

# Preimaginal and Adult Experience Modulates the Thermal Response Behavior of Ants

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## Summary

Colonies of social insects display an amazing degree of flexibility in dealing with long-term and short-term perturbations in their environment. The key organizational element of insect societies is division of labor. Recent literature suggests that interindividual variability in response thresholds plays an important role in the emergence of division of labor among workers (reviewed in [1, 2]). Genetic variation can only partly explain the variability among workers. Here we document the effects of both preimaginal and adult thermal experience on the behavioral differentiation of *Camponotus rufipes* ant workers. We show that preimaginal temperature (22°C or 32°C during pupal stage) affects temperature-response thresholds and temperature preferences of adult brood-tending workers. We further show that brood-carrying experience gathered as adult during several repeated temperature increases modifies thermal behavior. Experienced workers showed a faster transition from first sensing the temperature stimulus to responding with brood translocation. Developmental plasticity of workers provides a colony with flexibility in dealing with thermal variations and constitutes an important mechanism underlying interindividual variability. Adult thermal experience further fine tunes the behavioral response thresholds and reinforces behavioral differentiation among workers.

## Results and Discussion

Colonies of *Camponotus rufipes* build above-ground nest structures. Nest mounds are permeated by several brood chambers, and both daily and seasonal cycles in nest temperatures occur (Figure 1). As in the majority of ant species, workers regulate the temperature of their brood by relocating it among the numerous nest chambers, selecting temperatures most beneficial for brood development [3]. We used this brood-carrying behavior to investigate the impact of preimaginal and adult thermal experience on the temperature-response behavior of adult workers.

### Preimaginal Thermal Experience

We exposed a total of 702 *C. rufipes* pupae to one of two ecologically relevant temperatures (32°C: 382 pupae; 22°C: 320 pupae). Time from pupation to eclosion was less than half in pupae that developed at 32°C compared to 22°C (13.6 ± 1.8 days and 34.2 ± 3.0 days, respectively;  $T = 88.69$ ;  $p < 0.001$ ,  $t$  test). Mortality rates did not significantly differ between the two treatment groups (32°C: 35.9%; 22°C: 41.3%; Pearson's  $\chi^2 = 2.14$ ;  $p = 0.14$ ;  $\chi^2$  test). After

eclosion, workers were transferred to a 25°C climatic chamber, where they remained for  $33 \pm 4$  (range: 25–42) days before experiments started. We then compared the thermal behavior of the adult workers, addressing the question of whether individual temperature-response behavior was shaped by preimaginal thermal experience.

First, we exposed 12 worker groups (5–7 workers, 20 brood items) from each of the two treatments (groups@22 and groups@32) to a gradual increase in floor temperature of a test arena (A1; Arena Experiment) and recorded their behavioral responses. Temperature during pupal development had a significant effect on the thermal response behavior of the adult brood-tending workers (Figure 2). Within groups@22, the first worker picked up brood at significantly lower temperatures, i.e., had a lower response threshold, than within groups@32. Workers in groups@22 also moved the first brood item from A1 to a second, attached arena (A2) at lower temperatures, i.e., sooner, and completely removed all brood from A1 at lower temperatures than in groups@32 (Figure 2).

In groups@22, more workers participated in brood transfer compared to groups@32 ( $4.5 \pm 0.7$ ,  $n = 10$  groups and  $3.6 \pm 0.4$ ,  $n = 9$  groups, respectively;  $T = 3.39$ ;  $p < 0.01$ ;  $t$  test; only groups with six workers were considered).

Next, we examined the temperature preferred for brood location in groups of workers from the two treatments. Workers that carried brood out of the increasingly warm A1 were confronted with a choice of four different floor temperatures in the attached A2 (Arena Experiment; Figure S1, available online). In this short-term-preference test, brood was usually scattered across several of the four floor sections of A2. When comparing the floor sections containing the majority (median 85%, range 45%–100%) of brood items, the two treatment groups did not differ in their thermal preference for brood location ( $p = 0.4$ , Fisher's exact probability test).

