Apidologie (2024) 55:81

https://doi.org/10.1007/s13592-024-01121-4

Original article

Host-parasite interactions between *Xenoglossa pruinosa* (Apidae: Eucerini) and *Triepeolus remigatus* (Apidae: Epeolini) are characterized by tolerance and avoidance

Stephania Sandoval-Arango[1,2], Thomas C. Baker[1], and Margarita M. López-Uribe[1]

[1] Department of Entomology, The Pennsylvania State University, University Park, PA 16802, USA
[2] Present Address: USDA-ARS Bee Research Laboratory, Beltsville Agricultural Research Center, Beltsville, MD 20705, USA

Received 23 April 2024 – Revised 17 September 2024 – Accepted 20 September 2024

Abstract – In cleptoparasitic bees, host aggression and detection avoidance might be the main selective pressures shaping host-parasite interactions. However, the behavioral responses toward parasitism are unknown for most host species. In this study, we investigated the host-parasite interactions and behaviors of the cleptoparasitic bee *Triepeolus remigatus* when parasitizing the nests of its host, the squash bee *Xenoglossa* (*Peponapis*) *pruinosa*. Using circle-tube behavioral assays and direct observations at a nest aggregation of *X. pruinosa*, we assessed whether interactions between host and parasite were aggressive, tolerant, or avoidant and characterized the general parasitic behavior of *T. remigatus*. Our results reveal a lack of aggression between host and cuckoo bees, with interactions primarily characterized by tolerant and avoidant behaviors. Squash bees displayed minimal aggression toward both conspecifics and parasites. Interestingly, despite the absence of aggressive responses, *T. remigatus* preferred entering nests while the host was foraging, potentially indicating a strategy to avoid the discovery of parasitic visits. Furthermore, field observations provided insights into the parasitic behavior of *T. remigatus*, revealing primarily rapid visits to host nests without extensive inspection. The limited aggression and short time for nest visits observed in *T. remigatus* suggest adaptations to optimize parasitic success while minimizing host detection. Overall, our findings contribute to a better understanding of the behavior of open-cell parasites and provide a first accounting of the squash bee behavior when encountering parasitic bees. Further research is needed to elucidate the mechanisms underlying host-parasite coevolution and response to parasitism in ground-nesting bees.

behavior / cleptoparasites / ground nesting / host avoidance / solitary bees

1. INTRODUCTION

Brood parasites are a functional type of natural enemy that relies on heterospecific alloparental care by introducing their progeny into the nest of another individual (Pollock et al. 2021). Within this category, cleptoparasitism is a specialized form of brood parasitism that targets the provisions stored by the host for its offspring, which are then exploited by the parasite's brood (Bohart 1970; Litman 2019). In bees, cleptoparasitism has originated independently at least 20 times from nest-making ancestors, and nearly 2,800 species, or 14% of all bees, share this life-history trait (Cardinal et al. 2010; Litman et al. 2013; Sless et al. 2023). Most parasitic species are obligate and have lost the morphological structures associated with nesting behavior and

---

Corresponding author: S. Sandoval-Arango, s.sandoval793@gmail.com; M. M. López-Uribe, mml64@psu.edu
Manuscript editor: Cedric Alaux

pollen collection and transport (Litman 2019; Danforth et al. 2019). These bees are often called "cuckoo bees" due to their shared behavior with common cuckoo birds (Bohart 1970).

Cleptoparasitism is a major cause of brood mortality for bees, accounting for about 20% of brood loss, although this varies between host species (Wcislo 1996). Therefore, there is strong selective pressure on host species to protect their nest from intruders and cleptoparasites seeking to avoid detection by the host to successfully deposit their eggs in a nest (Litman 2019). Parasites have evolved three main strategies to usurp the host nest: (1) some species find nests with closed cells, and the adult female parasite re-opens the cell to kill the host egg/larva and lays her egg; (2) others re-open closed cells, but a hospicidal larva kills the host egg/larva, and finally (3) female parasites find nests that are still in the process of being provisioned and attack open cells by laying an egg that develops into a hospicidal larva (Rozen 1989; Danforth et al. 2019). Most species of brood parasitic bees are larval open-cell parasites (Litman et al. 2013; Sless et al. 2022, 2023). Because open-cell parasites attack hosts that are still actively provisioning their nest, it is hypothesized that they have strategies to avoid aggressive encounters with female hosts (Cane 1983; Litman 2019). These strategies involve morphological (e.g., modifications in the exoskeleton, Danforth et al. 2019), chemical (e.g., mimicry/camouflage, Polidori et al. 2020), and/or behavioral (e.g., host nest marking or host avoidance, Wuellner 1999; Litman et al. 2013) adaptations.

Nevertheless, several aspects of the life history of cuckoo bees are unknown, including whether host-parasitic relationships are primarily aggressive (Litman 2019; Danforth et al. 2019). Although it is assumed that parasitic females avoid the host female due to aggression (Wuellner and Hixon 1999), observations of this interaction are limited to a few species. In some cases, authors have observed host bees to aggressively evict parasites or chase them out of their nest (Thorp 1969; Batra 1978; Cane 1983; Torchio 1989; Sick et al. 1994). In other cases, no signs of aggression or guarding behavior were observed (Rust and Thorp 1973; Tengö and Bergström 1977; Wuellner and Hixon 1999). This response varies within genera and even between individuals of the same species when encountering different parasitic species (Rust and Thorp 1973; Batra 1978; Torchio 1989; Sick et al. 1994). If aggression is not found in these interactions, then it is typically assumed that parasites use a chemical strategy to conceal their presence, for example, to chemically mimic the odor of the host so that the intruder is not recognized (Polidori et al. 2020). However, chemical strategies have not been confirmed for most host-parasite pairs (Danforth et al. 2019), and in some cases, behavioral strategies, rather than chemical, seem to take center stage (Sick et al. 1994; Maggioni et al. 2023).

Disentangling how hosts and parasites interact, and placing these behaviors within the general context of strategies employed by parasitic bees to usurp a nest is key to understanding how brood parasitic lineages may have evolved from nest-building ancestors. Additionally, these interactions may reveal how similar selective pressures drive evolutionary transitions between one strategy to another and what drives convergence between distantly related lineages (Litman 2019). Similarly, because parasites play an important role in controlling and stabilizing host populations (Huyse et al. 2005; Greischar and Lively 2011), investigating host-parasite dynamics can enhance our understanding of host persistence over time and the health of host populations (Sheffield et al. 2013; Morelli et al. 2017). Since the hosts of cleptoparasitic bees are pollinators, understanding the trade-off of parasitic strategies and host responses to parasitism can improve our understanding of how and why pollinator populations fluctuate through time.

Here, we investigate the parasitic behavior of an open-cell cleptoparasite *Triepeolus remigatus* (Fabricius) (Apidae: Epeolini) and the interactions with its host, the squash bee *Xenoglossa* (*Peponapis*) *pruinosa* (Say) (Apidae: Eucerini). *Xenoglossa pruinosa* is a specialist pollinator of *Cucurbita* (squashes, gourds, and pumpkins) that has recently expanded its range following the domestication of its host plant from Mexico and southwestern North America into the temperate regions of North America (López-Uribe et al. 2016; Pope et al. 2023). Squash bees are solitary but often nest in aggregations near their host plant where populations of the parasite *T. remigatus* can also be found (Rightmyer 2008). Whether the interactions between hosts and parasites are aggressive or the parasite uses a strategy to avoid aggression by the host has not been investigated. We use circle-tube behavioral assays and direct observations at a nest aggregation of *X. pruinosa* to investigate whether interactions between host and parasite are aggressive and to characterize the parasitic behavior of *T. remigatus*. We also observe host-host interactions to test whether the reaction is specific to parasites or a generalized behavior against nest intruders. If the interactions are non-aggressive, it suggests that the parasites employ behavioral or chemical strategies to avoid aggression or the host bee is tolerant to the presence of the parasite.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted on a privately owned farm in Loganton, Pennsylvania, United States (41.036, – 77.276) during July–August of 2020 and 2021. The observations took place in a nest aggregation of the squash bee *X. pruinosa* located near *Cucurbita* crops such as pumpkin and squash, which are a pollen source for squash bees. The farm also cultivated other crops such as watermelon, radish, and tobacco and was surrounded by trees and wildflowers that served as nectar sources for the bees. Squash bees typically nested in bare soil next to the cucurbit crops or in soil with short legume cover crops, which facilitated the observation of host-parasite interactions at this site. All the observations and assays were conducted during the nesting peak of *X. pruinosa*, which typically lasts about two weeks from late July to early August. The parasitic bee *T. remigatus* was conspicuous at this nest aggregation for the duration of the study. Males and females typically emerged from the same nest aggregation as their host before the new generation of squash bees emerged and started nest construction. Other bee species nested near the squash bee aggregation including some species of *Lasioglossum*, while *Bombus* spp. and *Apis mellifera* collected pollen and nectar from the same cucurbit crops.

