Title:

Dominance hierarchy among workers changes with colony development in *Polistes japonicus* (Hymenoptera: Vespidae) paper wasp colonies with a small number of workers

Running head:

Dominance hierarchy changes with colony development

Authors:

Yoshihiro Ishikawa · Yoshihiro Y. Yamada · Makoto Matsuura · Morio Tsukada · Koji Tsuchida

Y. Ishikawa, Y. Y. Yamada (corresponding author), M. Matsuura, and M. Tsukada

Insect Ecology Laboratory, Graduate School of Bioresources, Mie University, Tsu, Mie 514-8507, Japan

E-mail: yamada-y@bio.mie-u.ac.jp; Tel.: +81 59 231 9498; Fax: +81 59 231 9540

K. Tsuchida

Laboratory of Insect Ecology, Faculty of Applied Biological Sciences, Gifu University, Yanagido 1-1, Gifu, Gifu 501-1193, Japan

Keywords emergence order · dominance hierarchy · *Polistella* · Polistinae · social wasp

Abstract. Dominance hierarchy in the primitively eusocial wasp *Polistes japonicus* was analysed in four colonies for two periods: (1) the first-brood period, when only early emerging workers are present on the nest, and (2) the mixed-brood period, when the first and second (last) broods are present on the nest. The rank in the dominance hierarchy was determined based on a sociogram showing a dominance–subordinance relationship for all pairs of workers. During the first-brood period, older workers were likely to be more dominant (older-dominance hierarchy), while the rank of workers was reversed during the mixed-brood period, with younger workers being likely to be more dominant (younger-dominance hierarchy). However, the oldest and youngest workers were not always the top-ranked workers in the dominance hierarchy during the first- and mixed-brood periods, respectively, and during the mixed-brood period no younger-dominance hierarchy was evident when the first or second brood was analysed separately. Higher-ranked workers displayed dominance behaviour more frequently, and the lowest-ranked worker hardly displayed dominance behaviour. Most workers displayed dominance behaviours primarily toward the worker ranked immediately below in the dominance hierarchy during the mixed-brood period but not during the first-brood period. The bodies of younger workers were larger for the mixed brood, but not for the first brood in some colonies or the second brood in all colonies. The association between body size and rank in the dominance hierarchy was negative during the first-brood period and positive during the mixed-brood period, with a nearly significant trend

also seen even when the analysis was limited to the second brood. To explain the above temporal change from an older-dominance hierarchy to a younger-dominance hierarchy, we propose the hypothesis that the probability of a worker inheriting the colony increases rapidly with colony development, and consequently younger larger workers attempt to move up the dominance hierarchy in order to produce their own offspring by becoming the superseder late in colony development, rather than working harmoniously so as to boost the overall production of reproductive progeny for a colony, which is the strategy adopted early in colony development.

Introduction

The subfamily Polistinae (paper wasps) comprises four tribes (Polistini, Epiponini, Mischocyttarini and Ropalidiini) and exhibits a dominance hierarchy among workers, as do many other social hymenopteran species (Michener, 1974; van Honk et al., 1981; Higashi et al., 1994; Monnin and Peeters, 1999). The dominance hierarchy in paper wasps is determined by frequent aggressive encounters among workers, in which one worker displays dominance behaviour over another, such as rushing, mounting or biting with the mandibles (Pardi, 1948; Gadagkar, 1980; Gadagkar and Joshi, 1982). The resulting rank in the dominance hierarchy usually determines the kind of labour performed by an individual worker: the frequency of foraging is higher for low-ranked workers, whereas high-ranked workers stay on the nest and perform intranidal tasks, but they are often lazy (Gamboa et al., 1990; O'Donnell, 1998). As a result, more-dominant workers are likely to live longer because foraging is riskier and physically and physiologically more demanding than intranidal tasks (O'Donnell, 1998; Heinsohn and Legge, 1999; Finkel and Holbrook, 2000; Cant and Field, 2001, 2005; Nilsson, 2002; Williams, 2008). Moreover, the top-ranked worker usually replaces the queen when she disappears (Pardi, 1948; Yoshikawa, 1963; Jeanne, 1972; Litte, 1977; West-Eberhard, 1978, 1981; Yamane, 1986; Bridge and Field, 2007), and thus more-dominant workers have more opportunities to produce their own progeny (Field and Cant, 2006; Field et al., 2006).

It has been considered that the main factor determining the dominance hierarchy in primitively eusocial wasps is not body size (Pardi, 1948; Strassmann and Meyer, 1983; Hughes and Strassmann, 1988; Reeve, 1991; Bridge and Field, 2007) but rather worker age: older workers are ranked higher in temperate regions (Pardi, 1948; Yoshikawa, 1956, 1963; Litte, 1979; Dew and Michener, 1981; Strassmann and Meyer, 1983; Miyano, 1986; Hughes and Strassmann, 1988; Iwahashi, 1989; Reeve, 1991) while younger workers are ranked higher in tropical regions (West-Eberhard, 1969, 1978, 1981; Jeanne, 1972; Yamane, 1986; Gadagkar, 1987; O'Donnell, 2001). However, there are some exceptions, such as *Parapolybia indica* (Suzuki, 2003), *Polistes instabilis* (Hughes and Strassmann, 1988), *Ropalidia marginata* (Gadagkar, 1980) and *Liostenogaster flavolineata* (Bridge and Field, 2007). [Note that Suzuki (2003) did not investigate the relationship between dominance hierarchy and emergence order, even though a relatively young worker inherits the colony when the foundress disappears in spite of *Parapolybia indica* being a temperate species.] A reasonable explanation for the first two exceptions is that the distributions of these species differ from those of their ancestral species.

Tsuji and Tsuji (2005) have recently developed a model in which the age-related dominance hierarchy is determined by the life expectancies of the colony and the superseding worker when that worker inherits the colony. Younger workers obtain lower fitness returns in temperate regions by superseding the foundress than by being workers because the colony ends soon thereafter and younger workers have limited chances for ovipositing after becoming the superseder. However, the reverse is true in tropical regions, where a younger worker that inherits the colony has a longer time for ovipositing and more workers to rear its progeny compared to in temperate regions, which is because the colony survives throughout the year with many workers. Furthermore, Tsuchida and Suzuki (2006) have proposed that a younger-dominance hierarchy (where younger workers are likely to be more dominant) is more likely in a larger colony and when the species exhibits a perennial life cycle. However, it should be noted that previous researches of dominance hierarchy have largely ignored the possibility of temporal changes in the dominance hierarchy. Moreover, studies of dominance hierarchy have been limited to only a small proportion of social-insect species; for example, only 19 of the 943 Polistinae species have been studied (Strassmann and Meyer, 1983; Arévalo et al., 2004; Tsuji and Tsuji, 2005; Tsuchida and Suzuki, 2006). Most data on the Polistini tribe (which comprises one genus, *Polistes*) have been derived from only 4 of the 12 subgenera (*Polistes* sensu stricto, *Megapolistes*, *Fuscopolistes* and *Aphanilopterus*). Observation of many species – particularly ones belonging to subgenera that have not been studied previously – is required to obtain a deeper understanding of dominance hierarchy.

In this paper, we describe the observed frequencies of dominance behaviour among workers and reveal the dominance hierarchy in *Polistes japonicus* (Hymenoptera: Vespidae), a member of the subgenus *Polistella*. We also present the effects of emergence order on the dominance hierarchy among workers. The relationships between body size and emergence order and between body size and dominance hierarchy are also examined. Our study has two novel features. Firstly, this is the first study to reveal the dominance hierarchy in the subgenus *Polistella*. Secondly, the dominance hierarchy was analysed for two periods to reveal possible temporal changes therein: (1) the early period (first-brood period), when only early emerging workers are present on the nest, and (2) the late period (mixed-brood period), when both young and old workers are present on the nest. This analysis has shown that there are temporal changes in dominance-determining mechanisms, as described below.

