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Research Article

Nesting Activity and Behavior of *Osmia cornifrons* (Hymenoptera: Megachilidae) Elucidated Using Videography

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Osmia cornifrons Radoszkowski (Hymenoptera: Megachilidae) is utilized as an alternate pollinator to *Apis mellifera* L. (Hymenoptera: Apidae) in early-season fruit crops. This study was conducted to investigate nesting activities and associated behaviors of *O. cornifrons*. *Osmia cornifrons* nesting activity was recorded by using a digital video recorder with infrared cameras. Nesting behavior of ten female *O. cornifrons* was observed, and the number of nesting trips per hour was recorded. Trends in daily activity were determined with regression analysis, and chi square analysis was used to determine if *O. cornifrons* spent a greater amount of time performing certain activities. The percentage of time required to gather nesting resources and complete nest construction activities was recorded from the video footage. Results of this study showed that pollen gathering was the most time-consuming gathering activity, requiring 221.6 ± 28.69 min per cell and cell provisioning was the most time-consuming intranest activity, requiring 28.9 min $\pm$ 3.97 min. We also found that *O. cornifrons* activity was correlated with time of day, temperature, and precipitation. Various nesting behaviors, including cell provisioning and partitioning, oviposition, grooming, resting and sleeping, nest-searching, and repairing behaviors, are described in this paper.

1. Introduction

Pollination services are both economically valuable [1] and essential to many crop production systems [2]. With colony collapse disorder and various pests threatening the honeybee [3] and issues such as habitat fragmentation and pesticides threatening wild pollinators [4], considerations for alternate pollination strategies by effectively managing solitary bees have become more relevant to agricultural production [5].

The Japanese hornfaced bee, *Osmia cornifrons* Radoszkowski (Hymenoptera: Megachilidae), is an important pollinator of rosaceous fruit crops such as apple and pear. Historically, *O. cornifrons* has been managed in Japan for apple pollination since the 1940s and was introduced into the United States for pollination in 1977 [6]. Additionally, *O. cornifrons* is being used for orchard pollination in Korea and China [7, 8]. *Osmia cornifrons* has been shown to be up to 80 times more effective at pollinating apples than *A. mellifera* [9] and has several benefits over *A. mellifera* such as flower constancy and consistent anther contact [10]. Despite these benefits, *O. cornifrons* remains an underutilized pollinator in the United States.

Understanding the nesting biology of *O. cornifrons* is important for management of the bees for growers, population managers (i.e., those who sell the bees to growers), and researchers. For example, by understanding *O. cornifrons* nesting biology, one can select release sites where *O. cornifrons* has access to adequate resources. Understanding the limiting factors of *O. cornifrons* activity, such as temperature thresholds, allows one to predict if *O. cornifrons* will be pollinating on a given day of the blooming season. In addition, knowing the nesting biology of *O. cornifrons* provides growers and researchers with insights into the biology of other *Osmia* bees such as *O. lignaria*, a managed solitary bee pollinator in the United States.

Observing nesting behavior of solitary bees such as *O. cornifrons* can be challenging because it is difficult to observe bees inside their nests. Despite this challenge, several aspects of *O. cornifrons* nesting biology have been described previously. Yamada et al. [11] described nesting behaviors of

O. cornifrons including cell provisioning, mud wall partitioning, and the time required to gather pollen and mud by utilizing glass tubes wrapped in paper as artificial nests. The paper could be removed from these glass tubes after the bee entered, which permitted *O. cornifrons* nesting activities to be observed. A major disadvantage of using glass tubes is that *O. cornifrons* could be disturbed by a sudden and un-natural increase in light levels in the innermost portion of the tube when the paper is removed from the glass tube; Lee et al. [12] noted that luminance is an important factor affecting *O. cornifrons* activity. In addition, the presence of visible observers has been found to alter the frequency of activities in some insects, such as damselfly nymphs [13].

