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Detection and description of four *Vespa mandarinia* (Hymenoptera, Vespidae) nests in western North America

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Abstract

Vespa mandarinia Smith 1852 is a semi-specialized predator of other social Hymenoptera and one of the two largest species of *Vespa*. Several individuals of this predatory wasp were detected in Canada and the United States in 2019, including an entire nest that was located and destroyed on Vancouver Island, British Columbia. The Washington State Department of Agriculture and the United States Department of Agriculture's Animal and Plant Health Inspection Service have collaborated to survey Washington State for *V. mandarinia* since 2020, using traps staffed by agency personnel, collaborators from local governments and nongovernmental organizations, and the general public. Trap data and public reports were used to select sites for live-trapping or net surveys, and live hornets captured in these efforts were subsequently collected and fitted with radio tags to locate nests. The survey ultimately led to the discovery of a *V. mandarinia* nest in October 2020, and three nests in August and September 2021. All of the nests were located within in red alder trees (*Alnus rubra*), with one just above the ground in a standing dead tree, and the other three in cavities ~2 to 5 meters above the ground in living trees. The number of combs in each nest varied between four and ten, cells between 418 and 1,329, and total hornets per nest between 449 and 1,474 (including immature and mature stages). Together, the four nests indicate an incipient population of *V. mandarinia* in the Cascadia region, and ongoing action by local, state, provincial, and federal governments, and residents of both countries is required to avoid the establishment of this exotic species in the region.

Keywords
community science, Eradication, radio-tracking, social Hymenoptera

Introduction

Vespa mandarinia Smith, 1855, is one of the 22 species of hornet (Vespidae: *Vespa*) (Smith-Pardo et al. 2020). Like all hornets, *V. mandarinia* is a eusocial predaceous wasp that feeds on many different types of insects. One aspect of its behavior (shared by the closely related *V. soror*) is the ability to mount group attacks on other social Hymenoptera, including honey bees (*Apis* spp.), resulting in rapid destruction of entire colonies of their prey (Matsuura and Sakagami 1973). This behavior makes it a perennial pest of apiaries throughout its native range, and it is a notable predator of *Apis mellifera*, which lacks effective defensive behaviors against *V. mandarinia* (Matsuura and Sakagami 1973; Arca et al. 2014; Mattila et al. 2020).

The first verified North American specimens of *V. mandarinia* outside of ports of entry were collected in British Columbia in 2019. Several wasps were observed that year on Vancouver Island, British Columbia, culminating in the location and eradication of an entire nest in the city of Nanaimo in September 2019 (Bérubé 2020). In December 2019, *V. mandarinia* workers were found approximately 90 km SW in Blaine, WA. The first confirmed specimen in the United States was a single dead worker that was collected on a porch (Wilson et al. 2020). Two additional specimens that had been collected earlier in the year were subsequently provided to the Washington State Department of Agriculture (WSDA), both of which were associated with beehive attacks – one hornet that had been "hawking" at a hive, and two specimens which were collected from a killed colony. Two colony losses that strongly resembled descriptions of *V. mandarinia* attacks in Japan (see Matsuura and Sakagami 1973) were also recorded in fall 2019 in the same region, although wasp specimens were not collected at either event. Based on the available evidence, WSDA, the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA APHIS), and the British Columbia Ministry of Agriculture implemented a robust trapping program in 2020, with the goal of early detection and eradication of any nascent *V. mandarinia* populations. The program included trapping by agency personnel and the general public and continuous public outreach to locate hornet populations. Because trapping hornet workers will not lead to eradication, WSDA also developed a protocol for capturing live hornets and tracking them to their nest, which could then be eliminated.

Public reporting

Washington State used active outreach to inform the public about *V. mandarinia* and encourage residents to report sightings. Potential hornet sightings were received via email, social media, phone calls, and through a purpose-built web application. All sightings were reviewed and positive/probable reports were used to inform trapping activities or initiate a site visit.

Lethal trapping

The basic survey approach was to use lethal traps and public reports to locate centers of hornet activity, and then shift to capturing live hornets that could be tracked back to nests. A variety of trapping approaches were identified from the literature and the experiences of beekeepers in the hornet's native range (Tatsuta and Makino 2003; Choi et al. 2012; Paschapur et al. 2022). Although there is considerable diversity in trapping approaches reported in the literature, many utilize a blend of fruit juices and ethanol. WSDA used bottle traps armed with orange juice and rice cooking wine (Makino and Sayama 2005; Okuda et al. 2011) because both components were available at grocery stores and promoted consistency across our collaborator and community science trapping programs. In 2020, traps were constructed from 1.65L (56 oz) clear plastic bottles with 2 cm square openings on 3 sides (Fig. 1). Each bottle contained a bait/killing solution comprising approximately 120 ml (4 oz) of orange juice and 120 ml (4 oz) of rice wine of at least 10% ABV. Captured hornets would subsequently drown in the bait. This approach was repeated in 2021, with the exception that the square-shaped openings were replaced by star-shaped openings due to concerns that the hornets might escape from the traps. This concern was raised when late-season captures of other insects in 2020 were so massive that they formed a solid surface inside the traps, allowing hornets to avoid the killing solution.