Materials and methods

Biology of *Polistes japonicus*

Three *Polistella* species are found in Japan: *P. japonicus*, *P. nipponensis* and *P. snelleni*. Around May an overwintered foundress of *P. japonicus* starts to found a nest, which eventually comprises 40–80 cells (Matsuura, 1995). Workers emerge in June and July, followed by the emergence of males and then reproductive females in August. There are around 10 workers and a maximum of 50 reproductive adults in a colony (Matsuura, 1995); this number of workers is as small as that for *P. nipponensis*.

Colonies and rearing conditions

Four colonies were reared for observation in a field cage (3.2 × 3.4 × 1.9–3.7 m) with a roof on the Mie University campus in Tsu, Mie, Japan over 3 years: 2002 (colonies A and B), 2003 (colony C) and 2004 (colony D). One wall of the cage was glazed and the remaining three walls were made of a vinyl chloride net with a 1 × 1 mm mesh, and the roof was constructed from corrugated clear-plastic sheets. The cage contained live trees (including *Neolitsea sericea*, *Prunus jamasakura* and *Dendropanax trifidus*) that provided nesting sites and nest materials for the wasps. Foundresses were collected in April in Tsu, reared in a small cage (11 × 15 × 8 cm) containing a honey solution as food, and released into the field cage early in May. Wasps were provided with flesh, honey and water placed on dishes on a table in the cage that were renewed every day. The flesh usually included lepidopteran larvae, adult cicadas (particularly their thoraxes), and honeybee larvae or pupae, most of which were split in half.

Workers were divided into the first and second broods, each of which comprised two to four individuals. The first brood was provisioned by the foundress and not by workers, while the second brood was provisioned mainly by workers. The former emerged continuously for 2–8 days and the latter started to emerge 3–7 days after the last emergence of the first brood, and completed their emergence in 4–12 days (Table 1).

Table 1

Observation and determination of dominance hierarchy

The head width of each newly emerged worker was measured as an index of body size with a vernier caliper to an accuracy of 0.05 mm. Workers were marked by attaching small pieces of differently coloured photographic paper labelled with numbers to the mesonotum with clear nail polish. The paper was kept as light as possible by removing its backing chartaceous part. The behaviours of individual wasps on the nest were recorded by a video camera and recorder. Video recording usually started at noon and finished at about 1800 hours, and was performed several times before male emergence in August. The total recording times were 72, 42, 72 and 84 h for colonies A, B, C and D, respectively, of which 48, 42, 12 and 12 h of observations were made before the emergence of the second brood: in colony B, the second brood was not produced and observation was limited to July.

Each episode of dominance behaviour was determined for each individual wasp by watching the videotape. The dominance behaviour was defined as aggressive contact of a target worker with another worker; that is, where a target worker rushed another worker or bit part of the body of another worker with its mandible. Episodes where a worker adopted a posture for rushing but did not actually rush or rushed but did not contact another worker were not counted. Vibration of the abdomen (Molina and O'Donnell, 2009) was often observed in foundresses but rarely observed in workers, and is not reported on here. Other dominance behaviours that are typically found in other species, such as the dominant worker buzzing its wings, stinging the subordinate, and rising on its legs above the subordinate

(Wilson, 1974; Spradbery, 1991), were not observed. The dominance hierarchy was determined based on a table listing the results of dominance contests as frequencies of episodes of dominance behaviour for all possible pairs of workers. Episodes of all kinds of dominance behaviour were counted without weightings. In each pair, one worker that displayed dominance behaviour over the other of the pair with a higher frequency was considered the dominant one of the pair. A worker was ranked based on the number of subordinate individuals for that worker minus the number of dominant individuals.

Statistical analysis

All statistical analyses were performed using the software package NCSS 2007. General linear model analysis (which is the same as ANCOVA in this application) was used to test whether the emergence order influenced the body size of workers, whether emergence order and body size influenced the rank in the dominance hierarchy, and whether this rank influenced the frequency of dominance behaviour. The model included two groups of factors: (1) the emergence order, rank in the dominance hierarchy and body size, and (2) colony characteristics (i.e. differences in the first factors among colonies). Data sets that did not conform to the normality assumption were log transformed to impose normality. Correlation analysis was applied separately to each colony when there was significant interaction between the two factors. Moreover, the following parameter was used to indicate the rank in the dominance hierarchy, emergence order and order of body size in order to exclude the influence of the total number of emerged workers: (order of a given worker – 1)/(number of workers – 1); this produced values of 0 and 1 for the first and last workers, respectively. The relationship between the frequency of dominance behaviour and the rank in the dominance hierarchy was also analysed using Spearman rank correlation analysis separately for each colony to examine whether the frequency of dominance behaviour can be used as an index for the rank in the dominance hierarchy. Higher-ranked workers reportedly display dominance hierarchy more frequently in many paper wasps (Wilson, 1974; Spradbery, 1991). All of the above analyses were performed separately for two periods: (1) the first-brood period, from the emergence of the last worker of the first brood to the emergence of the first worker of the second brood (usually from early to mid July), and (2) the mixed-brood period, from the emergence of the last worker of the second brood to the emergence of males in August (usually from late July to late August). Moreover, the analysis of the mixed-brood period was performed separately for first- and second-brood workers.

Furthermore, we analysed whether workers displayed dominance behaviour over the other workers at random. Whether the observed frequencies of dominance behaviours among the other workers conform to a random distribution was tested based on the probability that the observed highest frequency or a frequency higher than that is expected to occur if the target worker displays all dominance behaviours toward the other workers at random (i.e. according to a binomial distribution). This was done since the samples were too small to perform a familiar chi-square goodness-of-fit test.

Results

Basic characteristics of colonies

A foundress established a colony in the field cage by herself. The foundresses performed all kinds of extranidal and intranidal tasks before worker emergence, after which the foundresses rarely performed extranidal tasks except collecting nest materials, but they continued all intranidal tasks. The foundress exclusively laid eggs and it hardly received any dominance behaviour from workers with one exception in colony A, in which a worker of the second brood was dominant over the foundress, and finally replaced her (Y. Ishikawa, unpublished). In colonies A, B, C and D there were 49, 29, 79 and 39 cells, respectively, with 3, 4, 4 and 4 first-brood workers, and 5, 0, 3 and 2 second-brood workers emerging. One worker of the second brood (the fourth-emerging worker in colony A was missing immediately after emergence, so the actual number of workers was seven (Table 1).

Two, one and two males (so-called early males: Strassmann, 1981; Suzuki, 1985, 1997; Ono, 1989; Page et al., 1989) emerged before the last worker emerged in colonies A, B and D, respectively. These early males were removed from the colony by the observer since they might have interfered with the activity of workers.

The foundresses disappeared for unknown reasons from colonies A and D on 15 July 2002 and 12 August 2004, respectively (the foundress of colony A was found dead on the table for food supply on 15 July), and the top-ranked workers became superseders, which were observed ovipositing (a future paper will provide the details). Analyzing the data obtained before the foundress disappeared produced almost the same results as analyzing all of the data (i.e. including that obtained after the foundress disappeared), and hence the results of the latter analysis are presented here since they relate to longer observations.

Relationship between body size and emergence order

Analysis of all workers in the first and second broods revealed that earlier-emerging workers were likely to be smaller ($F_{1, 19} = 27.1$, $P < 0.001$; Fig. 1). In addition, the body sizes of workers were significantly associated with the colony ($F_{3, 19} = 10.3$, $P < 0.001$), but not with the interaction between emergence order and colony ($F_{3,\,16}$ = 1.39, P = 0.28). However, the influence of emergence order or colony on worker size disappeared when the analysis was limited to the second brood ($F_{1,\,5}$ = 0.045, P = 0.84 for emergence order; $F_{2,\,5}$ = 0.888, P = 0.47 for colony; $F_{2,\,3}$ = 0.433, P = 0.68 for the interaction). When the analysis was limited to the first brood, the relationship between worker size and emergence order differed between colonies ($F_{3,\,7}$ = 4.64, P = 0.043 for the interaction): earlier-emerging workers were significantly or nearly significantly smaller in colonies B and D (P = 0.010 and P = 0.056, respectively) but not in colonies A and C (P = 1.00 and P = 0.23, respectively).