This study investigated the nesting biology of *O. cornifrons* and described in detail the behaviors associated with nesting activities. There were four objectives in this study: (1) developing an unobtrusive and novel method to observe the nesting behavior of solitary bees, (2) investigating the factors that affect *O. cornifrons* activity levels, (3) determining how much time is allocated to gathering nesting resources and constructing the nest, and (4) describing the behaviors that occur during nest construction.

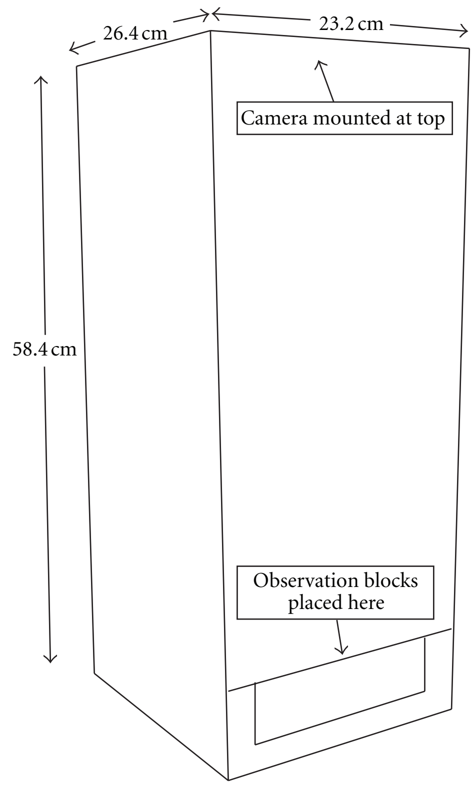

Figure 1: Diagram of camera housings for recording intranest behavior of *O. cornifrons*. The frame was made of white pine timber, and the walls were made from Masonite boards. The camera was mounted to the lid and faced down toward the observation blocks. A small groove was cut into the back of the frame to allow space for the camera cord.

Figure 2: An example observation nest block with *O. cornifrons* cocoons. The nest block was designed for videotaping nesting behavior of *O. cornifrons* by covering the top of the block with transparent plastic film.

2. Materials and Methods

2.1. Experimental Insects. *Osmia cornifrons* used in this experiment were acquired from a population that had been successfully established and managed for several years prior to the experiment on a blueberry farm in Independence, WV (N 39.46992, W 79.934651). In early November 2009, the bees were brought into the laboratory at West Virginia University (Monongalia County, WV) and placed into cold storage at 5°C for overwintering. On 9 May 2010, the bees were released in a residential area in Morgantown, WV, USA (N 39.666871, W 79.965523), where a power source for prolonged video recording of bee nest was readily available. Wilson et al. [14] stated that *O. cornifrons* could be successfully released and propagated on landscape plants in a city.

2.2. Developing a Protocol for Observing O. cornifrons In-Nest Activity. To effectively record in-nest activities of *O. cornifrons*, three camera housings were constructed from white pine and Masonite boards (Figure 1). An opening was cut into the front of the box to allow six observation nest blocks [15] to sit below the camera (Figure 2). A Masonite board roof with a 3.5 cm × 4 cm × 1.5 cm block of white pine attached to the center held an infrared camera (The Hawk Eye Nature Cam, West Linn, OR, USA) with the lens 44.3 cm from the bottom of the release box. The camera emits infrared light allowing for continuous observation without disturbing *O. cornifrons*. Cameras were connected to a 4-channel digital video recorder (DVR) (Falco Model LX-4PRO, Falco Pro Series, Taiwan) to record continuously for the entire duration of *O. cornifrons* nesting activity. The three camera housings were placed next to a building facing south and were covered with plastic to help shelter the nests from rain. A fourth camera was set outside the three camera housings facing the nest entrances. This camera was used to observe *O. cornifrons* searching behaviors and to record the weather. Nesting activities of *O. cornifrons* were recorded from 9 May 2010–1 June 2010.