2.2. Behavioral assays and field observations

To investigate whether there is aggression in the host-parasite interactions of *X. pruinosa* and *T. remigatus*, we studied their behavior using two methods. First, we performed circle-tube assays following the protocols by Pabalan et al. (2000) and Polidori et al. (2020) to test if the host bee reacts aggressively and differently with the cuckoo bee or a conspecific in a controlled environment (Figure 1a and b). Circle tubes are a standardized behavioral assay to compare levels of aggression in bees (Breed et al. 1978; Pabalan et al. 2000; Packer 2006; Smith et al. 2019; Polidori et al. 2020). We collected females of both species and set staged dyadic encounters in a circle-tube apparatus that consisted of a 50-cm-long clear sterile plastic tube of 3/8-inch inner diameter used to form the circle, and a 5-cm-long plastic tube of 5/8-inch inner diameter used to connect the two ends of the circle (Figure 1a). We collected females of the host bee while they were visiting the cucurbit flowers or while exiting their nests by placing overturned falcon tubes over the entrance. We netted cuckoo bees while they were flying near the host nest using an entomological net. The bees were briefly chilled in ice to facilitate placement in the circle-tube arena, with the second bee placed inside the tube 2 min after the first one was introduced. In interspecific trials, the cuckoo bee entered the circle tube first to simulate a situation where a squash bee returned to its nest to find an intruder. Each trial was recorded using a tripod-mounted camera for 15 min, a period that has been confirmed to detect aggressive

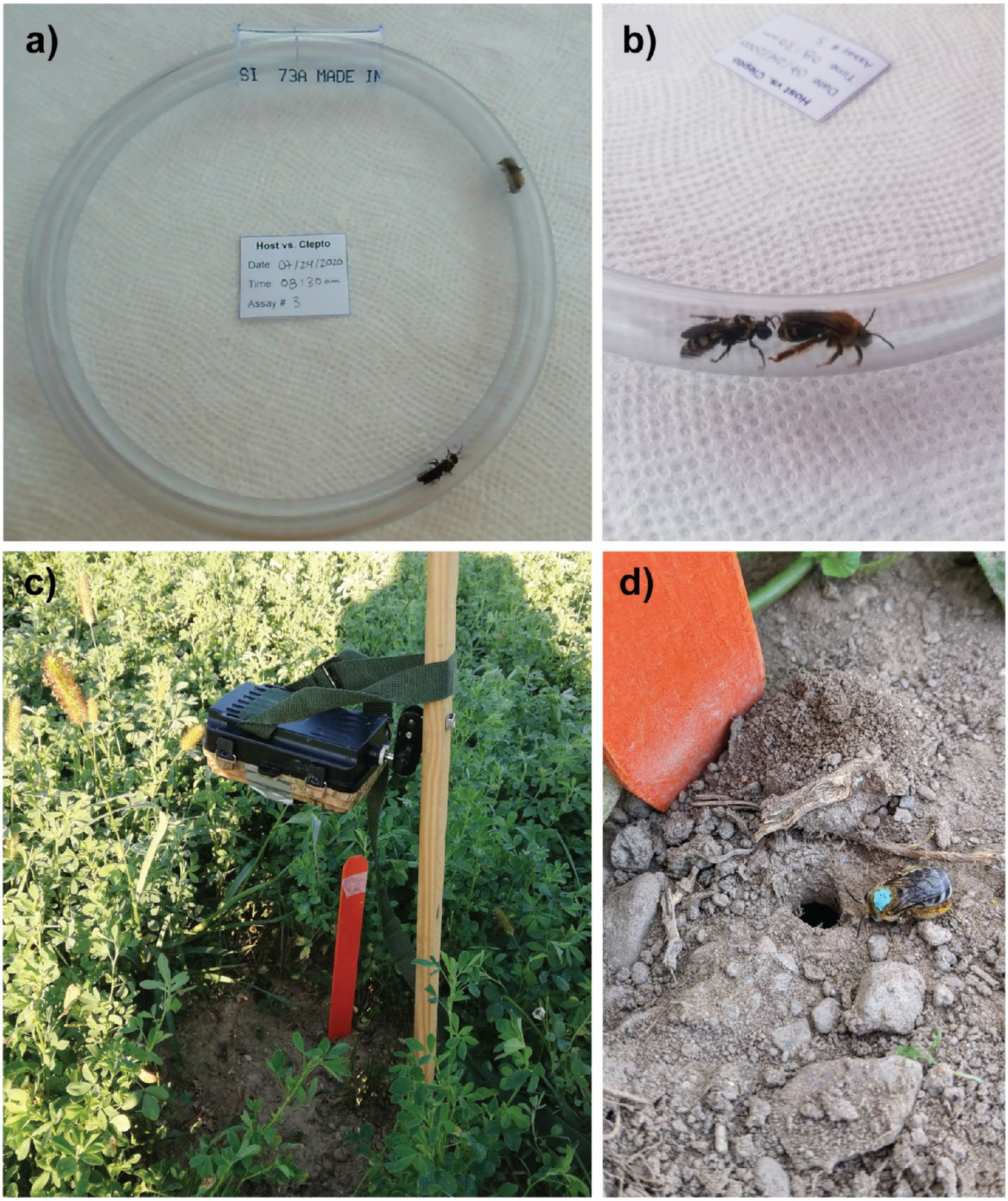

Figure 1 Set-up for circle-tube assays and field observations of interactions between *X. pruinosa* and *T. remigatus*. **a** Example of circle-tube assay between *X. pruinosa* and *T. remigatus*. **b** *T. remigatus* performing the "follow" behavior after *X. pruinosa*. **c** Field camera recording a nest entrance of *X. pruinosa* delimited by an orange tag. **d** *X. pruinosa* female with a blue mark in the mesosoma, standing next to her nest entrance

behavioral interactions in bees when they occur (Pabalan et al. 2000). All the behavioral assays were performed at the nesting site between 0630 and 1000 h local time during the peak foraging period of the squash bees. A total of 32 trials were performed, 16 each for conspecific and interspecific trials.

Second, we recorded videos at nest entrances of *X. pruinosa* and performed direct observations of the nesting site to investigate whether host and cuckoo bees behave differently in the nest environment versus the controlled environment of a circle-tube. The direct observations were used in combination with the videos to identify the main steps in the nest approaching and departure behavior of *T. remigatus* and identify any potential strategies that this parasite uses to avoid aggressive encounters with the squash bees. The videos were recorded at five nest entrances using T45 digital trail cameras (CamPark) with a 58-mm close-up macro lens attached (Vivitar) from approximately 0630 to 1000 h, for 1 week in 2020 and 2 weeks in 2021 (Figure 1c). The direct observations were performed for 10 min at each nest entrance every hour from 0700 to 1000 h, and any interactions were recorded in a field notebook. Because there can be multiple bees nesting next to each other, we marked all the individual bees that we could recognize at the aggregation with water-based Sharpie markers (Figure 1d).

