Journal of Sustainable Technology in Agriculture
Open Access | www.jostapubs.com | ISSN(online): 3107-6882

Original-Article

June 2026, Volume 2, Issue II. doi: 10.65287/josta.202606.bf39

Thermal limits of wasps and honey bees and response behaviour of honey bees against predatory wasps at the hive entrance

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Abstract

A study was conducted to examine the thermal limits and agonistic interactions between predatory wasps attacking honey bees and the honey bee species *Apis mellifera* L. and *Apis cerana* F. Thermoregulatory defence responses of honey bees and species-specific cumulative survival of wasps and bees were investigated, alongside wasp predatory behaviour parameters. Results revealed the highest bee-ball temperature of 48.53°C around *Vespa tropica*, while bees took the least time to form a bee ball around *Vespa basalis*. The maximum number of bees involved in the heat ball was recorded around *V. tropica* (51.67 bees) after 120 seconds. The cumulative survival temperatures of *V. auraria*, *V. basalis*, and *V. tropica* were 47°C, 49°C, and 50°C, respectively, after 5 minutes of heat exposure, and 46°C, 48°C, and 49°C, respectively, after 20 minutes of exposure. For both honey bee species, the cumulative survival temperatures were 53°C and 54°C during 5 minutes of exposure and 52°C and 53°C during 20 minutes of exposure.

Keywords: Agonistic interaction, Tolerance, Vespa, Survival, Heat balling, Exposure.

Received: 2026-06-08 | *Accepted:* 2026-06-25 | *Published:* 2026-06-28

1. Introduction

Honey bees play a vital role as pollinators in agricultural landscapes and natural ecosystems. They provide these services to over 75% of major global food crops (Klein *et al.* 2007), making their decline a significant concern for food security and biodiversity around the world (Goulson *et al.* 2015). Among biotic stressors affecting honey bee populations, predatory wasps have emerged as prominent enemies, especially in Asia. Species from the genus *Vespa* including *V. auraria*, *V. basalis*, *V. tropica* and *V. mandarinia* frequently attack honey bee colonies, killing forager bees, stealing their brood and in some cases leading to complete colony collapse (Tan *et al.* 2007; Monceau *et al.* 2014).

To counter these attacks, honey bees have evolved an array of defensive strategies, of which heat balling is one of the most advanced defence technique used by them. This behaviour involves a group of bees surrounding the predatory wasp and generating heat through muscular contractions to raise the internal ball temperature to a point where the wasp can die (Ono *et al.* 1987; Tan *et al.* 2005). This defence mechanism has been particularly well documented in *A. cerana* and *A. mellifera*, though variations exist in thermal thresholds, species responsiveness, and balling efficiency (Sugahara and Sakamoto 2009).

The effectiveness of heat balling depends significantly on the thermal limits of both the bees and the predatory wasps. *V. mandarinia*, for instance, has a thermal death point of 45–47°C, whereas honey bees can tolerate marginally higher temperatures (Tan *et al.* 2005; Motmayen *et al.* 2024). Although heat balling behavior is well-documented, significant knowledge gaps remain in our understanding of species-specific thermal tolerance among predatory wasps and the comparative defensive capabilities of various honey bee species. First, information on the heat tolerance of economically important wasp species such as *V. mandarinia, V. auraria, V. basalis* and *V. tropica* in the Himalayan region is limited. Second, previous studies have primarily focused on *A. cerana*, with less attention given to the heat balling efficiency of *A. mellifera* against various wasp species under controlled conditions. Third, there is a lack of quantitative data on the predatory behaviour parameters (attack frequency, reaction time, attack mode and site preference for attack) of different wasp species, which is essential for developing species-specific management strategies.

This study was designed to determine the thermal death limits of three predatory wasp species viz. *V. auraria*, *V. basalis* and *V. tropica*, and to evaluate the thermoregulatory defence response of *A. mellifera* and *A. cerana*. Additionally, this study assessed the survival of bees and wasps under controlled heat exposure in an incubator and quantified species specific predatory behaviours such as attack's frequency; reaction time to catch a bee; the number of wasps involved in a single attack and preferred sites of attack.