2.3. Determining Factors Affecting O. cornifrons Activity. To determine the daily activity pattern of *O. cornifrons*, the number of trips from observation nest blocks initiated per hour was recorded for ten bees from 15 May 2010–21 May 2010. Data were taken from the start of nesting to six days later. Only those trips where *O. cornifrons* gathered nesting materials (i.e., pollen or mud) were used to determine daily activity levels. The relationship between the number of trips *O. cornifrons* initiated and the time of day was determined using nonlinear regression analysis (SigmaPlot 11, Systat Software, Inc., San Jose, CA, USA).

To determine the effect of temperature on *O. cornifrons* activity levels, hourly climate data were obtained from a National Climate Data Center (NCDC) weather station located ca. 3.3 km from the study site. The weather station (i.e., MGTN RGNL-W L B HART FD AP located at N 39.642867, W 79.919947) is an automated surface observing system weather station which reports NCDC version 3 climate data. Bee activity data (i.e., number of trips initiated per hour) from 18 May 2010 (sunny day) were used to correlate temperature with activity. Correlation between precipitation and bee activity from 16-17 May 2010 (rainy days) was analyzed to determine the effect of precipitation on *O. cornifrons* activity. Because the weather station reported trace precipitation (<0.25 mm rain) without a numerical value, hours of trace precipitation are considered to be 0.025 mm of rain. Correlations of bee activities with temperature and precipitation were analyzed with Pearson's product moment correlation using SigmaPlot 11.

2.4. Intranest Activity of O. cornifrons. To determine the amount of time spent by *O. cornifrons* on different in-nest activities, video data were logged for ten bees from 15 May 2010–21 May 2010: three bees from camera 1, three bees from camera 2, and four bees from camera 3. Intranest activities included nest scouting, construction of preliminary plugs, cell provisioning, oviposition, cell partitioning, resting, grooming, sleeping, fighting, and other activities. For each activity, duration was measured as follows: (1) the start time was taken from the point at which the bee reached the area of the nest being constructed, (2) the stop time was taken from the point work activity ceased, (3) if the bee stayed in the nest for >20 s after building activity ceased, this extra time was recorded along with noting after work activities. A chi-square test determined if the time requirements of intranest activity differed significantly using SigmaPlot 11.

2.5. Gathering Activity of O. cornifrons. To determine the amount of time *O. cornifrons* requires for gathering nesting materials, time away from the nest was recorded for ten bees during every trip made. Trip times were recorded from the start of nesting (15 May 2010) until six days later (21 May 2010). Only trips in which nesting materials were brought back to the nest were used in data analysis. A threshold of 1 h was set for pollen gathering trips and 30 min for mud gathering trips. Any trips exceeding these thresholds were excluded from the data used in calculating the time requirements of gathering activities. The thresholds were not used to calculate the number of trips that *O. cornifrons* took to complete one part of a cell. This was done to account for trips in which *O. cornifrons* engaged in both gathering and nongathering activity (e.g., resting), while still being able to report an accurate number of trips required to complete the provisioning and partitioning of a cell. A chi-square test determined if time requirements of gathering activity differed significantly using SigmaPlot 11.

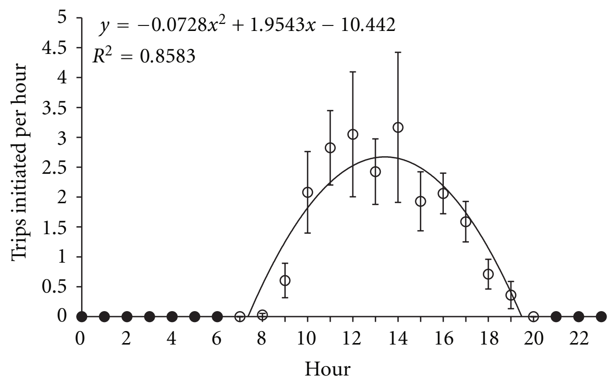

Figure 3: The average number of trips taken per hour by *O. cornifrons*. Hour 0 is 12:00 am and hour 23 is 11:00 pm. Error bars indicate standard error. Only the open circles were used to determine the regression equation.