Traps maintained by WSDA were mostly placed in Whatcom County in northwestern Washington State and maintained from June through November, covering the entire presumed area of potential hornet occupancy. In 2020, three traps were placed per square km, within a 2 km radius from any detection made through May 2020. Trap density was decreased to two traps/km^2 at a 4 km radius, and to one trap/km^2 at an 8 km radius. The maximum distance for the 2020 trapping areas was based on the maximum foraging distance of 8 km reported by Matsuura and Sakagami (1973). Traps were placed on branches in trees at ca. 2-2.2 meters high, depending on site characteristics and trapper height. In 2021, the trap density was reduced to 1/km^2 throughout the trapping area, but the geographic area of trap coverage was expanded. A series of traps testing alternative lures (e.g., isobutanol, 2-methyl butanol, and acetic acid; Landolt and Zhang 2016) was also maintained at eight sites in 2020 during the trapping season. Those results are not analyzed in this paper, but hornets caught using experimental lures are included in the results reported here.

Figure 1. A bottle trap used to survey for *V. mandarinia* by the Washington State Department of Agriculture, collaborating agencies, and community scientists.

Traps maintained by WSDA were inspected every 7 to 10 days, and each trap action (e.g., trap placement, service, specimen collected) was recorded using a smartphone. A short trap check interval was selected in part because the traps lacked a preservative, with longer trap return intervals potentially compromising DNA and morphological analysis of trap contents, in addition to being unpleasant to service. The short interval also allowed the agency to rapidly respond to captures and begin attempts to collect live specimens to track to a nest. In 2020, all trap contents were strained, sorted for field detection of *V. mandarinia*, and all bycatch collected into a sample bottle for further analysis. In 2021, contents were sorted in the field to detect *V. mandarinia*, with one trap randomly selected daily by each trapper for analysis of bycatch. Because trap contents were not returned to the lab in 2021, the agency initiated a quality control program by placing a preserved hornet in a random trap in each trapper's field area once a week to ensure suspect hornets were reported.

WSDA also recruited other agencies, nongovernmental organizations, and private residents (i.e., community scientists) to employ the same trapping protocol and expand the program more broadly in the state. This approach was also used in British Columbia, with community scientists staffing most traps. Instructions for constructing and servicing traps were provided on the WSDA website, and trap locations were logged by participants via an ArcGIS web app. These traps were located opportunistically and at the convenience of the participants, who were asked to check traps weekly. In 2020 the agency requested participants to send all trap contents to the WSDA Entomology Laboratory for analysis, in part to ensure hornets were not missed, and in part to analyze bycatch for impacts on non-hornet species. In 2021 the agency only requested trap contents from captures of potential hornets. In all, 1,681 traps were deployed in 2020 (797 WSDA, 263 collaborating agencies, 621 community science), and 1,648 total traps were deployed in 2021 (868 WSDA, 370 collaborating agencies, 410 community science) (Fig. 2).

Live trapping

An array of live traps was deployed near any hornet detections. Two live trap designs were used. One was based on a modified bottle trap incorporating a screen to separate the hornets from the attractant/kill solution. We also used translucent unitraps, again with a screen to isolate hornets from the killing solution. The unitraps were further modified by adding additional screened holes to the upper section to reduce heat and fumes inside of the trap, and potentially increase the chemical plume released from the baits (Fig. 3). Once deployed, live traps were checked daily, six days a week.

Tracking

Live hornets captured in traps or by net were chilled on ice and affixed with a radio tag for tracking back to a nest. Bluetooth tags constructed at the University of Washington, modified from tags developed to monitor bumble bee activity, were used for the first two tracking attempts. Subsequent tracking efforts employed VHF radio tags produced by Lotek (in 2020) or Advanced Telemetry Systems (in 2021). The initial attempt to glue a tag to a captive hornet, following the approach used by Iyer et al. (2019, 2020) was not successful. Bluetooth and VHF tags were subsequently attached by gluing them to dental floss or Teflon thread, and then looping this around the petiole of the insect and tightening it against the body (Fig. 4). After affixing the tag to a captive hornet, it was provided with commercially-produced jam or jelly, allowed to feed, and then followed with antenna-enhanced cell phones (for the Bluetooth tags) or commercially-produced receivers and Yagi antennas (for VHF tags) once the hornet commenced flying (Fig. 4).

Nest removal

Upon locating a nest, an electric vacuum with an in-line collection chamber was used to capture as many worker hornets as possible, followed by physical removal of the nests. The vacuum approach was preferred to insecticides to avoid contaminating sites and to

