

Original article

**Clustering of related workers in the honeybee colony
(*Apis mellifera* L.): adaptive process
or inevitable pattern?**

Robin F.A. MORITZ^{a*}, Robin M. CREWE^b, H. Randall HEPBURN^c

^a Institut für Zoologie, Molekulare Ökologie, Martin-Luther Universität Halle-Wittenberg,
Kröllwitzer Str. 44, 06099 Halle/Saale, Germany

^b Department of Zoology and Entomology, University of Pretoria, Pretoria, 0012, South Africa

^c Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140, South Africa

(Invited paper)

Abstract – Individually labeled freshly emerged honeybee workers (*Apis mellifera*) from three unrelated source colonies were introduced into five host colonies. The location of the workers during their first eight days of life was monitored. Workers from the same source colony tended to be found more often in the same area of the comb than workers from a different source colony. Although kin recognition among workers cannot be ruled out as a possible mechanism for this pattern, the results can be more readily explained by phenomena related to self-organized pattern formation, individual behavioral threshold variability and genetically determined worker task specialization.

Apis mellifera / kin recognition / spatial distribution / task specialization / pattern formation

1. INTRODUCTION

The honeybee queen is extremely polyandrous and as a consequence the colony is composed of numerous worker subfamilies, each having the same mother but different fathers [4]. This high intracolony genotypic variance has a number of implications for evolutionary biology [14], and among other aspects has made the honeybee a prime

test system for intranidal kin recognition [16]. Inclusive fitness theory predicts a high conflict potential among the subfamilies in the colony, fostering nepotistic behavior and kin recognition mechanisms. However, the impact of kin recognition and nepotistic behavior on colonial organization remains controversial [17, 19]. Whereas on several occasions nepotistic behavior has been claimed to be observed [16], there are also

* Correspondence and reprints
E-mail: r.moritz@zoologie.uni-halle.de

repeated indications for a lack of adaptive kin recognition in honeybees [6, 10, 20, 22, 24]. Generally the effects at the behavioral level were found to be weak [19] in spite of a wide variety of potentially available recognition cues [e.g., 2, 16, 23, 36].

Whereas the consequences of the queen's polyandry for intranidal recognition mechanisms among nest members are not very clear, they seem to be better understood for those mechanisms related to division of labor and worker task specialization [28, 31]. Genotypic variance is thought to be a major factor, tightly interwoven in the design of the honeybee colony [14, 25, 28]. Colonial organization is currently explained through the classical hierarchical pheromone signals on the one hand, and self-organized patterns on the other [29]. Whereas the significance of the pheromonal signals is believed to be well understood, the intricate and subtle mechanisms underlying self-organization among workers are currently the subject of intensive research [11]. Several examples are known where so-called 'cues' [38] rather than classical biological signals govern processes of colony organization. Indeed, self-organized patterns based on such cues seem rather inevitable in complex biological units such as the honeybee colony. Page and Mitchell [32] showed that on the basis of individual variability in behavioral thresholds, stable patterns are bound to emerge, explaining the establishment of phenomena such as division of labor and genetically determined specialized workers. The numerous subfamilies in the colony provide an excellent genetic basis for variance in individual behavioral thresholds [29]. It has been shown that pollen and nectar foragers have a genetically determined specific stimulus threshold for the release of a specific behavioral repertoire [35]. Stable patterns emerge if the action of the worker reduces or increases the threshold stimulus in the local environment, thereby regulating its own and other worker activities. Such classical feedback loop systems are believed to be the basis of many self-organized processes in insect societies in general [3].

The local conditions an individual worker experiences are clearly of great importance for its activities within this theoretical framework. By encountering specific situations and conditions in the colony, the worker will be exposed to an increasing array of stimuli that may or may not release behavioral responses depending on individual thresholds. Although worker bees exhibit a typical pattern during the course of age polyethism [21, 37], we certainly do not expect each and every worker to experience the identical local hive environment during its imaginal lifetime. Some workers may persist longer in the brood nest before visiting nest regions on the periphery than others, thus undergoing very individual nest experiences. It seems highly unlikely that these differences in individual experience will not influence the career of a worker in later life. Chance and random processes may play an important role, but in the light of the genetic variance for task specialization in older workers [32, 35] one might expect the location of young workers in the nest not to be random at all. Here we embarked on an investigation to see whether we could detect position differences among workers early in their imaginal lives, well before distinct task specialists had been established. In particular we wished to study whether there was a link between genotype and the location of workers in the hive during the first week of imaginal life.

2. MATERIALS AND METHODS

2.1. Host colonies

Five queenright observation hives were established, each with a single Langstroth frame containing brood of all stages on both sides at Rhodes University (Grahamstown, South Africa). The colonies were allowed to forage freely but received supplementary feeding with sugar candy if necessary to prevent absconding, which is a frequent phenomenon in African subspecies of

Apis mellifera [18]. A grid was drawn on the side panes of each observation hive dividing the frame into 54 squares (5×5 cm) with 9 columns and 6 rows.