2.3. Video scoring

For the circle-tube assays, we used modified behavioral categories from Pabalan et al. (2000) and Polidori et al. (2020) to score the behavior of both species in the videos (Table I). The main categories of behaviors included aggressive, tolerant/cooperative, and avoidant/withdrawal behaviors, and comprised 10 different behaviors. Different from Pabalan et al. (2000), we consider the "push" behavior as a tolerant/cooperative interaction because it was always exhibited as a response to the other bee not moving through the tube and not as aggression. For the field videos, we developed an ethogram to measure the frequency and duration of behaviors performed by *X. pruinosa* and *T. remigatus* at the nest aggregation (Table II) using categories based on Cane (1983) and Wuellner and Hixon (1999). We also scored the interactions between host and cuckoo bees when they occurred in the videos and whether they exhibited any of the aggressive, tolerant, or avoidant categories scored from the circle-tube assays (Table I), as well as whether a squash bee was present or not

Table I Ethogram of behaviors scored from circle-tube assays of *X. pruinosa* and *T. remigatus*

Behavioral category	Behaviors	Definition
Aggressive	C-posture	A bee curls her abdomen under the thorax with the body forming a c-shape, sting points at the other bee
	Bite	A bee closes her mandibles around a body part of the other bee. This is brief and not sustained for a continued period
	Mandibular hold	The mandibles of one bee appear clamped around the neck of the other bee for a continued period
	Leg kick	A bee rapidly kicks the other bee with her leg while the other bee is approaching
Tolerant/cooperative	Push	A bee pushes another with the end of its head or abdomen
	Pass	Bees encounter each other and accommodate to pass in the opposite direction
	Follow	A bee follows the other bee while they walk in the tube
	Stop in contact	A bee completely stops movement when encountering the other bee
Avoidant/withdrawal	Back/reverse walking	A bee walks backward when encountering the other bee
	Withdrawal	A bee makes a 180° turn away from the other bee and walks forward in the opposite direction

Modified from Pabalan et al. (2000) and Polidori et al. (2020)

Table II Ethogram of behaviors scored from field videos to characterize the nest approaching and departure behavior of *T. remigatus*

Behaviors	Definition
Flyby	A bee flies past the nest aggregation, often times slowly and performing a zig-zag movement
Hover	A bee flaps her wings continuously at a nest entrance without landing
Land	A bee touches the soil in or around the nest aggregation with her six legs
Inspect	A bee antennates at the nest entrance or introduces her head briefly into the entrance without introducing the rest of her body
Perch	A bee sits in nearby soil or vegetation while facing a nest entrance that was just inspected
Enter	A bee enters completely the host nest
Exit	A bee exits completely the host nest
Pre-departure grooming	A bee uses her legs to groom her head, antennae, wings, or metasoma while sitting at the host nest entrance
Depart	A bee leaves the area of the host nest that was visited
Post-departure grooming	A bee uses her legs to groom her head, antennae, wings, or metasoma while sitting in an area away from the host nest entrance
Soil-shuffling	A bee rubs her tarsi on the substrate and moves the soil

Modified from Cane (1983) and Wuellner and Hixon (1999)

at the aggregation while cuckoo bees were active near the nest entrances.

2.4. Statistical analyses

All the observations and interactions recorded in this study were for female *X. pruinosa* and *T. remigatus*. For the circle-tube assays, the data was not normally distributed; therefore, we used a Kruskal–Wallis test to look for differences between the number of interactions in each behavioral category observed in intra- and interspecific assays. For this, we combined the total number of interactions observed in each behavioral category, as some behaviors were infrequent. This test was followed by a Dunn's post hoc pairwise comparison test using a Bonferroni correction for multiple comparisons.

From the field video dataset, we aimed to investigate whether cuckoo bees enter empty or occupied nests. Additionally, we attempted to observe if there was a difference in interactions with squash bees at the nest entrance in both cases. However, we were unable to observe enough interactions between the two species, and cuckoo bees mostly entered empty nests. Instead, we calculated the relationship between squash bee foraging times and the number of parasites that visit the nest while the host is foraging using a linear regression. For this, we averaged the duration of foraging for each bee that performed more than one foraging trip or nest visit and compared only to the parasites that visited those specific nests. Because the parasite visits were not parametric and had a zero-skewed distribution, we used a square root transformation. All the analyses and visualization were performed in R v4.2.2 (R Core Team 2024) using the packages FSA (Ogle et al. 2023), ggplot2 (Wickham 2016), and Tidyverse (Wickham et al. 2019).

3. RESULTS

3.1. General observations

Squash bees at the nest aggregation were active between mid-July and late August in both 2020 and 2021. Identification of the total number of nests was challenging as new nests appeared throughout the season at the same time that females closed finished nests. Cuckoo bee activity varied by sex, with males emerging in mass earlier in the season between the 13th and 20th of July and females emerging in late July. After female emergence, parasitic males lived for another 1–2 weeks and mated. Female *T. remigatus* were observed searching for host nests mainly between the last week of July and the first week of August in both years, with a peak in activity between July 25th and August 5th. During the day, female *X. pruinosa* were active before we started recording at 0630 h local time, and contrary to this, male and female *T. remigatus* were frequently spotted sleeping in vegetation near the squash bee aggregation and were more active as the day got warmer, after 0730 h, with a peak activity period between 0800 and 0900 h local time. Additionally, female cuckoo bees were observed emerging from abandoned squash bee nests.

Intraspecific interactions between squash bees were tolerant at the nest aggregation and the cucurbit flowers. We observed that in some cases, squash bees make mistakes at recognizing their nests, and sometimes, the nest owner would kick the intruder with its legs, but we did not observe bees displaying aggressive behaviors such as stinging, biting, C-posture, or mandibular hold. Similarly, squash bees did not seem to acknowledge the presence of cuckoo bees near the aggregation or outside the nests as squash bees continued to fly in and out of their nests without performing guarding behaviors at the entrance or inspecting other bees. Additionally, several individuals of *T. remigatus* were observed nectaring in the same cucurbit flowers as the squash bees. Both *X. pruinosa* and *T. remigatus* were observed nectaring from the same wildflowers located near the aggregation, without displaying aggressive behaviors or reacting to each other's presence in a recognizable way. We did not observe squash or cuckoo bees antennating each other.

3.2. Circle-tube assays and aggressiveness of host-parasite interactions

Behavioral interactions in the circle-tube assays were analyzed for each behavioral category (aggressive/tolerant/avoidant) instead of each behavior individually because counts for some behaviors contained many zeros. Additionally, some behaviors were unique to one species and not performed by the other species during the assays. *Xenoglossa pruinosa* was the only species to perform the "leg kick" behavior in both intra- and interspecific assays, while *T. remigatus* was the only one to perform the "push" behavior in interspecific assays. The "C-posture" and "mandibular hold" behaviors were excluded from analyses because the bees did not perform these behaviors during the experiments (Table S1). Overall, we recorded 576 interactions.

Aggressive interactions accounted for 2% ($n = 12$) of the total number of behaviors performed, with 67% of the aggressive behaviors performed by *X. pruinosa* toward *T. remigatus*, represented mostly by leg kicks ($n = 7$). However, we did not find significant differences between intraspecific or interspecific interactions ($X^2 = 3.971$, $p = 0.137$, Figure 2a). Tolerant interactions were the most common and represented 65% of the total number of behaviors, with 63% of these being executed by *T. remigatus* toward *X. pruinosa*. We found significant differences in this category ($X^2 = 50.278$, $p < 0.0001$, Figure 2b), which were explained by differences in the number of interactions performed by *T. remigatus* toward *X. pruinosa* and not by how *X. pruinosa* interacted with *T. remigatus* or conspecifics (Dunn's *p*-adjusted < 0.0001 for differences in the number of interactions performed by *T. remigatus* in interspecific assays compared to the number of interactions performed by *X. pruinosa* in conspecific and interspecific assays). The most common behavior was "pass" ($n = 109$), followed by "stop on contact" ($n = 45$), and "push" ($n = 44$). Finally, avoidant interactions accounted for 33% of the observed behaviors and were most exhibited by *T. remigatus* (62%). Significant differences in this category ($X^2 = 16.860$, $p < 0.001$, Figure 2c) were driven by the higher number of interactions performed by *T. remigatus* in interspecific trials, compared to the number of interactions performed by squash bees in conspecific trials (Dunn's *p*-adjusted < 0.0001). The most common avoidant behavior was "withdrawal" ($n = 102$).