What makes our study new and different is that it looks at several things at once. Instead of just studying one species or one type of response, it compares the heat tolerance of different wasp species side-by-side, while also testing how two major honey bee species (*A. mellifera* and *A. cerana*) defend themselves, all under the same controlled conditions. On top of that, this is one of the first studies to document, how different wasp species behave as predators of honey bees in the Himalayan conditions. That matters because until now, we haven't had solid, species by species data from this region. So this gives us a much needed baseline to figure out which wasps are the real problem and how to manage them more strategically. The findings of this study will contribute to understanding the thermal ecology of bee wasp interactions and help identify species specific vulnerabilities. It will also provide a foundation for targeted management practices against predatory wasps of honey bees.

2. Matherials and methods

2.1. Study site

The study was conducted at the Bee Research Station, CSKHPKV, Nagrota Bagwan (32.1°N, 76.3°E; elevation ~650 m), located in Kangra district, Himachal Pradesh. The site lies in the lower western Himalayan region and experiences a subtropical to temperate climate, ideal for apiculture and wasp activity.

2.2. Heat balling of wasps

This study examined the response behaviour of *A. mellifera* against the predatory wasps by heat balling. Three colonies of almost equal strength in the apiary were selected. Wasps were collected alive from the field using insect net and maintained in ventilated containers with sugar solution for 12 hours prior to experimentation to allow acclimation. For attaching the wasp to the temperature meter, beekeeping gloves were used to prevent stinging and injury to the wasp. The adult wasps of three different species: *V. auraria, V. basalis* and *V. tropica* were gently attached to the tip of electronic temperature meter using a fine thread loop around the thorax, taking care not to restrict movement or cause injury. The temperature meter with the attached wasp was then carefully kept at the hive entrance to elicit the heat balling response from the bees. The temperature inside the bee ball was recorded after every 15 seconds. The highest temperature recorded inside the ball, the number of bees involved in balling the wasp and the time to make a ball was recorded as per the method of (Tan *et al.* 2005). This experiment was replicated three times.

2.3. Thermal limits of honey bees and wasps

Ten honey bee workers of both honey bees species, *A. mellifera* (n=10) and *A. cerana* (n=10) as well as adult workers of three different species of predatory wasps, *V. auraria* (n=10), *V. basalis* (n=10) and *V. tropica* (n=10) were all placed in separate cages (10x10x10cm). These cages were fitted with fine wire-mesh side panels, allowing enough ventilation for the wasps. These cages were kept in incubator at initial temperature of 43°C. The cage dimensions provided sufficient space for normal movement of the insects during the short-term heat tolerance assays while preventing overcrowding. All thermal tolerance experiments were conducted with three independent biological replicates. The three replicates were conducted on different days using insects collected from different colonies (for honey bees) or different foraging sites (for wasps) to account for natural variation in thermal tolerance.

The temperature in incubator was raised by 1°C after every 20 minutes of exposure until 54°C. These cages were removed after every 20 minutes of exposure to each temperature degree and were given a rest of 5 minutes before exposing to the next temperature level. The same experiment was done by locating the same number of bees and wasps inside cages into the incubator for 5 minutes; however in this case, they were not given the rest of 5 minutes and instead they were directly exposed to the next degree of temperature after the observation. The number of dead bees and wasps after exposure to every degree of temperature was recorded as per the method of (Tan *et al.* 2005).

Cumulative survival percentages were calculated based on the original cohort at the start of the experiment. For example, if 10 individuals were initially placed and 8 survived after exposure to a specific temperature, the cumulative survival at that temperature level would be 80%. The same wasps or bees that survived at a given temperature were subsequently exposed to the next temperature level. This approach accounts for cumulative mortality across increasing temperatures. The percentage at each temperature level represents the proportion of surviving individuals from the previous temperature level not relative to the initial cohort.

Incubator specifications and thermal tolerance assays

The thermal tolerance experiments were conducted using a BOD incubator with temperature control accuracy of ±0.5°C and a temperature range of 5-60°C. The incubator was equipped with an internal fan to ensure uniform temperature distribution, which was verified using calibrated thermocouples placed at different positions within the chamber. During the experiments, relative humidity inside the incubator was maintained at 60-70% using a water tray placed at the bottom of the chamber and humidity levels were monitored using a digital hygrometer.