We then analyzed the long-term temperature preference of groups of workers. Workers with brood were allowed to move onto a temperature gradient and remained undisturbed during 5 consecutive days and 4 nights (Gradient Experiment). Temperature during development had a significant effect on the temperature preference for brood location. Groups@22 consistently preferred higher temperatures for brood location compared to groups@32 tested in parallel on the same gradient (Table 1). During the first day after moving onto the gradient, workers often showed an overshooting temperature preference with brood scattered widely along the gradient. An overshooting response after being suddenly exposed to a change in stimulus has also been described in fire ants [4] and presumably explains why we found no difference in short-term temperature preference for brood location in the arena experiment. From the second day on, brood was moved in a daily cycle within a relatively limited temperature range on the gradient (Figure S2). A daily cycle was also found in short-term temperature preference and in temperature sensitivity (Table S1; Figure S3), corresponding to findings in ants [3, 5–8] and nonsocial insects [9, 10].

Our results clearly document that the thermal behavior of brood-tending workers is influenced by the temperature conditions experienced during their pupal development. This

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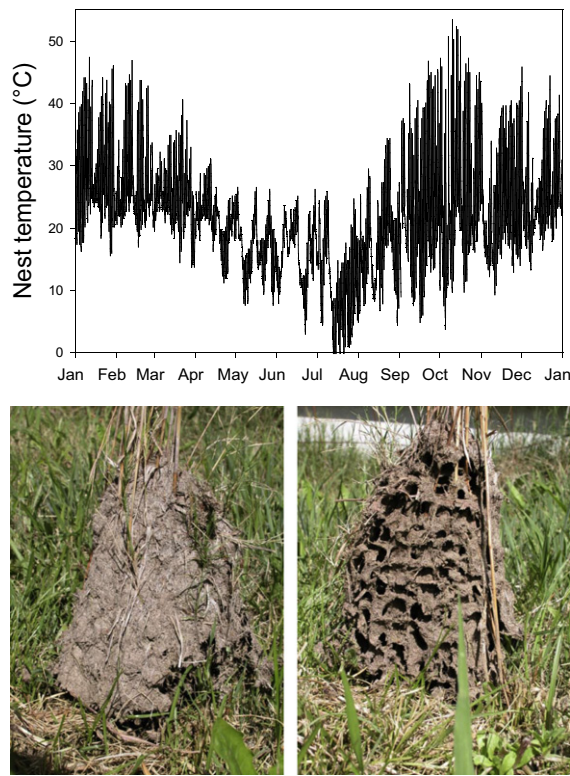


Figure 1. Colonies of *Camponotus rufipes* Experience Both Daily and Seasonal Cycles in Nest Temperature

Core nest temperature of a field nest measured every 90 min during one year in Formosa, Argentina with Gemini Tinytag data loggers. The above-ground nest structure is built with plant fragments (bottom left) and is permeated by numerous brood chambers in which different temperatures prevail (bottom right shows vertically opened nest). Pictures: O. Geissler.

developmental plasticity was expressed long after treatment. After eclosion and prior to the experiments, workers of both treatment groups had spent at least 3 weeks at 25°C. Thus, the differences found in thermal behavior were not induced by any recent experience causing e.g., habituation, but solely by the difference in temperature experienced during pupal development.

Numerous effects of preimaginal experience on adult behavior in insects are documented, e.g., preimaginal odor learning (imprinting) influencing both environmental and food preferences [11, 12] or brood recognition in ants [13]. In honey bees (*Apis mellifera*), deviation from the normal brood temperature has been shown to impair recruitment behavior and learning abilities [14, 15]. Given that honey bees are well known for their ability to keep the temperature of their brood exceedingly stable, it remains unclear whether and how these effects of temperature on adult behavior relate to division of labor and organization of work in a functioning colony.

The two temperatures selected for pupal development in our experiment reflect conditions actually occurring in nests of *C. rufipes* over the course of a year, and sometimes daily (Figure 1). Temperatures around 30°C represent the optimum developmental temperature reported for many ant species [3, 16], whereas temperatures exceeding 32°C will negatively affect development and can cause brood mortality [17].