Dominance hierarchy among workers

During the first-brood period, older workers were likely to be ranked higher in the dominance hierarchy ($F_{1,\,10}$ = 4.99, P = 0.050; Table 2, Fig. 2). The tendency was the same in all colonies; that is, this was not influenced by the colony ($F_{3,\,10}$ < 0.001, P = 1.00) and there was no interaction between emergence order and colony ($F_{3,\,7}$ = 0.245, P = 0.86). However, it should be noted that the oldest worker did not become the top-ranked worker in two colonies. In addition, smaller workers were likely to be ranked higher ($F_{1,\,10}$ = 9.79, P = 0.011 for body size; $F_{3,\,10}$ < 0.001, P = 1.00 for colony; $F_{3,\,7}$ = 0.282, P = 0.84 for the interaction; Fig. 3), because

Fig 2

Table 2

Fig 3

older workers were often smaller, as mentioned above (Fig. 1).

A hierarchy with older dominance ($r = 0.949$, $P = 0.051$) was present in mid July in colony B (which had no second brood), while in late July (no observation in August) the relationship between emergence order and rank in the dominance hierarchy was not significant ($r = 0.632$, $P = 0.37$), although the oldest worker was the top-ranked worker.

Analysis of all workers present during the mixed-brood period revealed that younger workers were likely to be ranked higher in the dominance hierarchy in all colonies ($F_{1, 16}$ = 11.0, $P = 0.004$ for emergence order; $F_{2, 16} = 0.001$, $P = 1.00$ for colony; $F_{2, 14} = 0.236$, $P = 0.79$ for the interaction; Table 2, Fig. 2; colony B was excluded from the analysis because it had no second brood). However, the youngest worker became the top-ranked worker in only one colony. Separate analysis of the first and second broods revealed no significant relationship between rank in the dominance hierarchy and emergence order in all colonies, suggesting that a younger-dominance hierarchy was due to a difference in the average rank in the dominance hierarchy between the first and second broods. Larger workers were likely to be ranked lower during the first-brood period($F_{1, 10} = 9.79$, $P = 0.011$ for body size; $F_{3, 10} < 0.001$, P = 1.00 for colony; $F_{3, 7} = 0.282$, $P = 0.84$ for the interaction; Fig. 3) and ranked higher during the mixed-brood period ($F_{1, 16} = 17.4$, $P = 0.001$ for body size; $F_{2, 16} = 0.044$, $P = 0.96$ for colony; $F_{2, 14} = 0.159$, $P = 0.85$ for the interaction; Fig. 3), because the body size was positively associated with the emergence order (Fig. 1). The effect of either the body size or the emergence order may be attributable to the strong association between these two features, and one of them may be independent of the rank in the dominance hierarchy. When the analysis was limited to the second brood, the effect of body size was nearly significant ($F_{1, 5}$ = 5.15, P = 0.073) but that of the emergence order was not significant ($F_{1, 5}$ = 0.079, P = 0.79). This suggests that body size is likely to be the main factor determining the dominance hierarchy during the mixed-brood period.

Several high-ranked workers performed most of the dominance behaviours observed in each colony, with low-ranked workers hardly displaying these behaviours during both the first- and mixed-brood periods (Fig. 4); consequently, higher-ranked workers displayed dominance behaviour at significantly higher frequencies (first-brood period: $F_{1, 10}$ = 25.4, P = 0.001 for rank; $F_{3, 10}$ = 2.47, P = 0.12 for colony; $F_{3, 7}$ = 3.77, P = 0.067 for the interaction; mixed-brood period: $F_{1, 16}$ = 51.2, P < 0.001 for rank; $F_{2, 16}$ = 0.237, P = 0.79 for colony; $F_{2, 14}$ = 0.592, P = 0.57 for the interaction; Fig. 4). In particular, the worker displaying the highest frequency of dominance behaviour became the top-ranked worker except in colony B, in which the top-ranked worker displayed dominance behaviour at nearly the highest frequency (Table 2). Spearman rank correlations between rank in the dominance hierarchy and the frequency of dominance behaviour were negative for all colonies for the two periods, and they were significant in most cases (Table 3). This was also the case when the Spearman rank correlation analysis was performed separately for the first and second broods during the mixed-brood period. This suggests that the frequency of dominance behaviour is a good indicator of the rank in the dominance hierarchy.

Displays of dominance behaviour toward other workers

During both the first- and mixed-brood periods, workers displayed most of the dominance behaviours toward particular workers (Table 2, Fig. 5). However, in the mixed-brood period (but not the first-brood period), a worker displayed dominance behaviours primarily toward the worker ranked immediately below it in the dominance hierarchy. Similar results were obtained when the frequency divided by the observation time in hours was used for the hourly frequency of dominance behaviour (data not presented).

Fig. 5

Discussion

The rank in the dominance hierarchy was more likely to be higher for older and younger workers during the first- and mixed-brood periods, respectively – this is the first report of the hierarchy changing from older dominance to younger dominance with colony development among primitively eusocial wasps. Although the sample was small, the tendency was found in all colonies studied and was statistically significant, suggesting that it is a common characteristic of *P. japonicus*. Moreover, a younger-dominance hierarchy was found during the mixed-brood period in the other three colonies; one was reared in the same cage before the present study and the other two were observed in the field, although the observation time was too short to allow the rank to be determined accurately (Y. Ishikawa, unpublished). *Polistes* wasps are distributed mainly in temperate areas, which indicates that the younger-dominance hierarchy does not derive from the ancestor. The following two points should be noted: (1) the oldest and youngest workers often failed to become the top-ranked worker during the first- and mixed-brood periods, respectively, which may often be the case in *Polistes* species (Strassmann and Meyer, 1983; Suzuki, 2003); and (2) body size rather than emergence order may determine the dominance hierarchy during the mixed-brood period, because larger workers tended to be ranked higher in the second brood while emergence order was not related to the rank in the dominance hierarchy for the second brood. However, worker size has been considered to be either a minor factor in determining the rank in the dominance hierarchy in many paper wasps (Klahn, 1981; Strassmann and Meyer, 1983; Hughes and Strassmann, 1988) or not related to it at all (Reeve, 1991). The sample in the present study was too small to draw a definitive conclusion, and hence further studies are required to confirm the influence of body size on the dominance hierarchy.

Neither the model of Tsuji and Tsuji (2005) nor the idea proposed by Tsuchida and

Suzuki (2006) as described in the Introduction explains why the hierarchy changes from older dominance to younger dominance in *P. japonicus*. Focusing on the future fitness prospects of workers, we propose the hypothesis that the temporal changes in mechanisms determining the dominance hierarchy in *P. japonicus* are caused by a high probability of a worker producing its own offspring by inheriting the colony due to a rapid reduction in the vigour of the foundress (Y. Ishikawa, unpublished) and there being only a small number of workers present (Bourke, 1999; Shreeves and Field, 2002). Actually, the foundress disappeared in two of the four *P. japonicus* colonies before the end of colony development, and the top-ranked worker inherited the colony and laid eggs. It appears that foundresses are more likely to lose their vigour in the field due to them performing physically and physiologically demanding foraging in the solo-founding period. Under such conditions in a species that forms colonies with a small number of workers, workers are considered to obtain better fitness returns by refraining from foraging for food in order to maintain their physical and physiological vigour and by increasing their ranks in the dominance hierarchy so as to increase the likelihood of replacing the foundress rather than becoming subordinates and foraging for food (Field and Cant, 2006; Field et al., 2006). Consequently, workers are expected to be more concerned about their rank in the dominance hierarchy during the mixed-brood period than during the first-brood period, which may have been reflected by dominance behaviour being displayed toward the worker ranked immediately below in the dominance hierarchy during the mixed-brood period, as seen in many social wasps (Downing and Jeanne, 1985; Miyano, 1986; Reeve and Gamboa, 1987; Hughes and Strassmann, 1988; Cant et al., 2006). Younger workers appear to be more likely to move up the dominance hierarchy because older workers are smaller and more physiologically and physically damaged due to them having worked hard for a longer time. Furthermore, an older worker appears to be uninterested in contests for a high rank in the dominance hierarchy because it will survive for a shorter time and lay fewer eggs than younger workers even if it replaces the foundress. Here it should be noted that younger workers should forage during the mixed-brood period in order to boost the overall production of reproductive adults for a colony, particularly because the larger size of younger workers makes them better foragers. However, for each younger worker the option of waiting for a chance to become the superseder is more profitable than the option of cooperatively rearing the offspring of the foundress.

