The influence of developmental temperatures on division of labour in honeybee colonies

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Contents

CHAPTER 1

Introduction

1.1. Division of labour

One of the primary characteristics of eusociality in insects is the division of labour among members of the same colony, in which sets of workers specialize in different sets of tasks (Michener 1969, Wilson 1975, Beshers et al. 2001). While reproductive individuals specialise in the production of offspring, a functionally sterile worker caste becomes responsible for brood rearing and foraging, and maintains the nest homeostasis (Schmickl and Crailsheim 2004). However, division of labour in social insects also takes place within the worker caste (Robinson 1992, Page and Erber 2002). Whereas several ant and termite species show an impressive worker polymorphism like the leaf-cutter ant *Atta sexdens* (Wheeler 1986, Winston 1980a,b), in the majority of social insects including the honeybees the worker caste is monomorphic and task allocation strongly depends on the age of the workers (Seeley 1995, Beshers and Fewell 2001). A general pattern of this temporal polyethism is that younger workers perform in-hive tasks like nest building and brood care, whereas older ones take the risk of foraging outside the colony (Rösch 1925, Beshers et al. 2001). However, this mechanism of task allocation does not follow a rigid pattern, and allows for flexible responses to environmental and intracolonial requirements, which may even reverse the behavioural development from outdoor to indoor worker (Rösch 1930, Robinson et al. 1989, Robinson 1992, Page et al. 1992, Robinson 2002). A loss of foragers in a colony leads to an earlier onset of foraging in workers, whereas the presence of brood and the lack of young nurse bees delays the behavioural development of older workers (Huang and Robinson 1996, LeConte et al. 2001, Leoncini et al. 2004). Plasticity in age polyethism is also achieved by genetic components. Due to the multiple mating of honeybee queens the colony is stuctured in several subfamilies (Taber 1958, Laidlaw and Page 1984) of wich some generate a higher proportion of precocious foragers than other subfamilies if older bees are lacking (Calderone and Page 1988, Giray and Robinson 1994, Robinson and Huang 1998). The shift in the behavioural patterns of honey bees goes along with physiological changes as it can be observed in glandular development. Wax glands for example are most active in bees with an age of three to 21 days (Rösch 1927, Lindauer 1952, Muller and Hepburn 1992) and the hypopharyngeal gland produces brood food in workers aged between three to 16 days (Lindauer 1952, Winston 1987). Physiological and behavioural developments are coordinated by hormones and in honeybees the juvenil hormone (JH) plays a central role for division of labour. It has been shown that the interplay of vitellogenin and JH is important for the transition from the in-hive worker to the forager, where JH acts as „behavioral pacemaker" reducing the age of first foraging (Jaycox et al. 1974, Robinson 1987, Huang et al. 1997, Robinson and Vargo 1997, Sullivan et al. 2000).

1.2. Thermoregulation

Although insects in general are ectotherms and their temperature depends on the environment many of them are able to regulate their body temperature to a certain degree. A favorable body temperature can be achieved passively by moving to a location with an adequate microclimate (Steiner 1929, Cloudsley-Thompson 1962), but it can also be achieved by actively generating metabolic heat (May 1979, Casey 1981, Tschinkel 1985, Jones and Oldroyd 2007). In social insects, the cooperation of many individuals allows temperature regulation not only on the individual level but as a feature of the whole colony, where especially the brood nest is under particular control (Jones and Oldroyd 2007). Endowed with strong flight muscles, social wasps and bees have the ability to directly incubate their brood (Himmer 1927, Jones and Oldroyd 2007). A highly precise regulation of the nest temperature is found in honeybees. The western honeybee (*Apis mellifera*) shows a mean brood temperature of around 35°C within a range of 32-36°C (Hess 1926, Himmer 1927, Dunham 1931, Wohlgemuth 1957, Koeniger 1978, Kronenberg and Heller 1982, Ritter 1982, Heinrich 1993). Honeybees sense temperature with thermo-receptors in their antennae (Heran 1952, Lacher 1964, Yokohari 1983) and it is assumed that a worker engages in nest thermoregulation, if the temperature it is exposed to exceeds an individual threshold (Jones et al. 2004, Weidenmüller 2004, Graham et al. 2006, Fehler et al. 2007, Jones and Oldroyd 2007). Honeybees increase their body temperature by activation of the flight muscles without moving the wings ("shivering") which can result in thorax temperatures exceeding 40°C (Esch 1960, Esch and Bastian 1968, Esch et al. 1991, Kleinhenz et al. 2003, Stabentheiner et al. 2003). Most workers and even the drones contribute to the colonial thermogenesis (Harrison 1987, Kovac et al. 2009). Older workers with strong flight muscles have a higher heating capacity than younger workers (Himmer 1925, Allen 1959, Stabentheiner and Schmaranzer 1987, Vollmann et al. 2004), but younger workers are usually located close to the brood nest (Seeley 1982) and hence are directly stimulated for brood heating. Heating workers press their warm thoraces firmly on capped brood cells to incubate the brood (Bujok et al. 2002). Sometimes empty cells, scattered in the sealed brood area, are entered by a heating workers, which is assumed to efficiently warm the pupae in the neighbouring cells

