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Seasonal Dynamics of Overwintered Queens and Workers of the Genus *Vespa* (Hymenoptera: Vespidae) in an Apiary in Daegu, South Korea

Jaehee Kim[1], Ohseok Kwon[2], Moon Bo Choi[3]*

[1]Department of Applied Biology, College of Agriculture and Life Sciences, Kyungpook National University, Daegu, Korea
[2]Institute of Plant Medicine, College of Agriculture and Life Sciences, Kyungpook National University, Daegu, Korea
[3]Institute of Agricultural Science and Technology, Kyungpook National University, Daegu, Korea

ABSTRACT

This study investigated the seasonal occurrence patterns of overwintered queens and hornet workers (*Vespa* spp.) collected over two years (2022 and 2024) at an apiary in Daegu, South Korea. Using hornet attractant traps, 744 individuals representing eight *Vespa* species were collected, of which *Vespa velutina* Lepeletier, 1836 and *Vespa crabro* Linnaeus, 1758 were the most frequently observed. The timing of the emergence of overwintered queens varied by species: *Vespa mandarinia* Smith, 1852 and *V. velutina* were the earliest to appear in early April, followed by *V. crabro*, *Vespa analis* Fabricius, 1775, and *Vespa ducalis* Smith, 1852. Workers began to emerge predominantly in mid-July, with populations peaking in August and September and declining sharply in October. Notably, following the application of a control method using an insecticide (clothianidin) in late July 2024, a marked decrease in the number of *V. velutina* workers was observed. This study highlights interspecific differences in the timing of colony development and provides foundational data for the effective management of hornets in apiary environments.

Keywords: Apiary, Insecticide, Reproduction, Seasonal variation, *Vespa*, Worker

Introduction

Species of the genus *Vespa* Linnaeus, 1758 (Hymenoptera: Vespidae) are apex predators of various arthropods and play critical regulatory roles in insect ecosystems (Brock *et al*., 2021; Richter, 2000). However, their potent venom and aggressive behavior pose risks to human safety (Choi *et al*., 2019), and certain species target honeybees, causing significant economic damage to apiculture (Norderud *et al*., 2021; Requier *et al*., 2023).

In recent years, the spread of *Vespa* species into regions such as Northeast Asia, Europe, and North America has raised concerns regarding their ecological, economic, and public health impacts (Lioy *et al*., 2022; Otis *et al*., 2023). The invasive alien species *Vespa velutina* Lepeletier, 1836, originally native to China, has expanded across Asia and Europe (Lioy *et al*., 2022), and was reported in the United States in 2023 (Hoebeke *et al*., 2024). Similarly, *Vespa mandarinia* Smith, 1852 drew international attention after its spread from Korea and Japan to North America in 2019 (Alaniz *et al*., 2021).

In invaded regions, various control efforts have been implemented to suppress hornet populations, reduce api-

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***Corresponding author:** Moon Bo Choi
e-mail kosinchoi@hanmail.net
https://orcid.org/0000-0001-7742-3704

ary damage, and mitigate broader ecological impacts (Beggs *et al*., 2011; Turchi & Derijard, 2018). However, most field-based control measures rely on direct collection using nets or hornet attractant traps, which are labor-intensive and offer short-term effectiveness (Beggs *et al*., 2011; Hsu *et al*., 2021; Lioy *et al*., 2020). Developing more sustainable and effective strategies requires a deeper understanding of *Vespa* biology, colony development, and foraging behavior; however, such ecological insights remain scarce for many species (Matsuura, 1984; Monceau *et al*., 2014).

Although *Vespa* species are frequently observed near apiaries (Chang *et al*., 1993; Choi & Kwon, 2015; Kim *et al*., 2024; Sim *et al*., 2014), only a limited subset directly threaten honeybees. This variation reflects interspecific differences in prey preferences and hunting behaviors (Matsuura, 1984; Matsuura & Yamane, 1990). In addition to predation, hornets may be drawn to sugar-rich resources, such as honey, pollen, and fermenting fruit (Couto *et al*., 2014; Paschapur *et al*., 2022), and abandoned hives or nearby areas serve as favorable nesting sites (Matsuura, 1971).

The seasonal activity of hornets is influenced by geographic and climatic variability, including local microclimates and annual weather fluctuations, which affect colony survival and growth (Choi & Kwon, 2015; Kim *et al*., 2020; Matsuura, 1991; Singha *et al*., 2023). The rise of invasive species has also led to shifts in the distribution of native hornets, introducing interspecific competition, and potentially altering colony cycles (Barbet-Massin *et al*., 2013; Choi *et al*., 2012a).

Early stage hornet colonies are often difficult to detect because of their high failure rates and small colony sizes (Spradbery, 1973), which limit the feasibility of direct observation. As an alternative, analyzing the seasonal occurrence of individuals collected using hornet attractant traps and distinguishing between overwintered queens and workers can provide valuable insights into colony development.

In the present study, a control method using insecticides was applied at the study apiary during fall (Hong & Jung, 2024; Kim *et al*., 2021), after which the abundance of certain *Vespa* species declined sharply. Although observational, these patterns highlight the potential influence of chemical control on hornet population dynamics and underscore the need for more rigorous experimental validation.

Here, we monitored *Vespa* activity over two years at an apiary in Daegu, South Korea, using hornet attractant traps. We examined the timing, duration, and frequency of the emergence of overwintered queens and workers across multiple species. These findings offer comparative insights into species-specific colony development and provide baseline ecological data for the development of more effective and ecologically informed hornet management strategies in apicultural environments.