Meanwhile, older workers were likely to be ranked higher during the first-brood period, which is explained as follows: The probability of a worker inheriting the colony is considered to be much lower during the first-brood period than during the mixed-brood period, due to the foundress maintaining a high vigour. Under these conditions, all workers are considered to adopt the option of boosting the total number of reproductive progeny per colony through cooperative rearing. Actually, intranidal and extranidal tasks were performed as often by high-ranked workers as by other workers during the first-brood period (Y. Ishikawa, unpublished). A hierarchy with older dominance during the first-brood period may be established based on only small differences in the amount of experience (Reeve, 1991), or emergence order is used only as a cue to avoid potentially costly dominance contests (Maynard Smith, 1982; Hughes and Strassmann, 1988; Reeve, 1991).

A worker displayed dominance behaviours primarily toward the worker ranked immediately below it in the dominance hierarchy during the mixed-brood period but not during the first-brood period. This suggests that the function of the dominance hierarchy differs between the first- and mixed-brood periods. In the mixed-brood period, its function is considered to be determining which workers have a chance to produce their own offspring (Cant et al., 2006). Meanwhile, the dominance hierarchy may promote efficient foraging during the first-brood period, as seen in *Ropalidia marginata* (Bruyndonckx et al., 2006).

The above hypothesis of temporal changes in dominance-determining mechanisms could be verified by detailed observations of behaviour of the foundress and workers and by investigating the physiological changes of the foundress in large samples of colonies. It would be helpful to examine whether the dominance hierarchy during the first-brood period changes after the vigour of the foundress is reduced experimentally (see Reeve and Gamboa, 1983, 1987) or which worker is the superseder after the foundress is artificially removed. Experiments for the mixed-brood period should be planned to examine whether there is a positive relationship between body size and rank in the dominance hierarchy for the second brood using a substantial number of colonies (to facilitate statistical analyses), and which type of dominance hierarchy is established among workers after removing the first or second brood. Furthermore, the probability of the foundress disappearing should be determined under true field conditions.

The optimal option for workers is likely to change with colony development in other paper wasp species, and also in other social wasps and bees, particularly in species with a small number of workers because the vigour of the foundress is expected to reduce during colony development and a worker is highly likely to become the superseder. Comparing the type of dominance hierarchy between early and late in colony development is considered to be highly effective for obtaining a comprehensive understanding of the social structure of social wasps and bees.

Acknowledgements

We thank two anonymous referees for helpful comments on the manuscript.

References

Arévalo E., Zhu Y., Carpenter J.M. and Strassmann J.E. 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. *BMC Evol. Biol.* **4**: 8

Bourk A.F.G. 1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* **12**: 245-257

Bridge C. and Field J. 2007. Queuing for dominance: gerontocracy and queue-jumping in the hover wasp *Liostenogaster flavolineata*. *Behav. Ecol. Sociobiol.* **61**: 1253-1259

Bruyndonckx N., Kardile S.P. and Gadagkar R. 2006. Dominance behaviour and regulation of foraging in the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *Behavioural Processes* **72**: 100-103

Cant M.A. and Field J. 2001. Helping effort and future fitness in cooperative animal societies. *Proc. R. Soc. Lond. B* **268**: 1959-1964

Cant M.A. and Field J. 2005. Helping effort in a dominance hierarchy. *Behav. Ecol.* **16**: 708-715

Cant M.A., Llop J.B. and Field J. 2006. Individual variation in social aggression and the probability of inheritance: theory and a field test. Am. Nat. **167**: 837-852

Dew H.E. and Michener C.D. 1981. Division of labor among workers of *Polistes metricus* (Hymenoptera: Vespidae): Laboratory foraging activities. *Insect. Soc.* **28**: 87-101

Downing H.A. and Jeanne R.L. 1985. Communication of status in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Z. Tierpsychol.* **67**: 78-96

Field J., Cronin A. and Bridge C. 2006. Future fitness and helping in social queues. *Nature* **441**: 214-217

Field J. and Cant M. 2006. Helping effort in primitively eusocial wasps. *Ann. Zool. Fennici* **43**: 481-487

Finkel T. and Holbrook N.J. 2000. Oxidants, oxidative stress and the biology of ageing. *Nature* **408**: 239-247

Gadagkar R. 1980. Dominance hierarchy and division of labour in the social wasp *Ropalidia marginata* (Lep.)(Hymenoptera: Vespidae). *Curr. Sci.* **49**: 772-775

Gadagkar R. and Joshi N.V. 1982. Behaviour of the Indian social wasp *Ropalidia cyathiformis* on a nest of separate combs (Hymenoptera: Vespidae). *J. Zool. London* **198**: 27-37

Gadakar R. 1987. Social structure and the determinants of queen status in the primitively eusocial wasp *Ropalidia cyathiformis*. In: *Chemistry and biology of social insects* (Eder J. and Rembold H., Eds), Verlag J. Peperny, München. pp 377-378

Gamboa G.J., Wacker T.L., Scope J.A., Cornell T.J. and Shellman-Reeve J. 1990. The mechanism of queen reguration of foraging by workers in paper wasps (*Polistes fuscatus*, Hymenoptera: Vespidae). *Ethology* **85**: 335-343

Heinsohn R. and Legge S. 1999. The cost of helping. *Trends Ecol. Evol.* **14**: 53-57

Higashi S., Ito F., Sugiura N. and Ohkawara K. 1994. Worker's age regulates the linear dominance hierarchy in the queenless ponerine ant, *Pachycondyla sublaevis* (Hymenoptera: Formicidae). *Anim. Behav.* **47**: 179-184

van Honk C.G.J., Röseler P.-F., Velthuis H.H.W. and Hoogeveen J.C. 1981. Factors influencing the egg laying of workers in a captive *Bombus terrestris* colony. *Behav. Ecol. Sociobiol.* **9**: 9-14

Hughes C.R. and Strassmann J.E. 1988. Age is more important than size in determining dominance among workers in the primitively eusocial wasp, *Polistes instabilis*. *Behaviour* **107**: 1-15

Iwahashi O. 1989. Society of *Ropalidia fasciata*. In: *Society of Ropalidia wasp* (Iwahashi O. and Yamane S., Eds), Tôkai University Press, Tokyo. pp 3-209 (in Japanese)

Jeanne R.L. 1972. Social biology of the neopropical wasp *Mischocyttarus drewseni*. *Bull. Mus. Comp. Zool.* **144**: 63-150

Klahn J.E. 1981. Alternative reproductive tactics of single foundresses of a social wasp, *Polistes fuscatus*. PhD thesis, University of Iowa

Litte M. 1977. Behavioral ecology of the social wasp, *Mischocyttarus mexicanus*. *Behav. Ecol. Sociobiol.* **2**: 229-246

Litte M. 1979. *Mischocyttarus flavitarsis* in Arizona: social and nesting biology of a polistine wasp. *Z. Tierpsychol.* **50**: 282-312

Matsuura M. 1995. General remarks on the Japanese social wasps: Polistinae. In: *Social* *wasps of Japan in color.* Hokkaido University Press, Sapporo. pp 309-322 (in Japanese)

Maynard Smith J. 1982. *Evolution and the theory of games.* Cambridge University Press, Cambridge. 224 pp

Michener C.D. 1974. *The social behavior of the bees.* Harvard University Press, Canbridge. 404 pp