(Kleinhenz et al. 2003, Fehler et al. 2007). Basile et al. (2008) showed that heating workers are supplied with energy via trophallaxis by their nestmates.

High environmental temperatures often require cooling of the brood. For cooling bees ventilate by wing fanning, evaporate water by tongue lashing or spreading droplets of water on the brood nest (Lindauer 1954, Kiechle 1961, Lensky 1964, Southwick and Moritz 1987). Moreover Starks and Gilley (1999) describe a behaviour termed „heat shielding“, where workers position themselves on hot interior regions especially on the broodnest to prevent overheating.

Additionally to the thermoregulation during the brood rearing period, honey bees maintain temperatures between 18 and 32°C also in the winter cluster with ambient temperatures far below 0°C (Hess 1926, Southwick and Mugaas 1971, Southwick 1987, Southwick and Heldmaier 1987). The individuals of the colony form a cluster with a warm core temperature and lower temperatures in the insulating mantle while the stored honey is consumed to metabolically produce heat (Owens 1971, Southwick 1985, Fahrenholz et al. 1989, Sasaki et al. 1990, Stabentheiner et al. 2003). Size, shape and tightness of a honey bee cluster depends on the ambient temperatures (Simpson 1961, Heinrich 1981, Myerscough 1993, Watmough and Camazine 1995, Sumpter and Broomhead 2000). Although overwintering as a colony is costly, it allows to start brood rearing already in early spring and is hence one reason for the ecological success of the honey bees (Seeley 1985, Winston 1987).

1.3. Impact of developmental temperatures

Brood nest temperatures in general are well regulated to about 35°C, but temporary deviations from the optimal temperature inevitably occur, especially at the edge of the brood nest (Rosenkranz and Engels 1994). Stronger deviations result in the death of the brood or in malformations of wings, stinger, proboscis or legs of the adult bees (Himmer 1927) or preclude ovary development in workers (Lin and Winston 1998). Smaller variations between 32 and 36°C, as it occurs in the brood nest, do not cause visible defects (Himmer 1927, Groh et al. 2004, Jones et al. 2005) but can affect wing morphology (Ken et al. 2005) or pigmentation of thorax and abdomen in *A. cerana* (Tsuruta et al. 1989). Additionally, developmental temperature influences the behavioural traits of adult workers. High temperatures of 36°C during pupal development have been shown to improve the olfactory learning ability of adult workers in proboscis extension reflex (PER) tests. Pupal developmental temperatures of 32°C however reduced the probability to dance as well as the number of performed waggle dance circuits (Tautz et al. 2003). Jones et al. (2005) confirmed these results and found improved short-term learning and memory abilities of adult workers experienced higher temperatures during their pupal development.

Groh et al. (2004) detected significant changes in the mushroom bodies of the honeybee's brain in response to the develomental temperature. As mushroom bodies are involved in learning and memory and influence division of labour in honeybees (Withers et al. 1993, Heisenberg 1998), develomental temperatures may have far reaching consequences for the social organization of the colony.

1.4. Study question

As developmental temperatures affect behavioural traits - particularly such involved in the outdoor activities of honey bees - they may well be an instrument for fine-tuning division of labour in the colony. Changes in environmental temperatures as well as a fluctuating colony size can influence brood temperatures and hence foraging thresholds of individual workers. Increasing proportions of foragers as a potential result of higher developmental temperatures will in turn reduce the proportion of in-hive bees, responsible for brood care. Developmental temperatures will then affect not only the foraging effort but also the population dynamics of the colony.

