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Research article

Flight activity and pollen resources of *Apis nigrocincta* and *Apis cerana* in Central Sulawesi, Indonesia

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Abstract

Importance of the work: *Apis nigrocincta* and *A. cerana* are important pollinators in Sulawesi; however, their flight activity patterns remain unstudied.

Objectives: To characterize the flight activity of *A. nigrocincta* and *A. cerana* bees and its relationship to environmental factors and pollen sources.

Materials & Methods: The flight activity of both honey bee species in lowland Central Sulawesi was observed during 0700–1600 hours and correlations between flight activity and environmental factors were analyzed. Bee pollen was collected from the hind legs of returning bees. Pollen acetolysis and color analysis were conducted to identify pollen sources.

Results: Flight activity was higher and pollen sources were more diverse in *A. cerana* than for *A. nigrocincta*. The latter only collected a single type of pollen from *Cocos nucifera*, which was the dominant pollen source for both species, indicating that environmental management is needed to ensure the sustainability of beekeeping with the native *A. nigrocincta* in the presence of the introduced *A. cerana*. *A. cerana* collected Gramineae pollen, with 12 pollen types from 9 families and 3 unidentified types of pollen. Bee pollen with a single predominant pollen type, such as *C. nucifera*, varied in color. General linear models revealed that light intensity and temperature negatively affected flight activity, in contrast to the results of other studies.

Main finding: In the apiaries of Central Sulawesi, the more widely distributed and adaptable *A. cerana* had higher flight activity and collected a greater diversity of pollen compared with the Sulawesi native *A. nigrocincta*.

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Introduction

Sulawesi in the Wallacea region was formed by the accretion of three tectonic plates approximately 50 million years ago (Hall, 1998). The island is home to a high diversity of native and endemic species, including the native honey bee *Apis nigrocincta* (Hadisoesilo et al., 1995; Hadisoesilo and Otis, 1996) and the endemic honey bee *A. dorsata binghamii* (Maa, 1953; Nagir et al., 2016). The distribution of *A. nigrocincta* is restricted to Sulawesi, Sangihe and the surrounding islands (Hadisoesilo et al., 1995; Otis, 1996). In addition, this species occurs sympatrically with *Apis cerana*, the Asian honey bee, which is widely distributed throughout Asia (Otis, 1996; Damus and Otis, 1997; Smith et al., 2000).

A. cerana bees are pollinators that provide various ecosystem services and improve the productivity of plants, such as cauliflower (Verma and Partap, 1994), *Jatropha curcas* (Atmowidi et al., 2008), strawberry (Klatt et al., 2014; Alpionita et al., 2021), cabbage (Stanley et al., 2017), green beans, cucumbers and tomatoes (Putra et al., 2020). *A. nigrocincta*, *A. cerana* and *A. dorsata binghami* visit coffee flowers adjacent to highland areas of Lore Lindu National Park, Central Sulawesi (Klein, 2009). However, the importance of honey bees as pollinators in lowland apiaries in Sulawesi has not yet been explored.

When honey bees visit flowers for nectar, they gather pollen and pack it into a pollen basket (corbicula) on their hind legs (Michener, 1999). Bees tend to associate nectar resources with flower color on an individual basis (Wells et al., 1983); furthermore, the pollen in the pollen basket is often mainly derived from a single plant species (Modro et al., 2009). Given that bee pollen has a specific color, it could potentially be used to identify the plants from which bees obtain pollen (Lloyd et al., 2017). Identification of the pollen sources of honey bees is essential for determining the plant species needed by the bees to ensure the sustainability of beekeeping (Dukku, 2013; Bareke et al., 2017), as well as for apiary management (Larinde et al., 2014).

Bees collect pollen during specific flight periods; for example, the foraging activity of *A. cerana* on mango flower peaks is from 0900 hours to 1000 hours (Deuri et al., 2018). The flight activity of *A. cerana* is also affected by environmental factors such as light intensity (Abrol, 1992). Temperature positively affects flight activity, whereas humidity and rainfall negatively affect flight activity (Deuri et al., 2018).