Mortality assessment criteria

Mortality of insects was assessed after each temperature exposure using standardized criteria. Insects were considered dead if they showed no movement of antennae, legs, or mouthparts upon gentle prodding with a fine brush and failed to exhibit coordinated movement within 60 seconds of observation.

2.4. Agonistic interactions between honey bees and predatory wasps

The *A. mellifera* colonies selected for conducting the observations on the incidence of predatory wasps were monitored for different agonistic interactions between honey bees and wasps. Observations were conducted at fortnightly intervals from July to November (the active wasp season in the Himalayan region), with a total of 10 observation periods over the five-month study period. Each observation period consisted of 10 minute observation sessions for each parameter, during the peak foraging activity of wasps.

2.5. Number of attacks by wasp/catch of honey bee

The number of attempts by a wasp of the three most prevalent species viz. *V. auraria*, *V. basalis* and *V. tropica* to catch a single honey bee was recorded. The reaction time or the time that a wasp of each species took to capture a bee was also recorded.

2.6. Type of wasp attack

The selected colonies were also observed for the number of wasps of each species associated in a single attack to the colony (Solitary or Group).

2.7. Site of attack

The colonies were observed for the preference of site of attack by the different species of wasp. The number of each species of wasp attacking to the colonies through different sites: hive entrance, ground level and disruption of bee foraging, were recorded.

2.8. Statistical analysis

The experiments were conducted using a completely randomized design (CRD) with three replications for each treatment combination. For the heat balling experiments, one factor analysis were used with three replications. For thermal tolerance assays, a three factorial design (Wasp species × Time interval × Temperature) was used for wasps and a three factorial design (Honey bee species × Time interval × Temperature) was used for bees. For predatory behaviour observations, a one factor analysis was employed.

The statistical analysis of observations recorded was done using the technique of analysis of variance for randomized block design for the interpretation of results as described by (Gomez and Gomez 1984). Analysis of Variance (ANOVA) for Randomized block experimental design (RBD) was performed at 5% level of significance, critical difference between the treatments was computed after the ANOVA for the treatments was found to be statistically significant.

3. Results

3.1. Average temperature variation in heat balling of predatory wasps by Apis mellifera

The variation of temperature inside bee ball was studied by attaching an adult worker of each of the three wasp species to the tip of thermometer and placing it in front of an *A. mellifera* hive. This study was conducted to examine the temperature variations and to determine the temperature at which different species of predatory wasps die during heat balling by *A. mellifera.* The study was conducted on three predatory wasp species: *V. auraria*, *V. basalis*, and *V. tropica.* The results for this experiment are presented in Table 1 which revealed species specific temperature variations during heat balling by honey bees against different predatory wasps, with *V. tropica* recording the highest temperature (48.53°C) followed by *V. auraria* recording the maximum temperature of (47.60°C) and *V. basalis* (45.77°C). These findings suggest that *V. tropica* is the most heat tolerant among the three species of wasps followed by *V. auraria* and *V. basalis.* The temperature inside the bee cluster was found to be lower than that inside the bee ball (42.73°C), suggesting that the bees concentrate their heat around the wasp as a defence behaviour rather than spreading it evenly throughout the cluster. This also shows that *A. mellifera* continues the balling activity to a level of temperature in which the wasp dies.

Wasp species	Temperature (°C)
V. auraria	47.60
V. basalis	45.77
V. tropica	48.53
Bee cluster	42.73
CD ($\alpha = 0.05$)	0.37

Table 1: Average temperature variation in heat balling of predatory wasps by *Apis mellifera*