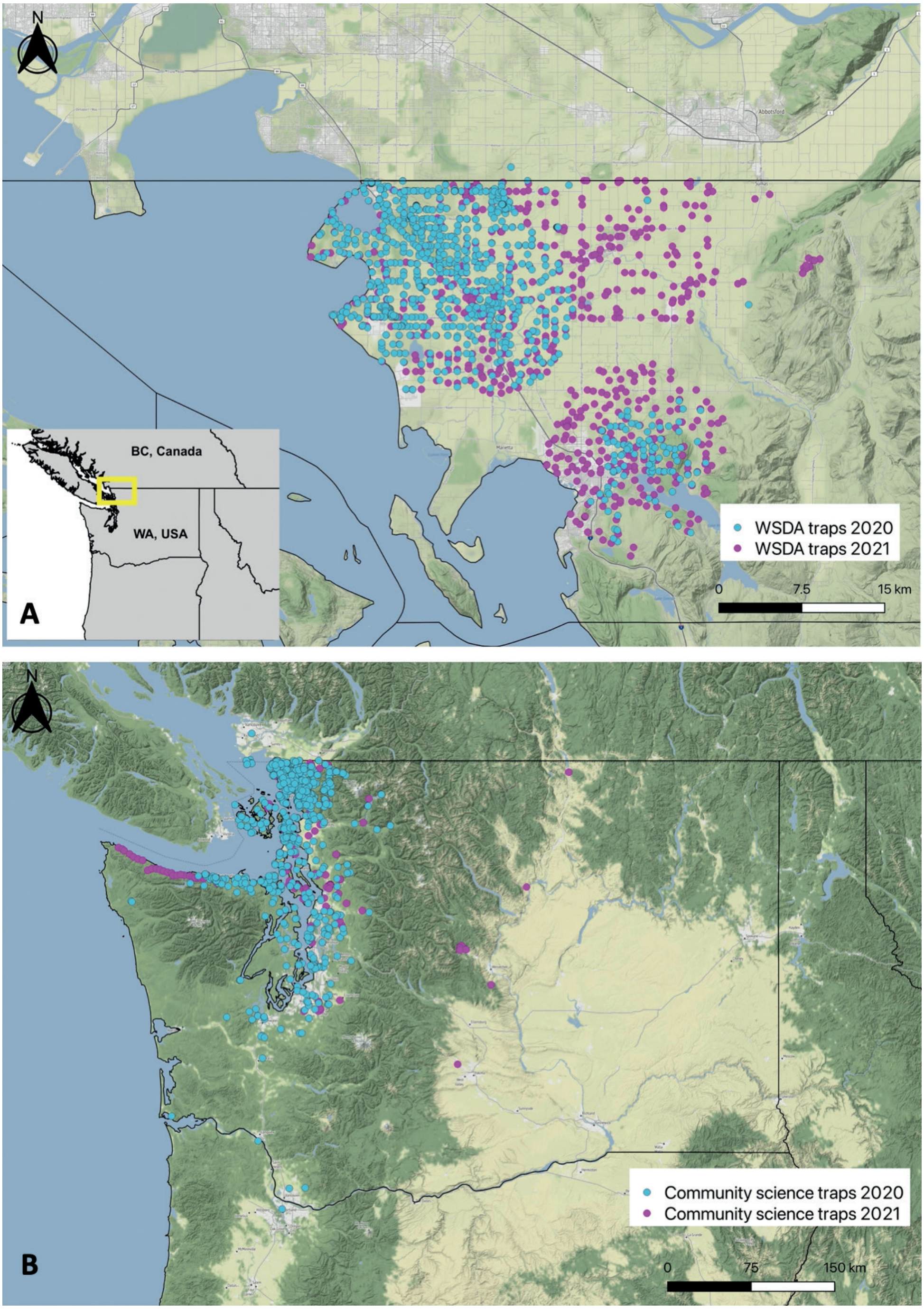

Figure 2. A map of bottle traps maintained by WSDA **B** map of bottle traps maintained by private residents and collaborating agencies. (Trap sites in British Columbia were not typically logged on the website and are thus underrepresented in these maps.) Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

Figure 3. Two styles of live traps used to collect *V. mandarinia* specimens for subsequent tracking back to an active nest.

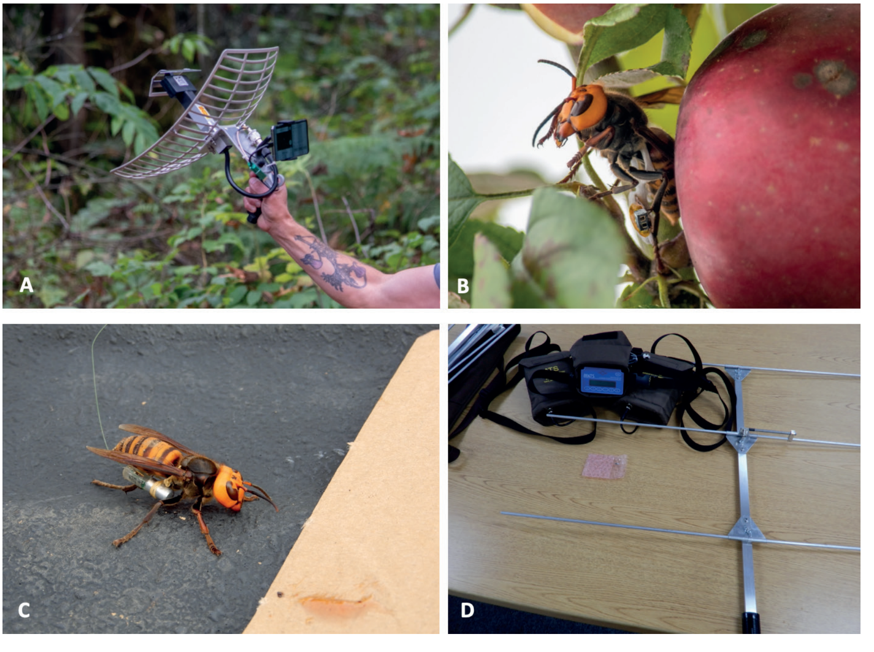

Figure 4. A antenna for Bluetooth tracking tag after Iyer et al. (2019) **B** *V. mandarinia* with affixed Bluetooth tag **C** *V. mandarinia* with ATS T-15 tag affixed **D** VHF receiver and Yagi antenna (Advanced Telemetry Systems).

