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Nest-Site Defense by Competing Honey Bee Swarms During House-Hunting

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Abstract

Cavity-nesting animals must often defend their homes against intruders, especially when the availability of suitable cavities is limited. Competition for nest sites is particularly strong when multiple groups of the same species migrate synchronously to found a new home. This may be the case for honey bees during the reproductive season, because neighboring colonies often cast swarms simultaneously, leading to potential competition for high-quality nesting cavities. To test the idea that honey bee swarms may compete for and defend potential nest sites as they search for a new home, we observed pairs of artificial swarms that were house-hunting concurrently. Workers from one swarm in each pair carried a gene influencing body color, so that the bees from the two swarms were easily distinguished. We set up a high-quality nest box and waited for nest-site scouts from each swarm to explore and recruit swarm mates to it. We recorded all the interactions between competing scouts at the nest box and found that when scouts from both swarms explored the box simultaneously they behaved agonistically toward bees from the other swarm. The level of aggression depended on the number of scouts from each swarm present at the nest box. When only one to three scouts from each swarm were at the box, they rarely fought. But when the scouts from one swarm outnumbered those from the other swarm (4–20 vs. one to three bees), those in the majority advertised their presence with a buzzing behavior at the entrance opening, and started mobbing and killing those in the minority. When one swarm gained clear control of the nest box (20+ vs. zero to one bees), some of its scouts guarded the box's entrance, preventing entry by foreign scouts. Our study exemplifies how cavity-nesting animals may compete for and defend suitable nesting sites.

Introduction

Competition for nest sites in cavity-nesting species can be strong, especially when the availability of suitable sites is low and multiple individuals are seeking a home in a given region with similar qualities. Competition for limited nest sites is widely observed in both vertebrates (e.g. fish, see Wiegmann & Baylis 1995; Kroon et al. 2000; Iguchi et al. 2004; Lindström & Pampoulie 2004; hole-nesting birds, see Newton 1994; Krist 2004; Banda & Blanco 2009; and reptiles, see Rand 1968; Rand & Rand 1976; Dugan et al. 1981) and invertebrates (e.g. wasps, see Mueller et al. 1992; Banks 1995; bees, see Alcock et al. 2006; and ants, see Foitzik & Heinze 1998).

Honey bees (*Apis mellifera*) live in colonies that reproduce by fissioning, whereby roughly two-thirds of the worker population leaves the nest with the mother queen as a swarm, while the remaining one-third of the workers stays behind with a new queen in the old nest (Martin 1963; Winston 1987). In a process that takes less than an hour, the swarm prepares for and then performs its departure with a special subset of workers, the nest-site scouts, producing the signals that initiate the swarm's mass exodus (Rangel & Seeley 2008; Rangel et al. 2010). Prior to the swarm's departure, the nest-site scouts, who comprise at most five percent of the swarm (Seeley et al. 1979), begin the house-hunting process by discovering and inspecting potential nesting cavities (Gilley 1998; Rangel et al. 2010). Once the swarm leaves the hive, it settles and then temporarily hangs from a tree branch where the search for a new nesting site continues with scouts exploring various sites of different qualities. When a scout finds an attractive cavity, she returns to the swarm and performs a waggle dance to recruit swarm mates to that site (Lindauer 1955; Seeley et al. 2006). The collective decision of where the swarm will move is reached through a process of competition among scouts that are visiting sites of different qualities, with the more attractive sites stimulating scouts to perform stronger waggle dances, leading to the fastest recruitment of uncommitted scouts to the site of highest quality (reviewed in Seeley & Visscher 2004; Seeley et al. 2006; Visscher 2007; Seeley 2010).

Because in temperate latitudes swarming occurs mainly in late May or early Jun. (Winston 1987), and usually on days with warm and sunny weather, it is very common that neighboring honey bee colonies cast swarms at approximately the same time. For this reason, it is possible that bivouacked swarms have to compete for nesting cavities with other nearby swarms, although the frequency of such conflicts is unknown. In this study we wanted to see whether multiple honey bee swarms that are house-hunting concurrently compete for and defend nest sites.

In a recent study, we used honey bee colonies housed in observation hives to determine the identity of the signalers that initiate a swarm's exodus from its hive. By labeling nest-site scouts at a nest box located a few hundred meters from the hive, and watching closely the scouts back at the hive, we found that it is nest-site scouts who perform the signals that initiate the swarm's mass exodus (Rangel et al. 2010). In two of the three trials conducted in this study, we also observed that over two hundred nest-site scouts remained inside the nest box while the swarm was leaving its hive. When we opened the box, we noticed that some of these bees were assuming the characteristic stance of bees that guard a nest entrance (described by Seeley 1985; see fig. 9.1 therein). These observations prompted us to ask in the present study the following questions regarding nest-site defense between competing swarms: During the house-hunting process, do scouts from multiple swarms ever inspect the same nest site at the same time? If they do, what types of interactions are observed at the site? What levels of aggression, if any, are observed between scouts from different swarms at the same nest site?