2.6. Description of O. cornifrons Behaviors. To describe *O. cornifrons* behaviors, 30 *O. cornifrons* were observed from the time nesting was initiated (15 May 2010) until nesting ceased or six days later (21 May 2010), whichever came first. Behaviors were divided into nesting behaviors and nonnesting behaviors. Any behaviors performed during nest constructing activities were considered nesting behaviors and all other behaviors were considered nonnesting behaviors. Nesting behaviors included scouting behavior, preliminary plug behavior, cell provisioning behavior, oviposition behavior, and cell partitioning behavior. Nonnesting behaviors included grooming behavior, resting behavior, sleeping behavior, fighting behavior, nest-searching behavior, nest repair, and nest supersedure. Additionally, other behaviors that did not fall under any of the listed categories were also recorded and described.

3. Results

3.1. Factors Affecting O. cornifrons Activity. Data of daily nesting activity of *O. cornifrons* was fitted with a second-order polynomial trend (Figure 3): $y = -0.0728x^2 + 1.9543x - 10.442$ (d.f. = 2, 13; $F = 33.30$; $P < 0.0001$; $r^2 = 0.86$), where y is the number of trips initiated per hour and x is time of day. Daily activity was tested for normality using the Shapiro-Wilk normality test and was found to be normally distributed ($W = 0.9053$; $P = 0.1346$; $\alpha = 0.05$). Variance of daily activity data was constant when disregarding the time of day based on the constant variance test ($P = 0.3642$). All nesting activities of *O. cornifrons* occurred between 7:00 am and 8:00 pm, and the most trips initiated per hour occurred between 10:00 am and 6:00 pm. *O. cornifrons* was not active on days when it rained (Figure 4).

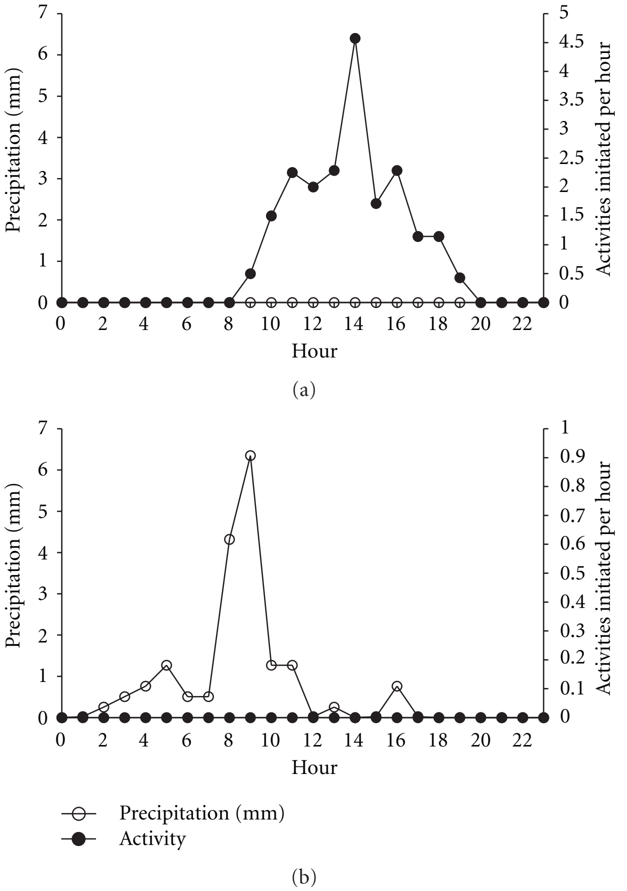

Figure 4: Relationship between *O. cornifrons* activity and precipitation on a day without rain (16 May 2010) (a) and a day with rain (17 May 2010) (b). Hour 0 is 12:00 am and hour 23 is 11:00 pm.

Individuals responded to rain by staying in their nests and occasionally walking to the nest entrance and looking out, but not exiting the nest.

Results of the Pearson product moment correlation test showed that activity and temperature were significantly correlated ($n = 24$; $\rho = 0.856$; $P < 0.0001$). The positive correlation coefficient indicates that *O. cornifrons* activity increased with temperature (Figure 5). *O. cornifrons* were not active below 13.9°C.