Based on these assumptions my thesis explores the impact of brood heating and pupal developmental temperatures on division of labour of the colony in the western honeybee (*Apis mellifera* L.):

1.) „A new device for continuous temperature measurement in brood cells of honeybees (*Apis mellifera*)" addresses the subject of temperature measurement in honeybee colonies and presents a new kind of multi-sensor thermometer.

2.) „Gaps or caps in honeybees brood nests: Does it really make a difference?" examines the question if honeybee workers take advantage of empty cells in the brood nest to improve the the efficiency of heating.

3.) „Pupal developmental temperature and behavioral specialization of honeybee workers (*Apis mellifera* L.)" delves into the influence of brood temperature on the performance of outside tasks by foragers.

4.) „Brood temperature, task division and colony survival in honeybees: a model" evaluates the importance of these empirical findings for the organization and viability of the colony.

1.5. References

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CHAPTER 2

A new device for continuous temperature measurement in brood cells of honeybees (*Apis mellifera*)

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Abstract

Nest temperature in honeybees is a crucial factor for the brood development and influences the task specialization of adult workers. Accurate and reliable data on temperature distributions are hence of major interest to understand colony function. We present a new device for temperature measurements in brood cells of honeybee combs. The instrument allows for a continuous temperature recording at the bottom of 768 brood cells. In contrast to previous techniques, we can record the complete temperature history of individual developing larvae under natural conditions in the hive. The device consists of a dense grid of thermistors, connected to a computer for the recording and display of the temperature data. Software is provided to graphically display the temperature profile across the comb in false colors.

CHAPTER 3

Gaps or caps in honeybees brood nests: Does it really make a difference?

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Abstract

Honeybee (*Apis mellifera*) workers maintain brood nest temperatures at about 35°C by activation of their flight muscles. In the capped brood area there are always some cells scattered containing no brood. These empty cells are called “gaps”. Recently honeybee workers were observed to enter these gaps when heating the brood. A theoretical model predicted a significant increase in the thermoregulation efficiency if workers took advantage of these gaps since the heat produced is directly transferred to the adjacent brood cells. We tested this model by recording temperatures of 7x7cm brood pieces with and without gaps using multi-sensor thermometers and experimental groups of 150 honeybee workers. We neither found differences in the slope of the temperature increase as predicted by the computer model nor in the maximal temperatures. We conclude that honeybee workers may not intentionally use empty cells in the nest for brood heating and the loss of brood due to the gaps may trade off the potentially higher heating efficiency.

CHAPTER 4

Pupal developmental temperature and behavioral specialization of honeybee workers (*Apis mellifera* L.)

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Abstract

Honeybees (*Apis mellifera*) are able to regulate the brood nest temperatures within a narrow range between 32°C and 36°C. Yet this small variation in brood temperature is sufficient to cause significant differences in the behavior of adult bees. To study the consequences of variation in pupal developmental temperature we raised honeybee brood under controlled temperature conditions (32°C, 34.5°C, 36°C) and individually marked more than 4400 bees, after emergence. We analyzed dancing, undertaking behavior, the age of first foraging flight, and forager task specialization of these workers. Animals raised under higher temperatures showed an increased probability to dance, foraged earlier in life, and were more often engaged in undertaking. Since the temperature profile in the brood nest may be an emergent property of the whole colony, we discuss how pupal developmental temperature can affect the overall organization of division of labor among the individuals in a self-organized process.

CHAPTER 5

Brood temperature, task division and colony survival in honeybees: a model

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Abstract

One of the mechanisms by which honeybees regulate division of labour among their colony members is age polyethism. Here the younger bees perform in-hive tasks such as heating and the older ones carry out tasks outside the hive such as foraging. Recently it has been shown that the higher developmental temperatures of the brood, which occur in the centre of the brood nest, reduce the age at which individuals start to forage once they are adult. It is unknown whether this effect has an impact on the survival of the colony. The aim of this paper is to study the consequences of the temperature gradient on the colony survival in a model on the basis of empirical data.