facilitate safe study of nests following extraction. A 1% cyfluthrin dust was on hand for any situations where the vacuum was impractical, but was never required. Once located, hornets were vacuumed from the nest opening early in the morning, typically just before or at dawn. After the majority of workers were captured using the vacuum, carbon dioxide was used to anesthetize any hornets remaining in the nest. Nest openings were sealed with foam or plastic wrap and the entire structure removed from the site for study, or, if hornet activity was low, partially studied in situ. Live adult hornets collected with the vacuum or found within the nests were placed on ice and transported to the laboratory for study. Protective suits constructed from a thick mesh were worn during all nest extraction activities.

Nest analysis

Nest cavities were measured in the laboratory or on site. Combs were separated, and the depth and width of each cell was measured in the laboratory using a digital caliper, with the exception of two combs from nest 4 that were provided to landowners before they could be measured. The caste of each adult hornet collected was recorded (queens and workers were distinguished by size), and immature stages were counted as egg, larva, or capped cell. Capped cells were opened for nest 4 and the sex of all pupae was recorded. We did not distinguish between pupae and prepupae for the other three. Two nests had abundant litter beneath the combs, which was retained and placed in Berlese funnels to collect other insects living within the nest cavity.

A subset of hornets was collected alive at each eradication event, chilled, weighed, and body length and mesosomal width measured with digital calipers. Length was measured by pressing the chilled hornet gently onto a flat surface, positioning the head so that it was vertical, and measuring between the frons and the tip of the metasoma. Care was taken to ensure that the metasoma was not artificially extended by pushing on it nor shortened by compressing it with the caliper. Mesosomal width was measured at the wing hinge. Most hornets were well-chilled throughout the measurements; any that showed signs of activity were chilled again and remeasured.

Results

Four hornets were found and one photograph was submitted by the public in 2019. In 2020, 15 hornets were captured in WSDA or community science traps, one was collected in a net by a WSDA entomologist, one was collected in a net by a community member, and 17 confirmed hornet reports were received through photographs or dead specimens. In 2021, four hornets were collected in traps, three were captured by WSDA entomologists, one was captured by a community member, and three were reported or found dead by community members (Table 1, Fig. 5).

Only a small amount of these detections led to opportunities to find nests. A homeowner report in late September 2020 was followed by a site visit by a WSDA entomologist, who was able to capture a foraging hornet with a net. The following day a Bluetooth tag was glued to the mesosoma of the hornet, but it failed to fly. It was initially supposed

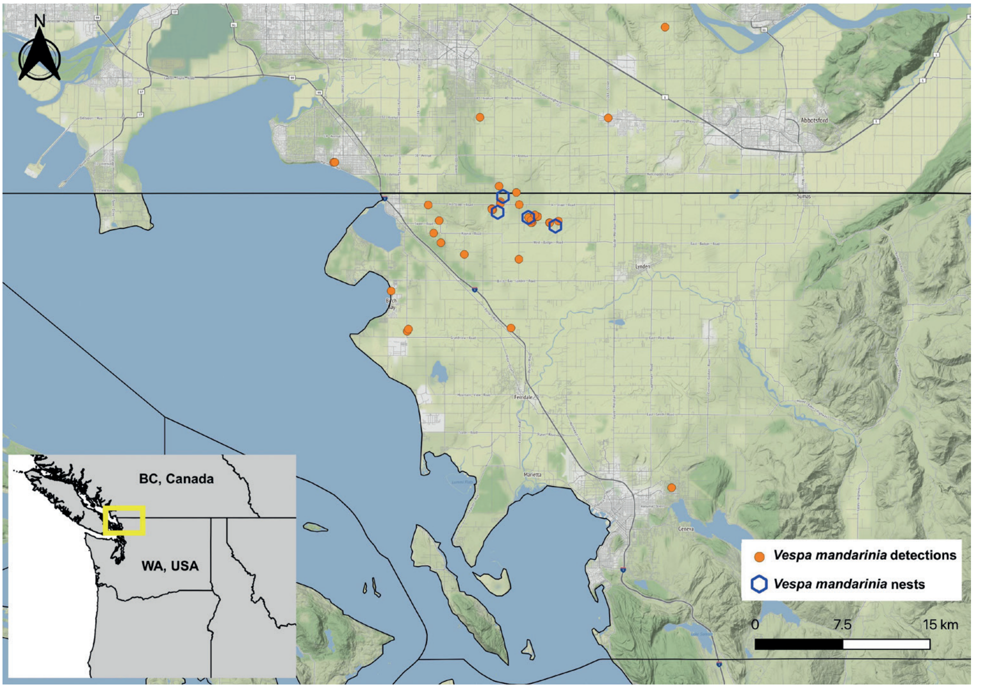

Figure 5. Map of confirmed *Vespa mandarinia* specimens and nests recorded from British Columbia and Washington State in 2020–2021. Details on the nest collected in British Columbia (not shown) in 2019 can be found in Bérubé, 2020. A single male specimen found in 2021 further south in Washington State was unrelated to these sightings and is also not included here. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