2.2. Focal workers

Under natural conditions the colony is composed of super- and half-sister families. Workers are thus related at least by $r = 0.25$. In order to show the potential genetic effects on the spatial distribution more clearly, we decided to experimentally increase the intracolony genetic variance to reveal its potential effects. We chose to introduce workers from three unrelated colonies into each of our observation colonies. Sealed worker brood frames each consisting of an *A. m. capensis*, an *A. m. scutellata* and a natural hybrid colony were placed in an incubator (35 °C, 60% r.h.). Emerging workers were collected daily and labeled individually with small colored and numbered tags (Opalithplättchen). The tags were glued to the thorax of the workers with the top of the number in the walking direction to avoid identification errors during later observations. One hundred workers of each type were placed in a jar and mixed before introduction into the colony. The workers were simultaneously introduced into the observation colony on the bottom board. This procedure ensured that differences in the spatial distribution of workers among the three genetic groups could not be due to the introduction procedure. The introduced workers positioned themselves on the comb of their choice within a few minutes. Since all focal workers were of the same age, potential behavioral differences among workers could not be due to age polyethism.

2.3. Observations

2.3.1. Queenright colonies

The introduced workers were left unobserved during the first three days to allow

for an undisturbed adaptation process in the host colony. Observations started after this period, using the following procedure. An observer read aloud the numbers of bees in each square beginning in the top left corner. Another person wrote down the numbers on a prepared protocol sheet. A census took about 15 minutes per frame side depending on the number of labeled workers on the comb. Six observation sessions were conducted per day for each colony. If a worker was found more than once during a census, only its first occurrence was recorded for further analysis. All workers observed in the same square were considered as ‘meeting’. Meeting of two workers under this definition thus does not involve any particular behavioral interaction among workers such as trophallaxis, grooming, or aggression. It simply refers to the distribution of the workers on the frame without assigning any subjective behavioral classification. After five days the experiment was terminated, and all labeled workers were removed from the colony. This was performed at night using a red light to keep disturbance within the colonies to a minimum.

2.3.2. Queenless colonies

It is known that workers of the studied races respond markedly differently in their reproductive behavior to queenless situations. *A. m. capensis* workers can develop into functional pseudoqueens in a week [37], producing a queenlike pheromone signal. This peculiar trait might interfere with the spatial distribution of the workers on the comb. We therefore removed the queens from three observation colonies and introduced another set of freshly emerged workers after 12 h as described above. Since *A. m. scutellata* brood frames were no longer available due to absconding problems, only workers from the *A. m. capensis* and hybrid colony were introduced. Observations were continued after three days as described above.

The data were entered into a computer using standard spread-sheet software (Microsoft Excel). Statistical evaluations were made using χ^2 contingency table analysis to detect deviation from random meeting of the workers on the comb.

3. RESULTS

Focal workers performing any of the classical tasks were rare, and most insects simply either sat or walked around in a seemingly random fashion. From all 25 192 observations, only in 53 cases could we classify worker behavior into any of the categories as defined by Seeley [38]. Although the majority of the three groups of focal workers were not involved in apparent tasks, their distributions in the colony deviated significantly from each other. In some extreme cases, workers of a certain group were almost exclusively found on one side of the frame, whereas others showed more even distributions. Figure 1 shows a typical example of the spatial distribution of the three worker groups on one frame side. Although these patterns changed over time, and we could not detect specific ‘home ranges’ of the various groups, the clustering of related bees was a persistent phenomenon. In colonies 1, 3 and 4 we consistently found on each observation day significant deviations from a homogeneous worker distribution, showing clustering of sister workers (χ^2 analysis, $P < 0.05$).

Table I shows the pooled data for all five observation days. In order to determine whether workers of the same subgroup were preferentially in the vicinity of each other, we tested whether the frequency of ‘meeting’ workers was higher within than between the subgroups with χ^2 analysis. Focal workers of the same origin met their own sister workers significantly more often than introduced workers from the other source colonies. In all queenright and queenless colonies, the observed number of met workers of the same subgroup was higher than

expected (significant in all colonies except 2 and 5, χ^2 contingency table, $P < 0.01$). If the data from the queenright colonies is presented in a way that shows the relative deviations (in %) from the expected frequencies under homogeneous distribution of meetings among the three types of workers (Fig. 2), we see that *A. m. scutellata* workers met workers of the same subgroup $11.8 \pm 3.6\%$ more frequently than expected. Hybrid bees showed a $5.1 \pm 1.4\%$ and *A. m. capensis* workers a $4.1 \pm 1.2\%$ bias in meeting frequencies.