The flight activity and pollen sources of the native Sulawesi honey bee (*A. nigrocincta*) and *A. cerana* have not yet been characterized. The aim of the current study was to study the flight activity and pollen sources of these two honey bee species in lowland areas at Jono Kalora Village, Parigi Moutong, Central Sulawesi by: 1) making observations of the flight activity of *A. cerana* and *A. nigrocincta*; (2) analyzing the correlation between flight activity and environmental factors; and (3) identifying the sources of the pollen taken by the two honey bee species using morphological characters.

Materials and Methods

Observations of flight activity

Observations of flight activity were made using one colony of *A. nigrocincta* from the Lompe Singgani (LS) apiary and one colony of *A. cerana* from the Kayu Manis (KM) apiary in Jono Kalora Village (Parigi Moutong Regency), Central Sulawesi (Table 1). The flight activities of honey bees were observed during 0700–1600 hours using the scan sampling method (Martin and Batteson, 1993), with three replication sets of observations carried out for each colony. Flight activity was recorded in 10 min intervals during 0700–1600 hours and was classified into three categories: 1) flying out (FO); 2) returning with pollen (RWP); and 3) returning without pollen (RWoP). Environmental parameters (light intensity, temperature and humidity) were measured every 10 min during the observation period.

Table 1 Bee pollen samples collected from hind legs of *Apis nigrocincta* and *A. cerana* in Jonokalora Village, Parigi Mountong, Central Sulawesi Province

Species	Apiary (altitude m amsl)	Coordinates	Sample code	Number of samples	Collector
A. nigrocincta	Lompe Singgani (37)	00˚ 47' 28.5"S, 120˚ 07' 59.3"E	An.LS.C1.1– An.LS.C1.11	11	NIS, RR, SB
cerana	Kayu Manis (62)	00˚ 48' 10.4"S, 120˚ 07' 59.6"E	Ac.KM.C1.1– Ac.KM.C1.24	24	

amsl = above mean sea level; An = *Apis nigrocincta*; Ac = *Apis cerana*; LS = Lompe Singgani; KM = Kayu Manis; C1 = Colony 1; 1(n) = sample number; NIS = Nurul Insani Shullia, RR= Rika Raffiudin; SB = Sri Bening

Pollen collection and color identification

Bee pollen was collected from the hind legs of returning honey bees using the direct method. The bee pollen was collected every 10 min during 0700–1600 hours after bee flight observations were made. In total, 11 bee pollen samples from *A. nigrocincta* and 24 samples from *A. cerana* were collected (Table 1).

The color of bee pollen was identified using the Color Picker from Image software (www.colorpickerfromimage.com). Pictures of bee pollen were taken using a stereomicroscope and Optilab camera with 4.5× magnification and were used for color identification in the Color Picker from Image application. The dominant color was used to determine the CMYK (cyan, magenta, yellow, black), RGB (red, green, blue) and HEX (hexadecimal) values. The HEX value was used to determine the color name in the ColorHexa (www.colorhexa.com) application.

Pollen preparation, identification and pollen type

Bee pollen samples from the hind legs were subject to acetolysis treatment to clear the exine layer; observations of pollen shape were made following the methods of Erdtman (1986) with some modifications. Pollen was observed using a compound microscope (Olympus CX31LEDRFS1) and an Indomicro camera. Pollen identifications were made using several characters: 1) pollen size, 2) polar view, 3) equatorial view, 4) aperture type and 5) exine ornament, and by consulting several sources: Huang (1972), Erdtman (1986), the database of the Australian Pollen and Spore Atlas (APSA, https://apsa.anu.edu.au/), Hamilton and Stevenson (2019) and Palynological Database 3.3 (PalDat 3.3, https://www.paldat.org/). Pollen type was determined from a sample of 200–300 pollen grains following the methods of Kiew and Muid (1991). Pollen was classified in the following categories: predominant pollen type (> 45%), secondary pollen type (16−45%), important minor pollen type (3−15%) and minor pollen type (< 3%) according to Kiew and Muid (1991).