that the wings were glued together while affixing the tag, but later examination showed that the wings were intact. We suspect instead that the hornet may have been chilled for too long. The homeowner captured another hornet the following week, which was successfully affixed with a Bluetooth tag by gluing it to floss and tying it around the hornet's petiole. The hornet successfully recovered and flew, but left the range of the antennas within an hour and was not detected again. Four hornets were collected alive in nearby traps the following week, two of which were affixed with VHF tags (NanoPin, Lotek Inc.). One of these was subsequently tracked for approximately 240 m from the release site to the first *V. mandarinia* nest located in the United States, and the second in North America. The nest was found in a cavity within a living red alder (*Alnus rubra* Bong.), approximately 2.4 m above the ground (Fig. 6a). A few more hornets were subsequently found in the vicinity of that nest after the nest was removed, but no more hornet nests were detected in 2020.

In 2021, several reports of hornets were received from a site located near the US/Canada border. Upon intensive trap placement and survey of the area, WSDA entomologists captured two hornets, which were subsequently tagged with VHF tags (T15, Advanced Telemetry Systems). One of these was successfully followed for about 625 m to the second nest detected in the US. Nest 2 was found within a completely dead alder tree, with the entrance at roughly ground level and combs extending both into the tree and below

Table 1. *Vespa mandarinia* specimens and confirmed sightings in British Columbia and Washington State, 2019–2021.

Date	State/ province	County (US)/ regional district (BC)	Caste	Method	Number	Notes
Aug-Sep 2019	BC	Vancouver Island	W, Q	found	many	Nanaimo nest; see Bérubé 2020 for more details
19-Oct-2019	WA	Whatcom	W	found	2	workers collected from killed *A. mellifera* colonies
22-Oct-2019	WA	Whatcom	W	found	1	dead worker, hornets observed hawking at apiary
13-Nov-2019	BC	Fraser Valley	Unk	photo only	1	
8-Dec-2019	WA	Whatcom	W	found	1	dead worker found on porch
10-May-2020	BC	Fraser Valley	W	hand capt.	1	
13-May-2020	BC	Fraser Valley	Q	found	1	queen found dead in garden
27-May-2020	WA	Whatcom	Q	found	1	queen found dead in driveway
6-Jun-2020	WA	Whatcom	Q	found	1	queen dead on porch
14-Jul-2020	WA	Whatcom	Q	trap	1	orange juice/rice wine trap, WSDA
29-Jul-2020	WA	Whatcom	M	trap	1	orange juice/rice wine trap, WSDA
17-Aug-2020	WA	Whatcom	Unk	photo only	1	
19-Aug-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, citizen science survey
21-Sep-2020	WA	Whatcom	W	hand capt.	1	sprayed with pesticide
25-Sep-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, citizen science survey
29-Sep-2020	WA	Whatcom	Unk	photo only	1	
29-Sep-2020	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
30-Sep-2020	WA	Whatcom	W	found	1	dead worker found in porch light
2-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
5-Oct-2020	WA	Whatcom	W	hand capt.	1	collected by private citizen
9-Oct-2020	BC	Fraser Valley	W	trap	1	orange juice/rice wine trap
9-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
15-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine/honey bee comb, WSDA
15-Oct-2020	WA	Whatcom	W	trap	1	isobutanol-acetic acid, WSDA
20-Oct-2020	WA	Whatcom	W	trap	1	orange juice/rice wine/honey bee comb, WSDA
20-Oct-2020	WA	Whatcom	W	trap	2	isobutanol-acetic acid, WSDA
21-Oct-2020	WA	Whatcom	W	trap	2	orange juice/rice wine/honey bee comb/ isobutanol, WSDA
24-Oct-2020	WA	Whatcom	W	nest erad.	many	US nest 1
27-Oct-2020	BC	Fraser Valley	M	hand capt.	1	feeding on pumpkin
29-Oct-2020	WA	Whatcom	M	found	1	sticky trap
29-Oct-2020	WA	Whatcom	W	found	1	found dead in water bowl
29-Oct-2020	WA	Whatcom	Q	found	3	found dead in water bowl
30-Oct-2020	WA	Whatcom	M	trap	1	orange juice/rice wine trap, WSDA
1-Nov-2020	WA	Whatcom	M	hand capt.	1	crawling in garage
4-Nov-2020	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
7-Nov-2020	BC	Fraser Valley	Q	hand capt.	1	crawling in house
12-Nov-2020	WA	Whatcom	M	hand capt.	1	crawling in driveway
4-Jun-2021	WA	Snohomish	M	found	1	found dead in yard
12-Aug-2021	WA	Whatcom	W	photo only	1	internet report
12-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
13-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
17-Aug-2021	WA	Whatcom	W	hand capt.	1	collected by private citizen
8-Sep-2021	WA	Whatcom	W	hand capt.	1	collected by WSDA entomologist
8-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
9-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
25-Aug-2021	WA	Whatcom	W	nest erad.	many	US nest 2
10-Sep-2021	WA	Whatcom	W	trap	1	orange juice/rice wine trap, WSDA
21-Sep-2021	WA	Whatcom	W	nest erad.	many	US nest 3
12-Sep-2021	WA	Whatcom	W	hand capt.	1	crawling in yard
23-Sep-2021	WA	Whatcom	W	nest erad.	many	US nest 4
22-Oct-2021	BC	Fraser Valley	W	trap	1	dead in Japanese beetle trap

