

# The mechanism underlying the regulation of work-related behaviors in the monomorphic ant, *Myrmica kotokui*

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**Abstract** The mechanism underlying the regulation of the work performed by the members of a colony is a crucial factor in the colonial life of eusocial organisms. If the response thresholds of the workers vary, greater-than-chance variation in the prevalence of work-related behaviors (i.e., in the “working degree”) is expected, and the distribution of these behaviors should be reestablished after demographic changes. We show that greater-than-chance variation in the working degree is restored after a demographic change in the ant *Myrmica kotokui*. The working degree varied markedly among workers, and the degree of variation could not be explained by chance alone. Moreover, the degree of variation could not be attributed to intrinsic factors such as reproductive potential or age. After a demographic change, some previously inactive workers started to work, whereas some previously active workers became inactive. These shifts resulted in the restoration of a substantial amount of variation in the working degree. These observations all support the hypothesis that variance in the response threshold is the basis of the regulation of work-related behaviors in this ant.

**Keywords** Regulation of work · Social insect · Response threshold model · *Myrmica kotokui* · Ant

## Introduction

Colonies of social insects are well suited to studies of group-level optimization because they are functional units

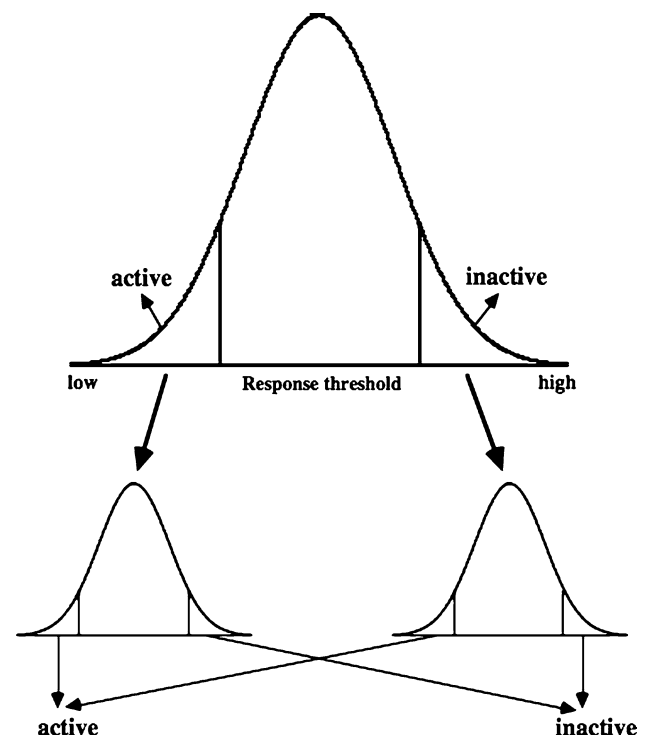
with high levels of cooperation among members (Wilson 1971; Oster and Wilson 1978; Seeley 1989; Hölldobler and Wilson 1990; Korb and Heinze 2004). The mechanisms regulating work-related behavior directly affect the efficiency of the colony as a whole. For this reason, such mechanisms are a focus of group-level adaptation in social insects (Korb and Heinze 2004). Accordingly, it is important to identify the mechanisms regulating work-related behavior in insect societies.

There are three main hypotheses for the basis of labor regulation in a social-insect colony: response threshold variation (RTM: Robinson 1992), foraging for work (FFW: Tofts and Franks 1992) and strict age polyethism (SAP: Wilson 1971). In RTM, a worker is assumed to execute a task if the task-related stimulus is higher than the worker’s response threshold. The response threshold for any given task is considered to vary among workers. A colony can allocate workers to required tasks on demand through this variation because increases in the task stimuli from unprocessed tasks induce insensitive workers to work. In FFW, a worker is assumed to search for unexecuted tasks. The processing of previously unprocessed tasks results from the search. In SAP, the tendency of workers to process tasks is strictly dependent on the age of the workers. Several studies have rejected the SAP hypothesis because removals of workers that performed specific tasks have been shown to induce other workers to execute those tasks (McDonald and Topoff 1985; Tripet and Nonacs 2004). Although the RTM and FFW hypotheses are not mutually exclusive, each mechanism has received partial support (Franks and Tofts 1994; Page et al. 1998; Pankiw and Page 2000; Jones et al. 2004; Weidenmüller 2004; see also Winston and Katz 1982; Robinson and Page 1995). Thus, further investigation is required to determine whether RTM or FFW is the basis of work performance in insect societies.