Data analysis

The false discovery rate (FDR) was used to determine which variables to include in the multivariate analysis. The FDR tests were performed using the FuzzySim package (Barbosa, 2015) in the R software package (R Core Team, 2020). The correlations between environmental parameters (temperature, humidity and light intensity) and the flight activity of honey bees were analyzed using general linear models (GLMs) in the R software package (R Core Team, 2020).

Results

Flight activity of A. nigrocincta and A. cerana and correlation with environmental factors

Observations of the flight activity of honey bees and bee pollen collection were carried out in a lowland area (37–62 m above mean sea level, amsl) of Central Sulawesi (Table 1). The number of bees observed in FO, RWP and RWoP peaked at 384; 63; and 474 bees for *A. nigrocincta* and 566; 279; and 404 bees for *A. cerana*, respectively (Figs. 1A–1C). Overall, the average numbers of *A. nigrocincta* at LS engaged in all three types of flight activity was slightly lower than for *A. cerana* at KM (Figs. 1A–1C).

The timing of the peak in FO (Fig. 1A) and RWP was similar for both *A. nigrocincta* and *A. cerana* and occurred in the early morning during 0700–0800 hours. This coincided with a period of moderate temperatures (approximately 30°C) and high humidity (Figs. 2A and 2B). FO was lowest at 1200 hours (Fig. 1A), which coincided with the hottest part of the day (approximately 40°C) and high light intensity (Fig. 2A and 2B). In the afternoon, the peak in FO (Fig. 1A) and RWoP (Fig. 1C) occurred during 1300–1400 hours and 1400–1500 hours for *A. cerana* and *A. nigrocincta*, respectively.

All environmental factors (temperature, humidity and light intensity) were used as predictor variables (FDR, $p < 0.001$). GLM analysis revealed diverse correlations between each flight activity type and environmental factors in both species (Table 2). FO and RWoP significantly decreased with temperature (Figs. 3A–3C, Table 2). Flight activity was lower when temperatures exceeded 40°C. Foraging bees experience a positive heat balance during flight at temperatures in the range 30–35°C (Cooper et al., 1985).

Humidity had a positive effect on flight activity, and its effect was significant for FO and RWP in *A. nigrocincta* and *A. cerana* (Figs. 3D–3F, Table 2). Light intensity had a significant negative effect on the flight activity of *A. nigrocincta* and *A. cerana*, with the exception of RWoP in *A. cerana* at KM (Figs. 3G–3I, Table 2)