We created a deterministic simulation of a honeybee colony (*Apis mellifera*) which we tuned to our empirical data. In the model in-hive bees regulate the temperature of the brood nest by their heating activities. These temperatures determine the age of first foraging in the newly emerging bees and thus the number of in-hive bees present in the colony. The results of the model show that variation in the onset of foraging due to the different developmental temperatures has little impact on the population dynamics and on the absolute number of bees heating the nest unless we increase this effect by several times to unrealistic values, where individuals start foraging up to 10 days earlier or later. Rather than on variation in the onset of foraging due to the temperature gradient it appears that the survival of the colony depends on a minimal number of bees available for heating at the beginning of the simulation.

CHAPTER 6

Summary

Honeybee nest temperature is a potentially crucial factor for population dynamic and division of labour in the colony, since it influences not only the development of the brood but also the behavioural performance of the workers in their later adult life. It is hence of particular interest to obtain accurate and reliable data on the temporal and spatial temperature distribution in the brood nest. In order to achieve this purpose, we developed a new device for temperature measurement in honeybee combs. Contrary to established techniques of temperature record in honeybee colonies (i.e. using thermocouples or infrared thermography), the new method allows a continuous temperature measurement in close proximity to the brood under near natural conditions in the colony and with a high spatial and temporal resolution. The instrument consists of a grid of 256 thermistors with a negative temperature coefficient, which results in a reduced resistance if temperature rises. The sensors are consecutively addressed by a personal computer and deliver a temperature pattern of 768 cells. Recorded data are stored by the computer in a text file and further processed with a specially developed software tool. This program graphically displays the temperature distribution for any timestep in false colour and provides parameters such as mean temperature, standard deviation, minimum and maximum temperature in given area of the comb as well as the number of cells in a certain temperature range (Chapter 2).

With the help of this instrument we were able to test the impact of empty cells in the brood nest for thermoregulation. Although honeybees form a compact brood nest, there are always some empty cells („gaps“) in the capped brood area due to the egg-laying behaviour of the queen or the removal of unviable eggs and larvae by the workers. Recently, workers were observed entering these gaps for brood incubation, which was assumed to be a very efficient way of brood heating, saving up to 37% of the incubation time. We tested these predictions by using the multi-sensor thermometers and inserting pieces of capped brood (7x7cm) with and without gaps into empty test combs. The brood was heated by groups of 150 in-hive workers. However, we neither found differences in the slope of the temperature increase nor in the maximal temperatures. We conclude, that honeybee workers do not intentionally use empty cells in the nest for brood heating but enter them only occasionally and hence gaps seem not to increase the efficiency of thermoregulation (Chapter 3).

Developmental temperatures in honeybees have been shown to influence the olfactory learning ability, the dancing behaviour and the synaptic organisation in the brain of adult

workers. To further improve our understanding of the impact of brood temperature on division of labour among members of the colony, we raised honeybee pupae in incubators set to 32, 34.5 and 36°C, marked the emerging bees individually and released them in observation hives. We investigated dancing activities, undertaking behaviour, age of first foraging and forager task specialisation. We found an increased probability to dance and to engage in undertaking as well as an earlier onset of foraging when bees developed under higher temperatures.

These results confirm former findings that brood temperature influences the behavioural performance of adult bees. Brood temperature might hence potentially affect the overall organization of the colony. The onset of foraging defines the transition from an in-hive to an outdoor worker and allocation of workers among these major fields of activity is critical for survival of the colony. It determines the investment in brood care and colony homeostasis on the one hand and in energy input as precondition for colony growth and winter survival on the other hand. Developmental temperature might fine-tune the proportion of in-hive bees and foragers in the colony by affecting the individual pace of behavioural development (Chapter 4).

We tested this hypothesis with the help of a deterministic computer model. In the simulation, the number of in-hive bees determines the temperature distribution in the brood nest. Workers developed under cool temperatures (32°C) start foraging 1 day later than workers developed under medium temperatures (35°C), whereas bees developed under hot temperatures (36°C) show a one day shortened in-hive period, which reflects our empirical findings. For the parametrization of the model, we conducted several experiments, using the multi-sensor thermometers described in chapter 2 to determine the heating efforts of foragers and in-hive bees, the impact of a single worker on the thermoregulation of the brood nest and the temperature gradient in brood combs. Results of the model were analyzed over a large parameter space. However, the results of the simulation suggest that the temperature effect, i.e. the acceleration of the behavioural development with increasing developmental temperatures, has only little impact on the population dynamic and the survival of the colony. Instead, the number of bees at the beginning of the simulation runs mainly determines the survival of the colony (Chapter 5).