3.2. Variation in bee numbers during heat balling of predatory wasps over time

During this study, the number of *A. mellifera* honey bees participating in the heat balling activity against different species of predatory wasps (*V. auraria*, *V. basalis*, and *V. tropica*) during different time intervals was investigated. The findings of this study which are presented in Table 2 revealed that the highest number of bees involved in heat balling of two predatory wasp species viz. *V. auraria* and *V. basalis*, was recorded within the first 90 seconds, with (41.33) for *V. auraria*, and (41.00) for *V. basalis.* However for *V. tropica* the most number of bees involved in heat balling was recorded after 120 seconds with (51.67). Beyond this, the number of participating bees in the ball gradually declined, for *V. auraria* and *V. basalis* after 120 second, while for *V. tropica* which maintained a relatively high level of involvement before gradually decreasing to 4.67 at 210 seconds. For *V. auraria* and *V. basalis*, the bees successfully killed the wasps within 180 seconds, after which the balling activity ceased. In case of *V. tropica*, however the activity continued up to 210 seconds before coming to an end. These results suggested that *V. tropica* had more tolerance towards the heat balling activity of bees compared to the other species, likely due to its general ability to resist high temperatures.

Time intervals (s)	*V. auraria*	*V. basalis*	*V. tropica*	Mean
After 15s	6.67	6.67	12.33	8.56
After 30s	14.33	13.33	22.33	16.67
After 60s	23.33	24.00	39.00	28.78
After 90s	41.33	41.00	48.33	43.56
After 120s	31.67	32.33	51.67	38.56
After 150s	19.00	20.67	42.33	27.33
After 180s	4.67	5.67	20.00	10.11
After 210s	0.00	0.00	4.67	1.56
Mean	17.63	17.96	30.08	
Factors	CD ($\alpha = 0.05$)			
S	2.89			
T	1.77			
S x T	5.01			

Table 2: Number of bees involved in heat balling of predatory wasps over time[1]

3.3. Cumulative survival of predatory wasps at different temperatures and exposure durations

Ten adult wasps of each species (*V. auraria*, *V. basalis*, and *V. tropica*) were placed in separate cages of diameter (10 × 10 × 10 cm) and exposed to different temperatures ranging from 43°C to 54°C for two time intervals (5 minutes and 20 minutes). The survival percentage was recorded after exposure to each temperature to determine the heat tolerance of each species (Table 3;Table 4).

In the 5-minute exposure, 100 per cent survival was observed in all of the three species at 43°C. At 44°C *V. auraria* and *V. tropica* showed 100 per cent survival, while *V. basalis*, showed a slight reduction in survival, showing 83.33 per cent survival. With every degree of rise in temperature, the survival was decreased. *V. basalis* recorded 67.59 per cent survival at 45°C, while the other two species showed no mortality. At 46°C, *V. auraria* recorded 80.00 per cent and *V. basalis* 47.62 per cent survival, while *V. tropica* remained unaffected. At 47°C, 71.03 per cent survival was observed for *V. auraria*, while *V. basalis* completely died at this degree of temperature and showed 0% survival, indicating that *V. basalis* could withstand the highest temperature of 46°C. *V. tropica* recorded only 93.33 per cent survival at the same temperature. *V. auraria* showed 65.56 per cent survival at 48°C and 0 percent survival at 49°C, suggesting that *V. auraria* could not tolerate temperature above 48°C. *V. tropica* did not survive beyond 50°C indicating stronger resistance to heat compared to other two species.

During 20-minute exposure, survival rates were comparatively lower at the same temperature levels compared to 5 minutes exposure. This temperature and time dependent mortality might be due to the cumulative physiological stress caused by prolonged heat exposure. *V. basalis* showed 90 per cent survival at 43°C and 69.72 per cent at 44°C, while *V. auraria* and *V. tropica* showed complete survival at these temperatures. *V. auraria* recorded 86.67 per cent survival at 45°C and 77.32 per cent at 46°C. *V. basalis* did not survive beyond 46°C, while *V. tropica* was minimally affected at this degree, showing 93.33 per cent survival. *V. auraria* showed 0 per cent survival at 48°C, suggesting that this species was completely intolerant to this temperature at this timing interval. However, *V. tropica* showed 61.90 per cent survival at this temperature. *V. tropica* again showed the highest tolerance towards heat as all of its individuals survived up to 49°C in 5 minutes exposure and up to 48°C in 20 minutes exposure.