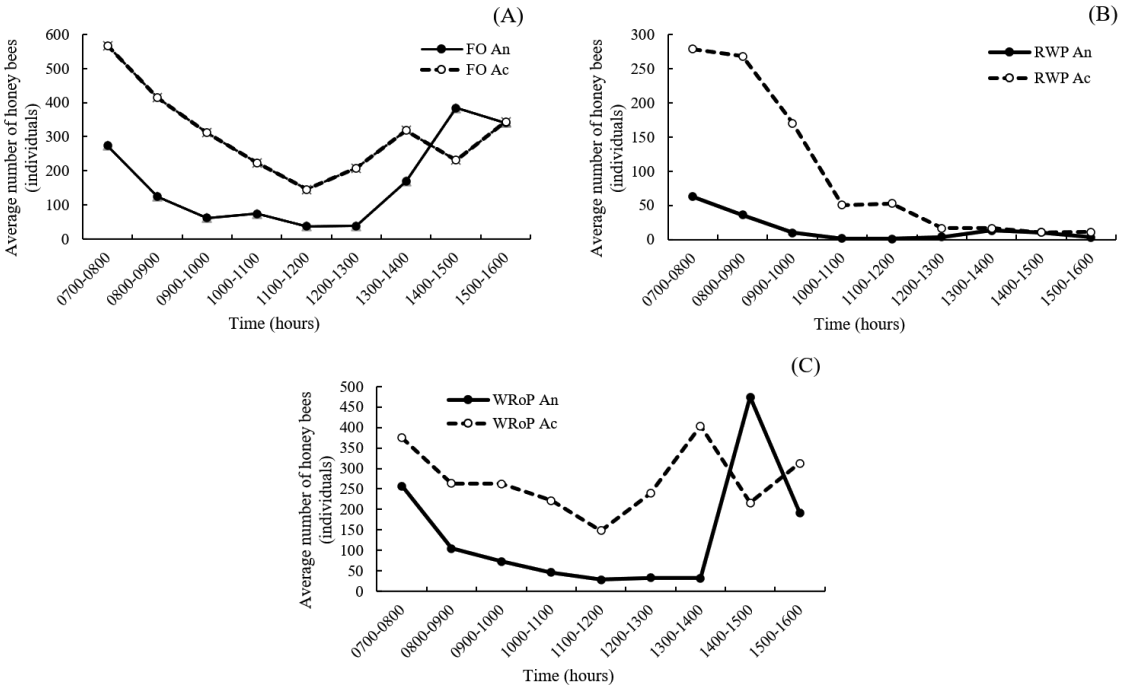

Fig. 1 Flight activity of *Apis nigrocincta* (An) from Lompe Singgani (LS) Apiary and *A. cerana* (Ac) from Kayu Manis Apiary in Parigi Moutong, Central Sulawesi: (A) flying out (FO); (B) returning with pollen (RWP); (C) returning without pollen (RWoP)

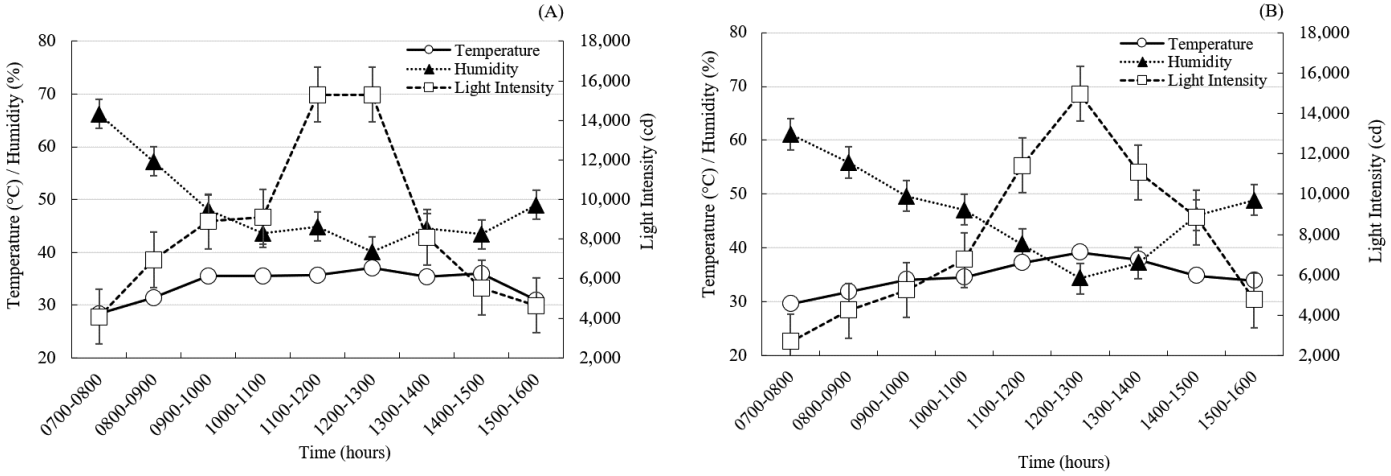

Fig. 2 Plot of temperature, humidity and light intensity observed during flight activities of: (A) *Apis nigrocincta* in Lompe Singgani (LS) Apiary; (B) *A. cerana* in Kayu Manis Apiary Central Sulawesi, where error bars indicate ± SD

Table 2 Generalized linear model analysis showing correlation between flight activity of *Apis nigrocincta* and *A. cerana* with temperature, humidity and light intensity

Activity	Species	Temperature		Humidity		Light Intensity	
		Estimate	*p*	Estimate	*p*	Estimate	*p*
FO	An	-1.928	> 0.1	1.7640	< 0.1	-0.006364	< 0.001
RWP		-0.6681	< 0.001	0.44279	< 0.001	-0.0005323	< 0.001
RWoP		-1.316	> 0.1	1.5050	> 0.1	-0.004899	< 0.01
FO	Ac	-9.196	< 0.001	3.294	< 0.001	-0.005706	< 0.001
RWP		-7.977	< 0.001	2.9751	< 0.001	-0.0041368	< 0.001
RWoP		-2.117	> 0.1	0.7437	> 0.1	-0.0006137	> 0.1