In the queenless colonies we see a similar pattern (Fig. 3). Both *A. m. capensis* ($11.2 \pm 2.5\%$) and hybrid ($4.5 \pm 1.5\%$) workers met significantly more frequently with workers of their own origin.

4. DISCUSSION

The vast majority of workers in our study did not show any of the behaviors typical of their age group. This is not in contrast to the classical reports on age polyethism and division of labor, but rather a result of our observation technique and the composition of the observation colonies. We did not focus on specific workers expressing a particular behavior as in the classical studies on division of labor [21, 36], but instead performed periodic scans over all workers irrespective of their activity. Moreover, most cells of the comb contained sealed brood or were filled with honey and pollen, leaving little opportunity for activities typical of young workers such as cell inspecting, cell cleaning and brood care [38]. So even workers with low thresholds for cell cleaning, nursing or other typical in-hive activities had few opportunities to perform these tasks.

We know that bees, depending on age and task specialization, reside in different regions of the nest. Our study was, however, corrected for age because all workers were simultaneously introduced on the day of emergence. Moreover, most workers were all engaged in the same task (being inactive),

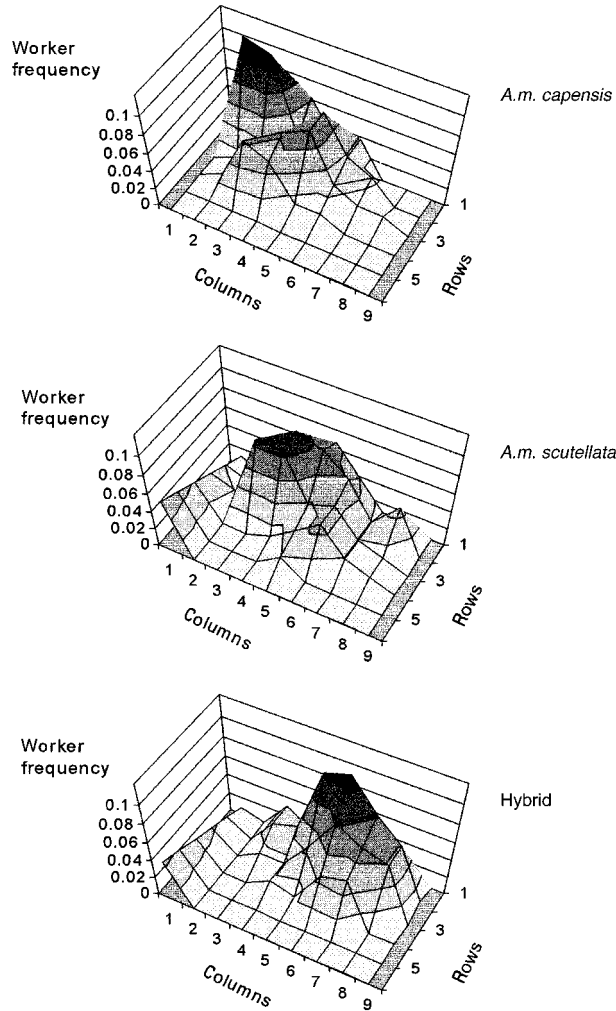


Figure 1. Distribution of focal *A. m. capensis*, *A. m. scutellata* and hybrid workers on a frame (example from frame side A of colony 1 on 11 Nov. 1998). The data represents the pooled frequencies of six observation sessions throughout the day based on 319 individual worker sightings. In this case, clustering is particularly obvious with *A. m. capensis* workers having the highest distribution in the upper left corner of the frame (row 2, column 2), *A. m. scutellata* is more to the right in the upper middle (row 2, column 4), and the hybrid workers are even further to the right towards the upper right corner (row 2, column 6) of the frame (row 1 = top of frame).

yet their spatial distribution in the colony was obviously not random at all. We compared three groups of sister workers within their home range in the brood nest area predicted by age polyethism. Sister workers were more frequently found in close proximity to each other on the comb than were the unrelated workers. Often distinct clustering of workers of a certain subgroup could be observed. What are the potential reasons for clustering of related workers? Is it an adaptive process or merely an inevitable pattern not governed by natural selection?

Related workers interacting more closely with each other could be a sign of nestmate or kin recognition. Many cues have been suggested as potential kin recognition signals in honeybees [2]. However, whether these signals were actually used by the insects in our current observations or in any other observations on honeybee colonies complying with the criteria of kin recognition remains to be proven. Although kin recognition mechanisms have been repeatedly claimed for honeybees, their impact, if detectable at all, was weak at best [7].

Table I. Numbers of focal workers meeting other focal workers in the observation colonies. The expected numbers for a homogeneous worker distribution are given in italics. They are derived from the number of observed meetings and not from the absolute numbers of workers in the colony. χ^2 values as well as the error levels are given. Focal workers show increased frequencies to meet with their sister workers. Note that the numbers of workers per genetic group are not equal in each host colony. Therefore the absolute numbers do not directly reflect the deviations from the expectations assuming random meeting. These are shown in Figures 2 and 3.