To determine whether honey bee swarms compete for and defend high-quality nesting cavities, we went to a small island devoid of natural nest sites and set up a pair of artificial swarms whose members were visually distinguishable. We then provided the two swarms with one attractive nest box and observed whether nest-site scouts from both swarms would explore the nest box at the same time. When we found that they would, we recorded all the interactions at the nest box between scouts from both swarms. Over several days, we noted the number of individuals from each swarm present at the nest box and the types of behaviors they performed, identifying the attacker(s) and the recipient(s) in all agonistic encounters.

Methods

Study Site and Bees

All observations were made at the Shoals Marine Laboratory on Appledore Island, Maine (42°58′N, 70°37′W). This wind-swept, 39-ha island lacks large trees with cavities and thus is devoid of natural nest sites for honey bees. This gave us confidence that nest-site scouts from our swarms would discover and become interested in the nest box we provided. Four medium-sized honey bee colonies were brought from the mainland (Ithaca, New York) in small hives. Two colonies were headed by naturally mated New World Carniolan queens (*Apis mellifera carnica*; Strachan Apiaries, Yuba City, California) whose workers had a dark-brown body color. The other two colonies were headed by cordovan queens that were artificially inseminated with sperm from cordovan drones using standard queen insemination procedures (Glenn Apiaries, Fallbrook, California). The workers of these queens were homozygous for the cordovan allele and so were visually distinctive; a bee that is homozygous for the recessive cordovan allele has a light-brown or 'blonde' body color, unlike the dark-brown or black body color of a non-cordovan, wild-type bee (e.g. see Taber 1955 for a description of how the cordovan genetic marker has been used to differentiate worker patrilines, and Getz et al. 1982 for how cordovan bees have been used in another behavioral study).

Swarm Preparation

We prepared an artificial swarm from each of the colonies brought from the mainland, but used only two colonies (one cordovan, one wild-type) at a time. To make an artificial swarm, we first located the colony's queen and placed her in a small cage (3.2 × 10 × 1.6 cm). Next, we used a metal funnel to shake 1.0 kg of bees (approx. 7700 workers, Mitchell 1970) into a swarm cage (15 × 25 × 35 cm) made of wood and covered on its two largest sides by wire screen to give the bees access to food and air. We placed the caged queen inside the swarm cage before sealing it, and kept the swarm cage in the shade. We fed each swarm *ad libitum* with a 50% (vol/vol) sucrose solution for 48–72 h, when copious wax scales were deposited by the bees on the floor of their cage. After this, the swarm cage was unsealed, the queen cage was attached to a swarm mount (see 'Set up of swarms'), and the workers were shaken onto the base of the mount. In less than an hour the workers were clustered around the queen cage in the center of the swarm mount. Like in natural swarms, scouts from our artificial swarms began searching for prospective nesting cavities.

Set Up of Nest Box

A nest box like that described by Seeley & Visscher (2003) was established 225 m from the swarms. The nest box was specially designed to enable us to observe the behaviors of bees both outside and inside the box. It was built with 2.0-cm-thick plywood, and was shaped as a cube that provided a 27-l cavity. The box had a 2.5-cm diameter entrance hole at the center of one of its side walls, and had another side wall left open. The nest box was bolted by its four corners to the outside of an observation hut so that the open wall of the nest box was aligned with a same-size opening on one of the hut's sides. A sheet of 3.2-mm-thick glass was placed over the opening so we could sit inside the hut and watch scout bees inside the nest box without disturbing them. The observation hut (244 × 113 × 113 cm) was constructed of plywood and assembled with bolts. Because all of the hut's interior surfaces were painted black, it provided a dark room inside which we observed bees in the nest box. Enough light for observing bees came in the nest box's entrance opening, but occasionally a flashlight was used to observe certain behaviors in better detail. Outside the entrance of the nest box, to expedite its discovery by nest-site scouts, we hung a vial containing the blend of pheromones produced by the honey bee's Nasonov gland (Bee Lure, Brushy Mountain Bee Farm, Moravian Falls, North Carolina), which bees usually release at their nest entrance to attract nest mates to their home (i.e. 'scenting behavior,' Winston 1987). The lure was removed as soon as scouts began visiting the nest box.

Set Up of Swarms

For each trial, we set up two swarms, one cordovan and one wild-type. Each swarm was placed on a swarm mount like that described by Seeley & Buhrman (1999, fig. 1 therein). Each mount consisted of a flat vertical board large enough for the bees to spread out upon as they clustered around the queen cage. This enabled us to monitor easily the bees on the swarm's surface. The swarms were set up beside the front and the back porches of the island's old Coast Guard building, approx. 20 m apart.