3.2. Intranest and Gathering Activities of O. cornifrons. The average total duration of labor required for cell completion (i.e., pollen provisioning, oviposition, and mud wall partitioning) was 51 min ± 6.5 min, and average time to complete the preliminary plug was 27 min ± 2.5 min. Provisioning the cell took most of the total time, requiring 29 ± 4.0 min (i.e., 57% of the total time to complete a cell). Building the mud-wall partition required 20 ± 1.8 min (i.e., 40% of the total time to complete a cell). Oviposition required only 3% of the total time to complete a cell, requiring 2 ± 0.7 min. Cell provisioning was the most time-consuming intranest activity, requiring 28.9 min ± 3.97 min.

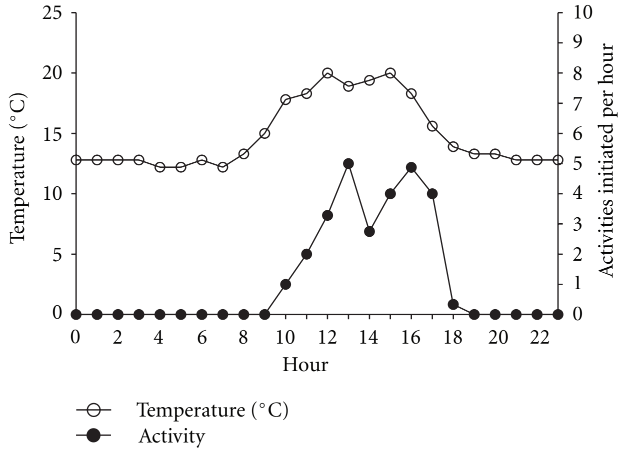

Figure 5: Relationship between *O. cornifrons* activity and temperature. Hour 0 is 12:00 am and hour 23 is 11:00 pm.

The total time required for *O. cornifrons* to gather pollen and mud for one cell was 255 ± 36.8 min, and gathering mud for a preliminary plug required 45 ± 13.7 min. Gathering pollen took 222 ± 28.7 min with an average of 19.8 trips. Gathering mud for the cell partition took 33 ± 8.1 min with an average of 11.5 trips.

3.3. Nesting Behaviors of O. cornifrons. Most nesting behaviors were distinct and consistent throughout the recorded video. Scouting behavior was the most variable behavior observed. When *O. cornifrons* searched for nests, they entered empty nests and moved to the back of the nest. Then they performed a series of forward and backward movements accompanied by turning upside down and left to right, inspecting the nest thoroughly. Finally, they turned and left the nests, occasionally coming back and performing these behaviors again.

During preliminary plug activity, *O. cornifrons* focused on plugging the upper edges of the nest, where the transparency film was attached to the observation block. During many of these trips, *O. cornifrons* moved back and forth repeatedly. This is likely a method used by the bees to measure distance [11]. They used their middle legs for support by holding them out perpendicular to their bodies and grasping the sides of the nest. Then, while holding mud with their mandibles, they bent their abdomen up until the apex of the abdomen was nearly in contact with the mandibles. Moving backwards, the mud ball was spread like a paste onto the nest surface. Use of the abdomen for nest building usually occurred during the preliminary plug activity and most often when the corner formed by the nest and the transparency film was being plugged. Although the use of abdomen during preliminary plug construction may be an artifact of the transparency film in this study, such behavior was observed in *O. lignaria* during mud gathering [16, 17] and mud wall construction [17].

Cell provisioning started when *Osmia cornifrons* females approached the rear of the nest where the pollen ball was being made. They then manipulated the pollen ball with their mandibles by either pecking at the pollen ball or pushing the pollen ball with the mandibles, using them like a shovel. During this time nectar from the crop was added to the pollen ball. After mandibulating the pollen ball, they turned in the nest and backed up so that their abdomen was over the pollen ball. Then they scraped the pollen from their scopa with their hind legs.

