Insectes Sociaux (2018) 65:473–481
https://doi.org/10.1007/s00040-018-0636-5

Insectes Sociaux

RESEARCH ARTICLE

The first brood emerges smaller, lighter, and with lower lipid stores in the paper wasp *Polistes jokahamae* (Hymenoptera: Vespidae)

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Received: 10 January 2018 / Revised: 27 May 2018 / Accepted: 5 June 2018 / Published online: 11 June 2018

Abstract

Workers and gynes (potential queens for the next spring) of temperate paper wasps are distinguishable based on their lipid stores a few weeks after emergence. However, it was not known whether the lipid stores of worker- and gyne-destined females differ at emergence. Newly emerged females of *Polistes jokahamae* were divided into three categories: the first brood, comprising worker-destined individuals that are nursed only by the queen; the second brood, comprising worker- and gyne-destined individuals that are nursed by the queen and workers and emerge before male emergence; and the third brood, comprising gyne-destined individuals that emerge after the emergence of the first males. The first brood produced smaller and lighter adults with lower lipid stores. These lipid stores were lower even after adjusting for head width, which suggests the presence of a preimaginal bias toward worker caste; such a bias was not detected in the second brood. After adjusting for head width, lipid stores increased with the wet mass in the second and third broods but not in the first brood, suggesting that the component proportion of lipid stores increased but that of some other nutrients decreased with increasing wet mass in the first brood. In addition, the head width, wet mass, and lipid stores (including lipid stores divided by the head width cubed) in the first brood increased with the emergence order, whereas the fatness (wet mass divided by the head width cubed) did not.

Keywords Caste-fate determination · Diapause · Eusocial insect · Gyne · Worker

Introduction

The origin of nonreproductive individuals (workers) in eusocial animals has been one of the main points of focus in sociobiology (Wilson 1971, 1975; Hunt 2012). One fruitful approach to understanding the origin of workers is to elucidate the mechanisms underlying caste-fate determination in primitively eusocial insects (see Smith et al. 2008), for which there are no critical morphological differences between the queen and workers (Michener 1964; Wilson 1971; Jeanne 2003). Primitive eusociality appears to represent an early stage of eusociality (Hunt 2012). In particular, eusociality of temperate paper wasps, a major group of primitive eusocial insects, may represent a very early stage, because the cues used for caste-fate determination include an abiotic one (photoperiod) (Bohm 1972; Judd 2018; Yoshimura and Yamada 2018). It suggests that temperate paper wasps are good, model insects for exploring the origin of workers.

The caste fate in temperate paper wasps is considered to be finally determined during the adult stage with a caste-fate-related bias generated by the nourishment levels and/or vibrations produced by the queen during the immature stage (O'Donnell 1998; Jeanne and Suryanarayanan 2011; Berens et al. 2015; Judd et al. 2015; Jandt et al. 2017; Judd 2018; Yoshimura and Yamada 2018). The caste fate of the paper wasps is affected by several cues after their emergence, including colony conditions (e.g., the colony size and the presence of the queen), the physiological state (e.g., lipid stores), and abiotic factors (e.g., photoperiod) (Bohm 1972; Solís and Strassmann 1990; Reeve et al. 1998; Tibbetts 2007; Judd 2018; Yoshimura and Yamada 2018). In advanced eusocial hymenopterans including honeybees and ants, for which there are clear morphological differences between the castes, the caste fate is typically determined by the qualitative and/or quantitative nourishment levels during the larval stage and/or pheromones (Wheeler 1986; Hartfelder and Emlen 2012), and the caste does not change after emergence. Moreover, genetic factors influence caste

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differentiation in some ants and bees (Smith et al. 2008; Hartfelder and Emlen 2012).

In temperate paper wasps, the first-brood females are nursed during their immature stage by the queen only, and emerging adults are usually smaller than the other broods and considered to be worker-destined individuals (Reeve 1991; Tsuchida 1991; Toth et al. 2009; Hunt 2012). The females that emerge at the same time as or later than males, which are called the third brood henceforth, are considered gyne-destined individuals (Suzuki 1986; Toth et al. 2009). The second brood is nursed by workers and the queen. Whether the second-brood females are destined to become workers or gynes is unclear in many species, with Suzuki (1986) suggesting that it varies between species. It was found that some of the second-brood adults of the temperate paper wasp *Polistes jokahamae* (nee *P. jadwigae*) Radoszkowski (Hymenoptera: Vespidae) (as used in the present study) are involved in foraging (Yoshimura and Yabuta unpubl.), whereas others stay on the nest with the third-brood adults until late autumn; two females originating in the second brood initiated the founding of a nest the following spring. The second-brood individuals may therefore change their castes after emergence depending on cues such as colony condition.