Data Collection at The Nest Box

After the two swarms and the nest box were set up, one of us waited at the nest box for the arrival of the first scout bees. Once scouts started to appear at the nest box, the observer there radioed to the person monitoring the swarms the body color of the scouts at the box. For each trial, the date and time of arrival of the first scouts from each swarm were noted. Once scouts from one or both swarms began to appear at the nest box, we recorded every 15 min (unless otherwise noted) the number of scouts from each swarm seen both outside and inside the nest box. To help us better describe the behaviors performed by scouts at the nest box, we videotaped these behaviors using a digital video camera (Sony DCR-TRV50, New York, NY, USA).

When two or more bees interacted at the nest box, we recorded the dates and times of the encounters and whether the interactions were: (1) between swarm mates, when scouts from the opposite swarm were not present at the nest box; (2) between swarm mates, when scouts from the opposite swarm were present at the nest box; or (3) between members of opposite swarms. When agonistic interactions occurred, we collected the following data: (1) the date and time of each interaction; (2) the type of the interaction, with a detailed description of all the behaviors; (3) the number of bees from each swarm involved in the interaction; and (4) to which swarm the attacker(s) and the recipient(s) belonged. If bees were killed inside the nest box, the date, time, and other details about the death were recorded. We concluded each trial when sufficient interactions between scouts from both swarms had been recorded at the nest box.

Experimental Manipulations at The Swarms

Because scout bees that find potential nest sites return to the swarm cluster and perform waggle dances to recruit other bees to their discoveries (Lindauer 1955), we checked for bees producing the waggle dance on the surface of each swarm every 15 min from approx. 0800 to 1700 hours (unless otherwise noted) on each day of the study. If a bee was dancing for a site other than the nest box, she was plucked off the swarm with forceps and killed, to prevent recruitment of bees to the non-nest-box site. When a scout appeared at the nest box, the person at the swarms watched to see if she would later produce a waggle dance advertising the nest box. Because nest-site scouts were not individually labeled, we relied on our ability to read waggle dances to determine whether a nest-site scout was dancing for the nest box, or for a different site, based on the distance and direction she communicated through her dances. If the scout danced, the person at the nest box was informed that recruits were likely to appear there soon.

On days when bees belonging to one swarm began to appear in high numbers (more than 10) at the nest box before bees from the other swarm had discovered the box, the person monitoring the swarms temporarily shut down the first swarm's scouting activity by sealing it off. To do this, a 'shroud' made of mesh fabric was placed over the swarm, preventing bees from returning to or leaving from the swarm. The shroud was kept 5 cm from the surface of the swarm by a wire frame that was attached to the swarm mount. The shroud was removed when bees from the other swarm began to appear at the nest box. After this, scouts from both swarms visited the nest box simultaneously. When we concluded a trial, each swarm was shaken into a hive at dusk and taken to a beeyard several hundred yards from the location of the swarms. Each swarm ceased its scouting after it was installed in a hive.

Data Analysis

The information that we report comes only from days on which we observed interactions at the nest box between scouts from both swarms. Video recordings were made to help us describe the scout bees' behaviors. Each video recording was made by following an individual bee and was analyzed at slow speed or frame-by-frame using a video editing deck (Sony DSR-30). For each video recording, we noted the duration of each behavior, the distance traveled by the bee (in mm), and information about the context in which the behavior was produced.

Results

We performed two trials with a different pair of swarms in each trial. In each trial, we recorded interactions at the nest box between scout bees from both swarms. The types of interactions and their durations depended on the number of bees from each swarm present at the time of the encounter; more aggressive interactions occurred when one swarm's scouts strongly outnumbered those from the other swarm and thus had control over the nest box. The types of agonistic behaviors observed at the nest box are described in Table 1. The less aggressive behaviors were guarding and chasing; the more aggressive behaviors were leg-pulling, grappling, stinging, and mobbing. The interactions that occurred in each trial are summarized below.

Trial 1

We set up the nest box and the first pair of swarms on 20 Jun. 2009. For the next 4 d the weather was rainy, cold, and windy, and scout bees did not fly from either swarm's cluster. On 25 Jun., the weather finally improved and scouts from the wild-type swarm began to visit the nest box. When only two or three wild-type bees were at the nest box, each one explored the box without interacting with her swarm mates. When more than three bees were present, some of them began to produce a curious nest-site buzzing behavior, which we describe below. When the number of wild-type scouts at the nest box grew large (i.e. >26 bees inside, five bees outside), we observed guarding behavior. At the end of the day, the number of wild-type bees inside the nest box had increased to above 60 and the nest-site buzzing behavior had stopped. After dusk, we found one wild-type bee and one cordovan bee dead inside the nest box. Possibly, they had stung each other.