Conlusion: This study confirms that pupal developmental temperature affects individual traits of adult honeybee workers. Workers developed under higher temperatures show an earlier onset of foraging as adults. However, this effect is only of minor importance for division of labour between in-hive duties and foraging on the colony level.

CHAPTER 7

Zusammenfassung

Die Temperatur im Brutnest der Honigbiene ist ein potentiell entscheidender Faktor für die Populationsdynamik und Arbeitsteilung im Bienenvolk, da sie nicht nur die Entwicklung der Brut sondern auch das Verhalten der Arbeiterinnen in ihrem späteren Leben als Adulte beeinflusst. Es ist daher von besonderem Interesse, genaue und zuverlässige Daten über die zeitliche und räumliche Temperaturverteilung im Brutnest zu erhalten. Zu diesem Zweck haben wir ein neuartiges Gerät für die Temperaturmessung in Bienenwaben entwickelt. Im Gegensatz zu etablierten Techniken der Temperaturaufnahme in Bienenvölkern (beispielsweise dem Einsatz von Thermoelementen oder Infrarotthermographie) erlaubt diese neue Methode eine kontinuierliche Temperaturmessung in unmittelbarer Nähe zur Brut und unter fast natürlichen Bedingungen innerhalb der Kolonie bei gleichzeitig hoher räumlicher wie zeitlicher Auflösung. Das Messgerät besteht aus einem Raster aus 256 Thermistoren mit negativem Temperaturkoeffizient, sogenannten Heißleitern, deren elektrischer Widerstand sinkt, wenn die Temperatur ansteigt. Die Sensoren werden nacheinander von einem Personal Computer angesteuert und liefern die Temperaturverteilung von 768 Zellen. Die aufgenommenen Daten werden in einer Textdatei abgespeichert und mittels einer speziell entwickelten Software weiterverarbeitet. Dieses Programm stellt die Temperaturverteilung zu jedem Zeitschritt graphisch dar und gibt Kenngrößen aus wie Durchschnittstemperatur, Standardabweichung, minimale und maximale Temperatur in einem gegebenen Bereich sowie die Anzahl der Zellen in einer bestimmten Temperaturspanne (siehe Kapitel 2).

Mit Hilfe dieses Messgerätes waren wir in der Lage, die Bedeutung von leeren Zellen im Brutnest für die Thermoregulation zu untersuchen. Obwohl Honigbienen ein kompaktes Brutnest anlegen, sind immer auch einzelne leere Zellen im verdeckelten Brutbereich vorhanden, die vom unregelmäßigen Eiablageverhalten der Königin oder dem Entfernen von Eiern oder Larven durch die Arbeiterinnen herrühren. Es wurde kürzlich beobachtet, dass

Arbeiterinnen in diesen leeren Zellen die umliegende Brut geheizt haben, wobei angenommen wurde, dass durch dieses Verhalten auf sehr effiziente Weise Wärme auf die Brut übertragen würde und dadurch bis zu 37% weniger Zeit für die Thermoregulation aufgewendet werden müsste. Wir haben diese Vorhersagen mit dem beschriebenen Messgerät überprüft, indem wir verdeckelte Brutstücke (7x7cm) mit und ohne leere Zellen in eine Testwabe eingefügt haben. Die Brut wurde von jeweils 150 Arbeiterinnen geheizt. Wir konnten dabei weder Unterschiede im Temperaturanstieg zu Beginn der Messungen noch bei den Höchsttemperaturen feststellen. Wir schließen daraus, dass Arbeiterinnen die Lücken im Brutnest nicht vorsätzlich sondern nur gelegentlich nutzen um darin zu heizen und diese leeren Zellen daher die Effizienz der Thermoregulation nicht verbessern (siehe Kapitel 3).