An = *A. nigrocincta*; Ac = *A. cerana*; FO = flying out; RWP = returning with pollen; RWoP = returning without pollen; $p < 00.5$= significant difference

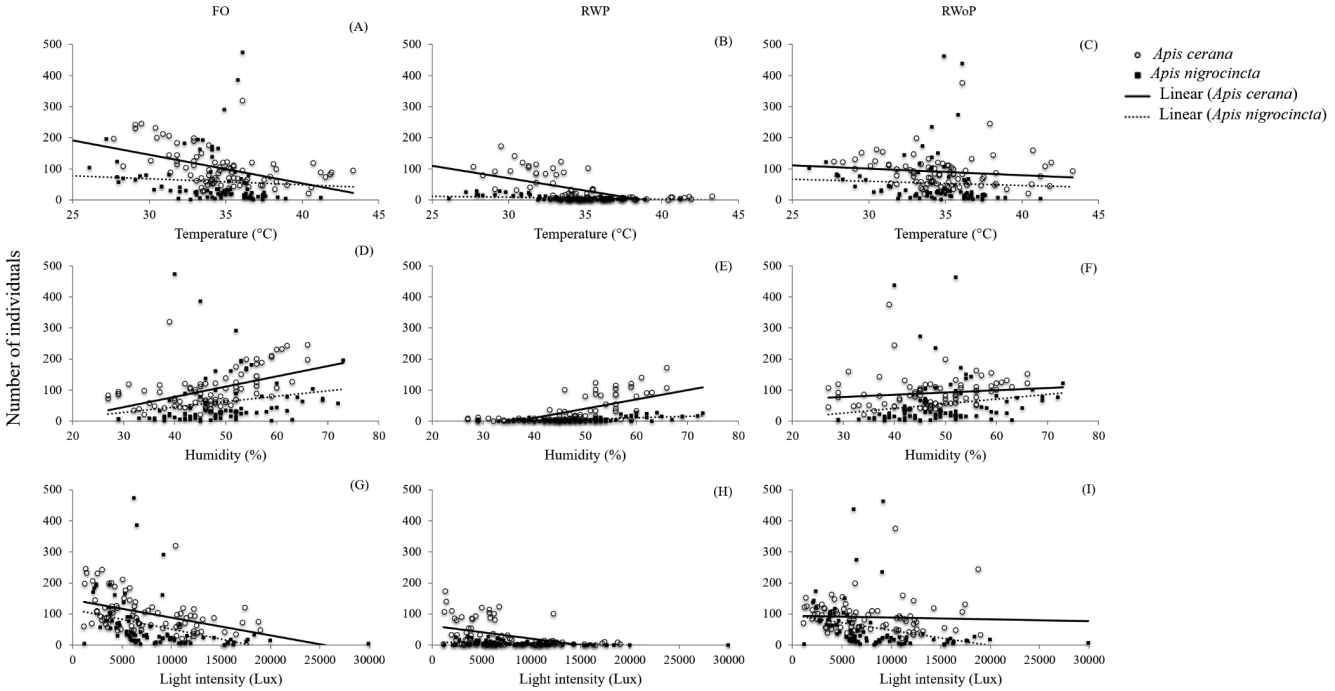

Fig. 3 Relationship between environmental factors: temperature (A–C); humidity (D–F); light intensity (G–I), with flight activity, where FO = flight out, RWP = returning with pollen and RWoP = returning without pollen

Pollen analysis and identification

Pollen identification on the basis of morphological characters revealed that *A. cerana* collected pollen from a more diverse set of plants than *A. nigrocincta* (Fig. 4, Table 3). In total, 24 bee pollen samples were obtained for *A. cerana* at KM, including 16 pollen types (1 Gramineae pollen type, 12 pollen types from 9 families and 3 unidentified types of pollen), as shown in Fig. 4. Furthermore, 12 of the 16 types of pollen were successfully identified to the species level, including 12 species and 8 families of plants differing in habitus (trees, shrubs and herbaceous plants), as shown in Table 3.