Table 1: Description of agonistic behaviors performed at the nest box by nest-site scouts from competing swarms during their house-hunting process

Behavior	Description of behavior
Increased level of aggression	
Guarding	When approached, a bee standing at the nest box entrance raises her front legs, projects her antennae forward, flares her wings, and often chases the intruder away
Chasing	A bee rushes toward another bee from behind as the chased bee runs away
Leg-pulling	A bee grabs the hind leg of another bee with her mandibles or front legs, and pulls her across the substrate, often for several minutes
Grappling	A bee grabs another bee from underneath the abdomen to avoid getting stung. They lock in position and move around trying to sting each other
Stinging	A bee protrudes her stinger while grappling with another bee, and inserts her sting in the other bee's abdomen. Venom is released. The soft inter-segmental membrane of the victim allows the stinging bee's sting to come out intact, thus the stinging bee may survive the attack and sting the victim repeatedly
Mobbing	A prolonged attack by two or more bees against another bee, often involving chasing, leg-pulling, grappling, and occasionally stinging

We recorded additional interactions between scouts from the two swarms on 26 Jun. Early on 26 Jun., we sealed off the wild-type swarm using the swarm shroud described above, to facilitate the discovery and exploration of the nest box by cordovan scouts. Some wild-type scouts had begun flying to the nest box before we sealed off their swarm, however, and by mid-morning we observed numerous wild-type scouts at the nest box (approx. 30 bees), with at least six to eight bees guarding the entrance. At 1020 hours, we noticed one cordovan bee approaching the nest box and attempting to enter it, but wild-type scouts guarding the box repeatedly repelled her. At approx. 1130 hours, we began removing wild-type bees from the nest box with an aspirator. This worked and by 1200 hours, one cordovan bee had entered the nest box, at which time there was only one wild-type bee there. Later that day, when there were equally low numbers of bees from both swarms at the nest box (i.e. one to three individuals), one-on-one aggressive interactions were observed. All the attacks were started by wild-type bees (Fig. 1a, b). At 1352 hours, a wild-type bee stung and killed a cordovan bee.

After 8 d of bad weather (27 Jun.–4 Jul.), the swarms reinstated their scouting activities on 5 Jul. On this day, two cordovan bees were visiting the nest box by 1100 hours, and one wild-type bee was being chased away constantly from the entrance by a cordovan bee. When the first wild-type bee managed to enter the nest box at 1215 hours, she was repeatedly chased and grabbed by the legs by one or two cordovan bees at a time, until she fled the nest

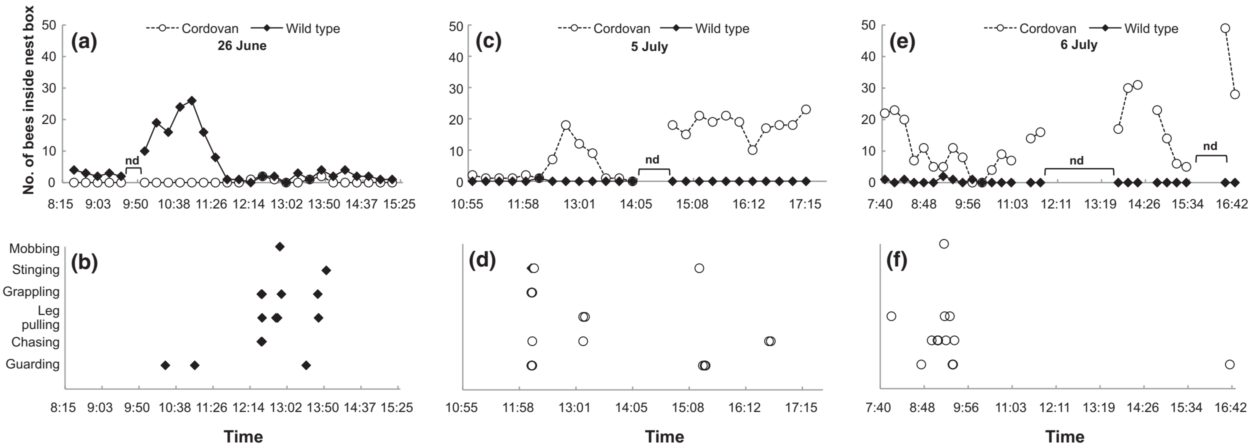

Fig. 1: Records of aggressive interactions between scouts from competing swarms at the nest box during trial 1. The top plots represent the number of bees from each swarm observed at the nest box. The bottom plots show the types of agonistic interactions observed between non-swarm mates. The identity of the attacker (cordovan or wild-type scout) is represented by either an open circle or a black diamond. The abbreviation 'n.d.' indicates that no data are available for a given sampling interval.

box and did not return (Fig. 1c, d). Over the rest of the day, the number of cordovan bees increased to nearly 20, and all the attacks consisted of mobbing (i.e. two to three bees against an individual bee) performed by cordovan bees against the one wild-type bee. When we made a night check up of the nest box (at 1945 hours), we found one cordovan bee and one wild-type bee twitching and dying, and two cordovan bees dead, inside the box.