Oviposition behavior looked deceptively similar to cell provisioning behavior. Before oviposition *O. cornifrons* mandibulated the pollen ball, and then turned to oviposit. The primary difference in behavior between oviposition and provisioning was that the abdomen moved vigorously during nest provisioning, but it was very still during oviposition.

Osmia cornifrons females started building a mud wall partition by creating a mud ring around the inner circumference of the nest. Building the ring usually took several trips, and the abdomen was occasionally used to spread mud around the ring in concentric circles. Once there was just a small opening left in the ring they placed mud in the hole and then rotated their entire body several times with their face seemingly directly in contact with the mud wall.

3.4. Nonnesting Behavior of O. cornifrons. Grooming behavior and resting behavior were the most commonly observed nonnesting behaviors. An *Osmia cornifrons* female often groomed itself right after provisioning a cell. Grooming entailed using the front legs to clean off the antennae as well as shaking the abdomen back and forth and rubbing it with the hind legs, seemingly to clean the scopa before the next pollen load was gathered. Frequently *O. cornifrons* would groom itself as it made a hasty exit from the nest. Usually the process did not take more than 20 s to complete and did not slow down nest building activity. When grooming took more than 20 s, it was often followed by resting activity. *Osmia cornifrons* was considered resting when it was in the nest but was not performing any noticeable activity.

Sleeping behavior was defined as all activity that occurred between the final trip of one day and the first trip made the following day. Most frequently, after the final activity of the day, *O. cornifrons* would move about the nest, seemingly giving the nest a thorough inspection. After inspection, activity would cease for several minutes at a time, and if *O. cornifrons* moved, it was only ca. 4 cm. Finally activity would cease for several hours at a time, and if the bee moved, it would most often simply turn sideways. The bees often slept sideways or upside down inside the nest. Many bees did not sleep in the nests at all but returned the next day. If it rained on the morning after a bee had been sleeping outside its nest, the bee did not return to its nest during the rainy day but did return the following day. Some *O. cornifrons* also slept in empty nests. In the morning, as light entered the nest entrances, *O. cornifrons* would begin to move again. Most often, *O. cornifrons* moved ca. 4 cm then ceased movement again for some time. Eventually *O. cornifrons* would go to the nest entrance and look outside. Sometimes they left immediately, but more frequently they moved back into the nest and waited. On a few occasions a bee took flight only to return a few minutes later and resume a resting state.

There was only one observation of an attempt to repair a damaged nest. The nest became damaged when one corner of the transparency film cover became detached from the nest, and when that occurred, one individual attempted to repair the uncovered area. First it spent a great deal of time inspecting the damaged area, then it began gathering mud and trying to patch the open area at the back of the nest. It made 13 trips and patched a large area of the opening but was unable to successfully close it. After the bee's unsuccessful attempt to repair the nest, it seemed to abandon the nest.

4. Discussion

Solitary bee activity levels might be affected by time of day, temperature, or precipitation. *Osmia cornifrons* has previously been observed foraging as early as 6:10 am and as late as 6:00 pm [18]. The earliest time *O. cornifrons* became active in our study was 8:00 am and activity continued until as late as 8:00 pm, a result similar to that recorded by Matsumoto and Maejima [18]. Lee et al. [12] reported that temperatures above 20°C caused an increase in *O. cornifrons* activity. Our study showed that the minimum temperature for *O. cornifrons* to be active was 13.9°C, and bee activity increased with temperature. Matsumoto and Maejima [18] observed *O. cornifrons* activity at temperatures as low as 10.7°C. The difference in the observed minimum temperature for *O. cornifrons* activity in our study and Matsumoto and Maejima's [18] observations may be due to temperature tolerance differences between populations of *O. cornifrons*. In our study, *O. cornifrons* did not fly on rainy days, though this might be attributed to low temperatures on those days; the maximum temperature on the rainy day analyzed in this study was 14.4°C which is 0.5°C above the determined minimum temperature threshold for activity. *O. cornifrons* was most active on warm, sunny days. Therefore, *O. cornifrons* can be expected to be most active from 10:00 am to 6:00 pm on warm days (>13.9°C) without precipitation.