Materials and Methods

Study site and trap configuration

This study was conducted at an apiary located near Palgongsan National Park in Daegu, South Korea (35°58'25.8"N, 128°39'48.2"E). The study area covered approximately 30 m^2. Five hornet attractant traps were deployed at 5-10 m intervals within the site (Kim *et al*., 2019). The attractant used in the traps was a mixture of plum extract and water at a 7:3 ratio. Given the relatively short distances between the traps and the wide foraging range of hornets, we assumed that the traps could potentially sample individuals from the same local population (Choi *et al*., 2012b). Therefore, the data from all traps were pooled for analysis.

Sampling schedule and frequency

For 2022, the survey focused on determining the emergence period of overwintered queens. Traps were installed on April 25 and collected seven times until July 30, when the queen activity ceased.

In 2024, to gain a more detailed understanding of species-specific queen emergence and seasonal dynamics of workers, traps were installed on April 7. Sampling was conducted 48 times between April 9 and October 22. During the expected emergence period of the new queens, traps were checked every 2-3 days to monitor the transition to the colony's cooperative phase. After mid-July, when workers began to appear, the sampling intervals were extended to approximately two weeks (Table 1).

Species and caste identification

Among the insects collected from the traps, individuals belonging to the genus *Vespa* were isolated and their species and caste were identified. Identification was performed using the taxonomic key provided by Smith-Pardo *et al*. (2020).

Results

Species composition and abundance of *Vespa* queens and workers over two years

Over the survey period, 748 individuals representing eight *Vespa* species were collected from the apiary. Among these, *V. velutina* (N=256, 34.2%) and *Vespa crabro* Linnaeus, 1758 (N=217, 29.0%) were the most frequently collected species, followed by *Vespa ducalis* Smith, 1852 (N=131, 17.5%), *V. mandarinia* (N=70, 9.36%), and *Vespa analis* Fabricius, 1775 (N=40, 5.4%). *Vespa dybowskii* André, 1884, *Vespa simillima* Smith, 1868, and *Vespa binghami* du Buysson, 1905 were collected in substantially

Table 1. Trap collection dates for *Vespa* sampling at the Daegu apiary from April to October in 2022 and 2024

Month	Year	Day												
April	2022	25*	-	-	-	-	-	-	-	-	-	-	-	-
	2024	07*	9	12	15	17	21	24	26	29	-	-	-	-
May	2022	8	23	30	-	-	-	-	-	-	-	-	-	-
	2024	1	3	6	8	10	13	15	17	19	22	24	27	29
June	2022	15	30	-	-	-	-	-	-	-	-	-	-	-
	2024	1	3	5	7	9	12	14	17	20	23	26	28	-
July	2022	2	30	-	-	-	-	-	-	-	-	-	-	-
	2024	2	5	8	10	12	15	18	26	-	-	-	-	-
August	2024	7	18	29	-	-	-	-	-	-	-	-	-	-
September	2024	12	22	-	-	-	-	-	-	-	-	-	-	-
October	2024	6	22	-	-	-	-	-	-	-	-	-	-	-

Values are presented as number.
-, not applicable.
*Trap installation date: April 25, 2022 and April 7, 2024.

lower numbers, generally fewer than 10 individuals each, and were thus considered minor components of the hornet community at the site (Fig. 1).

In 2022, 186 overwintered queens representing six species were collected. *V. velutina* was the dominant species (N=102, 54.8%), followed by *V. crabro* (N=29, 15.6%) and *V. mandarinia* (N=20, 10.8%; Figs. 1, 2).

In 2024, 562 individuals from eight species will be collected. The most frequently collected species was *V. crabro* (N=188, 33.7%), followed by *V. velutina* (N=154, 27.6%) and *V. ducalis* (N=113, 20.3%). Among these, 171 overwintered queens from eight species were identified, with *V. velutina* being the most dominant (N=51, 29.8%), followed by *V. crabro* (N=43, 25.1%) and *V. mandarinia* (N=37, 21.6%; Fig. 2).

In 2024, 391 workers from seven species were collected. *V. crabro* accounted for the highest proportion (N=145, 37.1%), followed by *V. velutina* (N=103, 26.3%) and *V. ducalis* (N=102, 26.1%; Fig. 3).

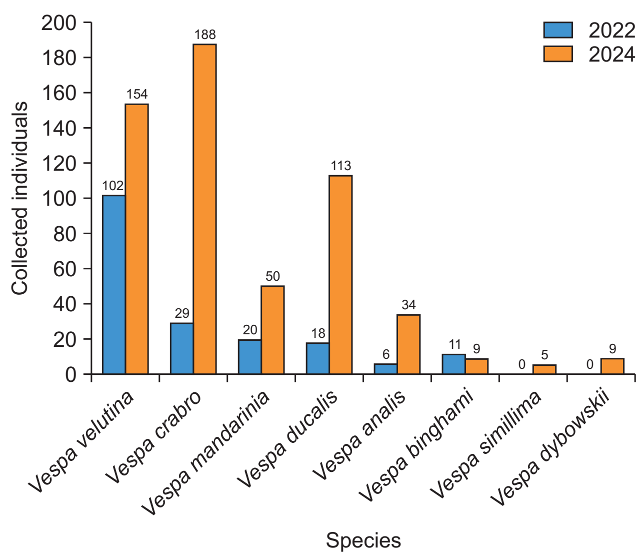

Fig. 1. Species and number of *Vespa* individuals collected through trapping over two years at the Daegu apiary.