All pollen collected from *A. cerana* was small (diameter 10–25 µm), with the exception of *C. nucifera* pollen (diameter 50–100 µm) (Table 3). The morphological characters of bee pollen from *A. cerana* varied with the dominant aperture and pollen shape from polar and equatorial views being tricorporate, spheroidal and sub-prolate, respectively. However, all 11 pollen samples collected from the hind tibia of *A. nigrocincta* were from *C. nucifera* (Fig. 4). *C. nucifera* pollen is circular from a polar view and prolate/compressed oval from an equatorial view; it is also characterized by a monocolpate/sulcate aperture and psilate exine ornament (Table 3). The most common type of bee pollen from the hind tibia of both *A. cerana* and *A. nigrocincta* was *C. nucifera*, which had pollen percentages of 51.14% and 100%, respectively (Table 3). This finding indicated that *A. cerana* foraged on a wider variety of plants than *A. nigrocincta*.

Fig. 4 Pollen type diversity collected by *Apis cerana* (type 1–16) and *A. nigrocincta* (only type 2) in Parigi Moutong Regency, Central Sulawesi and pollen identification: 1) *Ageratum conyzoides*; 2) *Cocos nucifera*; 3) *Desmodium* sp.; 4) *Euphorbia hirta*; 5) *Fibraurea tinctoria*; 6) Gramineae; 7) *Lannea coromandelica*; 8) *Lithocarpus glutinosus*; 9) *Mimosa pudica*; 10) *Saurauia oligolepis*; 11) *Saurauia hoeveniana*; 12) *Sphagneticola trilobata*; 13) *Tetracera scandens*; 14) Sp1; 15) Sp2; 16) Sp3; where E = equatorial; P=polar; Sp = unidentified pollen and bar scale = 20 µm

Table 3 Pollen type, morphological characters and pollen percentage of bee pollen collected from *Apis nigrocincta* and *A. cerana* in Parigi Moutong regency, Central Sulawesi

Bee species	Pollen from plant	Habitus	Polar side	Equatorial side	Aperture	Exine ornament	Polar size (height×width) µm	Equatorial size (height×width) µm	Pollen percentage (%)	Category
A. nigrocincta	*Cocos nucifera*	Trees	Circular	Prolate, Compressed oval	Monocolpate/ sulcate	Psilate	51.78−72.42× 45.30−64.26	54.2−80.31× 29.19−54.95	100	P
A. cerana	*Ageratum conyzoides*	Herbaceous	-	Spheroidal	Tricolporate	Echinate	-	17.99×17.81	0.02	M
	Cocos nucifera	Trees	Circular	Prolate, Compressed oval	Monocolpate/ sulcate	Psilate	51.78−72.42× 45.30−64.26	54.2−80.31× 29.19−54.95	51.14	P
	Desmodium sp.	Shrubs	Circular	Subprolate	Tricolporate	Reticulate	14.96−15.45× 14.69−14.93	13.84−14.32× 11.71−12.45	8.42	IM
	Euphorbia hirta	Herbaceous	Circular	Subprolate	Tricolporate	Reticulate	15.9−20.12× 15.78−19.68	15.08−19.31× 12.63−15.28	7.42	IM
	Fibraurea tinctoria	Shrubs	Circular	-	Tricolporate	Scabrate	11.65−13.60× 11.40−13.40	-	0.17	M
	Gramineae	Herbaceous	Circular	Spheroidal	Monoporate	Scabrate	88.27−95.58× 81.02−83.95	88.29−92.16× 74.23−76.56	9.14	IM
	Lannea coromandelica	Trees	Circular	Prolate	Tricolporate	Striate	11.9×11.57	19.43×12.59	1.60	M
	Lithocarpus glutinosus	Trees	Circular-lobate	-	Tricolporate	Reticulate	10.53−10.61× 10.13−10.17	-	0.26	M
	Mimosa pudica	Herbaceous	-	Oblate	Tetrad	Psilate	-	10.7×10.18	0.02	M
	Saurauia oligolepis	Trees	Circular	-	Tricolporate	Psilate	11.66×11.33	-	0.11	M
	Saurauia hoeveniana	Trees	-	Spheroidal	Tricolpate	Psilate	-	15.82×14.11	0.02	M
	Sphagneticola trilobata	Herbaceous	-	Spheroidal	Tricolporate	Echinate	-	15.85×15.84	0.02	M
	Tetracera scandens	Shrubs	Circular	Subprolate	Tricolpate	Reticulate	15.56−17.48× 15.12−15.71	15.65−17.89× 11.64−12.24	8.97	IM
	Sp1		Semi-angular	Prolate	Tricolpate	Verrucate/ Scabrate	15.83−17.27× 14.84−16.42	16.71−17.81× 10.63−13.32	5.00	IM
	Sp2		Circular	Subprolate	Tricolpate	Scabrate	14.94−15.64× 14.46−15.16	14.53−15.05× 12.22−12.88	6.09	IM
	Sp3		Circular	-	Tricolporate	Scabrate/ Reticulate	13.62−15.64× 13.41−15.34	17.14×15.05	1.61	M