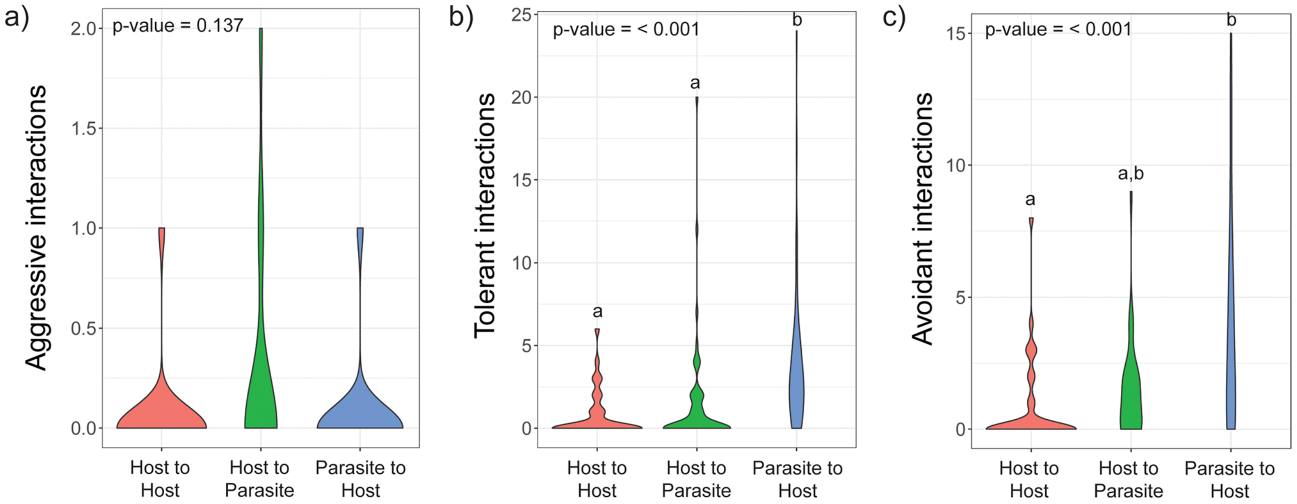

Figure 2 Violin-plots for the number of behavioral interactions in the circle-tube assays ($n = 16$). Represented here are the combined number of behaviors within each category: **a** aggressive, **b** tolerant, and **c** avoidant. *P*-values indicate significance in Kruskal–Wallis tests, and letters above plots indicate assays that are significantly different following a post hoc Dunn's test using the Bonferroni correction. Red, behaviors of *X. pruinosa* toward *X. pruinosa*; green, behaviors of *X. pruinosa* toward *T. remigatus*; blue, behaviors of *T. remigatus* toward *X. pruinosa*

3.3. Field videos and parasitic behavior of *T. remigatus*

The field cameras recorded a total of 182 h of video at the squash bee nest aggregation. Recording was not possible on several days throughout the season due to weather conditions, and on several occasions, squash bees were observed entering or leaving a nest a couple of times but were not observed anymore for the rest of the videos/season. Therefore, the number of squash bees included in analyses is smaller than the number of bees observed at the aggregation. We observed a total of 58 T. *remigatus* interacting with the squash bee nests (Table III, Table S3), but interactions between squash and cuckoo bees were minimal. Only on three occasions, we observed squash bees returning to their nests while *T. remigatus* individuals were sitting near the nest entrance. The squash bees did not react to the presence of the parasite and entered their nest normally. We observed cuckoo bees interacting with occupied nests six times, and on five of those occasions, the cuckoo bee completely entered the nest, while only once the bee departed after inspecting the entrance. Observations inside the nest aggregation were not possible, but we confirmed that *T. remigatus* departed the nests unharmed on all six occasions, and we did not observe the squash bees inspecting the entrance or outside the nest aggregation afterward. On 31 occasions, we observed cuckoo bees interacting with squash bee nests when the host was not present, either by inspecting or entering the nest (Figure 4). Finally, on 21 occasions, we could not determine whether the squash bee was present in the nest as we did not observe the host bee before or after cuckoo bees entered the nest.

Table III Frequency and average of the duration in seconds (Mean ± standard deviation) of foraging trips and nest visits of *X. pruinosa* and *T. remigatus* between 0630 and 1000 h

Species	*n*	Frequency (%)		Duration (Secs)	
		Foraging	Nest visit	Foraging	Nest visit
X. pruinosa	21	76	95	960 ± 643	316 ± 492
T. remigatus	58	-	64	-	64 ± 73

The number of squash bees nesting at the aggregation was larger than the number of bees that we initially recognized and marked. Sometimes, it was impossible to determine how many entrances were at an aggregation using the videos. Therefore, we examined data only for the 21 squash bees that we were able to confidently track in the videos (Table III, Table S2). Based on whether bees returned with pollen after leaving their nest, we were able to estimate squash bee foraging times, as well as the time they spent inside their nest compared to the amount of time that cuckoo bees spent visiting the same nests (Table III, Figure 3, Table S2-S3). Only 16 of the 21 *X. pruinosa* were actively foraging, and the duration of their trips was highly variable and in general longer than the duration of their or the cuckoo bees nest visits (Figure 3a, Table S2). For those 16 squash bees, we quantified the number of parasite visits and found a significant positive association between the duration of *X. pruinosa* foraging trips and the number of *T. remigatus* visits (Figure 3b, $R^2 = 0.504$, $p = 0.002$).

We characterized the nest approaching and departure behavior of *T. remigatus* to identify any potential strategies that this parasite might use to avoid aggression from *X. pruinosa* (Figure 4, Table S4). *Triepeolus remigatus* located host nests primarily by visually searching for entrance holes as we observed bees flying slowly in zigzags while skimming the soil. Transitions between behaviors are mostly linear as suggested by the frequencies of each behavior as well as the frequencies of transitions between different behaviors, and entering a host nest requires at least 3–4 preceding behaviors to occur. Most cuckoo bees entered the squash bee nests after landing at the entrance (64%), while some bees inspected the entrance (21%) before deciding to enter (8%) or depart (92%). Forty-three percent of the cuckoo bees that visited a nest exhibited pre-departure grooming behavior at the nest entrance, while only a small number of individuals (3%) performed post-departure grooming in an area away from the nest entrance. The soil shuffling behavior was only observed once (2%), and we never observed the perch behavior.