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Although FFW allows the existence of variable response thresholds among workers, in this case FFW should be considered a supplemental mechanism of RTM. If there is no variance in the response threshold, several predictions differ between the hypotheses. For example, a greater-than-chance variance in the working degree (the proportion of all worker behavior that is work-related) is expected only under RTM (see the following sections for the reason). Note that if the task stimuli vary, the working degree will vary in the absence of any variance in intrinsic response thresholds, especially if the number of behavioral observations is small. However, the use of a large number of behavioral observations will minimize this effect. For this reason, we conducted observations over a long period and made a large number of observations (see “Materials and methods”). As the variance in the working degree that would be expected based on chance alone can be estimated with simulations (see “Materials and methods”), we can conduct tests to determine which mechanism (FFW or RTM) is operating. However, several points should be addressed before any conclusions can be reached.

RTM predicts the presence of extremely inactive (“lazy”) workers in a colony because individuals with high thresholds for every task will work only rarely (Fewell and Bertram 1999; see also Fig. 1). Low levels of work-related behavior have been identified in major workers of polymorphic ants (Wilson 1976, 1984; Hasegawa 1993, but see Sempo and Detrain 2010). Long-term observations have also revealed the occurrence of lazy workers in monomorphic ants (Herbers and Cunnigum 1983; Nakata 1995). However, the inactivity of these workers may result from their reproductive effort. For example, reproductively active workers of *Pristomyrmex punctatus* (previously *P. pungens*) perform almost no tasks (Sasaki and Tsuji, 2003). Most of the previous studies of lazy workers have not investigated the reproductive potential of these workers. Consequently, the effects of such intrinsic factors, such as age and reproductive potential, on the working degree need to be examined. We investigated the behavioral changes associated with the removal of active (or inactive) workers from a colony of the typical monomorphic and monogynous ant, *Myrmica kotokui*. The above predictions were examined by comparing the working degree among workers before and after a demographic change. We posed the following four questions in this study to examine the mechanism underlying working regulation in this ant: (1) Is the variance in working degree greater than that expected based on chance alone? (2) Do the lazy workers start working in the absence of active workers? (3) Do certain active workers become inactive in the absence of inactive workers? (4) Is the distribution of the working degree restored after demographic changes? We also examined the effects of age and reproductive potential on the working



**Fig. 1** The schematic mechanism under which active and inactive workers are regularly produced as a result of variable response thresholds

degree of individuals. Based on the results of these investigations, we discuss the mechanism underlying the regulation of work-related behavior in *M. kotokui*.

## Materials and methods

### Study organism

*Myrmica kotokui* is a typical monomorphic ant (Kikuchi et al. 1999). In May of 2006 and 2007, five and three queenright colonies, respectively, were collected in the Tomakomai Experimental Forest of Hokkaido University in southwestern Hokkaido, Japan. *M. kotokui* is monogynous at this site (Kikuchi et al. 1999), and all of the collected colonies contained a single queen. The initial numbers of workers ranged from 225 to 421. The collected colonies were reared in the laboratory for 1 month before the experiments.

A total of eight experimental colonies (hereafter referred to as initial colonies) were established from each of these collected colonies. Each initial colony consisted of 150 workers, a queen, eggs and larvae. Each colony was housed in an artificial nest (plastic container with a plaster floor; 30 × 22 × 6 cm). A single square chamber (10 × 8 × 1 cm) was then set within the center of the box and was covered with a clear glass plate with a red

transparent cover. The nest space was connected to an adjacent foraging area by a 1-cm-long tunnel. Colonies were fed with commercially available insect food (Konchunomitsu DX<sup>TM</sup>, Marukan, Osaka, Japan) ad libitum.

All of the workers in a colony were individually marked with Paint Markers<sup>TM</sup> (Mitsubishi Inc., Tokyo, Japan). Ten colors and three marking points (between the eyes, pronotum and gaster) enabled us to discriminate 1000 individuals. New workers emerging from pupae were marked within a day. All the initial colonies were reared in the laboratory for 2 weeks before initiating behavioral observations.

**Behavioral observations**

To characterize the behavioral profile of each worker, we conducted observations using a scan-sampling method (Altmann 1974). During June 2006, preliminary observations of a colony were conducted to construct a behavioral catalog for this species. Worker behavior was recorded and divided into ten work and four non-work behaviors. The work behaviors were those that would directly benefit other colony members and included the following: attending the queen, attending the brood, attending other workers, trophallaxis with the queen, trophallaxis with the brood, trophallaxis with another worker, nest maintenance (chewing or licking nest material), foraging, transporting a live nestmate and handling colony materials (nest material or dead nestmate). Ants in the foraging area were considered to be foraging, irrespective of their behavior (walking or manipulating food). Four types of non-work behaviors were characterized: resting (i.e., stopping), self-grooming, eating food in the nest and walking.