Figure 6. A nest 1 (23 October 2020) **B** nest 2 (25 August 2021) **C** nest 3 (11 September 2021) **D** nest 4 (23 September 2021). Arrows indicate location of nest entrance.

ground (Fig. 6b). Soon after the detection and removal of the second nest, a homeowner captured a hornet using a makeshift trap, which was subsequently tagged and tracked 490 m from the release point to the third nest in the US, and fourth in North America. A public report also led to the capture of a fifth living hornet in 2021, which was tagged and tracked for 650 m to the fourth nest. Nests 3 and 4 were, like the first nest in 2020, located within red alder trees well above ground (nest 3 – ~2.2 m, and nest 4 – ~ 5.5 m; Fig. 6c, d).

All nest measurements and life stages are presented in Tables 2–6. The nests varied in the number of combs and total cells, ranging from 4 to 10 combs (Figs 7–8; Tables 2–4), and 418 to 1,329 cells (Tables 2–6). Nest 1, found late in 2020, contained 76 queens, and another 25 emerged while the nest was being studied. It was not possible to identify the foundress, which may have already died. Nine males were also recovered from nest 1. Only a single queen was found in each of the other nests. In each of these, the queen was not found until the nest was extracted, and in each case was the last adult hornet to be collected in the nest. The only other nest that contained adult males was nest 3 (the smallest), of which approximately 37% of adult hornets were males (Table 4). All capped cells from nest 4 were opened, and found to contain 23 male pupae, 112 female pupae, and 126 pre-pupae.

Table 2. Characteristics of *V. mandarinia* nest 1, collected 23 Oct 2020.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae[1]	Capped cells
1	238	21.82	10.34	0	0	0
2	212	44.49	11.52	0	6	9
3	177	34.74	12.53	0	8	41
4	137	32.8	12.08	0	30	58
5	98	29.20	12.81	0	12	0
6	31	18.91	11.22	6	7	0

[1]Only larvae still in the combs are represented here. Many larvae fell from the combs when CO2 was applied to the nest while it was still in the tree.

Table 3. Characteristics of *V. mandarinia* nest 2, collected 25 Aug 2021.

Comb	Total cells[1]	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1*#	79	21.66	9.65	18	12	28
2	86	24.40	10.56	12	9	62
3	129	26.47	10.78	25	52	47
4+	168	24.16	10.81	48	17	97
5	200	25.71	11.23	0	45	150
6	207	26.29	11.26	16	59	128
7	236	23.66	11.38	53	104	52
8*	170	27.39	11.75	66	104	0
9	54	22.06	11.53	54	0	0

* One cell with 2 eggs.
\# One cell with a larva and an egg.
+Two cells with 2 eggs.

Table 4. Characteristics of *V. mandarinia* nest 3, collected 11 Sep 2021.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1*	178	25.79	10.12	28	24	88
2	143	26.32	10.89	16	44	79
3	92	23.46	11.70	42	33	12
4	5	10.97	9.35	5	0	0

* One cell with 2 eggs.

Table 5. Characteristics of *V. mandarinia* nest 4, collected 23 Sep 2021.

Comb	Total cells	Mean cell depth	Mean cell width	Eggs	Larvae	Capped cells
1	93	22.75	9.80	6	20	31
2	91	23.89	10.28	2	15	52
3	88	25.75	11.08	2	16	56
4*	77	unmeasured	unmeasured	17	37	17
5	57	31.99	12.50	1	2	49
6	62	unmeasured	unmeasured	4	17	40
7	59	30.47	12.35	6	44	16
8	59	27.40	11.75	15	40	0
9	53	24.43	12.04	40	11	0
10	35	24.52	11.76	35	0	0

* One cell with 2 larvae, both appeared to be 2nd instar.

Table 6. Overview of *Vespa mandarinia* nests found in the United States, 2020–202021.

Nest	Collection date	Combs	Total cells	Eggs	Larvae	Capped cells	Workers	Males	Queens
1	23 Oct 2020	6	893	6	190[3]	108	112	9	76
2	25 Aug 2021	9	1329	292	422	564	195	0	1
3	11 Sep 2021	4	418	91	101	179	49	28	1
4	23 Sep 2021	10	674	128	202	261*	185	0	1

*23 of the capped cells contained male pupae, 112 contained female pupae, and 126 were prepupae.