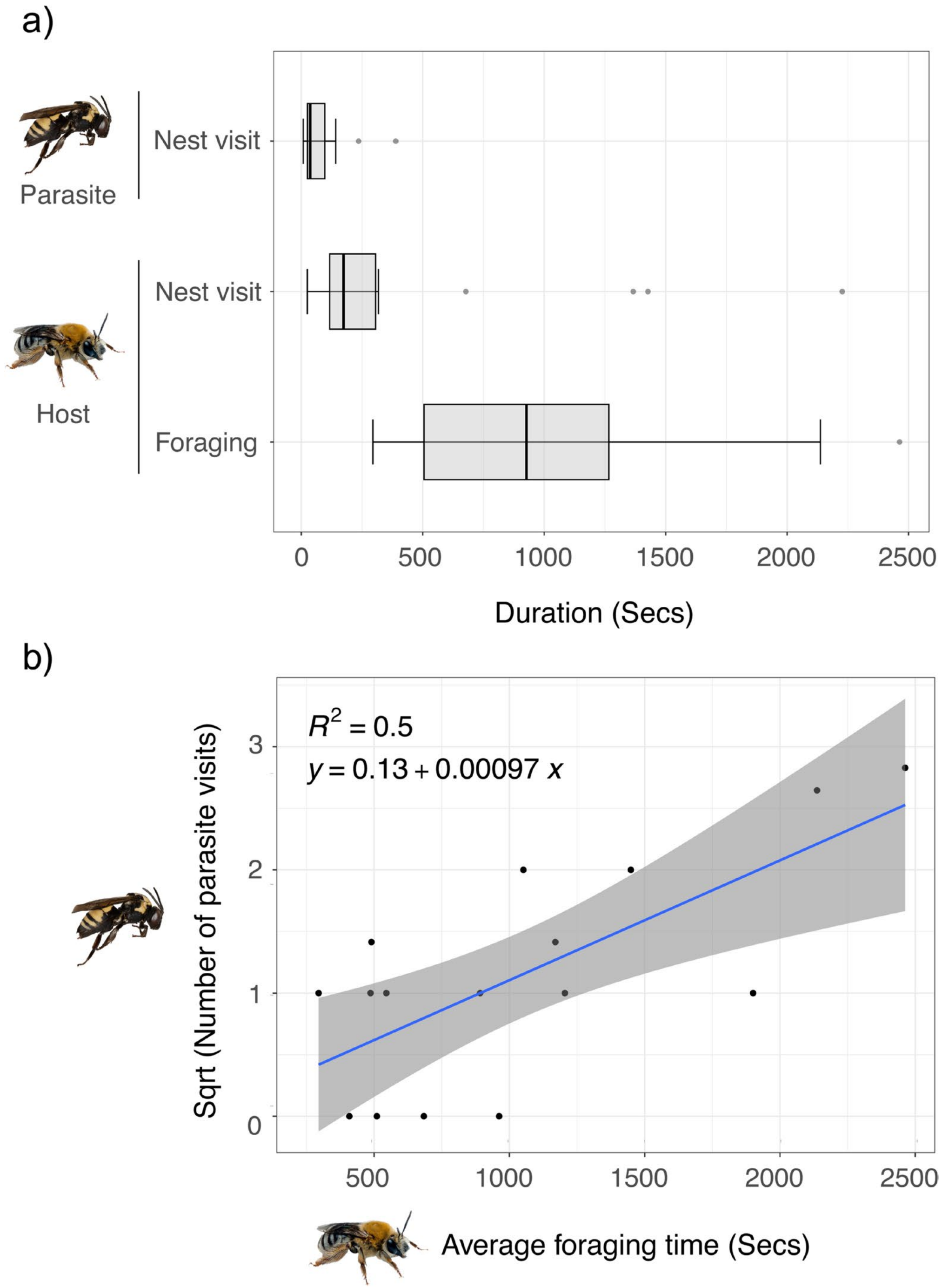

Figure 3 **a** Boxplots for the duration in seconds of foraging trips ($n = 16$) and nest visits or time spent in nest ($n = 20$) of *X. pruinosa* and nest visits of *T. remigatus* ($n = 37$). **b** Relationship between the number of parasite visits to nests (squared root transformed) and the average foraging time in seconds ($n = 16$) of *X. pruinosa*

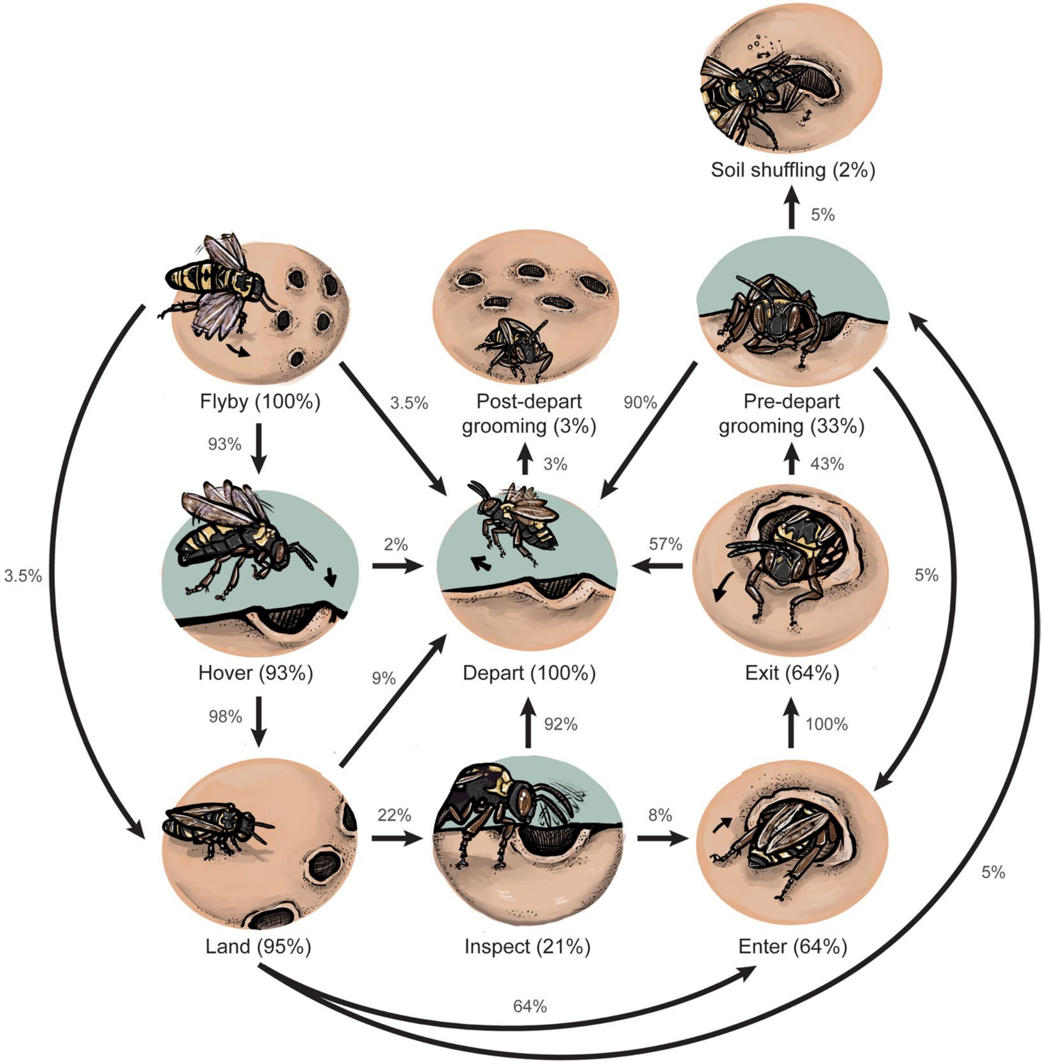

Figure 4 Behavioral components of the approaching and departure behavior of *T. remigatus*. The arrows show the direction of transitions between different behaviors. Numbers in black next to the behavior indicate the frequency (%) in which this behavior was observed for the total number of individuals ($n = 58$). Percentages in gray next to the connecting arrows indicate the frequency of transition from one behavior to another considering only the number of bees that performed that specific behavior. Illustrations by Nina Sokolov (https://ninasokolovart.weebly.com/)

4. DISCUSSION

Coevolutionary dynamics are theoretically common in host-parasite pairs, where the cost caused by parasitism selects hosts that can defend themselves against attacks by parasites while host defenses select parasite counterstrategies (Rothstein 2002; Criscione et al. 2005; Kilner and Langmore 2011; Castillo et al. 2022). In cleptoparasitic lineages, avoiding detection by the host is thought to be one of the main sources of selective pressure, since most parasites studied to date have strategies to avoid aggressive encounters with their hosts (Litman et al. 2013). Nevertheless, for most host-parasitic pairs, it is unknown whether aggression occurs in the first place and what constitutes a strategy to escape host detection, increasing the probability of survival of the parasitic offspring (Litman 2019). Here, we investigated the interactions between the squash bee *X. pruinosa* and its brood parasite *T. remigatus*. Overall, our results show a lack of aggression of *X. pruinosa* toward both conspecifics and parasites and a prevalence of tolerant behaviors in both host and parasite species.