Miyano S. 1986. Colony development, worker behavior and male production in orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). *Res. Popul. Ecol.* **28**: 347-361

Molina Y. and O'Donnell S. 2009. Worker reproductive competition affects division of labor in a primitively social paperwasp (*Polistes instabilis*). *Insect. Soc.* **56**: 14-20

Monnin T. and Peeters C. 1999. Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant. *Behav. Ecol.* **10**: 323-332

Nilsson J.-Å. 2002. Metabolic consequences of hard work. *Proc. R. Soc. Lond. B.* **269**: 1735-1739

O'Donnell S. 1998. Dominance and polyethism in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **43**: 327-331

O'Donnell S. 2001. Worker age, ovary development, and temporal polyethism in the swarm-founding wasp *Polybia occidentalis* (Hymenoptera: Vespidae). *J. Insect Behav.*

14: 201-213

Ono M. 1989. Multiple-comb nest founation by a single inseminated worker of the temperate paper wasp, *Polistes snelleni* Saussure (Hymenoptera, Vespidae). *J. Ethol.* **7**: 57-58

Page R.E., Post D.C. and Metcalf R.A. 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. *Am. Nat.* **134**: 731-748

Pardi L. 1948. Dominance order in *Polistes* wasp. *Physiol. Zool.* **21**: 1-13

Reeve H.K. 1991. *Polistes*. In: *The social biology of wasps* (Ross K.G. and Matthews R.W., Eds), Comstock Publishing Associates, A division of Cornell University Press, London. pp 99-148

Reeve H.K. and Gamboa G.J. 1983. Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **13**: 63-74

Reeve H.K. and Gamboa G.J. 1987. Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behaviour* **102**: 147-167

Shreeves G. and Field J. 2002. Group size and direct fitness in social queues. *Am. Nat.* **159**: 81-95.

Spradbery J.P. 1991. Evolution of queen number and queen control. In: *The social biology* *of wasps* (Ross K.G. and Matthews R.W., Eds), Comstock Publishing Associates, A division of Cornell University Press, London. pp 336-388

Strassmann J.E. 1981. Evolutionary implications of early male and satellite nest production in *Polistes exclamans* colony cycles. *Behav. Ecol. Sociobiol.* **8**: 55-64

Strassmann J.E. and Meyer D.C. 1983. Gerontocracy in the social wasp, *Polistes exclamans*. *Anim. Behav.* **31**: 431-438

Suzuki T. 1985. Mating and laying of female-producing eggs by orphaned workers of a paper wasp, *Polistes snelleni* (Hymenoptera, Vespidae). *Ann. Entomol. Soc. Am.* **78**: 736-739

Suzuki T. 1997. Worker mating in queen-right colonies of a temperate paper wasp. *Naturwissenchcaften* **84**: 304-305

Suzuki T. 2003. Queen replacement without gerontocracy in the paper wasp *Parapolybia indica* in temperate Japan. *Ethol. Ecol. Evol.* **15**: 191-196

Tsuchida K. and Suzuki T. 2006. Conflict over sex ratio and male production in paper wasps. *Ann. Zool. Fennici* **43**: 468-480

Tsuji K. and Tsuji N. 2005. Why is dominance hierarchy age-related in social insects? The relative longevity hypotesis. *Behav. Ecol. Sociobiol.* **58**: 517-526

West-Eberhard M.J. 1969. The social biology of Polistine wasp. *Misc. Publ. Mus. Zool. Univ. Mich.* **140**: 1-140

West-Eberhard M.J. 1978. Temporary queens in *Metapolybia* wasps: non-reproductive helpers without altruism? *Science* **200**: 441-443

West-Eberhard M.J. 1981. Intragroup selection and the evolution of insect societies. In: *Natural selection and social behavior: research and new theory.* Chirion Press, New York. pp 3-17

Williams J.B, Roberts S.P. and Elekonich M.M. 2008. Age and natural metabolically-intensive behavior affect oxidative stress and antioxidant mechanisms. *Exp. Gerontol.* **43**: 538-549.

Wilson E.O. 1974. Group effects and the control of nestmates. In: *Insect societies.* Harvard Uiversity Press, Cambridge. pp 296-305

Yamane So. 1986. The colony life cycle of the Sumatran paper wasp *Ropalidia* (*Icariola*) *variegata jacobsoni* (Buysson). With reference to the possible occurrence of serial polygyny (Hymenoptera: Vespidae). *Monit. Zool. Ital.* **20**: 135-161

Yoshikawa K. 1956. Compound nest experiments in *Polistes fadwigae* dalla Torre. Ecological studies of *Polistes* wasp IV. *J. Insect Polytech. Osaka City Univ.* **7**: 229-243

Yoshikawa K. 1963. Introductory studies on the life economy of polistene wasp II. Super individual stage 2. Division of labor among workers. *Jpn. J. Ecol.* **13**: 53-57

Figure captions

Fig. 1 Relationship between body size and emergence order (0, first; 1, last) among *P. japonicus* workers. Open and solid data points are for the first and second broods, respectively.

Fig. 2 Relationship between rank (0, top; 1, bottom) in the dominance hierarchy and emergence order among workers during the first-brood (a) and mixed-brood (b) periods.

Fig. 3 Relationship between rank in the dominance hierarchy and order of body size (0, largest; 1, smallest) during the first-brood (a) and mixed-brood (b) periods.

Fig. 4 Relationship between hourly frequency of dominance behaviour (frequency divided by hours spent on the nest by each individual) and rank in the dominance hierarchy during the first-brood (a) and mixed-brood (b) periods.

Fig. 5 Frequencies with which top-ranked and second-ranked workers displayed dominance behaviour toward other workers during the first-brood (a) and mixed-brood (b) periods.

Table 1. Emergence days of individual workers (expressed in days after the first emergence of workers)

Colony	Emergence order of individual workers							
	1	2	3	4	5	6	7	8
A	0(F) [a]	2(F)	3(F)	-	10(S)	11(S)	14(S)	22(S)
B	0(F)	1(F)	2(F)	3(F)	-	-	-	-
C	0(F)	2(F)	5(F)	7(F)	10(S)	14(S)	15(S)	-
D	0(F)	4(F)	6(F)	8(F)	14(S)	18(S)	-	-

[a] Letters within parentheses indicate the brood type: F, first; S, second.