A subsample of 366 hornets comprising 15 males, 249 workers, and 102 queens was measured from the four nests. Worker mass ranged from 0.36 g to 1.41 g, and males from 0.82 g to 1.3 g. Queens ranged between 1.84 g and 2.88 g (Fig. 9). The three foundress queens massed 2.7 g (nest 2), and 2.16 g (nests 3 and 4). Length of males ranged from 27.8 to 35.19 mm, workers from 21.83 to 37.08 mm, and queens from 36.93 to 44.15 mm. Mesosomal width of males was between 7.3 to 8.99 mm, workers from 6.2 to 9.1 mm, and queens from 8.94 to 10.96 mm. While queen mass was always appreciably larger than workers and males, there was slight overlap at the extremes of length and mesosomal width for a few individuals.

Other insects located in the nest included species of Staphylinidae, Elateridae, and Cantharidae commonly associated with decaying tree environments. Two species of flies were common in two nests, and have been recorded in other Vespidae nests (Table 7). Other invertebrates (e.g., Acari, Collembola, Annelida) were also collected in the Berlese funnels but were not enumerated.

Discussion

The nests located in the Pacific Northwest were generally somewhat smaller than those described by Matsuura and Sakagami (1973). The nest removed on Vancouver Island in mid-September 2019 contained approximately 400 cells and 200 adult hornets and was located in a subterranean burrow (Bérubé 2020). The largest nest reported here, collected in late August 2021, contained 1,329 cells, which is close to the size of the

Figure 7. Top – combs from nest 1, 23 Oct 2020; Bottom – combs from nest 2, 25 August 2021. Numbers next to the combs indicate the position in the nest (smaller numbers are older and higher in the nest). Comb characteristics are recorded in Tables 2–5.

Figure 8. Top – combs from nest 3, 11 September 2021; Bottom – combs from nest 4, 23 September 2021. Numbers next to the combs indicate the position in the nest (smaller numbers are older and higher in the nest). Comb characteristics are recorded in Tables 2–5.

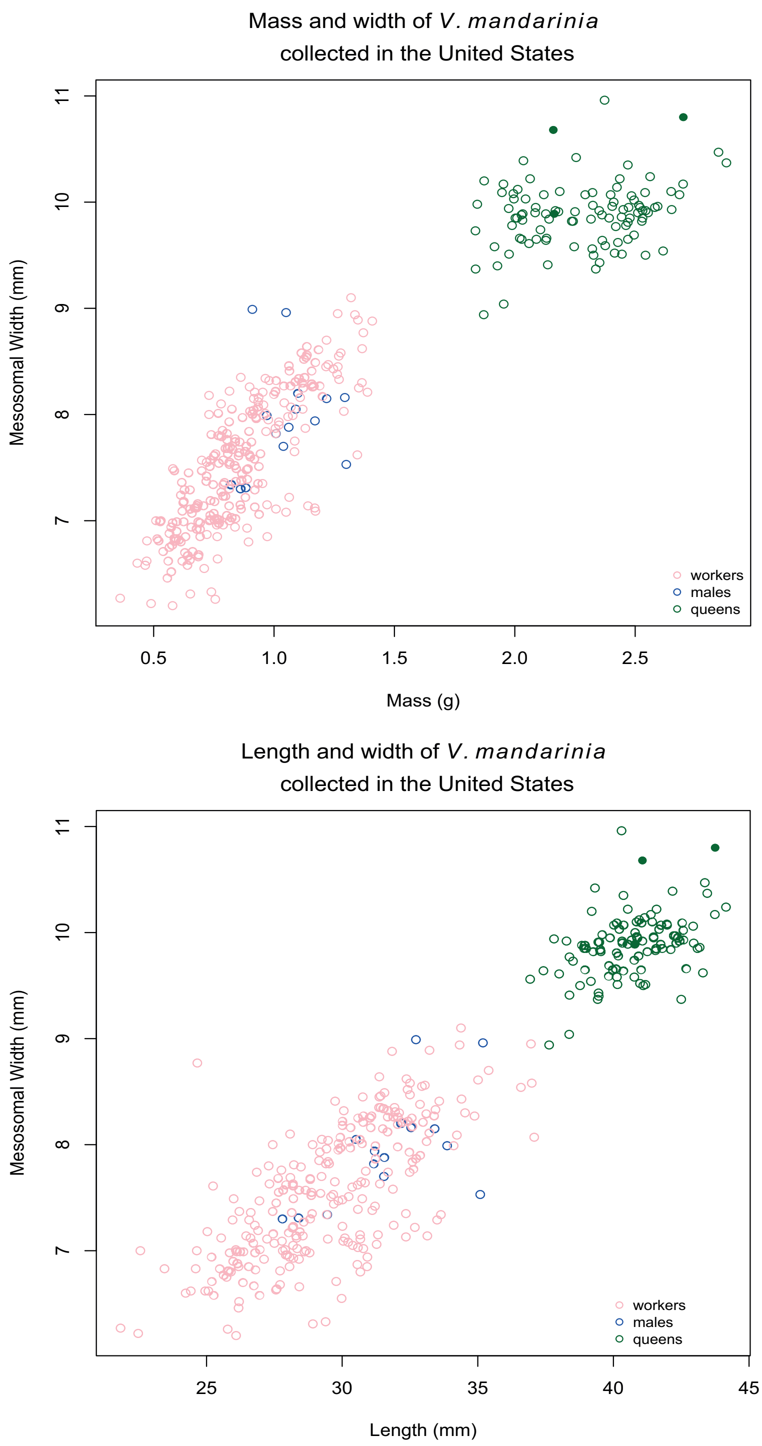

Figure 9. Body measurements of *V. mandarinia* collected from four nests in North America. The three foundress queens are represented with solid circles.