The lack of aggression between conspecifics of *X. pruinosa* was previously observed by Mathewson (1968) in Rhode Island and Hurd et al. (1974) in California (USA). In both studies, authors observed low intraspecific competition between females that would often interfere with one another and try to usurp each other's nests. When bees tried to enter nests that belonged to other females, they would leave quickly or the nest owner would evict them, without any signs of aggression. Černá et al. (2013) observed similar dynamics in nest aggregations of *Andrena*, *Anthophora*, *Colletes*, and *Osmia*, where there was frequent re-use of conspecific nests that resulted in contact between solitary females, but low levels of conflict in what they called "neighborhood societies." Low aggressiveness or tolerance in nest aggregations has been predicted to be a response to the cost of long-term protection against conspecific cleptoparasitism, where encountering other females is common, and defending a nest might cost time that could be used in foraging and nest construction (Broom et al. 2004; Černá et al. 2013).

The neighborhood dynamics in squash bees might explain the lack of aggression toward the cleptoparasite *T. remigatus*. We found that interactions between squash and cuckoo bees are mostly tolerant or avoidant, and the minimal aggression observed was limited to leg kicks and one bite. This tolerance might be exacerbated by the already tolerant interactions with conspecifics in the nest aggregation. The non-aggressiveness in the behavior of host and cuckoo bees has been observed for other species of *Triepeolus* and their hosts (Clement 1984; Wuellner and Hixon 1999) as well as other genera of cleptoparasites (Rust and Thorp 1973; Tengö and Bergström 1977; Garófalo and Rozen 2001; Maggioni et al. 2023). In all these cases, host bees did not react to the parasite's presence near the aggregation, and most cleptoparasites were observed perching near the nest and waiting for the host to leave before entering. This perching behavior was not observed in the present study, and it is unclear whether *T. remigatus* might be able to learn the location of the squash bee nest and return when the nest is empty as it has been suggested for other species within the same subfamily (Apidae: Nomadinae) (Cane 1983; Clement 1984; Wcislo 1996). We observed *T. remigatus* grooming at the entrance after 43% of nest visits, which might indicate the marking of nests that have been parasitized, as hypothesized by previous authors (Wuellner and Hixon 1999).

Several authors have suggested that non-aggressive interactions might indicate the use of a chemical strategy by the parasite (Litman 2019). These include chemical mimicry, camouflage, and chemical insignificance (Polidori et al. 2020). Cuckoo bees in the genus *Nomada* are assumed to use chemical mimicry to enter nests of their *Andrena* hosts as encounters between the two species are not aggressive, and similar chemical profiles have been found in the Dufour's gland of *Andrena* and the mandibular gland of *Nomada* (Tengö and Bergström 1977). Differently, *Stelis* cuckoo bees can visually recognize cavities with nests of other megachilids, primarily *Osmia*, and use chemical camouflage to avoid host aggression by chewing the margins of leaves of the host plant and spreading the droplet of liquid across their body (Torchio 1989). *Stelis* bees were also seen entering the nests, removing large bites of pollen/nectar resources from the provisions, and spreading the material on their bodies (Torchio 1989). Finally, some species of *Sphecodes* use chemical insignificance to enter nests of *Lasioglossum*. *Sphecodes* bees can easily kill guards and foragers of *Lasioglossum* spp. when entering their nests (Sick et al. 1994) and exhibit a very simple profile of cuticular hydrocarbons, lacking most chemicals present in the host cuticle (Polidori et al. 2020).

In other cases, no chemical integration has been found in the parasites (Sick et al. 1994; Maggioni et al. 2023), even though the host bees did not react to parasites approaching their nests and did not perform any distinctive behaviors when returning to cells visited by parasites. In the present study, we did not examine the chemical profiles of squash and cuckoo bees, but it is possible that *T. remigatus* uses a chemical strategy as it has been found in *Nomada*, *Stelis*, or *Sphecodes*. On the other hand, it is equally possible for chemical integration not to be part of the strategies employed by this parasite. Therefore, the chemical ecology of host-parasite interactions in this system requires further investigation.

We observed that cuckoo bees preferred entering nests while the host was foraging, and that longer foraging times resulted in more parasitic visits. This might indicate that parasites prefer to not encounter the host even though host-parasite interactions were not aggressive in our experiments. Squash bees spent an average of 960 s (or 16 min) foraging and 316 s (or 5.3 min) inside their nests, which is similar to observations by Hurd et al. (1974) in California where foraging times were on average 8.8–13.3 min and time inside nests were 7.6–9.2 min. In contrast, *T. remigatus* spent an average of 64 s (or ~ 1 min) visiting a host nest, which is faster than estimates for *Triepeolus eldredi* (7–20 min, Clement 1984) or *Triepeolus distinctus* (average of 2.75 min, Wuellner & Hixon 1999). In most cases, *T. remigatus* entered the host nest within 1 s of landing at the entrance and without extensive inspection, different from other cleptoparasites that exhibit a "sneak-thief" behavior where bees enter a host nest in a slow and measured manner (Eickwork and Abrams 1980). The speed of parasitic visits might indicate that squash bees that nest closer to their host plants have lower rates of parasitism, assuming that foraging trips would be shorter. Likewise, for populations of *X. pruinosa* that forage on wild *Cucurbita* species in part of their range (Hurd et al. 1971), instead of commercial crops, the availability of unfragmented habitats with abundant pollen and nesting resources might be important in reducing parasitism.

Litman et al. (2013) hypothesized that cleptoparasites likely exist at relatively low numbers to maintain density-dependent host-parasite equilibrium. However, considering the lack of aggression by *X. pruinosa*, the prevalence of *T. remigatus* at the nest aggregation, and the speed of the parasite visits compared to host foraging and nest visit times, it is difficult to understand how host populations persist through time. Maggioni et al. (2023) suggested that *Megachile parietina* might actively search and destroy parasitic eggs of *Stelis nasuta* and *Coelioxys aurolimbata* as a defense mechanism, and it is possible that *X. pruinosa* uses this strategy to reduce the impact of parasitism. There are currently no methods to successfully rear squash bees in laboratory conditions that would allow the observation of intranidal behavior, and therefore, it is not possible to confirm whether egg recognition is part of the defensive behavior of *X. pruinosa*. However, egg recognition is a fundamental strategy against parasitism in birds (Rothstein 1982; Lyon 2003) and might be an important strategy in bees that requires further examination.

Finally, the lack of aggression in squash bees could be a signature of a recent evolutionary association between *X. pruinosa* and *T. remigatus*. Considering that the ancestral host of *Triepeolus* is hypothesized to be an eucerine (Bohart 1970), it is possible that *T. remigatus* was a parasite of a different Eucerine and then switched hosts. At least 25 species of *Triepeolus* for which host records are known are parasites of Eucerine bees, most species parasitizing *Melissodes*, a genus of typically generalist pollinators of several plant species (Rightmyer 2008). Therefore, as squash bees diversified following the domestication of *Cucurbita* plants and occupied eastern North America in recent evolutionary times (López-Uribe et al. 2016; Pope et al. 2023), *T. remigatus* might have switched from a more generalized pattern of parasitism to attack exclusively squash bees. Host switches are common in *Sphecodes* (Habermannová et al. 2013) and have been suggested as a primary mode of speciation in other brood parasitic lineages (de Vienne et al. 2013), for example, in *Triepeolus*'s sister genus, *Epeolus* (Onuferko et al. 2019).