On 6 Jul., the cordovan swarm retained control of the nest box the entire day. By 0745 hours there were more than 20 cordovan bees inside the nest box and several were guarding the entrance. Nevertheless, one wild-type bee managed to get past the cordovan guards and enter the box at 0745 hours. At 0755 hours, one cordovan bee was stung and killed by the wild-type bee. Immediately after, the remaining cordovan bees mounted several mobbing attacks against the wild-type bee (Fig. 1e, f), but she was not killed. She left the nest box around 0930 hours, did not return, and did not recruit any swarm mates to the nest box. By the end of the afternoon, over 50 cordovan bees were at the nest box. At 1800 hours, we placed both swarms into hives and so ended the first trial.

Trial 2

We set up a second pair of swarms on 9 Jul., swapping the locations of the two swarm types from the first trial to exclude the possibility that one type of swarm was advantaged by a superior location for discovering the nest box. Having mastered our technique of shrouding one swarm to allow the other swarm to discover the nest box, we were more successful at getting scouts from both swarms to visit the nest box at the same time. On 9 Jul., cordovan scouts began visiting the nest box after 1100 hours, and by 1220 hours we counted over 20 cordovan bees at the box, which prompted us to shroud their swarm to allow recruitment by the wild-type scouts. This kept most, but not all (due to a leakage of bees during the sealing process), of the cordovan scouts from visiting the nest box. At 1618 hours, we observed two wild-type bees and one cordovan bee at the nest box, with occasional chasing and grappling interactions.

The cordovan swarm was kept shrouded in the morning of 10 Jul., although a few bees had leaked out overnight. By 0930 hours, there was one cordovan bee inside and one wild-type bee outside the nest box. We uncovered the cordovan swarm at 1050 hours and 5 min later there were three cordovan bees and one wild-type bee at the nest box entrance. Throughout the day we saw a maximum of three wild-type bees at the nest box, while the number of cordovan scouts fluctuated from zero to eight. The majority of the attacks were made by cordovan bees against wild-type bees, and the behaviors ranged from chasing to stinging and mobbing (Fig. 2a, b). Neither swarm increased its presence at the nest box to the high numbers seen the day before, but we observed many instances of mobbing by cordovan bees against wild-type bees (Fig. 2a, b). One of these mobbing events ended with a cordovan bee getting stung and killed by a wild-type bee, followed by the wild-type bee getting stung repeatedly, and ultimately killed, by cordovan bees. The many fights observed throughout the day resulted in another cordovan bee and four wild-type bees getting stung and killed. We shrouded both swarms at the end of the day to better control their presence at the nest box the next morning, but when we uncovered them, neither swarm visited the nest box that day.

Two days later, at 0945 hours on 12 Jul., we observed two cordovan bees and one wild-type bee inside the nest box. When the wild-type bee approached a cordovan bee at the nest box entrance, the cordovan bee chased the wild-type bee without hurting her (Fig. 2c, d). The number of bees inside the nest box remained low throughout the morning, fluctuating between zero and one for either swarm, and we saw no fighting. In the afternoon, the number of wild-type bees at the nest box increased to four, while only one cordovan bee remained interested in the nest box. At this point, wild-type bees performed attacks against cordovan bees, which included chasing, grappling, and mobbing (Fig. 2c, d). Because the number of bees visiting the nest box remained low throughout the trial, no buzzing behavior was observed in this trial. At the end of the day, the swarms were installed in hives, thus concluding the second trial.

The Nest-Site Buzzing Behavior

When one swarm had control of the nest box (i.e. its scouts strongly outnumbered those from the other swarm) but the total number of visitors remained rather low (i.e. around 8–20 bees), we often observed bees performing a curious behavior near the entrance opening whenever a flying bee approached the nest box, regardless of what swarm the visitor belonged to. In performing this behavior, when the flying bee attempted to land at the nest