What are the ecological implications of our findings on phenotypic plasticity in response to thermal conditions during

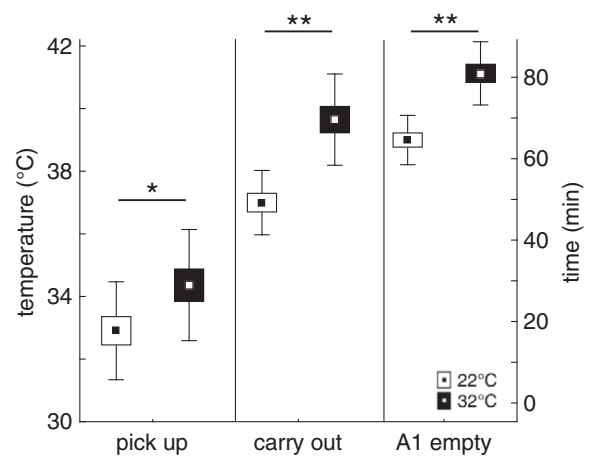


Figure 2. Preimaginal Thermal Experience Modulates Group Response to Increasing Temperatures

Twelve groups of workers+brood from each of the two treatments (22°C and 32°C pupal temperature) experienced a gradual increase in floor temperature in a test arena (A1; Arena Experiment). Group response differed depending on temperature experienced during pupal stage ( $F_{(3, 20)} = 10.79$ ;  $p < 0.001$ , one-way ANOVA). Within groups@22, the first brood was picked up at significantly lower temperatures than within groups@32 ( $p < 0.05$ ;  $n = 12$ ; least significant difference [LSD] post-hoc test), the first brood was carried out of A1 at lower temperatures ( $p < 0.001$ ;  $n = 12$ ), and A1 was completely emptied of brood at lower temperatures than in groups@32 ( $p < 0.001$ ;  $n = 12$ ). Means  $\pm$  standard error (SE) (boxes)  $\pm$  SD (whiskers) are shown.

development? *C. rufipes* workers that develop at 32°C exhibit higher heat tolerance before evacuating brood, fewer workers participate in brood carrying, and they select lower temperatures on the gradient than workers that develop at 22°C. In summer, temperatures exceeding 32°C are common in *C. rufipes* nests (Figure 1). Responding only to severely high temperatures and translocating brood to temperatures that are slightly below the optimum presumably prevents brood-tending workers in summer from having to relocate brood frequently, thus saving time and energy. In contrast, workers developing at lower temperatures, e.g., during springtime, have a lower heat tolerance, as shown by evacuation of brood

Table 1. Temperature Preference for Brood Location of Worker Groups from the Two Treatments (Gradient-Experiment).

Pupal Temperature	Group	Temperature Preference	
		Mean $\pm$ SD (°C)	Range (°C)
22°C	A	31.2 $\pm$ 0.4	29.1–33.5
22°C	B	31.6 $\pm$ 0.2	30.1–32.5
22°C	C	31.2 $\pm$ 0.2	30.4–33.4
22°C	D	31.1 $\pm$ 0.3	29.3–33.5
32°C	A	30.2 $\pm$ 0.5	27.7–31.9
32°C	B	30.2 $\pm$ 0.4	28.8–32.1
32°C	C	30.1 $\pm$ 0.5	29.9–34.6
32°C	D	29.9 $\pm$ 0.6	28.6–33.3

Mean location and range of distribution of 20 brood items on a temperature gradient (26°C–39°C), recorded every hour during 4 successive days and 3 nights ( $n = 83$  for each group; first day and night of the experiment did not enter analysis; see Figure S2). Groups from the 22°C treatment selected significantly higher mean temperatures for the location of brood: groups@22: 31.3°C  $\pm$  0.2°C; groups@32: 30.1°C  $\pm$  0.1°C;  $T = 13.76$ ;  $p < 0.01$ ; t test for paired samples.

