. First, sampling was restricted to a single location and time point, limiting the ability to assess spatial and temporal variation in parasitism and host-parasitoid interactions. Second, the developmental estimates are indirect and based on field-collected material, rather than controlled life-table experiments.

We did a preliminary attempt to establish a laboratory rearing of *L. mexicana* using third-instar *N. batesi* larvae; however, this was unsuccessful due to low parasitism rates (S. Hipólito-López, unpublished data). This highlights a key challenge for future research: identifying the ecological and physiological factors that govern successful parasitism. These may include host stage preference, oviposition behavior, adult nutrition, and microhabitat conditions.

In conclusion, the present study provides the first confirmed host record for *L. mexicana*, establishing its association with *N. batesi* in avocado agroecosystems. It also documents, for the first time, the males of this species and provides initial data on parasitism-rates, development times, and sex ratio. These findings contribute to a more complete understanding of the biology and ecology of a poorly known eucoiline parasitoid. From an applied perspective, the identification of a native parasitoid associated with *N. batesi* is particularly relevant given the increasing concern over the potential impact of this fly on avocado production. Although the parasitism rate observed here is relatively low, the presence of *L. mexicana* suggests that natural enemy complexes play a role in regulating *N. batesi* populations. Further research will be essential to determine its potential applicability in biological control programs.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Conceptualization: SPG, AMMC, SHL. Data curation: AMMC, OMG, SPG. Formal analysis: AMMC, SHL, SPG. Funding acquisition: SPG, AMMC, MCT. Investigation: GS, FEG, SPG, AMMC, SHL. Methodology: AMMC, SPG, SHL. Project administration: SPG, AMMC. Software: MCT, AMMC, SHL. Supervision: OMG, SPG. Validation: AMMC, FEG, SPG. Visualization: SPG, AMMC. Writing - original draft: AMMC, SHL, SPG. Writing - review and editing: SPG, AMMC, GS.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Additional figure

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