Es ist gezeigt worden, dass die Entwicklungstemperaturen bei Honigbienen das olfaktorische Lernen, das Tanzverhalten und die synaptische Organisation im Gehirn der adulten Arbeiterinnen beeinflussen. Um unser Verständnis der Bedeutung der Bruttemperatur auf die Arbeitsteilung zwischen den Mitgliedern einer Kolonie weiter zu verbessern, haben wir Honigbienen Puppen in Brutschränken bei 32, 34,5 und 36°C aufgezogen. Die geschlüpften Bienen wurden individuell markiert und in Beobachtungsstöcken freigelassen. Wir haben die Tanzaktivitäten, das Austragverhalten („undertaking“), das Alter des ersten Sammelfluges und Spezialisierungen für das Sammelgut untersucht. Dabei fanden wir bei Bienen, die sich unter höheren Temperaturen entwickelt hatten, eine erhöhte Wahrscheinlichkeit zu tanzen und Austragverhalten zu zeigen sowie einen frühereren Beginn der Sammeltätigkeit.

Diese Ergebnisse bestätigen frühere Forschungsergebnisse, wonach die Bruttemperatur das Verhalten der adulten Bienen beeinflusst. Sie kann sich daher potentiell auf die Gesamtorganisation des Bienenvolkes auswirken. Der Beginn der Sammeltätigkeit stellt für eine Arbeiterin den Übergang von Innendienst- zu Außendiensttätigkeiten dar und die Verteilung von Arbeiterinnen zwischen diesen beiden Hauptbetätigungsfeldern ist von entscheidender Bedeutung für das Überleben eines Bienenvolkes. Es werden dadurch die Investitionen festgelegt, die auf der einen Seite in die Aufzucht des Nachwuchses und der Aufrechterhaltung des Volkes fließen und auf der anderen Seite in den Energieeintrag, als Voraussetzung für die Volksentwicklung und eine erfolgreiche Überwinternug. Die Entwicklungstemperatur könnte sich als wichtiger Faktor zur Feineinstellung des Anteils der Innendienstbienen und der Sammlerinnen heraustellen, indem sie an den individuellen Geschwindigkeiten in der Verhaltensentwicklung angreift (siehe Kapitel 4).

Mit einem deterministischen Computermodell haben wir diese Hypothese überprüft. In der Simulation bestimmt die Anzahl der Innendienstbienen die Temperaturverteilung im Brutnest. Arbeiterinnen die sich unter kälteren Bedingungen (32°C) entwickelt haben beginnen ihre Sammeltätigkeit einen Tag später als Arbeiterinnen die sich unter mittleren Temperaturen (35°C) entwickelt haben, wohingegen Bienen, die sich unter höheren Temperaturen (36°C) entwickelt haben eine um einen Tag verkürzte Innendienstperiode zeigen, was unseren empirischen Befunden entspricht. Um das Modell zu parametrisieren haben wir verschiedene Experimente durchgeführt, bei denen wir mit Hilfe des in Kapitel 2 beschriebenen Temperaturmessgerätes die Heizleistungen von Sammlerinnen und Innendienstbienen bestimmten, den Anteil einer einzelnen Biene an der Thermoregulation des Brutnestes sowie den Temperaturgradienten in der Brutwabe. Die Ergebnisse des Modells wurden über einen weiten Bereich des Parameterraumes analysiert. Die Ergebnisse legen allerdings nahe, dass der Temperatureffekt, also die Beschleunigung der Verhaltensentwicklung durch höhere Enwicklungstemperaturen, nur einen geringen Einfluss auf die Populationsdynamik und das Überleben des Bienenvolkes hat. Stattdessen bestimmte in erster Linie die Anzahl der Bienen zu Beginn eines Simulationslaufes das Überleben des Bienenvolkes.

Schlussfolgerung: Diese Arbeit bestätigt, dass Entwicklungstemperaturen während der Puppenphase individuelle Eigenschaften von Arbeiterinnen der Honigbiene beeinflussen. Arbeiterinnen die sich bei höheren Temperaturen entwickelt haben, zeigten als Adulte einen früheren Beginn der Sammeltätigkeit. Dieser Effekt ist allerdings für die Arbeitsteilung zwischen Innendienst- und Sammeltätigkeiten im Bienenvolk nur von untergeordneter Bedeutung.