Table 2. Results of dominance contests for all pairs of workers in colonies

Colony	Worker ID	Worker ID[a]								Score[b]	Rank	Comparison with binominal distribution (*P*)[c]
		F1	F2	F3	F4	S5	S6	S7	S8			
First-brood period												
A	F1	-	13-25[d]	15-5	-	-	-	-	-	1-1	2	0.851
	F2	25-13	-	110-0	-	-	-	-	-	2-0	1	<0.001
	F3	5-15	0-110	-	-	-	-	-	-	0-2	3	0.063
B	F1	-	1-0	10-0	6-0	-	-	-	-	3-0	1	0.055
	F2	0-1	-	1-0	6-0	-	-	-	-	2-1	2	0.014
	F3	0-10	0-1	-	19-0	-	-	-	-	1-2	3	<0.001
	F4	0-6	0-6	0-19	-	-	-	-	-	0-3	4	-
C	F1	-	5-0	0-6	10-0	-	-	-	-	2-1	2	0.017
	F2	0-5	-	0-15	5-0	-	-	-	-	1-2	3	0.008
	F3	6-0	15-0	-	7-0	-	-	-	-	3-0	1	0.043
	F4	0-10	0-4	0-7	-	-	-	-	-	0-3	4	-
D	F1	-	9-0	6-0	2-1	-	-	-	-	3-0	1	0.151
	F2	0-9	-	1-0	0-3	-	-	-	-	1-2	3	0.667
	F3	0-6	0-1	-	0-4	-	-	-	-	0-3	4	-
	F4	1-2	3-0	4-0	-	-	-	-	-	2-1	2	0.517
Mixed-brood period												
A	F1	-	1-0	0-0	-	0-82	0-4	0-1	0-0	1-3	5	0.333
	F2	0-1	-	0-0	-	1-81	0-4	0-0	0-0	0-3	6	0.333
	F3	0-0	0-0	-	-	0-79	0-5	0-3	0-1	0-4	7	-
	S5[e]	82-0	81-1	79-0	-	-	179-0	68-0	16-0	6-0	1	<0.001
	S6	4-0	4-0	5-0	-	0-179	-	17-0	14-0	5-1	2	0.001
	S7	1-0	0-0	3-0	-	0-68	0-17	-	0-0	2-2	3	0.032
	S8	0-0	0-0	1-0	-	0-16	0-14	0-0	-	1-2	4	0.333
C	F1	-	1-0	0-0	3-0	1-1	0-3	0-3	-	2-2	4	0.071
	F2	0-1	-	1-8	2-0	0-2	0-3	0-2	-	1-5	6	0.148
	F3	0-0	8-1	-	10-0	70-0	1-27	1-11	-	3-2	3	<0.001
	F4	0-3	0-2	0-10	-	0-4	0-0	0-0	-	0-4	7	-
	S5	1-1	2-0	0-70	4-0	-	0-13	1-7	-	2-3	5	0.061
	S6	3-0	3-0	27-1	0-0	13-0	-	28-2	-	5-0	1	<0.001
	S7	3-0	2-0	11-1	0-0	7-1	2-28	-	-	4-1	2	0.002
D	F1	-	12-0	5-0	1-6	1-2	0-15	-	-	2-3	4	<0.001
	F2	0-12	-	0-1	0-4	0-6	0-9	-	-	0-5	6	-
	F3	0-5	1-0	-	0-7	0-0	0-13	-	-	1-3	5	0.400
	F4	6-1	4-0	7-0	-	0-28	0-21	-	-	3-2	3	0.075
	S5	2-1	6-0	0-0	28-0	-	2-70	-	-	3-1	2	<0.001
	S6[e]	15-0	9-0	13-0	21-0	70-2	-	-	-	5-0	1	<0.001

[a] Letter indicates the brood type (F, first; S, second), and the number indicates the emergence order.

[b]Score for the dominance contest, which indicates the numbers of subordinate (left) and

dominant (right) individuals for a target wasp. The dominance rank was determined based on the difference between the two numbers.

[c] Value of P indicates the probability that the observed highest frequency or a frequency higher than that is expected to occur if the target worker displays all dominance behaviours toward the other workers at random.

[d] Worker F1 displayed dominance behaviour toward worker F2 and received dominance behaviour from worker F2 with frequencies of 13 and 25, respectively.

[e] Superseder.

Table 3. Results of Spearman rank correlation analysis of the relationship between the rank in the dominance hierarchy and the frequency of dominance behaviour

Observation period	Brood	Colony	*R*	*P*
First brood	First	A	–1.000	<0.001
		B	–0.400	0.600
		C	–1.000	<0.001
		D	–1.000	<0.001
Mixed brood	First and second	A	–0.857	0.014
		C	–0.893	0.007
		D	–0.928	0.008
	First	A	-[a]	-
		C	–1.000	<0.001
		D	–0.738	0.262
	Second	A	–1.000	<0.001
		C	–1.000	<0.001
		D	–1.000	<0.001

[a] Analysis was impossible because two of the three workers were ranked the same.