Emergence timing of overwintered queens

Vespa velutina

In 2022, following trap installation on April 25, overwintered queens of *V. velutina* were predominantly collected during surveys on May 8 (N=51) and May 23 (N=38), indicating a sharp early peak in emergence. After May 30, the number of queens declined rapidly, with only 5-6 individuals collected intermittently in June. The last queen was collected on June 30.

In 2024, traps will be installed on April 7, and the first queen was collected on April 12. The highest number was recorded on April 29 (N=15), followed by consistent but declining collections of 3-4 individuals per survey until May 17, after which no further queens were collected. The final collection date for the queens was May 17.

These results indicate that *V. velutina* queens begin to emerge in early to mid-April, reach peak activity between late April and mid-May, and then decline sharply (Figs. 2, 4).

Vespa mandarinia

In 2022, the first queen was collected during the initial survey on May 8, and the queens continued to be collected in low numbers (≤6 individuals) until June 15, which

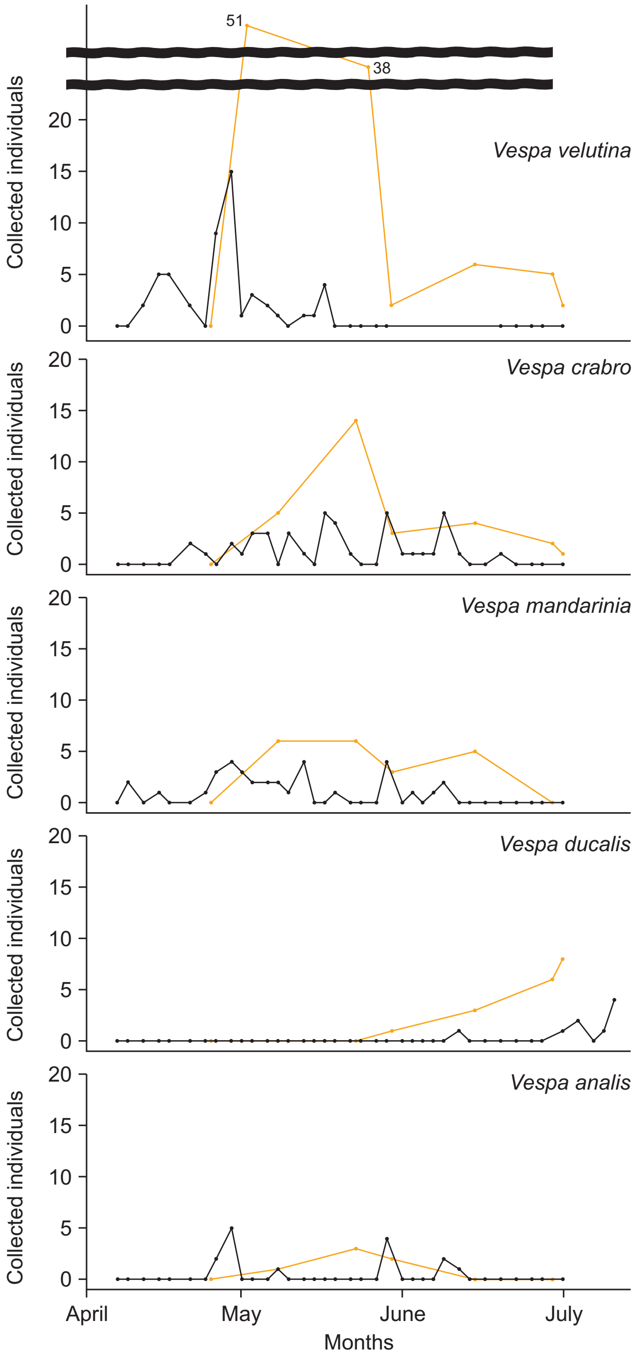

Fig. 2. Number of *Vespa* overwintered queens collected at the Daegu apiary from April to July in 2022 (yellow line) and 2024 (black line).