(-) = not identified; P = predominant; S = secondary; IM = important minor; M = minor

Five different colors of pollen were observed from the 24 bee pollen samples of *A. cerana* and 11 bee pollen samples of *A. nigrocincta* (Fig. 5). The predominant pollen of *C. nucifera* varied in color, with the most common color being dark yellow (Fig. 6). The predominant pollen of Gramineae and Sp2 was dark yellow.

Discussion

Insect-plant interactions shape ecological communities and the circadian clock of visiting insects to flowers (Bloch et al., 2017). Nectar and pollen are the main rewards that insects, including bees, receive from visiting flowers (Nepi et al., 2018). Pollen is an important food resource collected by bee workers, especially for the development of larvae (Nicholls and de Ibarra, 2016).

Both bees and flowers might have mutual influences on each other's circadian clock systems (Bloch et al., 2017). FO and RWP peaked at 0700–0800 hours for *A. cerana* and *A. nigrocincta*. This is consistent with a previous study showing that the foraging activity peak of *A. cerana* on sunflowers was during 0800–0900 hours in a highland area (1,030 m amsl) in Mongolia (Yang et al., 2020). In a highland area of Bandung (ca. 700 m amsl), Indonesia, the foraging activity peaks of *A. cerana* on the flowers of cucumber and green bean were during 1000–1100 hours and 1100–1200 hours, respectively (Putra et al., 2020). Temperatures are inversely correlated with wing loading and the thoracic temperature of bees, which have a substantial effect on their flying ability while foraging (Cooper et al., 1985). Bees can delay foraging activity until conditions for flying improve. *A. cerana* trades smaller foraging efficiency for greater metabolic efficiency (Tan et al., 2012). The low availability of natural resources, such as pollen, during the hottest part of the day (Cooper et al., 1985) might also contribute to the decreased foraging activity of bees during this period.

A. nigrocincta which is native to Sulawesi only collected pollen from a single species (*C. nucifera*) even though up to 10 plant species were blooming next to *C. nucifera* plants during the observation period at LS. In contrast, *A. cerana* collected 16 types of pollen, of which *C. nucifera* was also the most common source of pollen for this widely distributed Asian honey bee (Fig. 4, Table 3). The specificity of *A. nigrocincta* to the native plant is consistent with the selectivity of *A. koschevnikovi*, a honey bee native to Sumatera, which only visited a single plant species while *A. cerana* on the same island collected pollen from 56 plant species (Jasmi personal communication, November 2021). The current study is the first to characterize the flight activity and pollen collection behavior of *A. nigrocincta* in the lowland region of Sulawesi. *A. nigrocincta* has been reported to visit coffee flowers in agroforest adjacent to Lore Lindu National Park, Central Sulawesi (Klein, 2009). However, it should be noted that the aforementioned study was conducted in a highland area and the pollen collection habits of *A. nigrocincta* were not examined in that study.