The caste-fate-related bias generated during the immature stage in temperate paper wasps includes differences in adult size and nutritional status (Judd et al. 2010). Lipid stores appear to be particularly important due to gynes requiring ample lipid stores for overwintering and gyne-destined adults being likely to have higher lipid stores than worker-destined ones, in accordance with the diapause ground-plan hypothesis (Hunt 2006, 2007). This makes it fruitful to analyze differences in lipid stores as well as adult size among broods in order to obtain a deeper understanding of the mechanisms underlying caste-fate determination. It is particularly interesting to explore whether the lipid stores that the first brood reserves at emergence are lower than the lipid stores predicted based on the reduced body size. We are not aware of any such studies, with the exception of Judd et al. (2010) reporting the lipid stores (weight/wet mass) of gynes (not workers) at emergence and revealing that lipid stores were higher for gynes than for workers during the immature stage. In the present study, we compared lipid stores and wet mass (fresh body weight) while controlling for the body length (head width) using two new indexes: IRL (index of relative lipid stores) and IF (index of fatness), which quantify the relative lipid stores and wet mass normalized to the standard body volume as calculated from the head width, respectively.

In this study, we first compared the head width, wet mass, lipid stores, IRL, and IF of newly emerged wasps among the different broods of *P. jokahamae*. The first brood may not only be smaller but also have lower IRL and IF values. The second-brood adults may differ from the third-brood adults in one or more of the parameters related to body size and lipid stores. Second, we verified whether IRL is related to IF, including whether the relationships differ among the broods. An increase in IF is expected to induce one in IRL, but this is not guaranteed. If the relationship differs between the broods, the difference can be used for characterizing each brood. Third, we determined the relationships of lipid stores, IF, and IRL with the head width, including whether these relationships differ among the broods. Finally, we determined whether the above-five parameters increase with the emergence order in the first brood. The body length and wet mass reportedly increase with the emergence order among early-emerging workers in many paper wasps (Reeve 1991; Keeping 2002). We aimed to verify such a trend in *P. jokahamae* and elucidate whether the trend is also the same for IF, IRL, and lipid stores.

Materials and methods

Wasps

In total, 42 colonies were collected from Tsu and Suzuka, Mie and Fuso, Aichi, Japan in 2014 and 2016 from three sites that were within a 40-km-radius circle (Table 1). After removing the adults, the collected nests were individually

Table 1 Information about the samples

Nest[a]	Collection period and site			Sample size[b]
	Year	Date range	Site	
Pre-emergence	2014	May 31–June 3	Tsu and Suzuka, Mie; Fuso, Aichi	81 (11)
	2016	May 23–May 30	Tsu, Mie	64 (12)
Postemergence	2014	July 9–July 15	Tsu, Mie; Fuso, Aichi	72 (7)[c], 4 (2)[d]
	2016	July 2–July 24	Tsu, Mie	58 (8)[c], 14 (3)[d]
Postmale	2014	August 14	Tsu, Mie	21 (1)
	2016	August 10–August 18	Tsu, Mie	68 (3)

[a] Pre-emergence and postmale nests produced first- and third-brood adults, respectively. Many postemergence nests produced only second-brood adults, whereas some produced both second- and third-brood adults (the specific numbers are given in the column listing sample sizes)

[b] Numbers in parentheses are the numbers of nests

[c] Second-brood adults

[d] Third-brood adults

put in plastic cups (129 mm in diameter × 60 mm high) and kept in a room with the windows open and no light turned on at night. The nests were divided into the following three groups based on the degree of colony development or the collection dates: (1) pre-emergence nests, collected before the first workers emerged; (2) postemergence nests, collected between the emergence of the first workers and males, which produced mainly second-brood adults and also some third-brood adults; and (3) postmale nests, collected after the emergence of the first males, which produced third-brood adults. The postemergence nests were collected in July. These nests were considered to produce second-brood wasps that were nursed at least during the period from the third instar to the last instar by both the queen and workers, because the first brood usually begins to emerge in early June. Only individuals that were in cocoons when the nests were collected were analyzed. We identified the emergence order of each emerging adult by observing the collected nests every day.