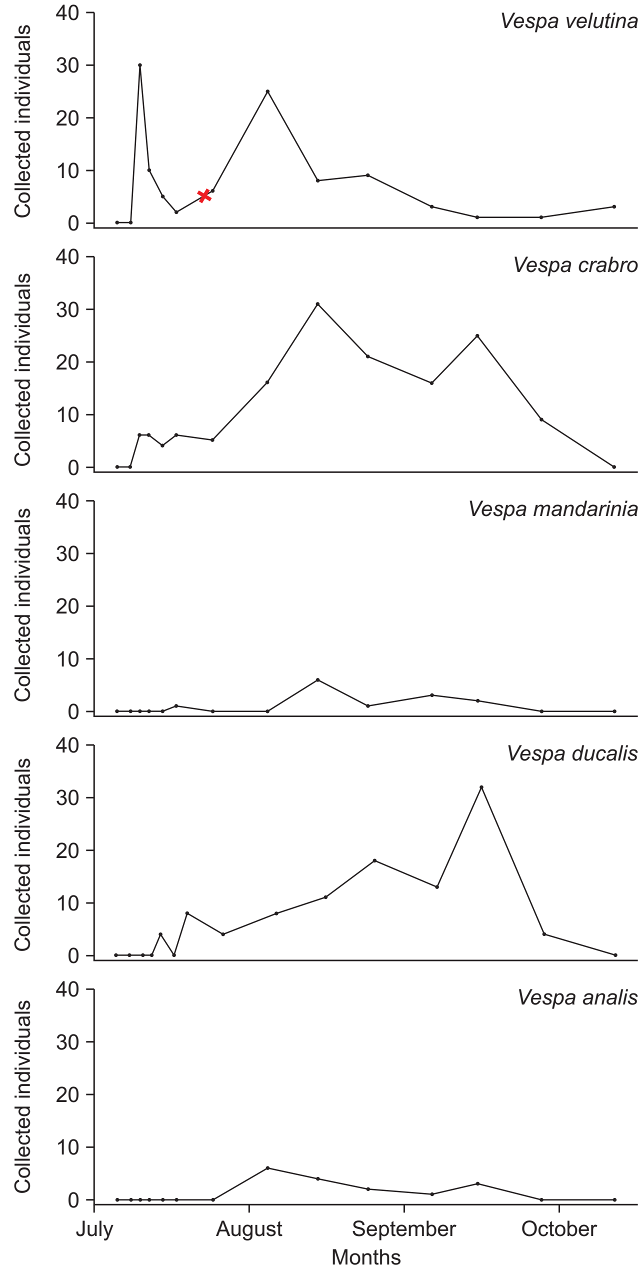

Fig. 3. Number of *Vespa* workers collected at the Daegu apiary from July to October in 2024 (the red X mark indicates the start of insecticide application on July 25, 2024).

In addition, three young queens were observed in the apiary on October 6, 2024 (Figs. 2, 4).

marked the final collection date.

In 2024, the first queen was collected on April 9, with sporadic collections continuing until June 9. Considering that queen activity in 2022 may have already begun before the start of sampling, it is likely that *V. mandarinia* also began its emergence period from early to mid-April.

Vespa crabro

In 2022, the first *V. crabro* queen was collected on May 8, and a peak of 14 individuals was observed on May 23. Queens were collected at a steady rate (3-5 individuals per survey) until their final collection on July 2.

In 2024, the first queen was recorded on April 21 and

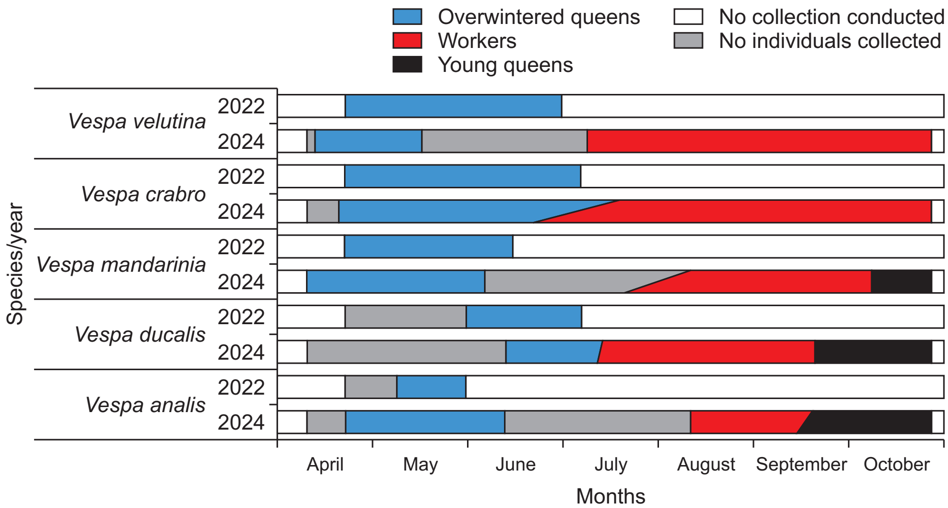

Fig. 4. Seasonal occurrence patterns of overwintered queens from five major *Vespa* species collected over two years at the Daegu apiary.

was continuously collected in low numbers (2-3 individuals) until June 20. Although no individuals were collected for approximately one month thereafter, one additional queen was captured on July 18. These findings suggest that *V. crabro* begins to emerge in late April and remains active until late June, with some individuals persisting into mid-July (Figs. 2, 4).

Vespa analis

In 2022, the first *V. analis* queen was collected on May 8, and the final individual was recorded on May 30. In 2024, the first queen was collected on April 26, followed by intermittent captures (1-5 individuals) until June 12 without a clear emergence peak. One young queen was observed on September 22, 2024. These results suggest that *V. analis* typically begins to emerge in late April (Figs. 2, 4).

Vespa ducalis

Among the studied species, *V. ducalis* exhibited the most recent queen emergence. In 2022, the first queen was collected on May 30, with collection continuing until July 2 (N=18). In 2024, the queens were collected from June 12 to July 12 (N=9). Notably, on July 12, the queen was collected alongside a worker, suggesting an active colony formation. Several young queens were also observed from mid to late October, 2024. These findings indicate that *V. ducalis* exhibits delayed emergence and colony initiation compared to the other species (Figs. 2, 4).

Other species

V. dybowskii, V. simillima, and *V. binghami* were collected in low numbers with sporadic emergence patterns. *V. binghami* queens were collected on May 8 and 23, 2022, and on April 26 and May 19, 2024, indicating intermittent activity between late April and mid-May. *V. dybowskii* queens were collected on April 26, April 29, and June 9, 2024 (N=4 in total), suggesting occasional emergence between late and early June. *V. simillima* queens were collected only on April 29 and May 10, 2024 (N=5), indicating a limited and short emergence window between late April and early May.

Emergence timing of workers

Vespa velutina

In the 2024 survey, the first *V. velutina* worker was collected on July 10. No individuals were collected on the previous sampling date (July 8), indicating a sudden and synchronized onset of worker activity. Within two days, 30 individuals were collected, representing a sharp increase in the population. The number of workers temporarily declined over the following three weeks; however, another peak was recorded on August 7 with 25 individuals. From September to October, the number of individuals dropped sharply, with only four workers collected in each of the two months (Figs. 3, 4).