After the definition of these behaviors, scan data were collected over a 32-day period from late July to late August. An observation cycle consisted of three continuous days of observations and one day without observations. In all, eight

observation cycles were conducted during the observation period. To minimize the effect of diurnal changes in social activity, each colony was scanned in the morning (9:00–10:00 hours), early afternoon (13:00–14:00 hours), and late afternoon (16:00–17:00 hours). As a result, each individual ant was observed a total of nine times per observation cycle, a total of 72 scans (9 observations × 8 cycles) for each individual. However, because we were unable to view the identification marks of ants at the back side of the transparent cover of the nest chamber during any given scan, the total number of behavioral records was less than 72 for some individuals. The degree of working (working degree) was calculated as the proportion of work behaviors relative to all behaviors of a worker. It is possible that the non-work behaviors may have unidentified functions for the colony (e.g., networking). However, the predictions of RTM are valid irrespective of the categorization of the behavior. Specifically, the restoration of a greater variance in the working degree is expected for any set of behavioral categories. It is of considerable interest to examine changes in the behavioral profiles of workers in response to demographic changes. Such an analysis is beyond the scope of this study and will be published elsewhere. Subsequent to the behavioral observations, all the workers from an initial colony (Colony ID; C2006-33, see Table 1) were stored in a deep freezer (−85 °C) to examine the relationship between the working degree and reproductive activity. Other colonies were used in the demographic change experiments (see later section).

**Variance in the working degree and its deviation from the value expected from chance alone**

It is possible that the observed variance in the working degree among individuals results from chance alone. Even if the response threshold does not vary among workers, we can still

**Table 1** Summary of usage of the experimental colonies

1st period			2nd period			
Colony ID	Number of workers	Behavioral observation	Usage	Selected workers	Number of workers	Behavioral observation
C2006-01	150	72	D	Inactive	30	72
C2006-33	150	72	BM	–	–	–
C2006-41	150	72	D	Inactive	30	72
C2006-T2	150	72	D	Inactive	30	72
C2006-T3	150	72	D	Inactive	30	72
C2007-A	150	72	D	Active	30	72
C2007-I	150	72	D	Active	30	72
C2007-M	150	72	D	Active	30	72

All the colonies were observed during 1 month before biometric measurements or a demographic change. Usage after the first observation is presented for each colony. D means “demographic change” and BM means “biometric measurements”

expect two sources of variation in working degrees, i.e., an extrinsic variance in the task stimulus and variation due to chance alone. The former factor would not affect this study because we conducted observations over a long period and collected a large number of behavior records (72 per individual). Thus, it is hard to assume specific individuals were always under low (or high) task stimuli. To test whether the observed variance statistically deviates from the variance due to chance alone, we conducted a simulation. To generate a chance distribution of the working degrees, the probability of a work-related behavior during a time step was assumed to be the average frequency of work-related behaviors in each colony. In the simulation, we considered 150 individuals, each of which performed a work-related behavior according to the given probability during a time step. After 72 time steps, we calculated the variance in the obtained working degree among these 150 individuals. The simulation was repeated 1000 times, and the distribution of the variances generated by the simulation was estimated for each colony to obtain the distribution of the variance due to chance alone. The observed variance was then compared with the generated distribution. If the observed variance exceeded the 95 % area of the generated distribution, we considered the observed variance to have deviated significantly from the expected chance value.

#### Demographic change experiments

To test changes in the working degree of inactive (or active) workers, we removed active (or inactive) workers from the colonies. In each colony, the 30 most inactive (or active) workers were selected based on their working degree in the observed 72 scans, and the other workers were removed from the colony. Only uninjured workers with more than 50 scans at the end of the first observation period were selected for the experiments. The brood/worker ratios in the new colonies (termed recolonized colonies) were held at the same levels ( $\pm 5$  %) as those of the initial colonies by adjusting the number of larvae. The 120 removed workers were stored in 99.9 % ethanol for biometric analysis. The most inactive workers were recolonized in 2006 (4 colonies) and the most active workers in 2007 (3 colonies). Simultaneous examinations of the behavioral changes in both active and inactive workers from the same colony were impossible because there was only a single queen in a colony. Behavioral observations were conducted using the procedure described above. Table 1 clarifies the structure of the data by specifying the use of each colony.