Totals of 23 pre-emergence, 15 postemergence, and 4 postmale nests were collected in the 2 years, which produced 145, 148, and 89 adult females, respectively (see Table 1 for the numbers of the first-, second-, and third-brood adults). Lipid stores were measured only for individuals collected in 2014 since the adults emerging in 2016 were used in another experiment. We therefore measured lipid stores of 81, 72, and 25 females emerging from the first, second, and third broods, respectively (Table 1).

Measurements

The head width and wet mass of newly emerged adults were measured using calipers with a precision of 0.01 mm and using an electronic balance with a precision of 0.0001 g, respectively. All measurements were completed on the emergence day.

After measuring the head width and wet mass, the females that newly emerged in 2014 were kept in a freezer (– 20 °C) so that the lipid stores in the gaster could be analyzed. The lipid stores in the gaster were removed using diethyl ether extraction (see Tibbetts et al. 2011). Lipid stores were estimated by calculating the difference in dry weight between before and after extraction.

Indexes for fatness and relative lipid stores

The two indexes we introduced—one for fatness (IF) and the other for relative lipid stores (IRL)—were calculated as the wet mass and gross lipid stores divided by the cube of the head width, respectively. The standard body volume is assumed to be proportional to the head width cubed. Thus, IF and IRL are indexes that control for the effects of the head width; that is, they represent the relative wet mass and lipid stores normalized to the standard body volume as calculated from the head width, respectively. If IRL is related to IF, lipid stores are predicted by both the head width and IF. IF values are determined not only by whether the contents of the gaster are light or heavy but also by whether the gaster is shrunken or swollen. However, the latter characteristic is considered the main mechanism because the variation of the actual IF (see "Results") is too large to be explained by differences in weight/volume ratio among the main three nutrients (including in the provided water solution): lipids, carbohydrates, and proteins.

Data analysis

We compared the head width, wet mass, lipid stores, IF, and IRL among the first, second, and third broods using a mixed linear model with the brood and colony included as fixed and random factors, respectively. When a difference was detected between the broods, a Holm's sequential Bonferroni multiple-comparison test (Holm 1979, Rice 1989) was performed to identify pairs exhibiting statistically significant differences.

The relationship between IRL and IF was analyzed using a mixed linear model with the brood and IF included as fixed factors and the colony as a random factor. The relationships of lipid stores, IRL, and IF with the head width were also analyzed using a mixed linear model: the brood and the head width were included as fixed factors and the colony as a random factor. This analysis was performed using only the samples collected in 2014 to enable exact comparisons between these relationships. The cube of head width was used when analyzing the effects of the head width on lipid stores since this parameter was considered to be linearly related to the body volume rather than the body length. This was verified by calculating AIC (Akaike's Information Criterion) scores: 640.7 for the head width, 638.3 for the head width cubed.

The effects of the emergence order on the head width, wet mass, lipid stores, IF, and IRL were analyzed using a mixed linear model with the colony included as a random factor. Only the samples collected in 2014 were used for this analysis to enable exact comparisons between the relationships of the emergence order with the above-five parameters; note that lipid stores were not measured in 2016. When multiple wasps emerged on the same day in the same nest, the same number (the mean of their emergence orders) was assigned to them.

The statistical tests were implemented using the "lem4" and "lmerTest" packages in R (version 3.4.3; R Foundation 2017) for the mixed linear models and using the "multcomp" package for the multiple-comparison tests.

Results

Comparisons of head width, wet mass, lipid stores, IF, and IRL among different broods

The values of head width ($\chi_2^2=75.4$, $P<0.001$), wet mass ($\chi_2^2=75.7$, $P<0.001$), lipid stores ($\chi_2^2=41.6$, $P<0.001$), IF ($\chi_2^2=22.9$, $P<0.001$), and IRL ($\chi_2^2=36.5$, $P<0.001$) differed among the broods (Fig. 1), with all of them being significantly lower in the first brood than in the second and third broods (sequential Bonferroni multiple-comparison test, $P<0.01$). This indicates that the first brood produced lighter and smaller adults with lower lipid stores. There were no significant differences between the second and third broods.