Colony # queenright	Worker type	<i>A. m. capensis</i>		<i>A. m. scutellata</i>		Hybrid		Chi ²	P
		Obs.	<i>Exp.</i>	Obs.	<i>Exp.</i>	Obs.	<i>Exp.</i>		
1	<i>capensis</i>	638	585.5	900	929.9	513	535.6	30.5	< 0.01
	<i>scutellata</i>			1 558	1 476.6	799	850.5		
	Hybrid					564	489.9		
2	<i>capensis</i>	320	311.6	481	486.2	234	237.3	5.5	NS
	<i>scutellata</i>			782	758.7	352	370.2		
	Hybrid					202	180.6		
3	<i>capensis</i>	384	356.4	312	303.8	509	544.8	39.7	< 0.01
	<i>scutellata</i>			302	258.9	413	464.3		
	Hybrid					920	820.8		
4	<i>capensis</i>	728	683.4	459	450.1	670	723.5	15.0	< 0.01
	<i>scutellata</i>			282	296.4	482	476.5		
	Hybrid					814	766.0		
5	<i>capensis</i>	150	148.1	64	67.5	203	201.4	1.4	NS
	<i>scutellata</i>			36	30.8	90	91.7		
	Hybrid					274	273.8		
queenless									
6	<i>capensis</i>	865	815.2			685	734.8	13.5	< 0.01
	Hybrid					712	662.2		
7	<i>capensis</i>	966	851.9			1 560	1 674.1	34.8	< 0.01
	Hybrid					3 404	3 290.0		
8	<i>capensis</i>	322	282.2			616	655.8	11.5	< 0.01
	Hybrid					1 564	1 524.2		

NS: non significant.

We cannot rule out a kin recognition mechanism as a possible explanation for our observations. The young workers might cluster because of support for each other in a way as yet unknown to us. However, clustering certainly did not occur because of the distribution of subfamilies in the brood. The queen in the host colony was unrelated to all introduced workers, and the focal worker-brood relatedness was zero. It seems difficult at this stage to interpret the clustering of related young workers as an adaptive kin

recognition process with an obvious immediate fitness advantage. It is true that laying workers may develop after loss of the queen, but then one might expect the phenomenon to be more strongly expressed under queenless conditions, where worker competition for reproduction occurs [27]. Clustering of related workers was similar in both queenright and queenless colonies.

In the light of the findings on self-organization mechanisms in honeybee colony

Figure 2. Mean relative differences between observed and expected meeting frequencies under a homogeneous distribution of the bees listed in Table I from all queenright colonies ($n = 5$). A positive deviation indicates a higher meeting frequency than expected under a random distribution of workers. Focal workers of all three groups met more frequently with their sisters than with the unrelated focal workers. □ : *A. m. capensis*; ▨ : hybrid; ▩ : *A. m. scutellata*.

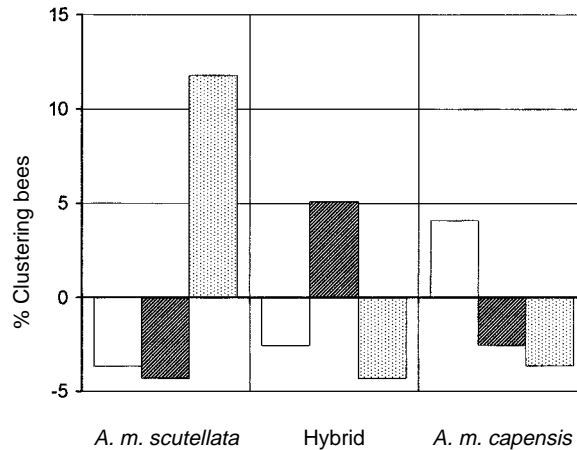
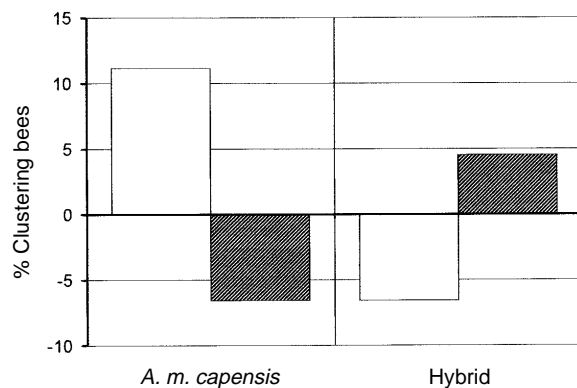


Figure 3. Mean relative differences of the expected meeting frequencies of the focal workers in the queenless colonies. As in the queenright case, here also related workers met more frequently than unrelated workers. □ : *A. m. capensis*; ▨ : hybrid.



organization [e.g., 8, 10, 12, 26] it seems helpful to consider this concept to explain inhomogeneous spatial worker distribution. It is well established that workers performing a specific task are preferentially found in specific nest areas [13, 42]. An extreme example may be that observed by Tautz and Lindauer [41] in dancing foragers which have specific individual dance floors in the nest that they use for communication on the comb. In our study we found clustering of young related workers well before any specific task specialization had been developed. It seems thus unlikely that specific tasks forced the workers into the various regions on the comb. Nevertheless, workers appar-

ently have preferences for particular locations in the nest. If workers utilize very subtle cues to spatially distribute themselves in the hive, it may well be that related workers use similar cues in a similar way.