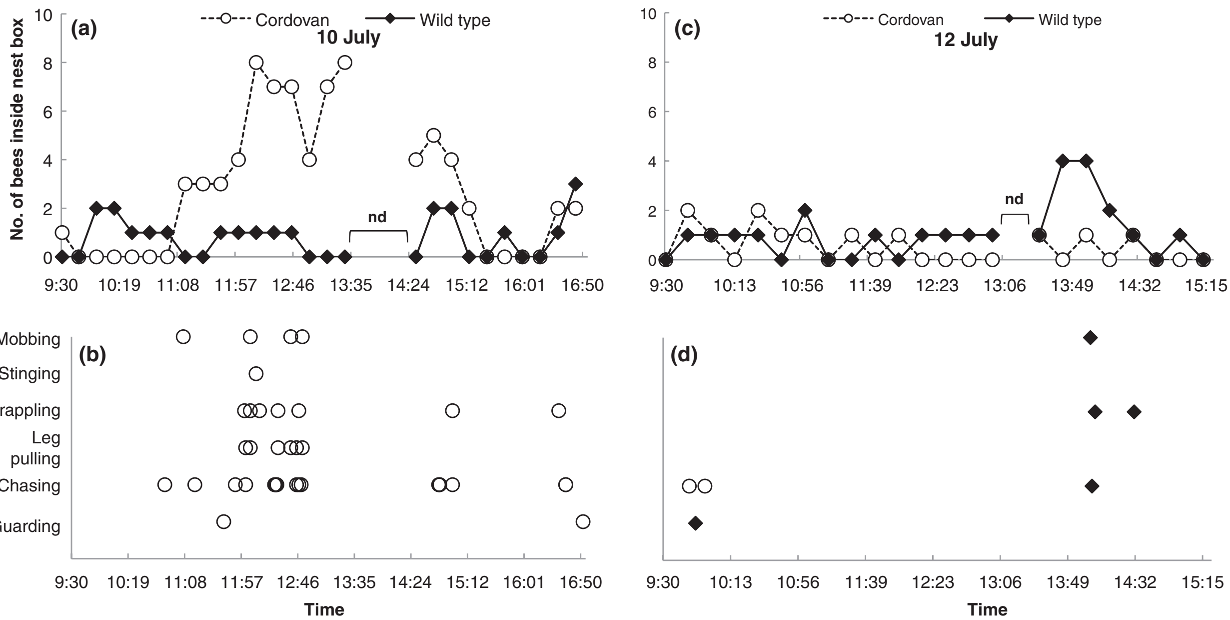

Fig. 2: Records of aggressive interactions between scouts from competing swarms at the nest box during trial 2. The top plots show the number of bees from each swarm observed at the nest box. The bottom plots show the types of agonistic interactions observed between non-swarm mates. The identity of the attacker (cordovan or wild-type scout) is represented by either an open circle or a black diamond. The abbreviation 'n.d.' indicates that no data are available for a given sampling interval.

box entrance, the other bee would run rapidly about near the entrance hole, moving in a zig-zag motion, partially opening her wings, and head-butting the newcomer while performing a buzzing behavior (Fig. 3). The buzzing bee often moved inside the nest box while remaining close to the entrance hole. The buzzing bee also spent time (1) buzzing while contacting other bees; (2) buzzing without contacting any bee; (3) contacting other bees without buzzing; (4) flying from the nest box entrance; or (5) standing inside the nest box near the entrance hole. Fig. 4 shows the percentages of time spent in each activity by bees performing the nest-site buzzing behavior.

Discussion

Our results demonstrate that when multiple honey bee swarms are searching for a home at the same time, they may explore the same potential nest sites, especially if the availability of these sites is low. Our findings also demonstrate that when this concurrent exploration happens, the nest-site scouts from competing swarms may defend a site by engaging in agonistic interactions that vary in the level of aggression depending on the number of nest-site scouts belonging to each swarm at the time of the encounters. While the interactions at the nest box between scouts from both swarms varied between trials and days, we observed consistent patterns of behavior depending on the number of bees from each swarm present together at the nest box. As shown in Fig. 5, we distinguished four levels of nest-site control, each one characterized by a certain number of bees from each swarm and a particular set of behaviors. The four levels are as follows:

Level 1: Neither swarm has control of the nest site and scouts from both are present in low numbers. At this level, each swarm has one to three bees at the site, and there are few violent interactions between non-swarm mates. These consist of one-on-one fights that last briefly, for just a few seconds, and that are rarely lethal. The nest-site buzzing behavior is not produced, and newly arriving scouts explore the site peacefully. When a bee encounters a swarm mate, they interact without aggression for several seconds.

Level 2: One swarm has weak control of the nest site with 4–20 bees there, and members of the other swarm are not present. The nest-site buzzing behavior is sometimes observed. Heavy scenting is done by bees at the entrance. The interactions between bees are peaceful.

Level 3: One swarm has weak control of the nest site, and members of the other swarm are present in low numbers. At this level, there are 4–30 bees from the swarm in the majority, and only one to three bees