The majority of time that *O. cornifrons* spent performing nesting activities was used for gathering pollen and provisioning the nest, which agrees with information reported by Lee et al. [12]. The average number of cells in *O. cornifrons* nests is 9.5 [15], and results of this study showed that the average number of trips to complete a cell was 31.3. This means that it takes an average of 297 trips for *O. cornifrons* to complete a nest, though this could vary as the nesting season progresses. Comparatively, *O. lignaria* was found to require an average of 32.4 trips to provision a cell and 6.9 trips to construct a mud wall [17] and was found to construct 3.64 cells per nest on average [19].

In addition to observing *O. cornifrons* behaviors described previously, two unusual behaviors were observed that have not been described in detail previously. First, one case of nest supersedure was observed in this study. An *O. cornifrons* female had oviposited in the back of its nest and began building a mud wall. For an unknown reason the bee seemed to abandon the nest but may have been a victim of predation. Two days later, another bee entered the nest, destroyed the original egg, laid a new egg, and finished the mud wall.

Second, *O. cornifrons* females sometimes seemed to have difficulty relocating their nests. Many times a female would enter a nest and immediately turn around and leave, then enter an adjacent nest. Sometimes a bee would enter two or three nearby nests before finally entering its own nest. When *O. cornifrons* entered a nest occupied by another female *O. cornifrons*, fighting took place. During fighting, *O. cornifrons* utilized its mandibles to fight off intruding *O. cornifrons*. Also during fighting, *O. cornifrons* would bend its abdomen forward putting its body in a C-shape. It was difficult to observe from the video footage if the abdominal behavior was being used for offensive or defensive purposes. The duration of fighting was usually several minutes, and most often the original bee displaced the intruder. On some occasions nest constructing activity was interrupted by intruding bees. When an interruption like this occurred, the bee failed to complete the activity it had been working on prior to the interruption and instead inspected the back of the nest and began the behavior all over again.

Osmia cornifrons behaviors described by Yamada et al. [11] were found to be similar to those observed with the video in our study. This indicates that *O. cornifrons* is likely not disturbed by using glass tubes to view their nesting behaviors. Still, the video method has advantages over using glass tubes which make it a valuable tool for studying solitary bees: (1) it does not require the physical presence of the researcher, (2) it can gather data on activities nonstop for weeks at a time which is nearly impossible to do otherwise, (3) video footage can be rewound, sped up, or slowed down as needed to analyze the data, and (4) video footage can be archived and used in other studies. The biggest disadvantages of using the video are the power requirements to run the equipment, the time-consuming nature of watching video footage, the cost of the equipment, and the possibility of technological failure.

This study showed that *O. cornifrons* was most active between 10:00 am and 6:00 pm, and they spent most of their active time gathering pollen and provisioning their nests. It also showed that temperature and precipitation have strong effects on the activity of *O. cornifrons*. This information is important as it can be used to avoid pesticide application during *O. cornifrons* peak activity. Our results indicate that pesticide application should be avoided between the hours of 11:00 am and 4:00 pm to reduce direct contact with foraging *O. cornifrons*.

Ideally, pesticide application should not occur between 7:00 am and 8:00 pm, but this is an impractical recommendation for most growers. Furthermore, observations of *O. cornifrons* sleep habits indicate that they frequently sleep outside the nest, which means that it may be impossible to completely avoid affecting *O. cornifrons* with pesticide sprays. Previous management practice has been to place *O. cornifrons* in the field seven to ten days before crop bloom [10]. From the data gathered it is recommended that growers wait for several days of temperatures above 13.9°C so that the bees can maintain activity after emergence. Releasing *O. cornifrons* in colder weather than this will hinder their ability to perform pollination duties and may cause the bees harm as they cannot forage in the cold temperatures. Additionally, this type of data would be useful in investigating seasonal age differences in the time to provision a brood cell and determining the effect of pesticides on *O. cornifrons* behavior by comparing video footage of *O. cornifrons* in treated and untreated fields.