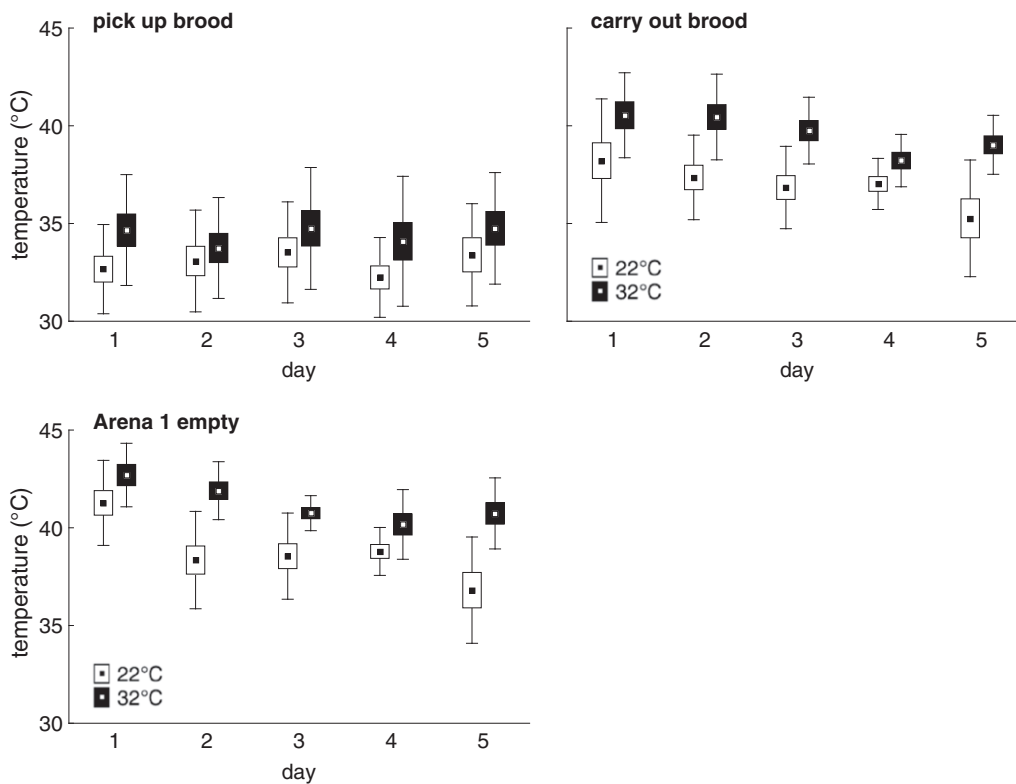


Figure 3. Adult Thermal Experience Modulates Group Response to Temperature Increase

Twelve groups of workers from each of the two treatments were tested on four ( $n = 20$ ) or five ( $n = 4$ ) consecutive days (Arena Experiment). With increasing experience, the temperature at which the first brood in each group was picked up did not change significantly ( $F_{(8, 98)} = 0.52$ ;  $p = 0.8$ ; ANOVA for repeated measurements). However, the first brood was carried out of A1 at significantly lower temperatures ( $F_{(8, 90)} = 2.46$ ;  $p < 0.05$ ), and A1 was emptied of brood at significantly lower temperatures with increasing experience ( $F_{(8, 86)} = 4.00$ ;  $p < 0.01$ ). Means  $\pm$  SE (boxes)  $\pm$  SD (whiskers) are shown.

at lower temperatures. These workers experience superoptimal nest temperatures less frequently; instead, nest temperature in spring often lies far below the optimum for brood development. Therefore, heat may represent a rare and valuable resource. Under such conditions, workers may utilize the available heat maximally by responding in large numbers and selecting the upmost edge of the temperature range beneficial for brood development, with only a low risk of exposing brood to superoptimal temperature conditions. Thus, differences in thermal experience during the pupal stage between spring and summer workers may lead to different strategies in coping with the naturally occurring daily temperature cycle. Similar strategies for the control of brood temperature are known from interspecific comparisons of related ant species [6] and honey bees [18] from different climates, where nurse workers from tropical species exhibit a higher heat tolerance than those from temperate species.