85mm

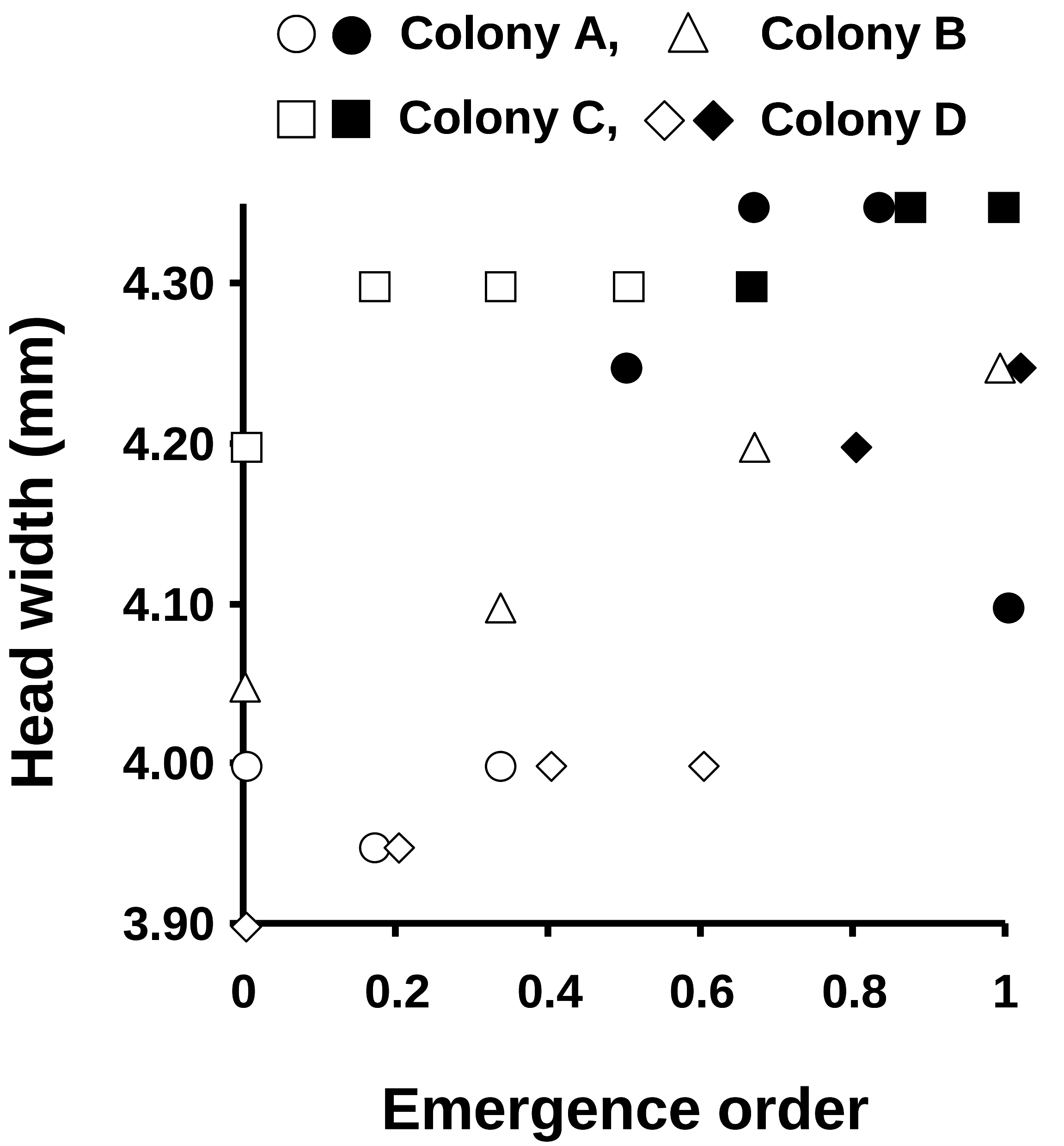
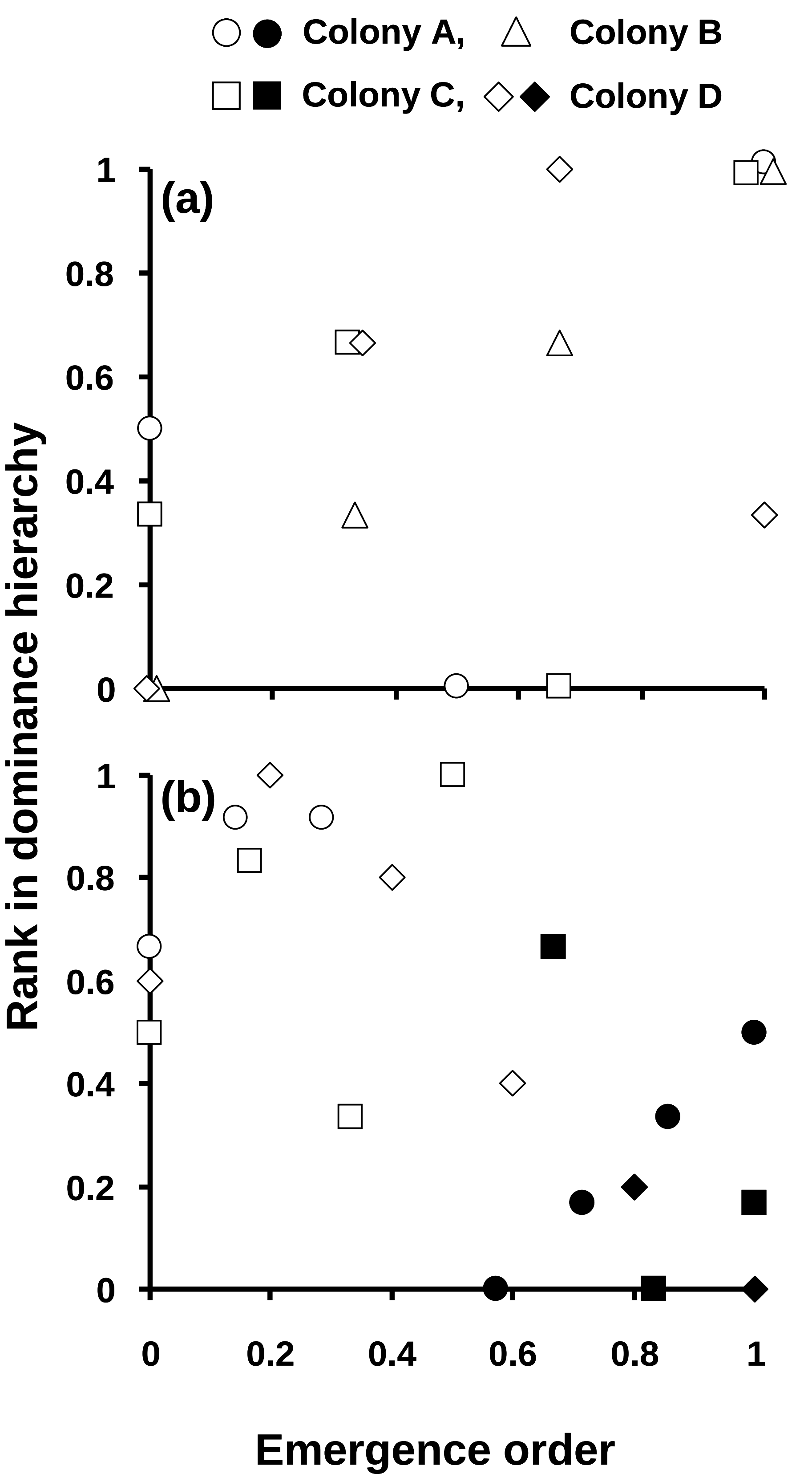
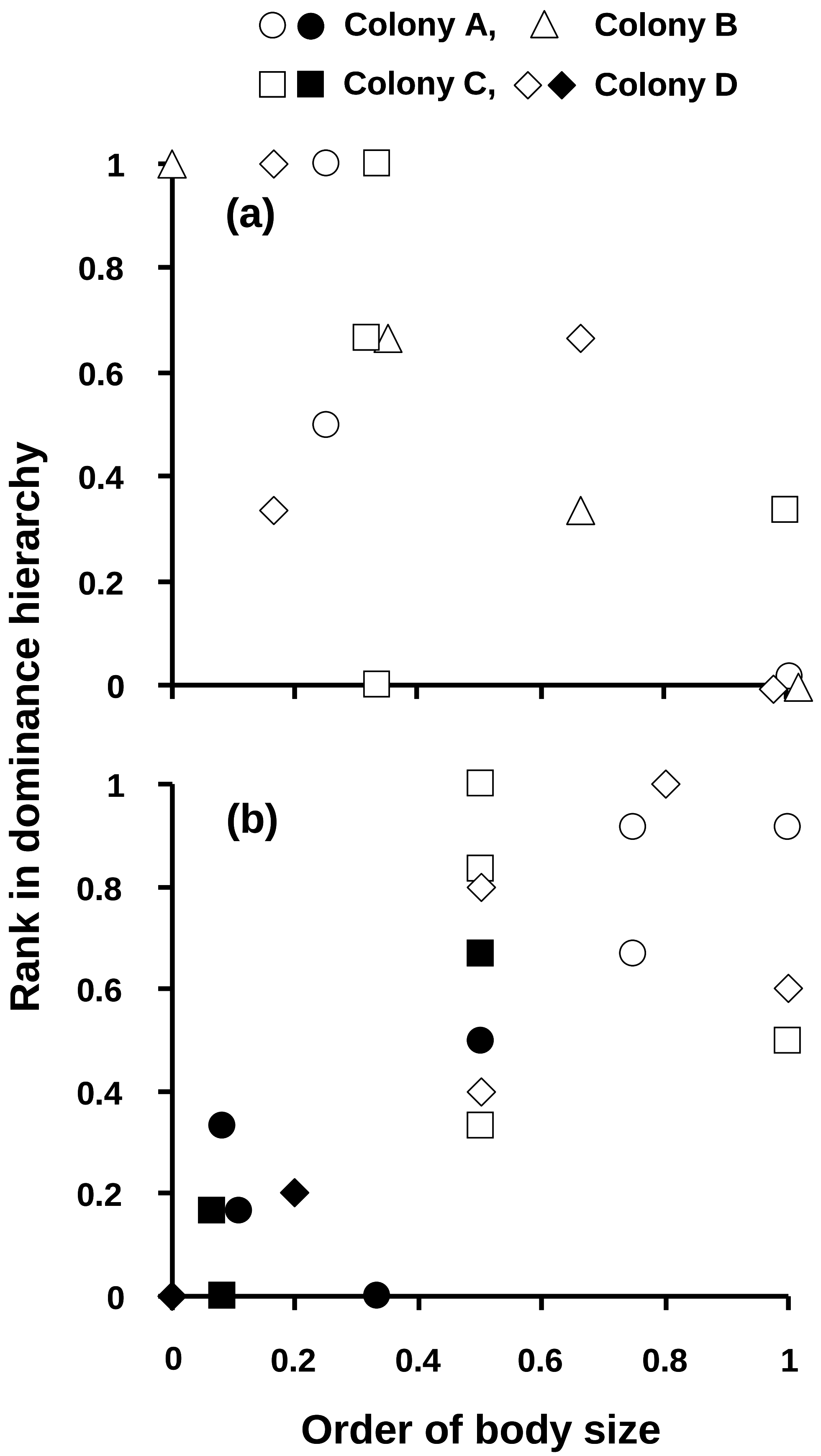

○ ● Colony A, △ Colony B
□ ■ Colony C, ◇ ◆ Colony D
Head width (mm)
4.30
4.20
4.10
4.00
3.90
0
0.2
0.4
0.6
0.8
1
Emergence order

Fig. 1


Colony A,
Colony B
Colony C,
Colony D
(a)
(b)
Rank in dominance hierarchy
0
0.2
0.4
0.6
0.8
1
Emergence order

85mm

Fig.2


Colony A,
Colony B
Colony C,
Colony D
(a)
(b)
Rank in dominance hierarchy
1
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
0.8
Order of body size