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[1] S = Wasp species; T = Time interval

Temperature (°C)	Cumulative survival of predatory wasp (%)			
		5 mins exposure		
	V. auraria	***V. basalis***	***V. tropica***	**Mean**
43	100.00	100.00	100.00	100.00
44	100.00	83.33	100.00	94.44
45	100.00	67.59	100.00	89.20
46	80.00	47.62	100.00	75.87
47	71.03	0.00	93.33	54.79
48	65.56	0.00	71.11	45.56
49	0.00	0.00	55.56	18.52
50	0.00	0.00	0.00	0.00
Factors				CD ($\alpha = 0.05$)
T				1.79
S				*NS*
Temp				*NS*
T x S				*NS*
T x Temp				5.07
S x T				6.20
T x S x Temp				8.77

Table 3: Cumulative survival of predatory wasps of honey bees at different temperatures and 5 mins exposure durations[2]

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[2] S = Wasp species; T = Time interval; Temp = Temperature

Temperature (°C)	Cumulative survival of predatory wasp (%)			
	20 mins exposure			
	V. auraria	***V. basalis***	***V. tropica***	**Mean**
43	100.00	90.00	100.00	96.67
44	100.00	69.72	100.00	89.91
45	86.67	69.72	100.00	85.46
46	77.32	0.00	93.33	56.88
47	59.52	0.00	75.19	44.90
48	0.00	0.00	61.90	20.63
49	0.00	0.00	0.00	0.00
50	0.00	0.00	0.00	0.00
Factors				CD ($\alpha = 0.05$)
T				1.79
S				*NS*
Temp				*NS*
T x S				*NS*
T x Temp				5.07
S x T				6.20
T x S x Temp				8.77

Table 4: Cumulative survival of predatory wasps of honey bees at different temperatures and 20 mins exposure durations[3]

3.4. Cumulative survival of honey bees Apis mellifera and A. cerana at different temperatures and exposure periods

In similar experiment, ten bees of each species (*A. mellifera* and *A. cerana*) were placed in separate cages of diameter (10 × 10 × 10 cm) and exposed to various temperature degrees inside an incubator from 43°C to 54°C, under two time durations of 5 minutes and 20 minutes. Survival percentage with increase in each temperature and duration was noted to assess thermal tolerance limits of honey bee species (Table 5;Table 6).

At the 5-minute exposure, both of the honey bee species exhibited 100 per cent survival up to 49°C. At 50°C, *A. mellifera* showed a slight reduction with 93.33 per cent survival while all of *A. cerana* workers were still alive. *A. mellifera*, recorded 71.48 per cent survival at 51°C and 44.44 per cent at 52°C. All of the remaining workers of *A. mellifera* died at 53°C. *A. cerana* displayed relatively higher heat resistance in early stages, remaining unaffected up to 50°C, while it showed 93.33 per cent and 67.78 per cent survival at 51°C and 52°C respectively, before reaching 36.51% at 53°C. The rest of the remaining workers of this honey bee species died at 54°C, suggesting that *A. cerana* bees can not tolerate temperatures above 53°C. During

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[3] S = Wasp species; T = Time interval; Temp = Temperature

the 20-minute exposure, mortality occurred at lower temperatures which might be due to longer exposure period causing exhaustion of the bees. *A. mellifera* remained unaffected till 48°C but exhibited a slight reduction in survival (93.33%) at 49°C. The survival decreased sharply to 53.71 per cent at 50°C and 33.33% at 51°C, while all of the remaining bee workers died at 52°C. *A. cerana* showed no mortality up to 51°C while the first reduction in survival was recorded at 50°C (73.33%) and at 51°C (72.02%). There was a 55.71 per cent survival at 52°C before reaching complete mortality at 53°C.

Our results suggest that *A. cerana* has slightly higher tolerance compared to *A. mellifera* which might be due to its evolutionary adaptation to the warmer conditions in its native regions in Asia, while *A. mellifera* which is a native species of Europe is slightly more susceptible.