#### Effects of ant age

In the behavioral observation component of the study, newly emerged workers were marked individually within a day.

Their behaviors were recorded as for the other workers. If a worker died during the observation period, its behaviors during the 3 weeks before its death were examined. Because all the workers used in the study were dark colored at the establishment of the initial colonies, the workers that died were assumed to be mature. However, the ages of these workers were unknown. In this study, the workers that died were termed before-death workers. We examined changes in the working degree over time in the young workers and in the before-death workers. We calculated the working degree for every three-day period for the 3 weeks after (or before) the birth (or the death) of the ants and analyzed the data with a generalized linear model (GLM) to detect any trends in the working degree over time. The average working degree was then compared between young and before-death workers based on data from individuals with a minimum of 50 scans.

#### Effects of body size and reproductive potential

For the frozen colony (C2006-33), we measured the head width of workers (i.e., the width across the eyes). The length of the longest ovariole was also measured for each of the workers using a binocular microscope (SZH-ILLD, OLYMPUS, Tokyo) with a micrometer (to 0.01 mm). These measurements were used as an index of body size and reproductive development, respectively, and the reproductive potential of individuals was inferred from the length of the ovariole relative to the head width (i.e., ovariole length/head width). We correlated the working degree with the body size or the reproductive potential.

#### Statistics

For the GLM analysis, we used a logit-link function and binomial errors because proportional data is binomially distributed (Crawley 2002); however, pseudo-binomial errors were used instead of binomial errors if overdispersion of the residuals was observed within a dataset (Crawley 2002). Pearson's product-moment correlation was used to detect correlation between the working degree and the size or the reproductive potential. A meta-analysis was conducted to unify the results across multiple colonies. Differences in the average values were tested with a *t* test. It might appear that all of the analyses should be conducted with a multivariate GLM with age and reproductive potential as explanatory variables. However, as live workers are required in the demographic change experiments, reproductive potential was measured in a single colony reared for this purpose. This data structure did not allow us to use a multivariate GLM. All of the proportion data were normalized with an arcsine transformation (Sokal and Rohlf 1994). All the statistical tests were performed with the R statistical package (version 2.4.0, R Development Core Team 2006).

## Results

### Effects of age

We observed nine young and six before-death workers. The working degree did not differ significantly between the young and the before-death workers ( $t$ -test,  $t = -2.041$ ,  $df = 13$ , n.s.). The GLM analysis did not detect any significant trends in the working degree over time in either age category (young workers; GLM-quasibinomial error [ $\chi^2$ -test],  $p = 0.85$ : before-death workers;  $p = 0.34$ ). Although these results show that the age of the individual ants did not affect the working degree, this conclusion does not imply a lack of age polyethism (a change in behavioral profile with age). In fact, the most frequently observed behavior among the before-death workers was foraging ( $30.7 \pm 22.5\%$ , average  $\pm 1$  SD), whereas young workers rarely engaged in foraging ( $0.5 \pm 1.4\%$ ). This difference is statistically significant ( $t$ -test,  $t = -3.846$ ,  $df = 13$ ,  $p = 0.02$ ). These findings show that age polyethism occurred but that the working degree was not affected by the age of the workers. More detailed analyses of the relationship between age and work are important to investigate the flexible task allocation system in this species. Such an analysis is beyond the scope of this study, due to the limitation of space, but will be presented in a subsequent paper.

### Effects of body size and reproductive potential

The distribution of head width in all five colonies was unimodal in 2006 and did not deviate from normality (for all the colonies,  $p > 0.05$ , one-sample Kolmogorov–Smirnov test). *M. kotokui* is thus a typical monomorphic species. In all five colonies, a negative correlation was observed between head width and the working degree during the first observation period (for all the five colonies  $p < 0.05$ , Pearson's product-moment correlation: meta-analysis,  $p < 0.01$ ). This negative value denotes that the larger workers were more lazy. The working degree was not correlated with the reproductive potential of the dissected ants (Pearson's product-moment correlation,  $t = 0.179$ ,  $df = 102$ ,  $p = 0.859$ ). This lack of correlation indicates that although the large workers were relatively inactive, their laziness was not the result of a high reproductive potential.

### Distribution of the working degree in the initial colonies

Great variation in the working degree among workers occurred within colonies (left-hand panels of Figs. 2, 3). In each colony, although certain workers performed almost no work, most of the observed behaviors were work-related for some workers (Figs. 2a–d, 3a–c). In all of the seven

(four in 2006 and three in 2007) colonies examined, no overlap was observed between the observed variance and the variances generated by chance (Fig. 4). This result implies that the observed variances in the working degree cannot be attributed to chance alone.