Vespa mandarinia

The first *V. mandarinia* worker was collected on July 18, 2024. Thirteen individuals were collected during the survey period. Overall, the abundance remained low, with no clear increase or peak (Figs. 3, 4).

Vespa crabro

Similar to *V. velutina*, *V. crabro* workers first appeared on July 10, 2024. The population gradually increased, peaking at 31 individuals on August 18. From late August to September, 10-20 individuals were consistently collected during each sampling period. However, by early October, worker occurrence dropped sharply, with the last collection occurring on October 6 (Figs. 3, 4).

Vespa analis

The first worker of *V. analis* was collected on August 7, 2024. However, fewer than five individuals were collected in August and September, and no clear pattern of increase was observed (Figs. 3, 4).

Vespa ducalis

Despite having a relatively late queen emergence, *V. ducalis* workers first appeared on July 12, 2024, around the same time as the other species. Four samples were collected on the same day. Fewer than ten individuals were collected in mid-August, after which the population began to increase. On September 22, 32 individuals were collected, which marked the peak in worker abundance. Worker numbers declined thereafter, with the last individuals (N=4) collected on October 6 (Figs. 3, 4).

Other species

For the remaining species, worker activity was minimal. *V. dybowskii* workers were collected sporadically between August and September. No *V. simillima* workers were collected during the survey period. *V. binghami* was represented by seven workers collected between early July and mid-September represented *V. binghami*. Overall, all three species exhibited limited sporadic worker activity.

Discussion

Vespa species observed in the apiary

Eight *Vespa* species were collected from the apiary during the study period. Among these, *V. velutina* was the most frequently collected species and was identified as the primary threat to apiaries. This species has now spread across South Korea and is the most prevalent hornet species near apiaries in most regions, contributing to widespread and significant damage (Choi & Kwon, 2015; Kim *et al*., 2025).

V. crabro and *V. ducalis* also appeared in relatively high numbers; however, these species tended to visit apiaries primarily to exploit floral resources rather than actively hunt honeybees. Consequently, their direct impact on apiculture is relatively minor (Matsuura & Yamane, 1990).

In contrast, although *V. mandarinia* was collected in smaller numbers, it poses a serious threat because of its tendency to engage in group attacks on beehives (Matsuura & Sakagami, 1973). Therefore, from a management perspective, *V. velutina* and *V. mandarinia* should be prioritized for control strategies in and around apiaries.

Emergence timing of overwintered queens

The sequences of overwintered queen emergence observed in the present study were *V. mandarinia*-*V. velutina*-*V. crabro*-*V. analis*-*V. ducalis*. *V. mandarinia* and *V. velutina* emerged the earliest in early April, followed by *V. crabro* and *V. analis* between late April and May. *V. ducalis* queens emerged in early June.

This emergence sequence closely aligns with previous observations in Japan by Matsuura (1984), who reported the queen emergence of *V. mandarinia* in April, *V. analis* and *V. crabro* in May, and *Vespa tropica* (Linnaeus, 1758), a species closely related to *V. ducalis*, between June 8 and 25.

Among the less frequently collected species, *V. binghami, V. simillima*, and *V. dybowskii* were primarily observed after late April. Notably, *V. velutina* exhibited an emergence pattern similar to that of *V. mandarinia*, with activity beginning in early April.

The overall advancement in emergence timing compared to earlier studies may be attributed to recent increases in average spring temperatures on the Korean Peninsula (An *et al*., 2011), which may accelerate the post-hibernation activity of overwintered queens (Spradbery, 1973).

Among all species, *V. ducalis* exhibited the latest colony initiation. This may reflect an adaptive strategy linked to its specialized ecological niche as a predator of paper wasps, with emergence timing synchronized with the development of its prey colonies (Archer, 1991; Matsuura, 1984; Starr, 1992).

From a methodological standpoint, the 2022 survey had wider intervals between site visits, limiting the precision of the emergence timing data. In contrast, the 2024 survey employed a shorter sampling interval, allowing for a more accurate tracking of emergence patterns.

Overall, most species ceased external activity from early to mid-June, after which queens were seldomly collected. This is likely due to the shift in colony dynamics around mid-June, when the first workers begin to emerge and the queens remain in the nest to focus on reproduction.

Seasonal emergence patterns of workers

This study examined the timing and abundance of hornet workers in an apiary. Most workers began to appear between early and mid-July, although in some species, the first individuals were not collected until mid-August. Worker abundance generally increased over time, peaking in August and September, followed by a sharp decline in October. This trend is consistent with previous reports on the life history of *Vespa* species, in which worker activity typically intensifies in mid-summer and lessens during autumn (Chang *et al.,* 1993; Choi & Kwon, 2015; Matsuura & Yamane, 1990).

Interestingly, the current study showed a brief gap in worker collection between mid-June and early July. This may be attributed to the behavioral characteristics of early emerging workers, who are often smaller and less experienced in foraging. These individuals may avoid high-risk environments, such as apiaries, or escape from traps more easily because of their smaller size or less aggressive behavior (personal observation by Choi). Such traits could influence the frequency of their appearance at the apiary and the likelihood of their being collected by traps.