Relationship between IRL and IF

An interaction between the brood and IF ($\chi_2^2=6.6$, $P=0.037$) was detected (Fig. 2), suggesting the effect of IF differed among the broods. Thus, separate analyses for the different broods were performed and significant differences between the broods were detected by comparing IRL-values at IF values of 2.7, 3.0, or 3.3. The relationship between IRL and IF was significant in the second brood ($\chi_1^2=9.1$, $P=0.003$) and third brood ($\chi_1^2=8.4$, $P=0.004$), but not in the first brood ($\chi_1^2=0.008$, $P=0.978$). This indicates that while controlling for the effects of the head width, high lipid stores were caused by heavy weights in the second and third broods, but not in the first brood. In addition, the analysis of a mixture of the second and third broods revealed no differences between the two broods. Whilst adjusting for IF, IRL was significantly higher in the second and third broods than in the first brood (sequential Bonferroni

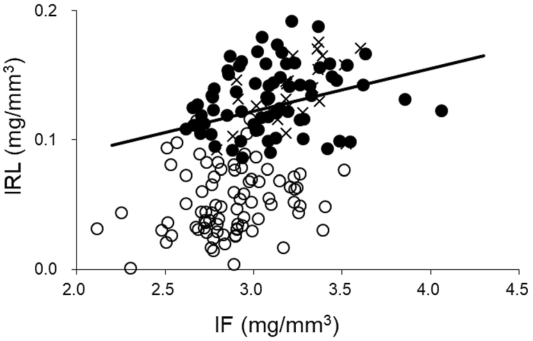

Fig. 2 Relationship between IRL and IF in different broods. A positive correlation was found in the second and third broods but not in the first brood. The line indicates the best-fit linear model for the second and third broods combined; no significant difference was detected between these two broods

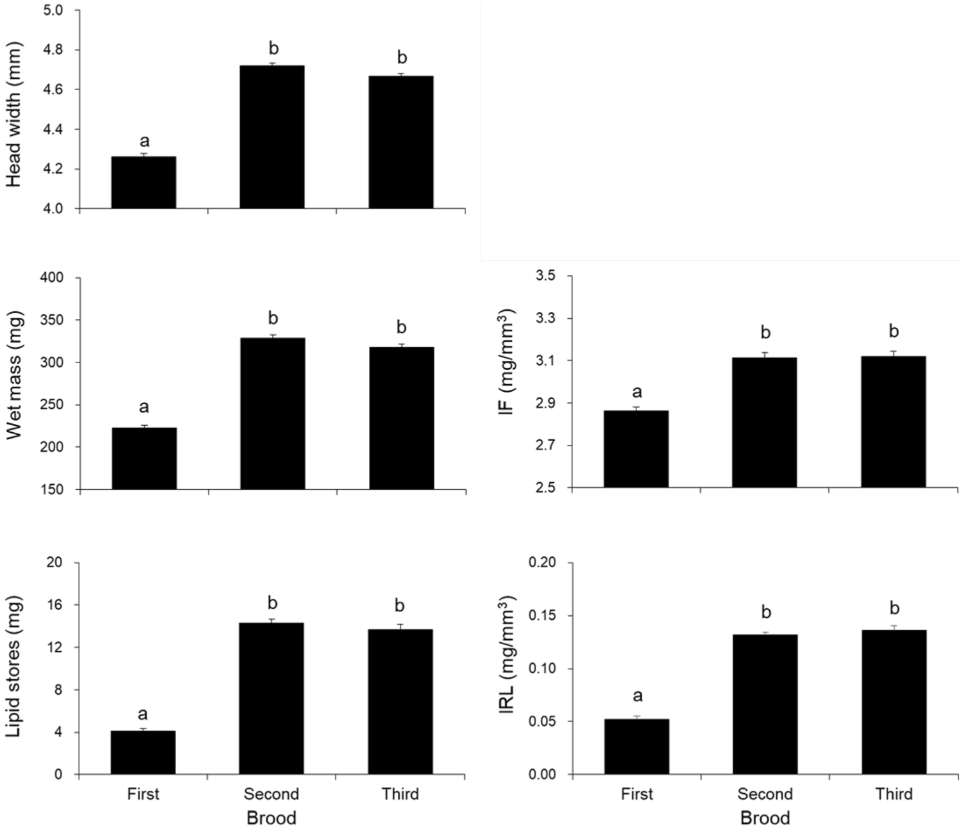

Fig. 1 Head width, wet mass, lipid stores, index of fatness (IF), and index of relative lipid stores (IRL) in the first, second, and third broods. Data are mean and SE values. Different letters above bars indicate significant differences in sequential Bonferroni multiple-comparison tests ($P<0.01$)