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APPENDIX

Curriculum vitae

Personal information

Name:	Matthias Adolf Becher
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Education

2003-2010:	PhD at the Martin-Luther Universität Halle-Wittenberg, Germany. Dissertation thesis: The influence of developmental temperatures on division of labour in honeybee colonies Supervised by Prof. Dr. Robin F.A. Moritz and Prof. Dr. Charlotte K. Hemelrijk
2002-2003:	Diploma thesis: “Classification of the extinction risk of animal populations on the basis of population dynamic parameters” at the Julius-Maximilians Universität, Würzburg, Germany. Supervised by Prof. Dr. H.-J. Poethke
1999-2003:	Study of Bioloy (Zoology, Microbiology, Botany) at the Julius-Maximilians Universität, Würzburg, Germany
1996-1999:	Basic studies in Biology at the Ruprechts-Karls-Universität, Heidelberg, Germany
1994-1995:	Civilian service
1985-1994:	Grammar School: Kurpfalz-Gymnasium Schriesheim, Germany

Publications and Editorial work

Becher MA, Scharpenberg H, Moritz RFA (2009) Pupal developmental temperature determines foraging specialisation of adult honeybee workers (*Apis mellifera* L.). J Comp Phys A 195:973-679 (DOI: 10.1007/s00359-009-0442-7)

Becher MA, Moritz RFA (2009) A new device for continuous temperature measurement in brood cells of honey bees (*Apis mellifera*). Apidologie 40:577-584 (DOI: 10.1051/apido/2009031)

Becher MA, Hildenbrandt H, Hemelrijk CK, Moritz RFA: Brood temperature, Task division and Colony survival in honeybees: a model. Ecological Modelling (DOI: 10.1016/j.ecolmodel.2009.11.016)

Becher MA, Moritz RFA: Gaps or caps in honey bees brood nests: Does it really make a difference? in prep.

Kaatz HH, **Becher M**, Moritz RFA (Eds.) (2005) Bees, ants and termites: applied and fundamental research. International Union for the Study of Social Insects (German speaking section), Halle

Declaration on the Author Contributions

1. A new device for continuous temperature measurement in brood cells of honeybees (*Apis mellifera*)
Apidologie (2009) 40:577-584. DOI: 10.1051/apido/2009031
Becher MA, Moritz RFA

I constructed the prototype of the device, developed the software and wrote the manuscript. RFA Moritz supervised the project and provided helpful technical suggestions.

2. Gaps or caps in honeybees brood nests: Does it really make a difference?
Becher MA, Moritz RFA
submitted to Naturwissenschaften, rejected (28. December 2009) with opportunity to resubmit

I performed the experiments, analysed the data and wrote the manuscript. RFA Moritz supervised the work and provided helpful discussions.

3. Pupal developmental temperature and behavioral specialization of honeybee workers (*Apis mellifera* L.)
Journal of Comparative Physiology A (2009) 195:673–679 DOI: 10.1007/s00359-009-0442-7
Becher MA, Scharpenberg H, Moritz RFA

I performed the experiments, analysed the results and wrote the manuscript. H Scharpenberg helped with the data collection in the first year. RFA Moritz supervised the work and provided helpful discussions.

4. Brood temperature, task division and colony survival in honeybees: A model
Ecological Modelling (2009) DOI: 10.1016/j.ecolmodel.2009.11.016
Matthias A. Becher, Hanno Hildenbrandt, Charlotte K. Hemelrijk, Robin F.A. Moritz

I designed, performed and analysed the empirical experiments. I further developed the model, performed the analysis and wrote the manuscript. H Hildenbrandt provided helpful suggestions for a first version of the model. CK Hemelrijk supervised a part of the project and edited the manuscript. RFA Moritz supervised the project and made valueable suggestions.

Erklärung

Hiermit erkläre ich, dass diese Arbeit von mir bisher weder der Naturwissenschaftlichen Fakultät I der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht wurde.
Ich erkläre, dass ich mich bisher noch nicht um den Doktorgrad beworben habe.
Ferner erkläre ich, dass ich diese Arbeit selbständig und nur unter Zuhilfenahme der angegebenen Hilfsmittel und Literatur angefertigt habe.

Halle (Saale), den 6. Januar 2010

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Matthias A. Becher