A particularly notable case was observed for *V. velutina* (Fig. 3). This species exhibited a sudden spike in worker abundance around July 10, with 30 individuals collected after a period of no capture. This sudden emergence coincided with approximately 250 mm of heavy rainfall recorded the day before and morning of sampling (KMA, 2024). It is likely that adverse weather conditions previously suppressed foraging activity, leading to delayed but concentrated post-rain emergence. Given the strong preference of *V. velutina* for honeybee predation (Norderud *et al*., 2021), such intensified activity near the apiary was expected.

However, these results were based on observations from a single apiary and may not reflect broader patterns of worker emergence across different landscapes. Factors such as topography, microclimate, vegetation, and local management practices also affect hornet activity. Thus, these findings should be interpreted with caution and should be supported by further studies across diverse geographical regions.

Implementation and effects of insecticide-based control

In this study, an insecticide-based control method targeting *V. velutina* was applied by the beekeeper at the apiary. The treatment was conducted beginning on July 25, using a method in which hornets were collected, treated with a neonicotinoid insecticide on the thorax and abdomen, and then released. The active ingredient used was clothianidin, a commercially available chloronicotinyl compound (International Organization for Standardization name: 3-[(2-chloro-1,3-thiazol-5-yl) methyl]-2-methyl-1-nitroguanidine; SG Hankooksamgong).

Immediately following the treatment, no sharp decline in trap collection was observed. According to previous studies, clothianidin, when applied at the recommended concentrations, can induce high mortality in adults within 6 hours and in larvae within 48 hours (Hong & Jung, 2024). Furthermore, this compound has been reported to spread throughout colonies within 24 hours, exerting a colony-wide effect (Kim *et al*., 2021). In theory, a noticeable population decline should have occurred within two days of application. However, as of August 7 sampling, 25 *V. velutina* workers were still being collected.

This delayed response may be due to the timing of the treatment, which coincides with the peak period of nest relocation in *V. velutina* (Diéguez-Antón *et al*., 2022). It is possible that newly arrived colonies that were not exposed to the insecticide subsequently established foraging routes for the apiaries. Hornet larvae are protected during pupation by cocoons, which form a sterile microenvironment that may prevent sufficient penetration by insecticides (Shabtai & Ishay, 1998). Given that pupation lasts approximately 16-19 days (Archer & Penney, 2012; Dong & Wang, 1989), and that clothianidin degrades naturally within approximately one week, it is plausible that newly emerged adults developed after the insecticide's effective period had passed.

Despite these factors, the sustained application of the insecticide by the beekeeper likely contributed to the cumulative control effects over time. The number of *V. velutina* workers declined markedly from late August onward and did not recover until mid-October. These results suggested that the insecticide-based method had at least moderate efficacy in suppressing *V. velutina* activity.

Clothianidin, a neonicotinoid, is widely regarded by local beekeepers as an effective control agent for *V. velutina* (Hong & Jung, 2024). The findings of this study support the potential utility of such methods in mitigating hornet-related damage to apiaries. However, the repeated use of insecticides raises concerns about their unintended impacts on non-target organisms and residual contamination within apiaries. Therefore, future efforts should prioritize the development of more sustainable and ecologically responsible control strategies.

Conclusion

This study confirmed that *V. velutina* was the most damaging hornet species in the surveyed apiary in Daegu, with *V. mandarinia* posing a significant threat due to its capacity for group predation. In contrast, *V. crabro* and *V. ducalis* were frequently observed, but posed minimal direct risk to honeybee colonies.

The emergence patterns of overwintered queens varied by species, with most queens ceasing external activity by mid-June, coinciding with the transition to worker production. Workers began emerging in mid-July, peaked in August and September, and declined sharply in October. Notably, a substantial reduction in *V. velutina* was observed following insecticide treatment, indicating the effectiveness of the control method.

Nevertheless, owing to the potential risks of repeated insecticide use, particularly with respect to non-target species and environmental safety, future research should explore more sustainable and eco-friendly approaches to hornet management. This study provides baseline ecological data on hornet phenology and behavior in apiary environments that can inform the development of effective targeted management strategies.

Author Contributions

Conceptualization: Moon Bo Choi, Jaehee Kim. Data curation: Jaehee Kim. Formal analysis: Jaehee Kim. Funding acquisition: Moon Bo Choi. Investigation: Moon Bo

Choi, Jaehee Kim. Methodology: Moon Bo Choi. Project administration: Ohseok Kwon, Moon Bo Choi. Resources: Moon Bo Choi. Software: Moon Bo Choi, Jaehee Kim. Supervision: Ohseok Kwon, Moon Bo Choi. Validation: Ohseok Kwon, Moon Bo Choi. Visualization: Moon Bo Choi, Jaehee Kim. Writing – original draft: Jaehee Kim. Writing – review & editing: Moon Bo Choi, Jaehee Kim.

Conflict of Interest

The authors declare that they have no competing interests.

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References

Alaniz, A.J., Carvajal, M.A., and Vergara, P.M. (2021). Giants are coming? Predicting the potential spread and impacts of the giant Asian hornet (Vespa mandarinia, Hymenoptera:Vespidae) in the USA. *Pest Management Science*, 77, 104-112. https://doi.org/10.1002/ps.6063

An, S.I., Ha, K.J., Seo, K.H., Yeh, S.W., Min, S.K., and Ho, C.H. (2011). A review of recent climate trends and causes over the Korean peninsula. *Journal of Climate Change Research*, 2, 237-251.

Archer, M.E. (1991). Taxonomy and bionomics of the Vespa tropica group (Hym., Vespinae). *Entomologist's Monthly Magazine*, 127, 225-232.