85mm

Fig. 3

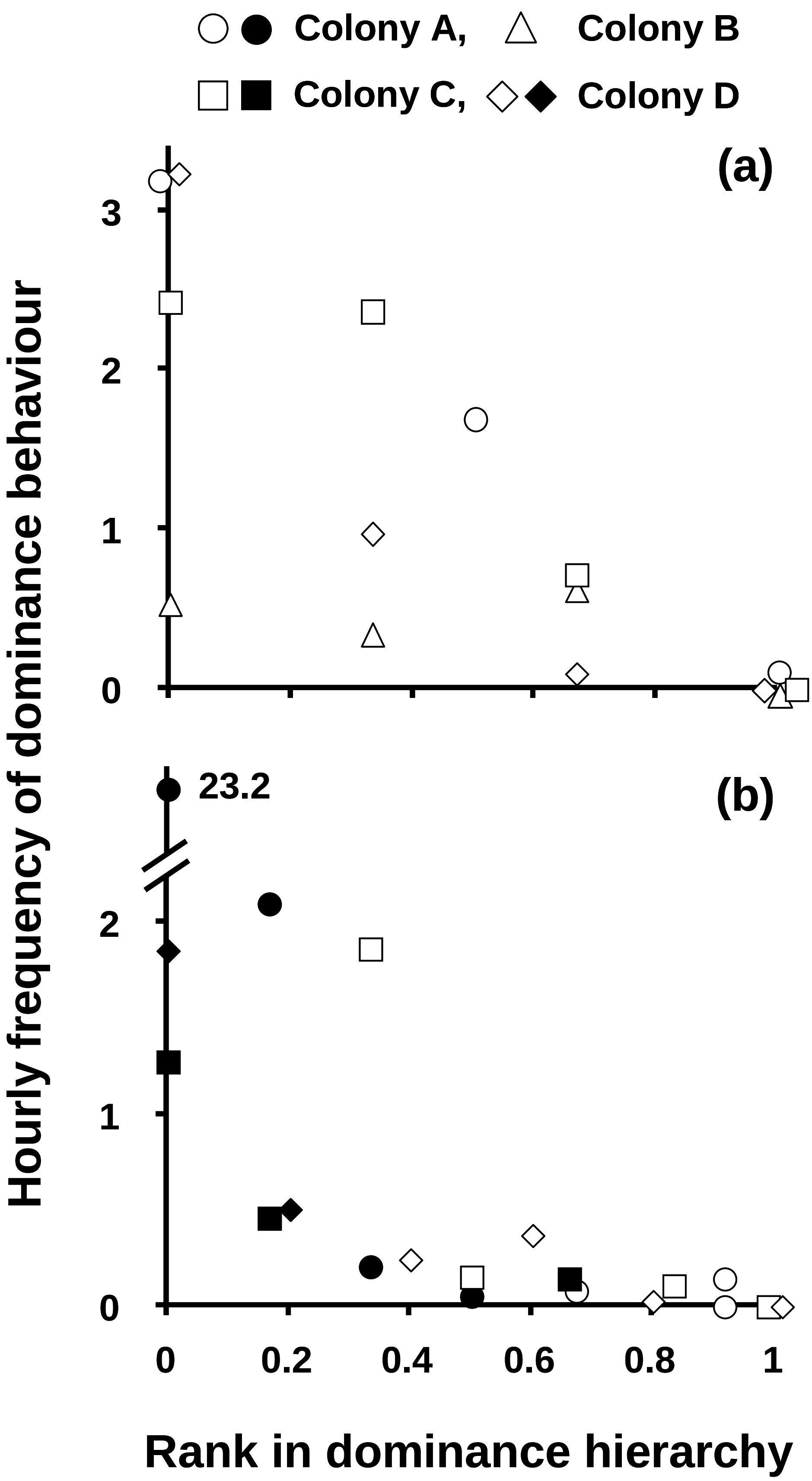

Colony A,
Colony B
Colony C,
Colony D
(a)
(b)
23.2
0
1
2
3
0.2
0.4
0.6
0.8
Hourly frequency of dominance behaviour
Rank in dominance hierarchy

Fig. 4

85mm

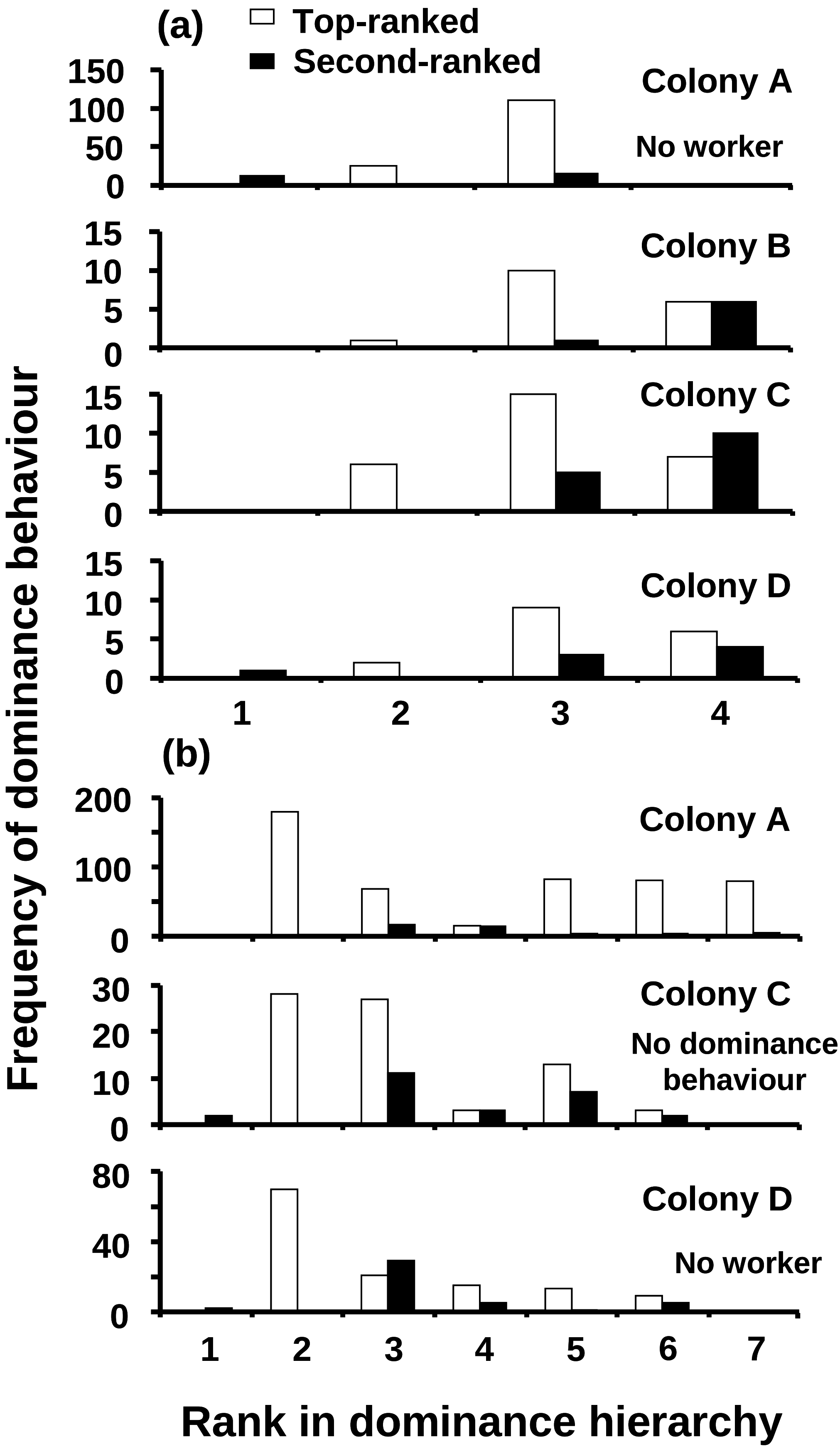

(a)
Top-ranked
Second-ranked
Colony A
No worker
150
100
50
0
Colony B
15
10
5
0
Colony C
15
10
5
0
Colony D
15
10
5
0
1
2
3
4
(b)
Colony A
200
100
0
Colony C
No dominance behaviour
30
20
10
0
Colony D
No worker
80
40
0
1
2
3
4
5
6
7
Frequency of dominance behaviour
Rank in dominance hierarchy

Fig. 5

85mm

624