Cues as simple as nest temperature have been shown to be important for establishing self-organized processes in honeybee colonies [26], and this could equally well be important for spatial worker distribution. Age has been shown to have a strong effect on the temperature preferences of workers. Only older worker bees can cope with the cooler temperatures of the nest periphery [1], whereas the younger bees are found within the warm center of the nest [40]. The

spatial position of a worker bee may thus correspond to simple cues such as intranidal temperature profile, and depend on individual thresholds for temperature preferences. If the threshold variance is due to genetic variance, then we would expect related bees to cluster in similar sites in the nest. Thus rather than identifying a potential kin 'signal' from a fellow bee [5], it may be a simple nest environmental cue that forces the bees into a particular region of the nest. The results would be indistinguishable in our observations.

Irrespective of the proximate mechanisms causing the clustering of related workers in different nest areas, it would be surprising if this had no consequences on worker specialization in later life. Individual experience does affect behavioral responses, and we do not expect workers experiencing different nest environments to have identical behavioral response thresholds in later life. If the location of a worker in the colony interferes with the behavioral threshold settings, then the switches for task specialization in honeybees may be set much earlier in the life of a worker honeybee than has been addressed so far [27].

Our results on clustering of related workers in the colony may be similar to those of Oldroyd et al. [30]. They found that dancing workers were preferentially followed by their super-sister workers, and discussed this as a possible adaptive process where kin recognition allows specialized workers to interact more efficiently for the needs of the colony. Yet already Oldroyd et al. [30] clearly saw the limitations of the analysis, and cautioned that the "data should not be taken as unequivocal evidence for subfamily recognition" (p. 128 in [30]), suggesting that task specialization was an equally valid explanation of their results. Although adaptive processes are plausible and cannot be excluded, there remains a paucity of studies showing clear evidence of any kin recognition mechanism among honeybee workers, and there is as yet no clear evidence of

increased colony efficiency due to increased super-sister interactions. We favor a more parsimonious explanation requiring fewer assumptions and necessary mechanisms for clustering of related workers. If genetic task specialization determines the spatial position of a worker in the colony, then this is sufficient to explain clustering of related workers in the colony. In the interpretation of our study, we use this very argument but turn it around. We found an inhomogeneous spatial distribution of bees which were not performing any particular task, and argue that these positional differences among the young workers may contribute to the development of specific task preferences in later life (e.g., water foragers versus nectar foragers). We are well aware that we have no full experimental evidence yet to support the latter part our hypothesis (task specialization in later life). Nevertheless, in the light of the well-developed theoretical concepts of colonial organization and the empirical evidence of task specialization [3], the search for the mechanisms causing this pattern in spatial worker distribution and the identification of the consequences for the ontogeny of task specialization seem highly rewarding for understanding the colonial organization of the honeybee. The theory of subfamily task specialization within colonies is based on genotype-environment interactions. These can start very early in the life of a honeybee worker, and we should not necessarily expect a worker with a given genotype which is specializing in one task in a colony to specialize in the same task in another colony.

ACKNOWLEDGMENTS

We wish to thank A.M.D. Schmidt-Moritz, R.P.C. Moritz, R.K.C. Moritz, R.L.V. Moritz, R.L.M. Moritz and R.W.K. Moritz for helping with the behavioral observations. This work was facilitated by a South African Humboldt Research Award to R.F.A.M. and by financial support from the Deutsche Forschungsgemeinschaft.

Résumé – Regroupement d’ouvrières apparentées dans la colonie d’abeilles (*Apis mellifera* L.) : processus adaptatif ou structure inévitable ? Chez *Apis mellifera* la polyandrie de la reine conduit à la coexistence dans la colonie de nombreuses demi-fratries. La théorie de l’adéquation adaptative globale (« inclusive fitness ») prédit un potentiel conflictuel élevé entre les fratries qui favorise des mécanismes tels que la reconnaissance de parentèle et le népotisme. En même temps, la variabilité génétique combinée au polyéthisme lié à l’âge représente une base importante pour la division du travail et la spécialisation des abeilles dans la colonie.