Archer, M.E., and Penney, D. (2012). *Vespine Wasps of the World: Behaviour, Ecology & Taxonomy of the Vespinae*. Siri Scientific Press.

Barbet-Massin, M., Rome, Q., Muller, F., Perrard, A., Villemant, C., and Jiguet, F. (2013). Climate change increases the risk of invasion by the Yellow-legged hornet. *Biological Conservation*, 157, 4-10. https://doi.org/10.1016/j.biocon.2012.09.015

Beggs, J.R., Brockerhoff, E.G., Corley, J.C., Kenis, M., Masciocchi, M., Muller, F., *et al.* (2011). Ecological effects and management of invasive alien Vespidae. *BioControl*, 56, 505-526. https://doi.org/10.1007/s10526-011-9389-z

Brock, R.E., Cini, A., and Sumner, S. (2021). Ecosystem services provided by aculeate wasps. *Biological Reviews of the Cambridge Philosophical Society*, 96, 1645-1675. https://doi.org/10.1111/brv.12719

Chang, Y., Lee, M., Yim, Y., and Youn, Y. (1993). Species and visiting patterns of wasps (Hymenoptera: Vespoidea) in an apiary. *Journal of Apiculture*, 8, 22-28.

Choi, M.B., Kim, T.G., and Kwon, O. (2019). Recent trends in wasp nest removal and Hymenoptera stings in South Korea. *Journal of Medical Entomology*, 56, 254-260. https://doi.org/10.1093/jme/tjy144

Choi, M.B., and Kwon, O. (2015). Occurrence of Hymenoptera (wasps and bees) and their foraging in the southwestern part of Jirisan National Park, South Korea. *Journal of Ecology and Environment*, 38, 367-374. https://doi.org/10.5141/ecoenv.2015.038

Choi, M.B., Martin, S.J., and Lee, J.W. (2012a). Distribution, spread, and impact of the invasive hornet *Vespa velutina* in South Korea. *Journal of Asia-Pacific Entomology*, 15, 473-477. https://doi.org/10.1016/j.aspen.2011.11.004

Choi, M.B., Park, B.A., and Lee, J.W. (2012b). The species diversity and distribution of Vespidae in Southeast region (Sangdong-eup, Gimsatgat-myeon, Jungdong-myeon) of Yeongwol-gun, Gangwon-do, Korea. *Journal of Korean Nature*, 5, 305-310. https://doi.org/10.7229/jkn.2012.5.4.305

Couto, A., Monceau, K., Bonnard, O., Thiéry, D., and Sandoz, J.C. (2014). Olfactory attraction of the hornet *Vespa velutina* to honeybee colony odors and pheromones. *PLoS One*, 9, e115943. https://doi.org/10.1371/journal.pone.0115943

Diéguez-Antón, A., Escuredo, O., Seijo, M.C., and Rodríguez-Flores, M.S. (2022). Embryo, relocation and secondary nests of the invasive species *Vespa velutina* in Galicia (NW Spain). *Animals (Basel)*, 12, 2781. https://doi.org/10.3390/ani12202781

Dong, D., and Wang, Y. (1989). A preliminary study on the biology of wasps Vespavelutina auraria Smith and Vespatropica ducalis Smith (Hymenoptera: Vespidae). *Zoological Research*, 10, 155-162.

Hoebeke, E.R., Bartlett, L.J., Evans, M., Freeman, B.E., and Wares, J.P. (2024). First records of *Vespa velutina* (Lepeletier) (Color form *Nigrithorax*) (Hymenoptera: Vespidae) in North America, an invasive pest of domesticated honeybees. *Proceedings of the Entomological Society of Washington*, 126, 193-205. https://doi.org/10.4289/0013-8797.126.2.193

Hong, D., and Jung, C. (2024). Evaluation of the susceptibility of several insecticides to honey bee pest, *Vespa velutina nigrithorax* (Hymenoptera: Vespidae). *Korean Journal of Applied Entomology*, 63, 13-23. https://doi.org/10.5656/KSAE.2024.01.1.044

Hsu, K.T., Chen, C.H., Chen, Z.H., Hong, S.S., Wang, C.T., and Chen, W.P. (2021). *Beehive with low-energy of high-voltage shock against killer hornets*. Paper presented at 2021 International Conference on Electronic Communications, Internet of Things and Big Data (ICEIB), Yilan County, Taiwan.

Kim, I.K., Kim, C.J., Choi, J.H., Kang, H.J., and Choi, M.B. (2025). Stylopization by Xenos spp. (Xenidae, Strepsiptera) in invasive alien hornet, Vespa velutina, in South Korea. *Parasite*, 32, 10. https://doi.org/10.1051/parasite/2025004

Kim, J., Choi, Y.S., Kang, E.J., Kim, S., Kim, K., Park, B., *et al*. (2021). Evaluation of control efficiency against Vespa spp. (Family: Vespadae) using method of release after applying pesticide to the Vespa body. *Journal of Apiculture*, 36, 105-110. https://doi.org/10.17519/apiculture.2021.09.36.3.105

Kim, S., Park, B., Min, S., and Kim, D. (2024). Occurrence patterns of major wasp species around near apiary in Wanju, Jeollabuk-do. *Journal of Apiculture*, 39, 175-184. https://doi.org/10.17519/apiculture.2024.09.39.3.175

Kim, W.M., Kim, S.Y., and Song, W. (2020). Microhabitat characteristics affecting the occurrence and diversity of queen hornets (genus *Vespa*) in an urban green area. *Landscape* *and Ecological Engineering*, 16, 173-186. https://doi.org/10.1007/s11355-020-00415-w

Kim, W.M., Kim, S.Y., Song, W., and Choi, M.B. (2019). Ecological characteristics of hornets (genus *Vespa*) considering environmental spatial information in urban children's parks. *Korean Journal of Environment and Ecology*, 33, 506-514. https://doi.org/10.13047/KJEE.2019.33.5.506

Korea Meterological Administraion (KMA). (2024). Open MET DATA portal. *KMA*. Retrieved March 19, 2025 from https://data.kma.go.kr/resources/html/en/aowdp.html.