Triepeolus remigatus is a parasite of at least another species of squash bee, *Xenoglossa strenua* (Bohart 1966), with records mentioning

Dieunomia and *Centris* as possible hosts, although these associations have not been confirmed (Rightmyer 2008). Switching to parasitize species with specialized pollen-collecting strategies might be an advantage against competition with other cleptoparasites and might lead to host specialization. This might also represent an advantage for the squash bees if they become inaccessible to other parasites unable to consume this specific type of pollen (Danforth et al. 2019). Therefore, a recent association between the two species and the initial advantage of decreasing competition might explain a lack of defenses by the squash bees. However, adaptations for using feeding resources from cucurbits might make it harder for *T. remigatus* to switch to other host groups with different nesting behaviors (Lim et al. 2022), and as the parasitic pressure increases, host bees might evolve strategies to counterattack parasitism. Future studies investigating the phylogeny and ancestral host associations of *Triepeolus* will help clarify whether *T. remigatus* and closely related species have a correspondent association with closely related *Xenoglossa* that are pollen specialists, and whose ancestors are predicted to be oligolectic (Dorchin et al. 2021). Furthermore, our research highlights the need for a better understanding of how the evolution of nest aggregations and resource specialization have mediated host-parasitic associations in bees and the evolution of specialized cleptoparasitism.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-024-01121-4.

ACKNOWLEDGEMENTS

We would like to thank the Kauffman family in Loganton, Pennsylvania, for allowing the observation of host-parasite interactions on their farm. We thank Laura Jones for finding the nest aggregation investigated in the present study and facilitating conversations with the farm owners. We are thankful to Mila Paiva, Jacob Lucabeche, Lizette Cambron-Kopco, and Avehi Singh for their help in the field. Additionally, we thank Grace Gutierrez for help processing videos of the squash bee aggregation. This project was funded by an Apes Valentes Student Award from the Center for Pollinator Research at Penn State. SSA thanks Fulbright and the Ministry of Science and Technology in Colombia (Minciencias) for a Fulbright-Minciencias fellowship to support doctoral studies in the United States. MMLU was supported by an NSF CAREER Award (DEB-2046474), the USDA NIFA Appropriations under Projects PEN04716, and the Pennsylvania State University Lorenzo L. Langstroth Endowment.

AUTHOR CONTRIBUTION

All authors contributed to the study's conception and design. Material preparation, data collection, experiments, and analysis were performed by Stephania Sandoval-Arango. The first draft of the manuscript was written by Stephania Sandoval-Arango and Margarita M. López-Uribe, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

FUNDING

This study was funded by an Apes Valentes Student Award from the Center for Pollinator Research at the Pennsylvania State University. SSA received a Fulbright-Minciencias fellowship to support doctoral studies in the United States from Fulbright and the Ministry of Science and Technology in Colombia (Minciencias). MMLU was supported by an NSF CAREER Award (DEB-2046474), the USDA NIFA Appropriations under Projects PEN04716, and the Pennsylvania State University Lorenzo L. Langstroth Endowment.

DATA AVAILABILITY

All data supporting the findings of this study are available within the paper and its Supplementary Information.

DECLARATIONS

Ethics approval and consent to participate This study did not require ethics approval.

Competing interests The authors declare no competing interests.

REFERENCES

Batra S (1978) Aggression, Territoriality, Mating and Nest Aggression of Some Solitary Bees (Hymenoptera: Halictidae, Megachilidae, Colletidae, Anthophoridae). J Kansas Entomol Soc 51:547–559

Bohart GE (1966) Notes on *Triepeolus remigatus* (Fabricius), a "Cuckoo Bee" Parasite of the Squash Bee, *Xenoglossa strenua* (Cresson) (Hymenoptera: Apoidea). Pan Pac Entomol 42:255–262

Bohart GE (1970) The Evolution of Parasitism Among Bees. Utah State University, Logan

Breed MD, Silverman JM, Bell WJ (1978) Agonistic behavior, social interactions, and behavioral specialization in a primitively eusocial bee. Insectes Soc 25:351–364

Broom M, Luther RM, Ruxton GD (2004) Resistance is useless?-extensions to the game theory of kleptoparasitism. Bull Math Biol 66:1645–1658. https://doi.org/10.1016/j.bulm.2004.03.009

Cane JH (1983) Olfactory evaluation of *Andrena* host nest suitability by kleptoparasitic *Nomada* bees (Hymenoptera: Apoidea). Anim Behav 31:138–144. https://doi.org/10.1016/S0003-3472(83)80181-X

Cardinal S, Straka J, Danforth BN (2010) Comprehensive phylogeny of apid bees reveals the evolutionary origins and antiquity of cleptoparasitism. Proc Natl Acad Sci USA 107:16207–16211. https://doi.org/10.1073/pnas.1006299107

Castillo R, Wurdack M, Pauli T, Keller A, Feldhaar H, Polidori C, Niehuis O, Schmitt T (2022) Evidence for a chemical arms race between cuckoo wasps of the genus *Hedychrum* and their distantly related host apoid wasps. BMC Ecol Evo 22:138. https://doi.org/10.1186/s12862-022-02093-8

Černá K, Straka J, Munclinger P (2013) Population structure of pioneer specialist solitary bee *Andrena vaga* (Hymenoptera: Andrenidae) in central Europe: the effect of habitat fragmentation or evolutionary history? Conserv Genet 14:875–883. https://doi.org/10.1007/s10592-013-0482-y

Clement S (1984) Observations on the Behavior of *Triepeolus nr. Eldredi* Cockerell (Hymenoptera: Anthophoridae). The Pan-Pacific Entomologist 60:300–303

Criscione CD, Poulin R, Blouin MS (2005) Molecular ecology of parasites: elucidating ecological and microevolutionary processes. Mol Ecol 14:2247–2257. https://doi.org/10.1111/j.1365-294X.2005.02587.x

Danforth BN, Minckley RL, Neff JL (2019) The Solitary Bees. Princeton University Press, New Jersey

de Vienne DM, Refrégier G, López-Villavicencio M, Tellier A, Hood ME, Giraud T (2013) Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytol 198:347–385. https://doi.org/10.1111/nph.12150

Dorchin A, Shafir A, Neumann FH, Langgut D, Vereecken NJ, Mayrose I (2021) Bee flowers drive macroevolutionary diversification in long-horned bees. Proc R Soc B 288:20210533. https://doi.org/10.1098/rspb.2021.0533

Eickwork GC, Abrams J (1980) Parasitism of sweat bees in the genus *Agapostemon* by cuckoo bees in the genus *Nomada* (Hymenoptera: Halictidae, Anthophoridae). Pan Pac Entomol 56:144–152

Garófalo CA, Rozen JG (2001) Parasitic Behavior of *Exaerete smaragdina* with Descriptions of Its Mature Oocyte and Larval Instars (Hymenoptera: Apidae: Euglossini). Am Mus Novit 3349:1–28. https://doi.org/10.1206/0003-0082(2001)349

Greischar MA, Lively CM (2011) Parasites can simplify host-population dynamics and reduce extinction risk. Evol Ecol Res 13:557–569

Habermannová J, Bogusch P, Straka J (2013) Flexible Host Choice and Common Host Switches in the Evolution of Generalist and Specialist Cuckoo Bees (Anthophila: *Sphecodes*). PLoS ONE 8:e64537. https://doi.org/10.1371/journal.pone.0064537

Hurd PD, Linsley EG, Whitaker TW (1971) Squash and gourd bees (*Peponapis*, *Xenoglossa*) and the origin of the cultivated *Cucurbita*. Evolution 25:218–234. https://doi.org/10.2307/2406514

Huyse T, Poulin R, Théron A (2005) Speciation in parasites: a population genetics approach. Trends Parasitol 21:469–475. https://doi.org/10.1016/j.pt.2005.08.009

Kilner RM, Langmore NE (2011) Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. Biol Rev 86:836–852. https://doi.org/10.1111/j.1469-185X.2010.00173.x