The pollen of *C. nucifera* was the most common in the tibia of both *A. nigrocincta* and *A. cerana*. The flowers of *C. nucifera* provide nectar and pollen in a single inflorescence composed of numerous male flowers that are available throughout the year

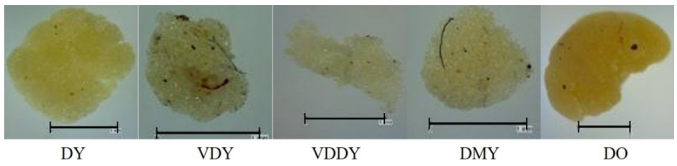

Fig. 5 Color type of bee pollen collected from hind tibia of *Apis nigrocincta* and *A. cerana* in Parigi Moutong, Central Sulawesi, where DY = dark yellow, VDY = very dark yellow, VDDY = very dark desaturated yellow, DMY = dark moderate yellow, DO = dark orange and scale bar = 1 mm

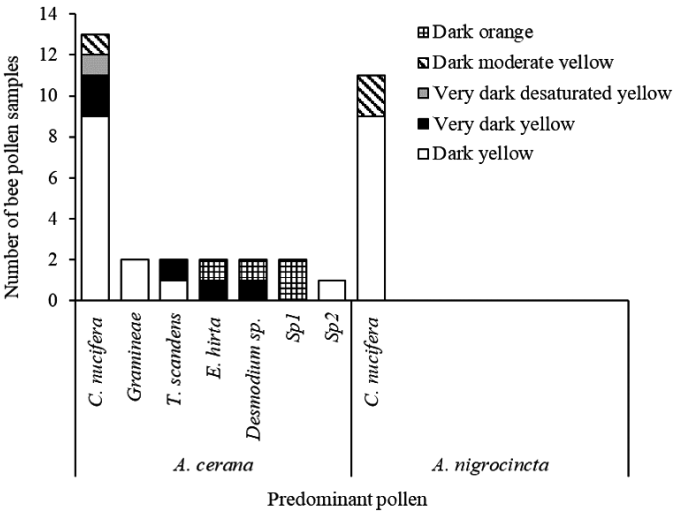

Fig. 6 Number of bee pollen samples with color type based on predominant pollen

(Thomas and Josephrajkumar, 2013; Agussalim et al., 2017; Jasmi, 2017). The pollen of *C. nucifera* is highly nutritious with total soluble protein, total carbohydrate and free amino acid contents of 190.6 mg/g, 6.8 mg/g and 95.0 mg/g, respectively (Sharma et al., 2009). *C. nucifera* pollen also has several fatty acids and high antioxidant activity (Araújo et al., 2017).

Five color types were observed among the 24 and 11 bee pollen samples from *A. cerana* and *A. nigrocincta*, respectively: dark yellow, dark moderate yellow, very dark desaturated yellow, very dark yellow and dark orange. Bee pollen with the most common pollen (from *C. nucifera*) had four different colors. All four colors of the *C. nucifera* pollen were collected by *A. cerana*, whereas only two colors of *C. nucifera* pollen were collected by *A. nigrocincta*. Variation in bee pollen color within a species has also been observed for *Vernonia* spp. in Brazil; *A. mellifera* foraging on *Vernonia* spp. collected both light brown and light beige pollen (Modro et al., 2009). Variation in the color of pollen might be related to its storage time; for example, the white pollen of *Centaurea iberica* changes to yellow after a year of storage (Joujeh et al., 2019).

Observations of the flight activity and the identification of bee pollen indicated that *A. cerana*, which is an introduced species, shows high environmental adaptability compared with the Sulawesi native *A. nigrocincta*. It is believed that *A. cerana* was introduced to Sulawesi in the 1970s from Java for use in beekeeping (unpublished data). The highly adaptable honey bee *A. cerana* on Sulawesi might compete with *A. nigrocincta*. Koetz (2013) as suggested by *A. cerana* competing with *A. mellifera* in apiaries in northeastern Australia. Therefore, environmental management is needed to ensure the sustainability of beekeeping when the native *A. nigrocincta* is in the presence of *A. cerana*. The results of the current study indicated that the maintenance of nectar and pollen resources requires careful attention. In apiaries with both *A. nigrocincta* and *A. cerana*, the number of *A. cerana* colonies also needs to be considered.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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