In addition to providing a colony with workers adapted for seasonal variations, developmental plasticity may also represent an important mechanism providing the colony with inter-individual variability among workers present in the nest at one time. Brood chambers providing the most beneficial temperatures may already be occupied, and brood will therefore be distributed across several chambers with varying temperatures. Consequently, workers emerging at the same time will differ in their preimaginal temperature experience and thus in their temperature-response thresholds, resulting in division of labor for the task of brood carrying. Differences in temperature or other environmental factors during brood development

not only may influence temperature-response thresholds, but also may impact response thresholds for other task-related stimuli. If indeed interindividual variability is beneficial for colony organization, increased plasticity in response to, e.g., environmental perturbations may be a trait selected for, especially in species with low genetic diversity within colonies [19]. The main focus of studies investigating the proximate mechanisms underlying interindividual variability in social insects has so far been on the genetic basis of variance. The benefits gained by an increased genetic diversity through multiple mating have been documented (reviewed in [20]). Similarly, the unusually high genetic recombination rates found in social Hymenoptera have been discussed as a mechanism increasing worker diversity [20, 21]. We propose that susceptibility to environmental fluctuations represents a further important factor generating variance in behavioral traits.

#### Adult Thermal Experience

The ecological success of social insects is often attributed to an increase in efficiency through division of labor, on the basis of the assumption that specialists are more effective in performing their tasks compared to generalists (e.g., [22–25], but see [26]). The importance of experience has been shown for successful task execution in the context of foraging (e.g., [23, 27, 28]); however, little is known about the link between experience, individual response thresholds, and individual efficiency [29]. We repeatedly exposed groups of individually marked workers to a temperature increase (Arena Experiment). Our results show that the thermal response behavior

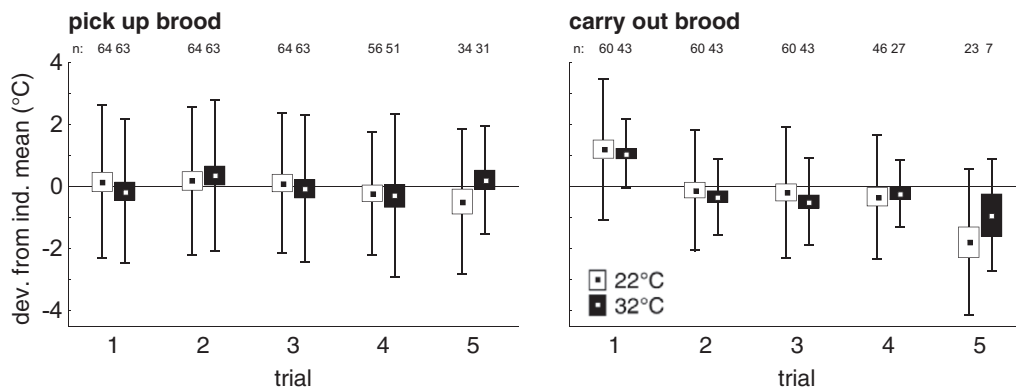


Figure 4. Adult Thermal Experience Modulates Individual Response Thresholds

Experience gathered in the course of five successive trials did not significantly modify the temperature at which a worker first picked up brood when floor temperature of a test arena increased (A1; Arena Experiment; workers from 22°C pupal temperature and 32°C pupal temperature; both  $p > 0.05$ ; Spearman-Rank correlation). However, with increasing experience, the temperature at which a worker first carried out brood of A1 decreased significantly (Rho:  $-0.29$  and  $-0.38$  for workers from groups@22 and groups@32, respectively; both  $p < 0.05$ ; Spearman-Rank correlation). For every trial in which a worker responded, the difference between responded temperature in this trial and mean individual response temperature across all responded trials was calculated. Individual response values were ordered successively, skipping nonresponded trials. Means  $\pm$  SE (boxes)  $\pm$  SD (whiskers) are shown. Numbers above symbols denote sample sizes. Only workers that responded at least three times were included into analysis.

of brood-tending *C. rufipes* workers is modified as a result of experience gathered in preceding similar situations.