Dans le présent travail nous avons cherché dans quelle mesure la structure de la parenté a une influence sur la répartition spatiale des ouvrières. Pour ce faire nous avons marqué individuellement 100 ouvrières nées provenant de trois colonies mères non apparentées et de race différente (*A. m. capensis*, *A. m. scutellata* et leur hybride naturel) et les avons introduites dans huit colonies d’observations, cinq ayant une reine et les trois autres étant orphelines. Les ruches d’observation ont été constituées de cadres de couvain operculé couverts d’ouvrières. Sur les parois vitrées des ruches d’observation a été tracée une grille comportant 54 carrés (9 colonnes et 6 rangées). La position des ouvrières introduites a été notée six fois par jour et la répartition spatiale des groupes d’ouvrières obtenue (Fig. 1). Si des ouvrières sont observées dans le même carré, ceci est considéré comme une « réunion ». Dans toutes les ruches d’observations les réunions entre ouvrières sœurs ont été plus nombreuses (Figs. 2, 3). Dans six des huit colonies d’observation les ouvrières apparentées se sont réunies significativement plus souvent que les non apparentées (Tab. I).

Ces observations concordent avec celles de Oldroyd et al. [30], qui rapportent l’existence de contacts plus nombreux entre ouvrières apparentées dans la communication dansée et interprètent cela comme un processus adaptatif. De nos données nous

concluons qu’il ne s’agit pas obligatoirement lors de ces « réunions » d’un processus adaptatif de reconnaissance de parentèle. Les ouvrières ne présentent aucune activité particulière qui pourrait laisser conclure à un processus de reconnaissance. Les activités telles que le toilettage mutuel ou la trophallaxie n’ont été observées entre ouvrières marquées que dans 53 cas sur 25 192. Même si nous ne pouvons exclure un éventuel profit adaptatif pour les ouvrières, celui-ci semble improbable. Nos observations s’accordent plutôt avec le concept d’auto-organisation de la colonie d’abeilles. Des stimuli simples (comme la température ou la présence de la reine) peuvent également conduire à une répartition des abeilles dans la colonie qui ne soit pas due au hasard. Lorsqu’il existe pour des préférences concernant le milieu des valeurs-seuils différentes selon les fratries, on peut aboutir à l’émergence d’une structure semblable à celle que nous avons observée. Tant qu’il n’y a pas de preuve d’un mécanisme de reconnaissance de la parenté dans la colonie d’abeilles, l’émergence d’une structure autoorganisée nous semble une explication plus plausible que le regroupement d’ouvrières apparentées.

***Apis mellifera* / reconnaissance parentèle / répartition spatiale / spécialisation de tâches / émergence de structure**

Zusammenfassung – Aggregation verwandter Arbeiterinnen im Bienenvolk (*Apis mellifera* L.): Adaptiver Prozess oder zwangsläufige Musterbildung? Die Polyandrie der Bienenkönigin führt dazu, dass zahlreiche Halbgeschwisterfamilien im Bienenvolk koexistieren. Dies führt zu einem hohen Konfliktpotential zwischen den Familien, und die inklusive Fitness Theorie sagt Phänomene wie Verwandtenerkennung und nepotistisches Verhalten als adaptive Merkmale voraus. Zugleich stellt die genetische Variabilität zusammen mit dem altersbedingten Polyethismus eine

wichtige Basis für die Arbeitsteilung und die Spezialisierung von Honigbienen im Bienenvolk dar. In der vorliegenden Arbeit untersuchen wir, inwieweit die Verwandtschaftsstruktur Einfluss auf die räumliche Verteilung der Arbeiterinnen nimmt. Wir haben hierzu je 100 frisch geschlüpfte, individuell markierte Arbeiterinnen von drei unverwandten Muttervölkern verschiedener Rassen (*Apis mellifera capensis*, *A. m. scutellata* und deren natürliche Hybride) in fünf weiselrichtige und drei weisellose Beobachtungsvölker gegeben. Die Beobachtungsvölker waren mit einer mit Arbeiterinnen besetzten, verdeckelten Brutwabe bestückt. Auf die Glasseitenwände der Beobachtungskästen wurde eine Gittermatrix mit 9×6 Feldern aufgezeichnet. Die Positionen der eingebrachten Arbeiterinnen wurden sechs mal täglich protokolliert und die räumliche Verteilung der Arbeiterinnengruppen erfasst (Abb. 1). Wurden Arbeiterinnen im gleichen Feld beobachtet, so wurde dies als "Begegnung" gewertet. In allen Beobachtungsvölkern wurden häufiger Begegnungen zwischen Geschwisterarbeiterinnen beobachtet. (Abb. 2, Abb. 3). In sechs der acht Beobachtungsvölker begegneten sich verwandte Arbeiterinnen signifikant häufiger als unverwandte (Tab. I).