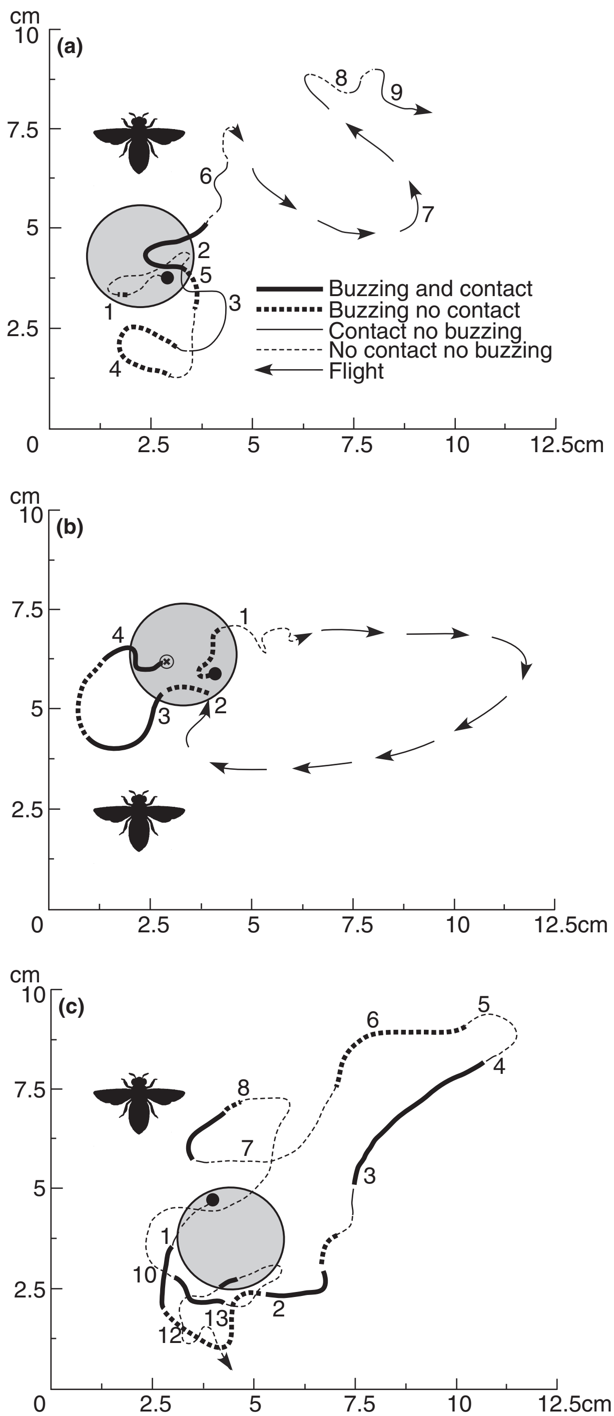

Fig. 3: Detailed view of the travel patterns, taken from videorecordings, of nest-site scouts producing the buzzing behavior near the entrance opening of the nest box. Each record depicts a different bee (a–c). The numbers next to the line denote the time elapsed (in seconds) as the bee moved across the front of the nest box. In each diagram, the large grey circle represents the entrance hole, the black circle indicates the starting point of the behavioral sequence, and an open circle with an 'x' represents when the bee entered the nest box and disappeared from the camera's view.

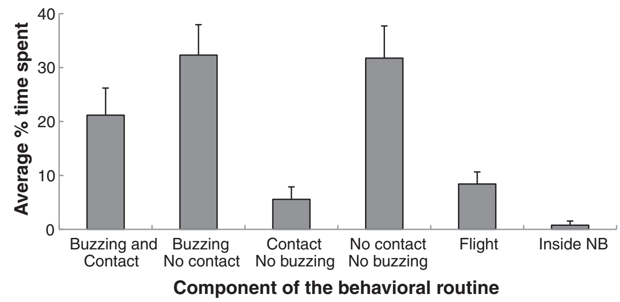

Fig. 4: Average percentage (±SE) of time spent producing each component of the nest-site buzzing behavior by nest-site scouts (n = 17).

from the swarm in the minority. When the scouts in the majority outnumber those in the minority by at least two bees, aggression toward bees from the swarm in the minority is common. The fights can still be one-on-one, but when the majority group outnumbers the other by a higher amount (i.e. eight against one), mobbing becomes prevalent. The nest-site buzzing behavior is common. Guarding at the nest box is not observed, although occasional attacks are seen in the air outside the entrance. The majority of fights do not end in deaths, and most aggressive interactions involve chasing and grappling directed toward bees in the minority.

Level 4: One swarm has strong control of the nest site. When one swarm has more than 20 bees at the nest site, and the other swarm has no bees there, the nest-site buzzing behavior is stopped and guarding is started. When there are 20–30 scouts outside, they react defensively toward visitors from both the swarms allowing swarm mates to enter, but chasing away non-swarm mates. Usually, bees from the competing swarm do not approach the nest site closely. If there are few scouts guarding the entrance, and a bee of the minority swarm enters the nest site, she will be mobbed and so has a low likelihood of escaping alive.

The variation in the levels of aggression observed at the nest box between individuals from competing swarms can be understood as different combat strategies, as proposed by Lanchester's (1916) theory of combat between two warring armies (Wallis 1968; Taylor 1984). In particular, our results are consistent with Lanchester's 'square law', which assumes that, in battles between two battling groups, all the individuals on both sides are equally vulnerable to attack from every individual on the opposing side. In this type of contest, individuals are eliminated at a rate that is proportional to the number of individuals on the other side (as described in Franks & Partridge 1993, Wilson et al. 2002). Lanchester's square law