In groups that experienced the same temperature increase several times, the temperature at which the first brood item was picked up remained unchanged over successive trials. However, the first brood item was carried out of the test arena A1, and A1 was completely emptied of brood, at lower temperatures, i.e., sooner with increasing experience (Figure 3). This change in group response was based on a change in individual response behavior. Whereas the first response to an increase in temperature measured in each worker, picking up brood, remained unchanged, response thresholds for carrying brood out of A1 decreased, i.e., workers carried out brood at lower temperatures and therefore sooner over successive trials (Figure 4).

Reinforcement of response thresholds through experience has been suggested in theoretical work [30] and empirically demonstrated for thermoregulating bumble bees [29]. Our results show reinforcement of only one of the two measured behavioral thresholds in *C. rufipes* workers. Although the initial behavioral response, i.e., picking up brood, is not modified through experience, the behavioral transition to an effective behavioral response (carrying away brood) is accelerated with experience. Thus, experienced workers are no more sensitive to the stimulus than inexperienced workers, but they are far more effective. This is an important distinction, not detected in previous studies [29] and not considered in existing threshold models [2, 30].

Experiencing success in performing a task (foraging) has been shown to generate behavioral differentiation among ant workers [31]. Similarly, a change in the behavioral response thresholds of experienced brood-carrying individuals modulates the response at the colony level, resulting in an acceleration of the whole process of brood translocation [25]. Behavioral differentiation among workers in an insect colony can thus arise from differences in recent experience at performing a task.

Our findings demonstrate that heterogeneity among workers is increased through variability in both preimaginal and adult experience. Colony phenotype is a product not

only of the genetic variability among workers in a colony; it is also shaped by individual experience. We are only beginning to understand the role of individual experience in the social organization of insect societies.

#### Experimental Procedures

##### Animals

Experiments were performed in the laboratory with workers from one *C. rufipes* colony (founding queen collected at La Pedrera, Uruguay in 2002). The colony was kept in a climatic chamber at 25°C and 50% relative humidity (RH). A large colony fragment including all brood stages was moved to a separate box. From this box, two experimental groups were established by collecting all newly spun pupae every morning and equally distributing them between two climatic chambers (22°C and 32°C), where they were kept together with 5–10 previously marked workers in small plastic boxes (pupae boxes) with plaster floors (8.5 × 8.5 × 6 cm). Pupae boxes in the two climatic chambers were checked for emerged workers (callows) every morning. Callows were transferred to new nest boxes together with five uniformly marked adult workers and brood taken from the colony and placed in the 25°C climatic chamber in groups of five to seven callows of about the same age (referred to as groups@22 or groups@32 herein). Workers were individually marked and remained in the 25°C chamber for 33 ± 4 (25–42) days before they were tested. All boxes received fresh food daily (sucrose water, Bhatkar diet [32], and frozen cockroaches) and experienced a light-dark 12:12 hr regime (lights-on: 8:00 a.m.).

##### Arena Experiment

Arena 1 (A1; 7.5 × 5.5 × 2 cm) connected to Arena 2 (A2; 7 × 4 × 2 cm) via a tube (7 cm) that could be closed by a sliding door (see Figure S1). Both arenas had water-filled containers at two sides, keeping RH between 50% and 60%. A1 was placed on a heating plate connected to a water bath that could be programmed to a gradual temperature increase (F25 ME, Julabo Labortechnik GmbH; Germany). The floor of A2 contained four independent heat sources inserted from underneath (Peltier elements; 1.5 × 1.5 cm) and separated by a narrow plastic strip to avoid heat conduction between the plates. The heat sources were feedback controlled ( $\pm 0.7^\circ\text{C}$ ). The temperatures on the four floor sections of A2 were 28°C–29.5°C (section 1), 30°C–31.5°C (section 2), 32.5°C–33.5°C (section 3), and 34°C–35°C (section 4). Floor temperature of A1 and of the four sections of A2 was measured and recorded with thermal sensors (K-type; NiCr–Ni-type) connected to a thermometer with corresponding software (Conrad Electronics 309/K204).