Diese Beobachtungen stehen im Einklang mit denen von Oldroyd et al. [30], die ebenfalls über vermehrte Kontakte verwandter Arbeiterinnen bei der Tanzkommunikation berichten und dies als adaptiven Prozess interpretierten. Wir schließen aus unseren Daten, dass es sich nicht notwendigerweise um adaptive Verwandtenerkennung handelt. Die Arbeiterinnen zeigten bei den "Begegnungen" keine besonderen Aktivitäten, die auf einen Erkennungsprozess hätten schließen lassen können. Tätigkeiten wie gegenseitiges Putzen oder Trophallaxe zwischen markierten Bienen wurde nur in 53 von insgesamt 25 192 Fällen beobachtet. Auch wenn wir einen möglichen adaptiven Nutzen für die Arbeiterinnen nicht ausschließen können, scheint dies eher unwahrscheinlich. Unsere Beobachtungen

lassen sich eher mit einem Konzept der Selbstorganisation im Bienenvolk in Einklang bringen. Einfache Stimuli (wie z.B. Temperatur, Anwesenheit der Königin) können ebenfalls dazu führen, dass sich Arbeiterinnen nicht zufällig im Bienenvolk verteilen. Wenn zwischen Geschwistergruppen unterschiedliche Schwellenwerte für Umweltpräferenzen existieren, kann es zu einer gleichen Musterbildung kommen, wie wir sie beobachtet haben. Solange es keinen Nachweis für einen Mechanismus der Verwandtenerkennung im Bienenvolk gibt, erscheint uns die selbstorganisierte Musterbildung eher als plausible Erklärung für die Aggregation verwandter Arbeiterinnen im Bienenvolk geeignet zu sein.

***Apis mellifera* / Verwandtererkennung / räumliche Verteilung / Spezialisierung / Musterbildung**

REFERENCES

- [1] Allen M.D., Respiration of worker honeybees of different ages at different temperatures, *J. Exp. Biol.* 36 (1959) 92–101.
- [2] Arnold G., Quenet J.M., Masson C., De Schepper B., Estoup A., Gasqui P., Kin recognition in honeybees, *Nature* 379 (1996) 498.
- [3] Bonabeau E., Theraulaz G., Deneubourg J.-L., Aron S., Camazine S., Self-organization in social insects, *Trends Ecol. Evol.* 12 (1997) 188–193.
- [4] Boomsma J.J.C., Ratnieks F.L.W., Paternity in eusocial Hymenoptera, *Phil. Trans. R. Soc. Lond. B* 351 (1996) 941–957.
- [5] Breed M.D., Chemical cues in kin recognition: criteria for identification, experimental approaches, and the honeybee as an example, in: Vander Meer R.K., Breed M.D., Winston M.L., Espelie K.E. (Eds.), *Pheromone Communication in Social Insects*, Westview Press, Boulder, CO, 1998, pp. 57–78.
- [6] Breed M.D., Velthuis H.H.W., Robinson G.E., Do worker honeybees discriminate among unrelated and related larvae phenotypes? *Ann. Entomol. Soc. Am.* 77 (1984) 737–739.
- [7] Breed M.D., Welch C.K., Cruz R., Kin discrimination within honeybee colonies: an analysis of the evidence, *Behav. Process.* 33 (1994) 25–40.
- [8] Camazine S., Self-organizing pattern formation on the combs of honeybee colonies, *Behav. Ecol. Sociobiol.* 28 (1991) 61–76.