Table 7. Insects collected from litter below three *V. mandarinia* nests in Washington State, USA.

Order	Family	Species	Nest
Diptera	Scatopsidae	*Coboldia fuscipes* (Meigen, 1830)	1, 4
		Scatopse notata (Linnaeus, 1758)	1
	Phoridae	*Dohrniphora cornuta* (Bigot, 1857)	1
		Triphleba lugubris (Meigen, 1830)	1, 3, 4
		Megaselia sp.	4
	Sphaeroceridae	*Minilimosina parva* (Malloch, 1913)	1
	Milichiidae	*Leptometopa latipes* (Meigen, 1830)	1
	Fanniidae	*Fannia incisurata* (Zetterstedt, 1838)	1
Coleoptera	Staphylinidae	*Quedius* sp.	1
		Hylota ochracea Casey, 1906	1
		Phloeopora oregona Casey, 1906	1
		Crataraea suturalis (Mannerheim, 1830)	3
		Silusa californica (Bernhauer, 1905)	1, 4
		Scydmaenus ovipennis Casey, 1897	1
		Euplectus confluens LeConte, 1849	4
		Lobrathium subseriatum LeConte 1880	4
		Medon pugetense Hatch, 1957	4
	Elateridae	*Limoniscus* sp.	1
	Leiodidae	*Ptomaphagus nevadicus* Horn 1880	1
	Cantharidae	*Silis lutea* LeConte, 1853	1
	Corylophidae	*Sericoderus lateralis* (Gyllenhal, 1827)	3
	Histeridae	*Bacanius hatchi* Wenzel, 1960	3

smallest nest (collected in December) reported by Matsuura and Sakagami (1973). It is possible that the August nest would have continued to grow and may have approached the more typical size reported for nests in Japan. However, nests described by Matsuura and Sakagami (1973) were collected from south-central Japan, and more southerly nests may be able to expand more quickly to large sizes. Although details about nests from northern parts of the hornet's range are sparse, two nests collected on Hokkaido (Yamane and Makino 1977) each comprised five combs, with 675 cells (col. Aug 26, 1973) and 1141 cells (col. Sep 15, 1976). The nests removed in Washington State and British Columbia seem to be in accord with these northern records, so it is also possible that the nests we removed were typically sized for this latitude and climate.

One factor that may have impacted nest size and shape, particularly for nests 1, 3, and 4, was the constraining geometry of the tree cavity they were located within. The shape of the combs mirrored the internal shape of the cavities, and it is possible that workers could not use the space as efficiently as a nest in excavated soil. Indeed, the nest with the greatest number of cells reported here was nest 2, collected in August and the only one of the Washington nests not wholly confined to a tree cavity. Nest 3 seemed exceptionally small and contained a high proportion of males early in the season. The high number of males so early in the season is suggestive of inbreeding effects causing the production of diploid males (Van Wilgenburg et al. 2006; Darrouzet et al. 2015), which may have contributed to the very small nest size. Body measurements of all castes indicate that the largest workers and smallest queens could be confused if mesosomal width or body length is the only characteristic available for distinguishing between them, a phenomenon observed in other Vespidae (O'Donnell 1998).

It is interesting that all of the nests we located were in tree cavities in alder trees, with three of them high above the ground in still-living trees. Even though this is a small sample size, it is unexpected based on the most comprehensive reports of other nest sites (Matsuura and Sakagami 1973), where less than 16% of nests were reported from any sort of tree cavity. However, other data suggests that nests in cavities are somewhat more frequent (Choi et al. unpublished), and two of the three *V. mandarinia* nests reported by Yamane and Makino (1977) from Hokkaido were in tree hollows, although no further description is provided. Even so, the proportion of tree cavity nests in our results seems unusual. This could be a result of heavily saturated ground in the study area at the time queens are establishing nests, with more than 650 mm of total precipitation typical during the winter and spring months. Alternatively, nests from 2021 could have been established by queens that successfully dispersed from the 2020 nest after imprinting on the cues of their natal home, biasing nest selection towards alders.

No hornets were detected in British Columbia or Washington State in 2022. It is too early to feel confident that the species has been prevented from establishing, and several years of survey remain to be conducted. Some of the findings described in this paper suggest that small population effects may be impeding establishment, i.e., the unseasonably high number of males observed in nest 3. However, the characteristics of the other three nests, and our observations of foraging behavior and analysis of the local prey base (unpublished) concur with climate modeling (Alaniz et al. 2020; Zhu et al. 2020; Nuñez-Penichet et al. 2021) in suggesting that the region provides viable habitat for this species. Those results, and the recent spread of other hornet species outside of their range in multiple countries, are evidence that Vespidae require further study to either prevent, or mitigate the effects of, future introductions.

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