Lim K, Lee S, Orr M, Lee S (2022) Harrison's rule corroborated for the body size of cleptoparasitic cuckoo bees (Hymenoptera: Apidae: Nomadinae) and their hosts. Sci Rep 12:10984. https://doi.org/10.1038/s41598-022-14938-9

Litman JR (2019) Under the radar: detection avoidance in brood parasitic bees. Phil Trans R Soc B 374:20180196. https://doi.org/10.1098/rstb.2018.0196

Litman JR, Praz CJ, Danforth BN, Griswold TL, Cardinal S (2013) Origins, Evolution, and

Diversification of Cleptoparasitic Lineages in Long-tongued bees. Evolution 67:2982–2998. https://doi.org/10.1111/evo.12161

López-Uribe MM, Cane JH, Minckley RL, Danforth BN (2016) Crop domestication facilitated rapid geographical expansion of a specialist pollinator, the squash bee *Peponapis pruinosa*. Proc R Soc B 283:20160443. https://doi.org/10.1098/rspb.2016.0443

Lyon BE (2003) Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature 422:495–499. https://doi.org/10.1038/nature01505

Maggioni M, Moldoveanu OC, Zamponi E, Quaranta M, Monterastelli E, Dani FR (2023) Lack of evidence for chemical integration of the cuckoo-bee *Stelis nasuta* (Latreille, 1809) and *Coelioxys aurolimbata* (Förster, 1853) with their main host *Megachile parietina* (Geoffroy, 1785). Apidologie 54:53. https://doi.org/10.1007/s13592-023-01031-x

Mathewson JA (1968) Nest Construction and Life History of the Eastern Cucurbit Bee, *Peponapis pruinosa* (Hymenoptera: Apoidea). J Kansas Entomol Soc 41:255–261

Morelli F, Møller AP, Nelson E, Benedetti Y, Liang W, Šímová P, Moretti M, Tryjanowski P (2017) The common cuckoo is an effective indicator of high bird species richness in Asia and Europe. Sci Rep 7:4376. https://doi.org/10.1038/s41598-017-04794-3

Onuferko TM, Bogusch P, Ferrari RR, Packer L (2019) Phylogeny and biogeography of the cleptoparasitic bee genus *Epeolus* (Hymenoptera: Apidae) and cophylogenetic analysis with its host bee genus *Colletes* (Hymenoptera: Colletidae). Mol Phylogenet Evol 141:106603. https://doi.org/10.1016/j.ympev.2019.106603

Pabalan N, Davey KG, Packer L (2000) Escalation of Aggressive Interactions During Staged Encounters in *Halictus ligatus* Say (Hymenoptera: Halictidae), with a Comparison of Circle Tube Behaviors with Other Halictine Species. Journal of Insect Behavior 13:627–650

Packer L (2006) Use of artificial arenas to predict the social organization of halictine bees: Data for fourteen species from Chile. Insectes Soc 53:307–315

Polidori C, Geyer M, Schmitt T (2020) Do *Sphecodes* cuckoo bees use chemical insignificance to invade the nests of their social *Lasioglossum* bee hosts? Apidologie 51:147–162. https://doi.org/10.1007/s13592-019-00692-x

Pollock HS, Hoover JP, Uy FMK, Hauber ME (2021) Brood Parasites Are a Heterogeneous and Functionally Distinct Class of Natural Enemies. Trends Parasitol 37:588–596. https://doi.org/10.1016/j.pt.2021.02.005

Pope NS, Singh A, Childers AK, Kapheim KM, Evans JD, López-Uribe MM (2023) The expansion of agriculture has shaped the recent evolutionary history of a specialized squash pollinator. Proc Natl Acad Sci USA 120:e2208116120. https://doi.org/10.1073/pnas.2208116120

Rothstein SI (1982) Mechanisms of avian egg recognition: Which egg parameters elicit responses by rejecter species? Behav Ecol Sociobiol 11:229–239. https://doi.org/10.1007/BF00299299

Rothstein SI (2002) Phylogeny, specialization, and brood parasite-host coevolution: some possible pitfalls of parsimony. Behav Ecol 13:1–10. https://doi.org/10.1093/beheco/13.1.1

Rozen JG (1989) Morphology and systematic significance of first instars of the cleptoparasitic bee tribe Epeolini (Anthophoridae, Nomadinae). American Museum of Natural History, New York, p c1989

Rust RW, Thorp RW (1973) The Biology of *Stelis chlorocyanea*, a Parasite of *Osmia nigrifrons* (Hymenoptera: Megachilidae). J Kansas Entomol Soc 46:548–562

Sheffield CS, Pindar A, Packer L, Kevan PG (2013) The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. Apidologie 44:501–510. https://doi.org/10.1007/s13592-013-0200-2

Sick M, Ayasse M, Tengö J, Engels W, Lübke G, Francke W (1994) Host-parasite relationships in six species of *Sphecodes* bees and their halictid hosts: Nest intrusion, intranidal behavior, and Dufour's gland volatiles (Hymenoptera: Halictidae). J Insect Behav 7:101–117. https://doi.org/10.1007/BF01989830

Sless TJL, Branstetter MG, Gillung JP, Krichilsky EA, Tobin KB, Straka J, Rozen JG, Freitas FV, Martins AC, Bossert S, Searle JB, Danforth BN (2022) Phylogenetic relationships and the evolution of host preferences in the largest clade of brood parasitic bees (Apidae: Nomadinae). Mol Phylogenet Evol 166:107326. https://doi.org/10.1016/j.ympev.2021.107326

Sless TJL, Danforth BN, Searle JB (2023) Evolutionary Origins and Patterns of Diversification in Animal Brood Parasitism. Am Nat 202:107–121. https://doi.org/10.1086/724839

Smith A, Simons M, Bazarko V, Seid M (2019) The influence of sociality, caste, and size on behavior in a facultatively eusocial bee. Insect Soc 66:153–163. https://doi.org/10.1007/s00040-018-00679-4

Tengö J, Bergström G (1977) Cleptoparasitism and Odor Mimetism in Bees: Do *Nomada* Males Imitate the Odor of *Andrena* Females? Science 196:1117–1119. https://doi.org/10.1126/science.196.4294.1117

Thorp RW (1969) Ecology and Behavior of *Melecta separata callura* (Hymenoptera: Anthophoridae). Am Midl Nat 82:338–345. https://doi.org/10.2307/2423782

Torchio PF (1989) Biology, Immature Development, and Adaptive Behavior of *Stelis montana*, a Cleptoparasite of *Osmia* (Hymenoptera: Megachilidae). Ann Entomol Soc Am 82:616–632. https://doi.org/10.1093/aesa/82.5.616

Wcislo WT (1996) Parasitism rates in relation to nest site in bees and wasps (Hymenoptera: Apoidea). J Insect Behav 9:643–656. https://doi.org/10.1007/BF02213885

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York

Hurd PD, Linsley EG, Michelbacher AD (1974) Ecology of the squash and gourd bee, Peponapis pruinosa, on cultivated cucurbits in California (Hymenoptera: Apoidea). Smithsonian Contributions to Zoology 1–17. https://doi.org/10.5479/si.00810282.168

Ogle DH, Doll JC, Wheeler AP, Dinno A (2023) FSA: Simple Fisheries Stock Assessment Methods

R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Rightmyer MG (2008) A review of the cleptoparasitic bee genus Triepeolus (Hymenoptera: Apidae)-Part I. Zootaxa 1710. https://doi.org/10.11646/zootaxa.1710.1.1

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. Journal of Open Source Software 4:1686. https://doi.org/10.21105/joss.01686

Wuellner CT, Hixon MS (1999) Behavior of a cleptoparasitic bee, Triepeolus distinctus (Hymenoptera: Nomadinae), before departing from the nest of its host, Dieunomia triangulifera (Hymenoptera: Halictidae). In: Entomological contributions in memory of Byron A. Alexander. University of Kansas Natural History Museum Special Publication, pp 143–150