Temperature (°C)		**Cumulative survival of honey bees (%)**	
	5 minutes		
	Apis mellifera	*Apis cerana*	Mean
49	100.00	100.00	100.00
50	93.33	100.00	96.67
51	71.48	93.33	82.41
52	44.44	67.78	56.11
53	0.00	36.51	18.26
54	0.00	0.00	0.00
Mean	51.54	66.27	58.91
Factor			CD ($\alpha = 0.05$)
T			*NS*
HS			*NS*
Temp			4.57
T x HS			3.73
T × Temp			6.47
S × Temp			6.47
T ×HS × Temp			9.14

Table 5: Cumulative survival of honey bees (*Apis mellifera* and *Apis cerana*) at different temperatures and 5 mins exposure duration[4]

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[4] HS = Honeybee species; T = Time interval; Temp = Temperature

Temperature (°C)	**Cumulative survival of honey bees (%)**		
	20 minutes		
	Apis mellifera	*Apis cerana*	Mean
49	93.33	100.00	96.67
50	53.71	73.33	63.52
51	33.33	72.02	52.68
52	0.00	55.71	27.86
53	0.00	0.00	0.00
54	0.00	0.00	0.00
Mean	30.06	50.18	40.12
Factor			CD ($\alpha = 0.05$)
T			*NS*
HS			*NS*
Temp			4.57
T x HS			3.73
T × Temp			6.47
S × Temp			6.47
T ×HS × Temp			9.14

Table 6: Cumulative survival of honey bees (*Apis mellifera* and *Apis cerana*) at different temperatures and 20 mins exposure duration[5]

3.5. Quantification of predatory behaviour of different wasp species in Apis mellifera apiary

To study the predatory behaviour of different wasp species, an experiment was conducted to evaluate different predatory behaviour parameters of wasps on *A. mellifera* apiary. This study analyzed number of attacks by different species, their reaction time to catch a bee, type of attack, whether solitary or group, and preference of different wasp species for the site of attack (Hive entrance, ground level or disruption of foraging). The observations on this aspect were recorded for ten minutes for each parameter. The results of this study that are presented in Table 7 reveal that *V. auraria* exhibited the highest attack frequency (2.13), followed by *V. basalis* (0.70) and *V. tropica* (0.36), suggesting that *V. auraria* is the most abundant species. The reaction time for attacks varied significantly, with *V. auraria* being the fastest and most agile among species to react and catch a bee (8.08 seconds). *V. basalis* was the weakest among species taking (31.04 seconds to capture a bee while *V. tropica* required comparatively shorter time than *V. basalis* and longer than *V. auraria* (24.08 seconds) to capture a bee. These results documented species specific differences in predatory behaviour and abilities of wasp species. Solitary attacks were the dominant mode of predation across wasp species, with *V. auraria*, *V. basalis* and *V. tropica* recording (1.51, 0.70 and 0.36 attacks, respectively. Among species, only *V. auraria* used to attack the colonies in group while *V. basalis* and *V. tropica* preferred attacking solitary. This could also be due to the less abundance of the later two species in the

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[5] HS = Honeybee species; T = Time interval; Temp = Temperature

apiary. Assessment of attack on different sites of the colonies revealed that the hive entrance was the preferred location for predation, particularly for *V. auraria* (1.46 attacks) and *V. tropica* (0.29 attacks), while *V. basalis* preferred targeting and catching honeybees at ground level (0.60 attacks). Only *V. auraria* was observed to disrupt the foraging activity of the bees with (0.35 attacks) catches during foraging of the bees, while the other two species did not show this tendency.

Wasp species			**Type of attack**			**Site of attack**	
	No. of attacks	**Reaction time (s)**	**Solitary**	**Group**	**Hive entrance**	**Ground level**	**Disruption of foraging**
V. auraria	2.13	8.08	1.51	0.61	1.46	0.31	0.35
V. basalis	0.70	31.04	0.70	0.00	0.10	0.60	0.00
V. tropica	0.36	24.08	0.36	0.00	0.29	0.08	0.00
CD ($\alpha = 0.05$)	**0.27**	**0.89**	**0.15**	**0.21**	**0.24**	**0.17**	**0.23**

Table 7: Quantification of predatory behaviour of different species of wasps in *Apis mellifera* apiary ($N = 10$ colonies)