multiple-comparison test, $P < 0.001$), with no significant difference detected in IRL between the second and third broods. Thus, assuming that IF is determined by whether the abdomen is swollen or shrunken, lower lipid stores per unit body volume rather than lower IF were responsible for the lower IRL in the first-brood adults.

Relationships of lipid stores, IF, and IRL with head width

Lipid stores had a significant positive correlation with the head width, and the trend was the same in all broods, with no interaction between the head width and brood detected (Table 2; Fig. 3). However, the brood significantly influenced lipid stores; after adjusting for head width, the first-brood adults had lower lipid stores than the second- and third-brood ones (sequential Bonferroni multiple-comparison test, $P < 0.001$), with no difference between the second and third broods.

IF was not related to the head width in any broods (Table 2; Fig. 3). Meanwhile, IRL had a significant positive correlation with the head width, with no effects of interaction between the head width and brood (Table 2; Fig. 3). The brood significantly affected IRL; after adjusting for head width, the first-brood adults had lower IRL than the second- and third-brood ones (sequential Bonferroni multiple-comparison test $P < 0.001$), with no difference between the second and third broods.

Effects of emergence order on head width, wet mass, lipid stores, IF, and IRL in the first brood

The pre-emergence nests each produced 1–11 first-brood adults. The parameters except IF increased with increasing emergence orders till the fifth emergence order and reached plateaus after that, and the analysis were performed separately for the first five emerging adults (sample size 101) and the sixth to eleventh emerging adults (sample size 44). The latter group exhibited no significant relationship between the five parameters and emergence order. Regarding the former group, the head width ($t_{81.4} = 6.4$, $P < 0.001$), wet mass ($t_{84.6} = 4.3$, $P < 0.001$), lipid stores ($t_{40.8} = 3.1$, $P = 0.004$), and IRL ($t_{40.4} = 2.3$, $P = 0.026$) had significant positive correlations with the

Table 2 Statistical results for the effects of head width and brood on lipid stores, index of fatness (IF), and index of relative lipid stores (IRL)

Response variable	Factors	χ^2	*df*	P^a
Lipid stores	Head width cubed	74.9	1	< 0.001
	Brood	18.2	2	< 0.001
	Interaction	1.3	2	0.517
IF	Head width	0.01	1	0.904
	Brood	4.9	2	0.087
	Interaction	2.6	2	0.271
IRL	Head width	20.2	1	< 0.001
	Brood	2.9	2	< 0.001
	Interaction	2.9	2	0.230

[a] When the interaction was not significant, *P* values were calculated using a statistical model without the interaction