Two factors that cause the working degree to vary are the variance in the intrinsic response threshold and the variance in the extrinsic task stimulus. If the variance in the extrinsic task stimulus is large, the working degree will vary, especially if the number of behavioral observations is small. For example, if a small stimulus does not result in work but a large stimulus does, the possible values of the working degree for two behavioral observations are 0, 0.5 and 1.0. However, the values of the working degree will tend to cluster around 0.5 as the number of behavioral observations increases. Thus, the use of a large number of observations over a long period will eliminate the effect of the variance in the extrinsic task stimulus. We collected 72 observations per month per individual. For this reason, the significant deviations from the variance in the working degree expected from chance alone strongly suggested that the intrinsic response thresholds varied.

### Restoration of the distribution of the working degree after the demographic change

In Figs. 2 and 3, the right-hand panels show the distribution of the working degree after the demographic change in each colony. Although only the most lazy (Figs. 2e–h) or most active (Figs. 3d–f) workers were left in the colony, large variations in the working degree were restored after the demographic change. When active workers were removed from the colony, the average working degree decreased in three of four colonies (Fig. 2;  $t$ -test,  $p < 0.01$  for 3/4 colonies; meta-analysis,  $p < 0.01$ ). When inactive workers were removed, the average working degree increased in two of three colonies (Fig. 3;  $t$ -test,  $p < 0.05$  for 2/3 colonies; meta-analysis,  $p < 0.05$ ). There is, however, no significant difference in the overall average of the working degree between the cases of removal of inactive workers (combining Fig. 2e–h) and removal of active workers (combining 3d–f;  $t$ -test,  $t = -1.765$ ,  $df = 203$ ,  $p = 0.79$ ).