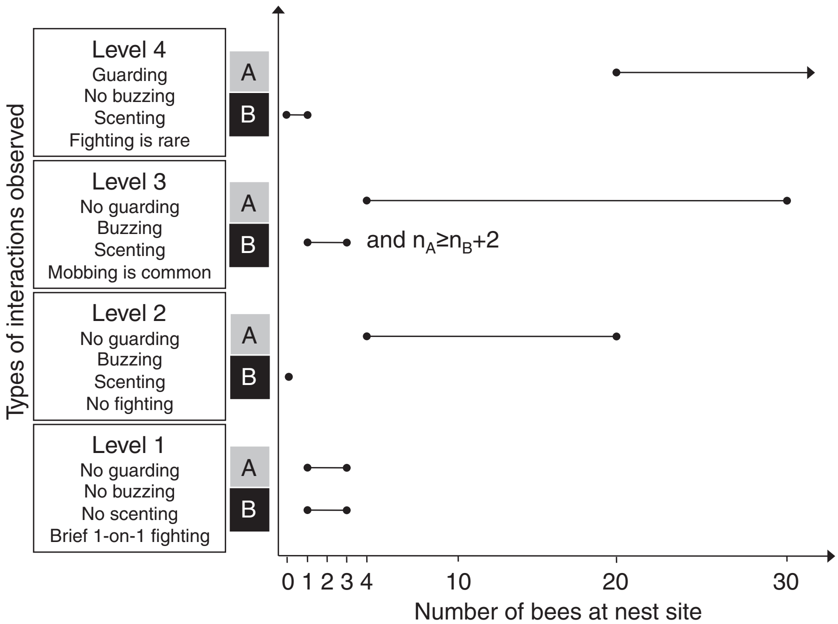

Fig. 5: Summary of the four levels of interaction observed between nest-site scouts from two swarms competing for ownership of a potential nest site. The types of agonistic interactions depend on the number of bees from each swarm present at the site. A and B refer to the two swarms, while n_A and n_B represent the number of scouts from the two swarms.

predicts that the larger an army is relative to its enemy, the fewer members it will lose. This square law shows the utility of mounting a concentrated attack in which members of one side gang up, or 'mob' individuals from the opposing side. Minimizing losses in this scenario depends mainly on superior number of individuals, not on superior fighting value of individuals. Lanchester's square law offers a good explanation to our observation that the scouts from one swarm only conducted deadly attacks against scouts from the other when the number of individuals present at the nest box from one swarm greatly exceeded those from the other swarm. Furthermore, our observation that the swarm that had a higher number of individuals at the nest box proceeded to take the opportunity to guard the narrow entrance to the disputed hive is a further example of the benefits that the group in the majority obtained from concentrated numbers.

One of the behaviors performed at the nest box entrance by scouts, the nest-site buzzing behavior, has not been previously described in detail. Previous studies of house-hunting honey bees anecdotally mention the production of what was presumed to be the buzz-run signal by scouts at nest sites, possibly to signal bees at the nest site to return to their swarm (Lindauer 1955; Seeley et al. 1979; Camazine et al. 1999). One study in particular (Camazine et al. 1999) reported that 'buzz-running generally began first on the nest site, and in many cases rather little buzz-running occurred on the swarm prior to swarm take off'. However, none of these studies provides a detailed description of this buzzing behavior at nest sites, and thus to date, its form and message remain a mystery.

The nest-site buzzing behavior that we observed is similar in form to the buzz-run signal that nest-site scouts perform to release a swarm's take off from the bivouac site (Visscher & Seeley 2007). In producing this signal, a bee encounters lethargic bees in the swarm cluster and rouses them to greater activity by moving in a zig-zag motion with her wings spread as she buzzes through them. After a few seconds the bee breaks contact with the cluster of quiescent bees while she continues to buzz and ultimately flies off the swarm (described in Rittschof & Seeley 2008). The message of this signal is now known: 'time to go'. In contrast to the bees producing buzz-runs to release a swarm's take off, bees performing the nest-site buzzing behavior contact swarm mates and non-swarm mates alike, and their behavioral routine typically starts with the buzzing bee coming out of the nest box entrance. Bees might produce the buzzing behavior near the entrance opening to provide visual beacons to swarm mates approaching the nest box, or they might produce the behavior to show their readiness to attack and defend a site and thus discourage non-swarm mates from attempting to land at an already dominated nest box. Future work needs to examine nest-site buzzers more closely to determine the exact message of their (presumed) signal.

Even though in this study we easily witnessed two swarms competing for the same scarce resource of a high-quality nest site, it is possible that this phenomenon is not common. However, this study demonstrates that under certain conditions (i.e. when suitable nesting cavities are scarce), the scout bees from neighboring honey bee swarms will compete for and defend sites of high quality. Furthermore, the scouts appear to follow sophisticated rules of site defense. The level of aggression between scouts from different swarms depends on the number of scouts from each swarm present at the time of the encounters, such that strong aggression is only observed when scouts from one swarm highly outnumber the other. Thus, scouts seem to assess their swarm's control of a site and adjust their guarding and fighting behaviors accordingly. Furthermore, we report a curious behavior, the nest-site buzzing behavior, which scouts seem to produce as part of their repertoire of aggressive behaviors to defend a high-quality nest site. Is this a signal used by scout bees to indicate resource-holding potential? The answer must await further study.

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