- [9] Camazine S., Sneyd J., A model of collective nectar source selection by honey bees: self-organization through simple rules, *J. Theor. Biol.* 149 (1991) 547–571.
- [10] Carlin N., Frumhoff P., Nepotism in the honeybee, *Nature* 346 (1990) 706.
- [11] Detrain C., Pasteels J., Deneubourg J., *Information Processing in Social Insects*, Birkhäuser, Basel, Switzerland, 1999.
- [12] de Vries H., Biesmeijer J.C., Modelling collective foraging by means of individual behavior rules in honeybees, *Behav. Ecol. Sociobiol.* 44 (1998) 109–129.
- [13] Frumhoff P.C., Schneider S., The social consequences of honeybee polyandry: the effects of kinship on worker interactions within colonies, *Anim. Behav.* 35 (1987) 255–262.
- [14] Fuchs S., Moritz R.F.A., Evolution of extreme polyandry in the honeybee, *Apis mellifera* L., *Behav. Ecol. Sociobiol.* 45 (1999) 269–275.
- [15] Getz W.M., The honey bee as a model kin recognition system, in: Hepper P.G. (Ed.), *Kin Recognition*, Cambridge Univ. Press, Cambridge, UK, 1991, pp. 358–412.
- [16] Getz W.M., Smith K.B., Olfactory sensitivity and discrimination of mixtures in the honeybee, *J. Comp. Physiol. A* 160 (1987) 239–245.
- [17] Grafen A., Do animals really recognize kin? *Anim. Behav.* 39 (1990) 42–44.
- [18] Hepburn H.R., Reece S., Neumann P., Moritz R.F.A., Radloff S.E., Absconding in honeybees (*Apis mellifera*) in relation to queen status and mode of worker reproduction, *Insectes Soc.* 46 (1999) 323–326.
- [19] Keller L., Indiscriminate altruism: unduly nice parents and siblings, *Trends Ecol. Evol.* 12 (1997) 99–103.
- [20] Kryger P., Moritz R.F.A., Lack of kin recognition in swarming honeybees, *Behav. Ecol. Sociobiol.* 40 (1997) 271–276.
- [21] Lindauer M., Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat, *Z. Vergl. Physiol.* 36 (1952) 299–345.
- [22] Moritz R.F.A., Kin recognition in honeybees: experimental artefact or biological reality?, in: Goodman L.J., Fisher R.C. (Eds.), *The Behaviour and Physiology of Honeybees*, CAB International, Oxon, UK, 1991, pp. 48–59.
- [23] Moritz R.F.A., Crewe R.M., Chemical signals of queens in kin recognition of honeybees (*Apis mellifera* L.), *J. Comp. Physiol. A* 164 (1988) 83–89.
- [24] Moritz R.F.A., Heilser T., Super- and half-sister discrimination by honeybee workers (*Apis mellifera*) in a trophallactic bioassay, *Insectes Soc.* 39 (1992) 365–372.
- [25] Moritz R.F.A., Southwick E.E., *Bees as Superorganisms – An Evolutionary Reality*, Springer Verlag, Heidelberg, Germany, 1992.
- [26] Moritz R.F.A., Kryger P., Self-organization of circadian rhythms in groups of honeybees (*Apis mellifera* L.), *Behav. Ecol. Sociobiol.* 34 (1994) 211–215.
- [27] Moritz R.F.A., Kryger P., Allsopp M., Competition for royalty in bees, *Nature* 384 (1996) 31.
- [28] Moritz R.F.A., Fuchs S., Organization of honeybee colonies: characteristics and consequences of a superorganism concept, *Apidologie* 29 (1998) 7–21.
- [29] Moritz R.F.A., Page R.E., Behavioral threshold variability: costs and benefits in insect societies, in: Detrain C., Pasteels J., Deneubourg J. (Eds.), *Information Processing in Social Insects*, Birkhäuser, Basel, Switzerland, 1999, pp. 203–215.
- [30] Oldroyd B.P., Rinderer T.E., Bucu S.M., Honeybees dance with their super-sisters, *Anim. Behav.* 42 (1991) 121–129.
- [31] Page R.E., Robinson G.E., The genetics of division of labor in honeybee colonies, *Adv. Insect Physiol.* 23 (1991) 117–169.
- [32] Page R.E., Mitchell S.D., Self-organization and the evolution of division of labor, *Apidologie* 29 (1998) 171–190.
- [33] Page R.E., Robinson G.E., Fondrk M.K., Genetic specialists, kin recognition and nepotism in honeybee colonies, *Nature* 338 (1989) 576–579.
- [34] Page R.E., Metcalf R.A., Metcalf R.L., Erickson E.H., Lampman R.L., Extractable hydrocarbons and kin recognition in the honeybee, *J. Chem. Ecol.* 17 (1991) 745–756.
- [35] Page R.E., Erber J., Fondrk M.K., The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.), *J. Comp. Physiol.* 182 (1998) 489–500.
- [36] Rösch G.A., Über die Bautätigkeit im Bienenvolk und das Alter der Baubiene. Weiterer Beitrag zur Frage nach Arbeitsteilung im Bienenstaat, *Z. Vergl. Physiol.* 6 (1927) 265–298.
- [37] Ruttner F., Hesse B., Rassenspezifische Unterschiede in der Ovaentwicklung und Eiablage von weisellosen Arbeiterinnen der Honigbiene *Apis mellifera*, *Apidologie* 12 (1981) 159–183.
- [38] Seeley T.D., *Honeybee Ecology. A Study of Adaptation in Social Life*, Princeton Univ. Press, Princeton, NJ, 1985.
- [39] Seeley T.D., Thoughts of information and integration in honey bee colonies, *Apidologie* 29 (1998) 67–80.
- [40] Southwick E.E., Social temperature control and heat production in honey bees, in: Mercer J.B. (Ed.), *Thermal Physiology*, Elsevier, Amsterdam, 1989, pp. 755–759.
- [41] Tautz J., Lindauer M., Honeybees establish specific sites on the comb for their waggle dance, *J. Comp. Physiol. A* 180 (1998) 537–539.
- [42] Trumbo S.T., Huang Z.Y., Robinson G.E., Division of labor between undertaker specialists and other middle-aged workers in honey bee colonies, *Behav. Ecol. Sociobiol.* 41 (1997) 151–163.