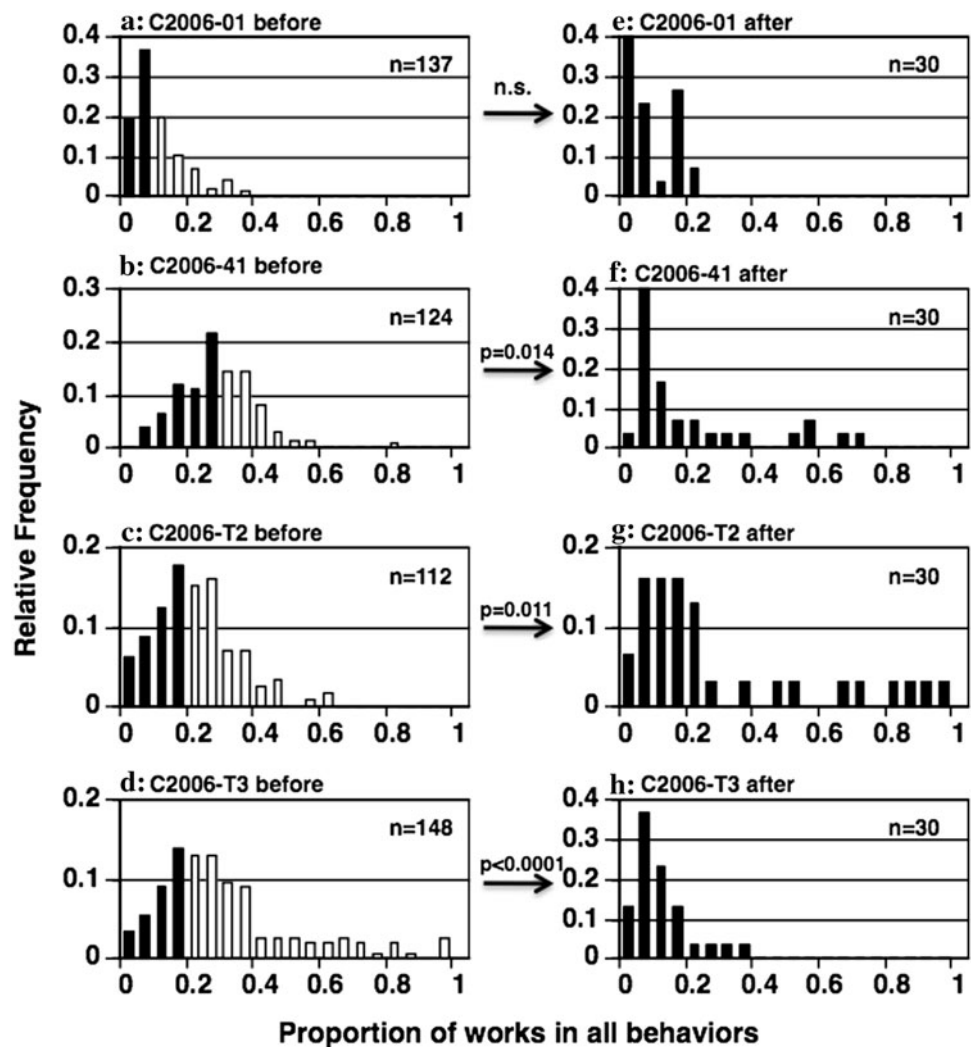
## Discussion

### Factors affecting the working degree

First, our results showed that the observed variations in the working degree could not be attributed to intrinsic factors, such as reproductive potential and age. High reproductive activity has been reported to be associated with laziness in



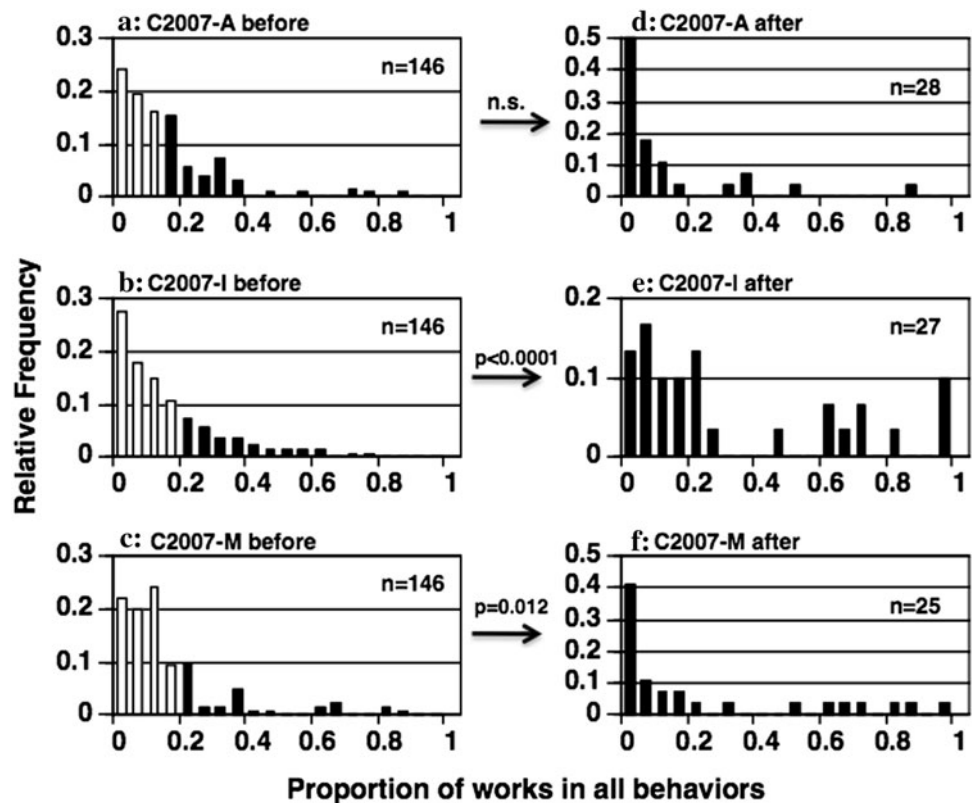
**Fig. 2** Changes in the working degree before and after the removal of active workers from the colonies. The *left-hand panels* show the distributions of the working degree before the demographic change; the *right-hand panels* show the corresponding distributions after the demographic change. The *white bars* in the *left-hand panels* represent the removed workers. The *p* values above the arrows represent the significance of the difference between the average working degree before and after the change



the ant *Pristomyrmex punctatus* (previously *P. pungens*; Sasaki and Tsuji 2003). In *M. kotokui*, however, because the degree of ovarian development was not correlated with the working degree, the observed laziness could not be explained by high reproductive activity. The GLM analyses revealed no correlation between age and the working degree, and the average working degree did not differ between the young and before-death workers. Nevertheless, this result does not mean that no age polyethism occurs in this species. The frequency of foraging was much greater in the before-death workers than in the young workers. This result shows that a behavioral change toward foraging occurred with age. However, the working degree itself was not determined by age. This result contradicts the hypothesis that SAP is the basis of working regulation in *M. kotokui* and is consistent with the results of several previous studies (Meudec and Lenoir 1982; McDnald and Topoff 1985; Tripet and Nonacs 2004). Accordingly, other factors are needed to explain the regulation of work-related behavior in *M. kotokui*.