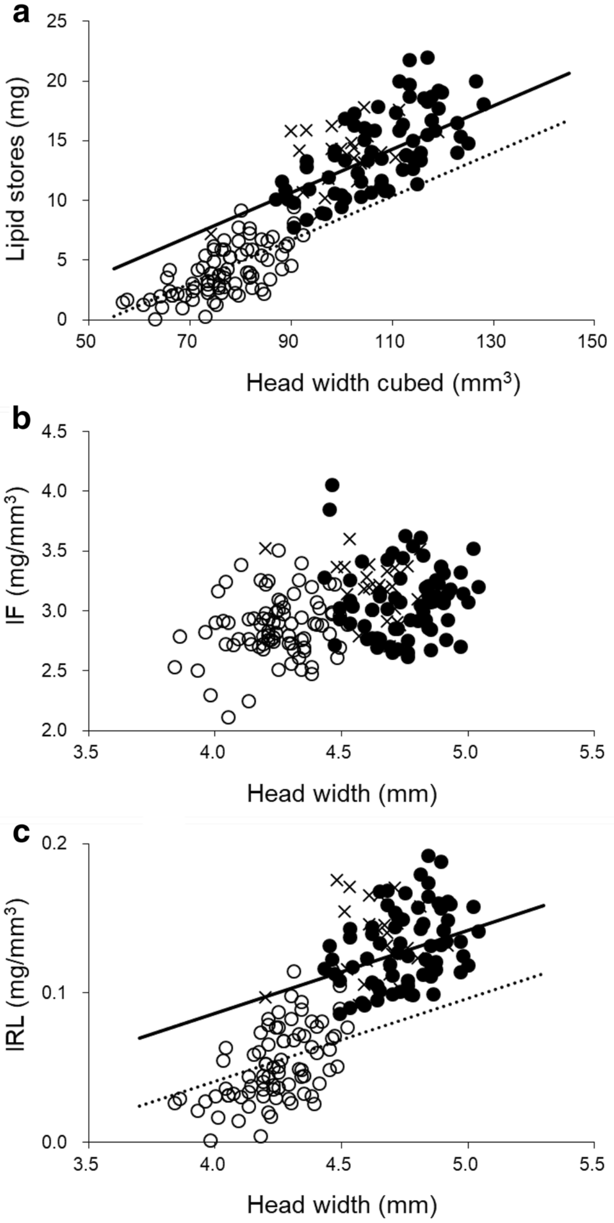

Fig. 3 Effect of head width on lipid stores (**a**), IF (**b**), and IRL (**c**). The broken and solid lines in panels a and c indicate the best-fit linear models for the first brood and for the second and third broods combined, respectively (see Table 2 for the statistical results). No significant difference was detected between the second and third broods. Regression lines are not drawn in panel **b** since head width had no significant effect

emergence order in the first brood (Fig. 4), whereas IF did not ($t_{86.2} = 1.0$, $P = 0.324$).

Discussion

The present results indicate that the first-brood adults emerged with a bias toward worker caste, which suggests that the first brood had a different plan for storing different nutrients as well as determining body size during the immature stage. The first brood produced smaller and lighter adults with lower lipid stores than the other broods. Even while controlling for the head width, the lipid stores of the first-brood adults were lower than those of the other broods. A particularly interesting finding was the positive correlation of IRL with the head width, with this relationship differing between the broods: IRL was lower in the first-brood adults than the other-brood adults after adjusting for head width. In addition, IRL was lower in the first brood than in the other broods after adjusting for IF, suggesting that lipid stores per unit body volume were lower in the first brood assuming IF to be determined by whether the abdomen is swollen or shrunken. Thus, there were brood-related differences in the values of IRL, in the relationships between IRL and IF, and in the relationship of IRL with the head width.

No difference in the body size, lipid stores, or related indexes was detected between the second and third broods, with no bias toward worker caste present in the second brood. These findings are in accordance with the observations that some second-brood adults became workers, whereas others became gynes. The second-brood adults appear to change their fates in response to the conditions of their nests and abiotic cues, as mentioned in "Introduction" (Solís and Strassmann 1990; Tibbetts 2007; Judd 2018; Yoshimura and Yamada 2018). However, second-brood adults with higher lipid stores at emergence might be more likely to be gynes, which indicates the need to survey the fate of individuals with different lipid stores at emergence. The lipid stores can be estimated accurately by simply measuring the head width and wet mass at emergence (see the last