Lioy, S., Bergamino, C., and Porporato, M. (2022). The invasive hornet *Vespa velutina*: distribution, impacts and management options. *CABI Reviews*, 2022. https://doi.org/10.1079/cabireviews202217030

Lioy, S., Laurino, D., Capello, M., Romano, A., Manino, A., and Porporato, M. (2020). Effectiveness and selectiveness of traps and baits for catching the invasive hornet *Vespa velutina*. *Insects*, 11, 706. https://doi.org/10.3390/insects11100706

Matsuura, M. (1971). Nesting sites of the Japanese Vespa species. *Kontyû*, 39, 43-54.

Matsuura, M. (1984). Comparative biology of the five Japanese species of the genus Vespa (Hymenoptera, Vespidae). *The Bulletin of the Faculty of Agriculture, Mie University*, 69, 1-131.

Matsuura, M. (1991). 7. Vespa and Provespa. In G.R. Kenneth, and W.M. Robert (Eds.), *The Social Biology of Wasps* (pp. 232-262). Cornell University Press.

Matsuura, M., and Sakagami, S.F. (1973). A bionomic sketch of the giant hornet, *Vespa mandarinia*, a serious pest for Japanese apiculture (with 12 text-figures and 5 tables). *Journal of the Faculty of Science, Hokkaido University Series 6, Zoology*, 19, 125-162.

Matsuura, M., and Yamane, S. (1990). *Biology of the Vespine Wasps*. Springer-Verlag.

Monceau, K., Bonnard, O., and Thiéry, D. (2014). *Vespa velutina*: a new invasive predator of honeybees in Europe. *Journal of Pest Science*, 87, 1-16. https://doi.org/10.1007/s10340-013-0537-3

Norderud, E.D., Powell, S.L., and Peterson, R.K.D. (2021). Risk assessment for the establishment of Vespa mandarinia (Hymenoptera: Vespidae) in the Pacific Northwest, United States. *Journal of Insect Science (Online)*, 21, 10. https://doi.org/10.1093/jisesa/ieab052

Otis, G.W., Taylor, B.A., and Mattila, H.R. (2023). Invasion potential of hornets (Hymenoptera: Vespidae: Vespa spp.). *Frontiers in Insect Science*, 3, 1145158. https://doi.org/10.3389/finsc.2023.1145158

Paschapur, A.U., Subbanna, A.R., Parihar, M., Bhat, S., Mishra, K.K., and Kant, L. (2022). Hornet pests of honey bees in the Indian Himalayas and a low cost trapping device for their eco-friendly management. *Emergent Life Sciences Research*, 8, 183-194. https://doi.org/10.31783/elsr.2022.81183194

Requier, F., Fournier, A., Pointeau, S., Rome, Q., and Courchamp, F. (2023). Economic costs of the invasive Yellow-legged hornet on honey bees. *The Science of the Total Environment*, 898, 165576. https://doi.org/10.1016/j.scitotenv.2023.165576

Richter, M.R. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology*, 45, 121-150. https://doi.org/10.1146/annurev.ento.45.1.121

Shabtai, Y., and Ishay, J.S. (1998). Hornet silk caps maintain a clean room environment: a device for filtering out bacteria and dust particles. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 120, 565-570. https://doi.org/10.1016/S1095-6433(98)10067-3

Sim, H., Lee, M., Choi, Y., Kim, H., Hong, I., Woo, S., *et al*. (2014). Pattern of emergence of Vespa velutina nigrithorax Buysson (Hymenoptera: Vespidae) on spring in south part of Korea. *Journal of Apiculture*, 29, 353-358. https://doi.org/10.17519/apiculture.2014.11.29.4.353

Singha, S., Saha, S., Nath, R., Kalla, P., Laskar, N., and Pal, S. (2023). Seasonal occurrence of greater banded hornet (Vespa tropica Linn.) in Western honey bee (Apis mellifera Linn.) colonies under terai agro-ecological region of West Bengal. *International Journal of Bio-resource and Stress Management*, 14, 808-813. https://doi.org/10.23910/1.2023.3474

Smith-Pardo, A.H., Carpenter, J.M., and Kimsey, L. (2020). The diversity of hornets in the genus *Vespa* (Hymenoptera: Vespidae; Vespinae), their importance and interceptions in the United States. *Insect Systematics and Diversity*, 4, 2. https://doi.org/10.1093/isd/ixaa006

Spradbery, J.P. (1973). *Wasps; an Account of the Biology and Natural History of Solitary and Social Wasps, with Particular Reference to Those of the British Isles*. Sidgwick & Jackson.

Starr, C.K. (1992). The social wasps (Hymenoptera: vespidae) of Taiwan. *Bulletin of the National Museum of Natural Science*, 3, 93-138.

Turchi, L., and Derijard, B. (2018). Options for the biological and physical control of *Vespa velutina nigrithorax* (Hym.: Vespidae) in Europe: a review. *Journal of Applied Entomology*, 142, 553-562. https://doi.org/https://doi.org/10.1111/jen.12515