Acknowledgments

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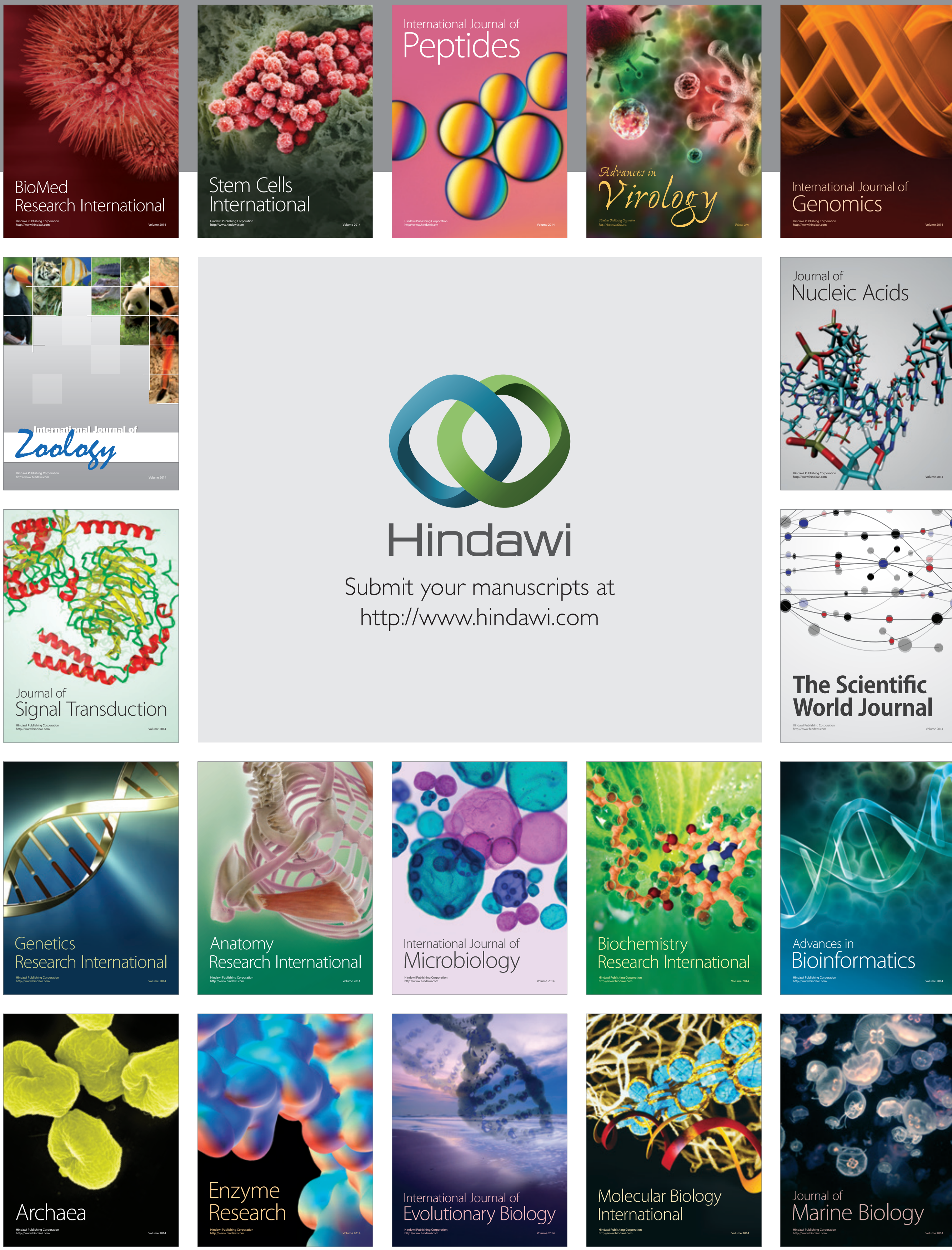
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