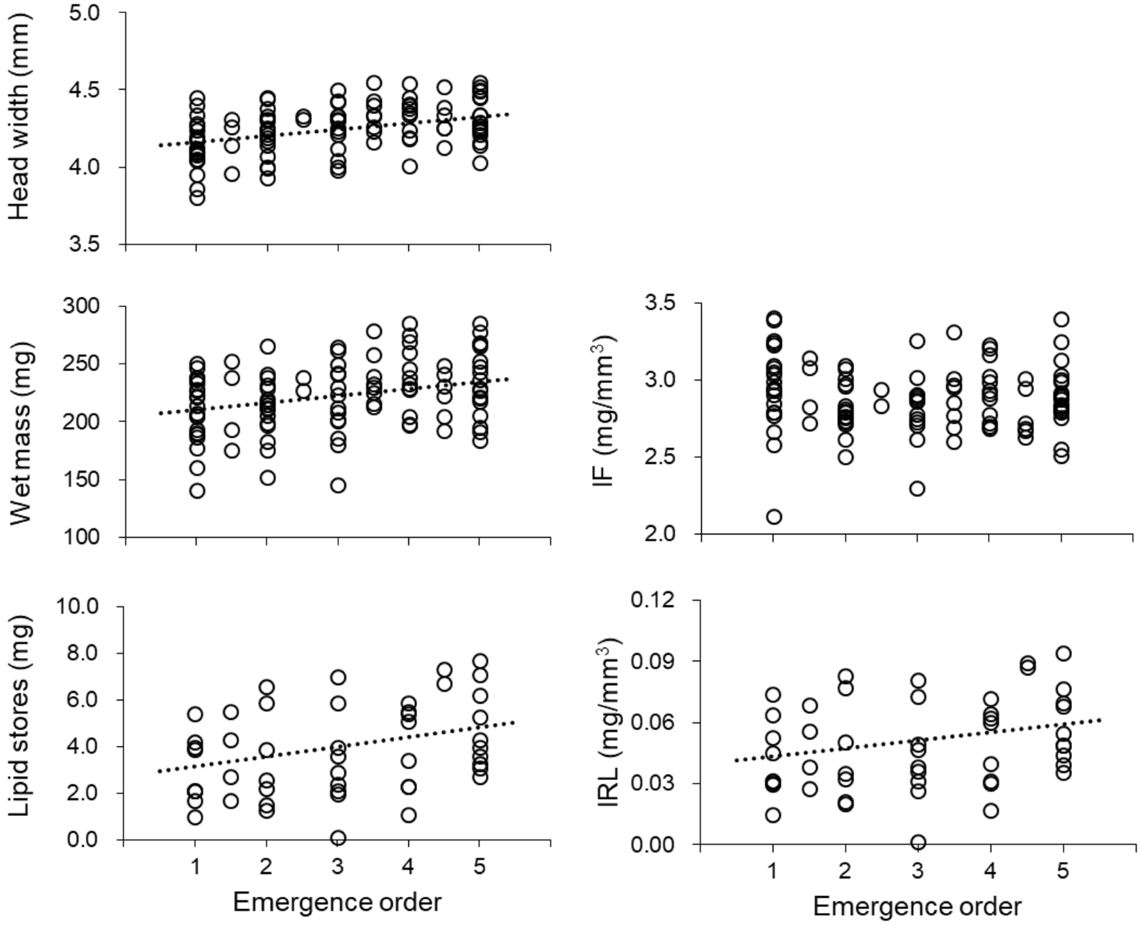

Fig. 4 Effects of emergence order on head width, wet mass, lipid stores, IF, and IRL in the first brood. The analysis was performed for the first-to-fifth emerging adults of the first brood. Four of the variables (the exception was IF) increased with the emergence order. Lines indicate the best-fit linear models

paragraph of "Discussion"), which makes such a survey both possible and likely to be conducted in the future.

First-brood females emerging later were larger and heavier, and had larger values of lipid stores and IRL, whereas IF did not change with the emergence order. These phenomena appear to reflect the wet mass, lipid stores, and IRL, each of which is related to the head width but not IF. This suggests that the component proportion of lipid stores increased and at the same time that of some other nutrients (e.g., proteins and carbohydrates) decreased as the head width or emergence order increased, given that IRL was not related to IF in the first brood.

Differences in the amount of provisions are considered to be insufficient to explain the caste-fate-related bias generated during the immature stage in primitive eusocial bees and wasps (Jeanne and Suryanarayanan 2011; Amsalem et al. 2015; Berens et al. 2015; Judd et al. 2015; Jandt et al. 2017). This view appears to also apply to our results because both the physiology and size of the first brood differed from those of the other broods. Moreover, it is possible that reduced amounts of provisions for the first brood are merely attributable to shorter days, cooler weather, or lack of foragers (only the queen forages), rather than regulation by the queen (Judd et al. 2015). Putative factors other than quantitative differences in provisions are as follows:

1. The queen provides qualitatively different food to the first brood. This strategy is adopted by the honeybee, *Apis mellifera*, with royal jelly being provided for queen-destined larvae (Hartfelder and Emlen 2012). The protein royalactin in royal jelly has recently been discovered to be responsible for driving queen development (Kamakura 2011). However, special diets for nursing queens have to our best knowledge not been reported in primitively eusocial insects.
2. The queen dispatches a signal (e.g., a pheromone or mechanical vibrations) to change the physiology of the first brood.
3. The queen forces the first brood to change its physiology using certain chemical and/or mechanical vibrations. This is similar to factor 2, except that the focal chemical or mechanical vibrations influence the physiology of the receiver directly rather than acting as a signal (see Peeters and Liebig 2009). Antennal drumming performed by the *P. fuscatus* queen creates bias toward worker caste in the first brood (Jeanne and Suryanarayanan 2011; Suryanarayanan et al. 2011; Jandt et al. 2017). Whether this action is a signal or directly affects the physiology of the offspring remains to be elucidated. Queen pheromone has been assumed to function as a primary factor for generating caste-fate-related bias in the bumblebee *Bombus terrestris* (Amsalem et al. 2015), but further analysis is required to confirm this.
4. Abiotic cues such as the day length change the physiology of the first brood. By rearing colonies under photoperiod-regulated conditions, Yoshimura and Yamada (2018) revealed that the day lengths during the pupal and adult stages affect caste-fate determinations in *P. jokahamae*, irrespective of the brood. When wasps experience long days during most of the pupal stage, smaller adults more likely mature eggs under both short and long days during the adult stage. This suggests that a caste-fate-related bias (lower IRL) is created in smaller wasps during the immature stage. Another particularly interesting observation was that when wasps experienced short days during most of the pupal stage, such effects of adult size were not present, suggesting that the caste-fate-related bias (lower IRL) does not occur for short days during the immature stage. Alternatively, the bias created during the immature stage is so small that it is overshadowed by the high-priority factor of day length during the adult stage. That study did not determine IRL, but suggests that pupae monitor the day length and change their physiology accordingly. The photoperiod might have been the main trigger for the caste-fate-related bias increasing during the immature stage in the present study. Further detailed research on the role of photoperiod in caste-fate determination is required in *P. jokahamae* and other paper wasps.

Most nonsocial insects decide to enter diapause in response to abiotic cues such as day length and temperature (Tauber et al. 1986; Danks 1987; Saunders 2002). Thus, as eusociality is advanced, mechanisms for the caste-fate-related bias appear to change from factor 4 through factors 2 and 3 to factor 1, as Judd (2018) suggested. Researchers have investigated the mechanisms underlying the caste-fate-related bias in some limited species so far, but researches on such mechanisms in many species are expected to lead to a deeper understanding of the evolutional process of eusociality.

Gyne-destined wasps emerging with higher lipid stores circumstantially supports the diapause ground-plan hypothesis (Hunt 2006, 2007), which assumes that eusociality originates in temperate solitary wasps: the characteristics of workers originate in nondiapausing wasps, whereas those of gynes originate in diapausing wasps. This assumption is challenged by the following two facts, as suggested by Kelstrup et al. (2017): (1) the phylogenic and biogeographical analysis of Santos et al. (2015) in *Polistes* paper wasps suggested that the genus originated in a tropical area, and (2) very few temperate solitary wasps overwinter as adults (Evans and West-Eberhard 1970). It might be fruitful to explore lipid stores of emerging adults in tropical paper wasps. If lipid stores and/or IRL increase with the emergence order in tropical paper wasps, the seasonal changes in them found in temperate paper wasps might be caused by factors unrelated to diapausing.

This study has verified the usefulness of two indexes: IF and IRL. We have used these indexes to obtain a better understanding of the mechanisms underlying brood-related differences in lipid stores: the first brood exhibits not only smallness but also a different plan for storing different nutrients. Moreover, since IRL is related to IF in the second and third broods, lipid stores are expected to be predicted by the two factors of the head width (the standard body volume as calculated from the head width) and IF, and indeed this has been confirmed (Yoshimura and Yamada unpubl.). Meanwhile, such a relationship between IRL and IF was not present in the first brood, and so IF is not the second predictor of lipid stores (Yoshimura and Yamada unpubl.). We expect that IRL and IF would also be useful when analyzing many other species.

Acknowledgements We thank the journal editor (Michael Breed) and two anonymous referees for constructive suggestions and comments.

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