Great variations in the working degree occurred among the workers in both the initial and the recolonized colonies (Figs. 2, 3). These variations could not be explained by chance alone (Fig. 4). This result is not consistent with any mechanism that does not include a greater-than-chance variation in the task processing rate among individuals. The variation in the working degree is due to chance alone in such a mechanism. A number of lazy workers began to work after the removal of active workers, whereas several active ants became inactive after the removal of lazy workers (Figs. 2, 3). Consequently, the large variations in the working degree were restored (Figs. 2, 3). These results are consistent with the predictions of RTM. Several previous studies have shown that task replacements by the remaining workers occur after the removal of workers engaged in specific tasks (Meudec and Lenoir 1982; McDnald and Topoff 1985; Tripet and Nonacs 2004). However, no study has demonstrated a shift in the opposite direction (active to lazy), although the occurrence of such a shift is an important prediction of RTM.

**Fig. 3** Changes in the working degree before and after the removal of inactive workers from the colonies. The *left-hand panels* show the distributions of the working degree before the demographic change; the *right-hand panels* show the corresponding distributions after the change. The *white bars* in the *left-hand panels* represent the removed workers. The *p* values above the *arrows* represent the significance of the difference between the average working degree before and after the change



Several studies have found variance in response thresholds for several tasks in social bees (Page et al. 1998; Pankiw and Page 2000; Jones et al. 2004; Weidenmüller 2004; see also Winston and Katz 1982; Robinson and Page 1995). Although additional studies are needed to determine whether the thresholds depend on the physiological status of an individual, as originally suggested (Robinson 1992; see also Franks and Tofts 1994), the present evidence, including this study, indicates that variations in response thresholds occur in insect societies. The RTM is compatible with FFW because the additional FFW under RTM will increase the task processing rates. Indeed, Tofts and Franks (1992) provided suggestive evidence of FFW in several social organisms. Thus, FFW still merits examination in social organisms. However, in *M. kotokui*, the observed distribution of working degree can not be attributed to chance alone, and this finding contradicts any mechanism that lacks a larger variation of the task processing rate among individuals than that occurring by chance.