In a first step, we measured the response of brood-tending workers to an increase in floor temperature. A group of 5–7 individually marked workers

together with brood (10 pupae and 10 larvae) was transferred to A1 and left undisturbed at  $30.6^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$  floor temperature for 60 min. During the following 110 min, floor temperature in A1 increased at a rate of  $0.13^{\circ}\text{C}/\text{min}$  to  $45.1^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$ . For each worker, we recorded the temperature at first picking up of brood (defined as holding brood between mandibles for at least 10 s while standing still or moving around) and at first carrying brood out of A1 to A2.

In a second step we measured the temperature preference of the brood-carrying workers by presenting them a choice of four different temperatures in A2. As soon as all brood had been moved from A1 to A2, the connection between both arenas was closed. One hundred and twenty minutes after the ramp in A1 had reached  $45^{\circ}\text{C}$ , the distribution of brood items on the different floor sections of A2 was recorded. The floor section containing the majority of brood items entered the analysis of short-term temperature preference. Workers and brood were then transferred back to their original nest box; the experimental arena was cleaned with 60% alcohol.

Experiments with each group were performed alternately in the morning and in the afternoon. Morning experiments started at 9:00; afternoon experiments started at 14:00. Twelve groups from each rearing temperature ( $22^{\circ}\text{C}$  versus  $32^{\circ}\text{C}$ ) were tested.

In order to evaluate experience-based changes in response behavior, each group of individually marked workers was exposed to the temperature increase on four ( $n = 20$ ) or five ( $n = 4$ ) consecutive days, alternating between morning and afternoon experiments for each group. Temperatures at first picking up of brood and at first moving a brood item out of A1 were noted for every individual in the group.

#### Gradient Experiment

A Plexiglas box ( $39 \times 3.5 \times 2$  cm) with a glass floor was placed on a feedback-controlled temperature gradient ( $26.0^{\circ}\text{C} \pm 1^{\circ}\text{C}$  to  $39^{\circ}\text{C} \pm 1^{\circ}\text{C}$ ). The box was divided into two thermally equal but separated parts by a water chamber, enabling the testing of two groups, one from each temperature group, simultaneously. RH in the box was 60%–80%, and food was provided. Boxes with groups consisting of 8–9 previously tested, individually marked workers and 20 pupae were connected to the cooler end of the gradient. Once workers had transferred all brood onto the gradient, they remained undisturbed under a 12:12 hr light:dark regime (lights on: 7:00) for 5 consecutive days and 4 nights. Location of the brood on the gradient was photographed every hour (Cyclon Webcam SL-6830, Speed Link, with VisionGS PE v1.50 Final by Sascha Keller). During the dark phase, the gradient was indirectly illuminated with a red light. Temperatures were recorded as described above. Pictures of the distribution of brood items on the gradient were analyzed with Microsoft Office Picture Manager 2003, Microsoft Corporation. Four groups of workers from each rearing temperature ( $22^{\circ}\text{C}$  versus  $32^{\circ}\text{C}$ ) were tested.

#### Data Analysis

Data were analyzed with STATISTICA for Windows, version 7.1 by StatSoft (2005). Probabilities and frequencies were tested with nonparametric statistics; for all other data that did not differ from normal distribution (Kolmogorov-Smirnov Test), parametric statistics were used. If not mentioned otherwise, results are given as mean  $\pm$  standard deviation (SD).

#### Supplemental Data

Supplemental Data include three figures and one table and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01760-6](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01760-6).

#### Acknowledgments

This study was supported by a HWP stipend to A.W. and by the Deutsche Forschungsgemeinschaft (SFB 554/TP E1). We thank four anonymous reviewers for thoughtful comments that helped improve the manuscript. We are indebted to A.G. Di Giacomo and the Götz family for providing facilities at the Reserva Ecológica El Bagual in Formosa, Argentina, where field data were collected.

Received: May 17, 2009

Revised: August 10, 2009

Accepted: August 28, 2009

Published online: November 12, 2009

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