4. Discussion

4.1. Temperature variation inside the bee ball

The study on temperature inside heat ball of honey bees revealed that *A. mellifera* bees are capable of killing wasps with lethal temperatures. Among the wasp species, *V. tropica* was the most tolerant of the species, standing temperatures up to (48.53°C), followed by *V. auraria* and *V. basalis.* The bee cluster itself recorded a lower temperature as compared to the wasp species, confirming that bees generate higher levels of heat around the wasp during their defence. Our observations of heat balling behaviour in honey bees align with previously documented studies of (Sugahara and Sakamoto 2009) from Japan who found that honey bees utilize the heat balling behaviour to defend against *V. mandarinia*, with bee balls reaching temperatures around 46°C. Also the present results are strongly supported by the findings of (Tan *et al.* 2005) who have documented wasp heat ball temperature of 45°C for *V. auraria.* (Ono *et al.* 1987) have also reported the heat ball temperature as 46°C for *V. auraria*, while, later work of (Ono *et al.* 1995) reported a temperature of 47°C, highlighting a notable concordance. Additionally, (Vaziritabar and Esmaeilzade 2019) reported a heat ball temperature of 47°C for *V. auraria.*

4.2. Number of bees involved in the bee ball

The study on the number of bees involved in heat balling revealed that a greater number of bees participated in balling the adult worker of *V. tropica* for a longer time period, supporting the idea that this species is more resistant to heat. These results are well aligned with the findings of (Baracchi *et al.* 2010) who documented that the number worker bees forming the ball around the hornet was strongly correlated with the maximum temperature inside the bee ball. The findings show that bees increase the heat inside the ball to a level where the wasp dies and that some wasps can resist this defensive tactic better than others.

4.3. Cumulative survival of bees and wasps in different temperatures and exposure periods

The cumulative survival data for wasps and bees after their exposure to different degrees of temperature and various exposure timings revealed that the ability of wasps vary in terms of their tolerance towards heat exposure. *V. basalis* was the least heat tolerant among the species, surviving only up to 46°C in a 5 minute exposure. *V. tropica* was most resistant, surviving up to 49°C and dying completely at 50°C. In contrast, honey bees, especially *A. cerana* tolerated higher temperatures than wasps. *A. cerana* could survive up to 53°C in 5 minutes exposure, while *A. mellifera* was not able to withstand the heat of 53°C. Longer time exposures increased mortality at lower temperatures with both wasps and bees dying in slightly lower temperatures than they used to die at short time exposure. Our findings on the heat tolerance levels among wasp species and honey bees are supported by (Sugahara and Sakamoto 2009) who reported that *A. cerana* could withstand slightly higher temperatures than wasps during heat balling.

The higher thermal tolerance observed in *A. cerana* compared to *A. mellifera* likely reflects its long evolutionary history in Asia, where it has co-evolved with various predatory wasp species over millions of years (Radloff *et al.* 2010). This adaptation has likely enhanced thermoregulatory mechanisms in *A. cerana*, including more efficient heat-shock protein expression, greater mitochondrial density for sustained thermogenesis and superior behavioural coordination during ball formation (King and MacRae 2015; Garrido *et al.* 2013; Stabentheiner *et al.* 2010; Tan *et al.* 2007). In contrast, A. mellifera, which originated in Europe and Africa, has had substantially less evolutionary exposure to Asian wasp predators, having been introduced to the region only recently (Ruttner 1988). The lower tolerance of A. mellifera may thus reflect its evolutionary history in environments with fewer high-temperature wasp predators.

The differential tolerance between honey bee species may also reflect adaptation to ambient temperatures in their native ranges, with A. cerana naturally inhabiting warmer tropical and subtropical regions where selection for heat tolerance has been stronger (Tan *et al.* 2007). Future genetic and physiological studies exploring the molecular basis of these differences would provide valuable insights into the mechanisms underlying species-specific thermal adaptations.

The findings are in close agreement with the findings of (Tan *et al.* 2005) who have also reported mortality of *A. mellifera* honey bees between 51 to 52°C. Among other similar studies, (Vaziritabar and Esmaeilzade 2019) have reported that wasps were dying at temperatures between 48°C and 49°C while *A. mellifera* were reported to die at 53–54°C.