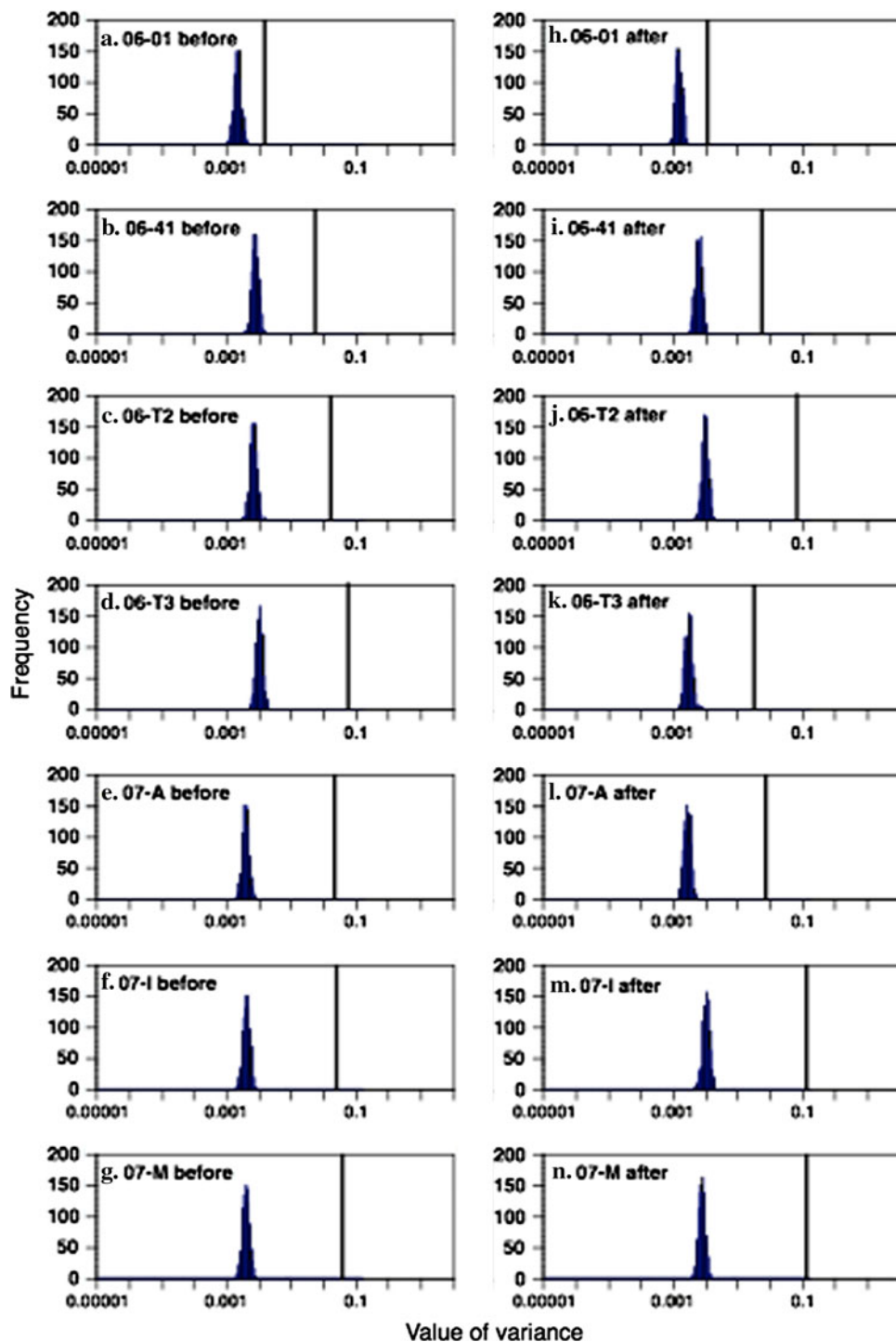
**Individual size and working degree**

Interestingly, larger individuals are lazier in *M. kotokui*. It is well known that major morphs in dimorphic ants rarely process tasks and have limited behavioral repertoires (reviewed in Hölldobler and Wilson 1990). Wilson (1985) showed that the labor activities of major workers of the

dimorphic ant, *Pheidole pubiventris*, increase in response to a relative decrease in minor workers. If major workers are assumed to have high thresholds, this pattern can be explained by the RTM (Bonabeau et al. 1996; Theraulaz et al. 1998). Although *M. kotokui* is a typical monomorphic ant, larger workers tend to be lazy. This result suggests that larger workers have higher response thresholds than smaller workers. One possible basis for this difference is that larger workers are excessively heavy. In *Temnothorax albipennis* (previously *Leptothorax albipennis*), the division of labor is related to the corpulence of the ants (Blanchard et al. 2000; Robinson et al. 2009). Hasegawa (1993) reported that the major workers of *Colobopsis nipponicus* are more corpulent and show smaller behavioral repertoires than the minor workers. Although ovarian development was not correlated with the working degree, larger workers of *M. kotokui* might be more corpulent than smaller workers. The relationship between corpulence and social activity should be investigated.

Another question that needs to be resolved is the source of the variation in the response thresholds. In the honeybee, the patriline of individuals appears to determine the threshold value (Jones et al. 2004), implying that response thresholds have a genetic basis. However, although a honeybee queen mates with many males, *M. kotokui* queens appear to mate with a single male (K. Ohkawara, pers. comm.). A low genetic diversity among workers is

**Fig. 4** The distribution of the simulated variances generated by chance alone (histograms) and the observed value of the variance (*thick vertical lines*). The *left-hand panels* are the results for the colonies before the demographic change, and the *right-hand panels* are the results after the change. All of the observed variances differ from the simulated distribution at a significance level of  $p < 0.0001$



expected in monogynous and monoandrous ant species. Thus, it is of interest to investigate how variation in response thresholds is produced in such species.

In many *M. kotokui* colonies in this study, the average value of the working degree and the variance of the working degree changed after the demographic change (see Figs. 2, 3). If a variance of the response thresholds are remained in a recolonized colony, a wide variation of the

working degree is still expected in the recolonized colony. However, because we selected relatively inactive (or active) workers for the recolonizations, the characteristics of the distribution of the response thresholds also changed. It is of interest to examine how such changes would affect the shape of distribution of the working degree. Ravary et al. (2007) showed that individual experiences affect task specialization in the parthenogenetic ant, *Cerapachys biroi*.



Their results suggest that task specialization is not determined by genotype alone. Dornhas (2008) showed that in an ant, specialists for a particular task did not have a higher task-processing efficiency than non-specialists. Consequently, such factors, in addition to the response threshold variance, merit further examination in terms of the regulation of work-related behavior in social organisms.

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