4.4. Predatory behaviour of wasp species

The observation on the predatory behaviour of different wasp species showed that *V. auraria* was the most aggressive and agile wasp across different species, attacking more frequently and also with quick reaction to catch the bees compared to the others. It was the only species which attacked in group, preferred attacking and catching the bees at the hive entrance, and also disrupted the foraging of bees. Only solitary attacks of *V. basalis* and *V. tropica* were observed on the colonies and these two species were not as damaging as *V. auraria* and were slower in capturing bees. The aggressive predatory behaviour of *V. auraria* observed in our study is consistent with previous findings of (Srivastva *et al.* 1995) who documented that *V. auraria* was one of the most aggressive predators of honey bee apiaries, capable of capturing bees rapidly and causing significant damage to the colony. (Motmayen *et al.* 2024) also reported *V. auraria* as the most agile and damaging wasp species attacking honey bee colonies followed by *V. basalis* and *V. tropica*.

5. Conclusion

The findings of this study reveal that *A. mellifera* employs targeted thermogenesis to destroy predatory wasps, with internal balling temperatures reaching lethal thresholds for wasps. Among predatory wasps, *V. tropica* displayed the highest heat tolerance and required prolonged exposure to succumb to balling. Besides more number of bees were observed to accumulate during heat balling of *V. tropica* compared to the other species. *V. basalis* exhibited the least tolerance to heat, dying in lower temperatures. Between the two honey bee species, *A. cerana* demonstrated slightly higher tolerance to heat. *V. auraria* was the most aggressive predator, with fast reaction times and a tendency for group attacks. This study emphasize the ecological significance of heat balling as a defence mechanism employed by honey bees against their predators. Besides, it reports important insights on ability of different species of predatory wasps to attack honey bee colonies and the need for species specific predator surveillance in Himalayan apiaries to protect colony health.

Practical recommendations for beekeepers

Based on the findings of this study, the following practical recommendations are offered for beekeepers in the Himalayan region:

- Species-specific surveillance: Beekeepers should prioritize monitoring for *V. auraria* during peak foraging periods, as this species exhibited the highest attack frequency and fastest reaction times.

- Hive entrance management: Since the hive entrance was identified as the primary site of attack, installing entrance reducers or wasp traps during periods of high wasp activity can reduce predation pressure.

- Colony strength maintenance: Stronger colonies with larger worker populations are better equipped to mount effective heat balling responses. Beekeepers should maintain colonies at optimal strength through proper nutrition and disease management.

- Trap placement: Based on site preference data, traps should be placed near the hive entrances for *V. auraria* and *V. tropica*, while ground-level traps may be more effective for *V. basalis*.

- Timing of interventions: The activity patterns of different wasp species should guide the timing of protective interventions. Early morning and late afternoon observations may help identify species-specific peak activity periods.

Future research recommendations

Future research should address the following priorities:

- Long-term climate change impacts: With increasing global temperatures, understanding how elevated ambient temperatures affect the efficacy of heat balling and the physiological costs to bees is critical.

- Chemical ecology: Exploring semiochemicals involved in bee-wasp interactions could lead to the development of repellents or attractants for more targeted wasp management.

- Population genetics: Studying the genetic diversity and phylogeography of both honey bees and predatory wasps would reveal patterns of adaptation and inform conservation strategies.

- Integrated pest management: Field trials evaluating the effectiveness of integrated management approaches combining physical, biological and behavioural control methods would provide practical guidance for beekeepers.

- Comparative studies: Expanding this work to include other honey bee species (*A. dorsata*, *A. florea*) and wasp species would provide a more comprehensive understanding of bee-wasp co-evolutionary dynamics.

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❗ Publication & Reviewer Details

Publication Information
- **Submitted:** *08 June 2026*

- **Accepted:** *25 June 2026*

- **Published (Online):** *28 June 2026*

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Journal of Sustainable Technology in Agriculture https://www.jostapubs.com/
PAPAYA Academic Press, Statoberry LLP, https://www.statoberry.com/papaya

June 2026, Volume 2, Issue II *Submitted:* 2026-06-08
`doi:10.65287/josta.202606.bf39` *Accepted:* 2026-06-25