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Division of labor by division of risk according to worker life expectancy in the honey bee (*Apis mellifera* L.)

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Abstract – The hypothesis that the division of labor in foraging honey bee workers is a consequence of division of risk among foragers with differing life expectancies was tested using a dynamic programming model and field experiment. Honey bee workers collecting water were captured in the middle of one cold day and one warm day in April, May and July. We investigated whether workers infected with *Nosema apis* or workers with worn wings undertake foraging in poorer weather conditions more often than do healthy workers or workers with unworn wings. On each pair of days, the ratio of diseased workers and workers with worn wings was usually significantly higher on the cold day than on the warm day. The result that risky tasks are more often undertaken by workers with shorter life expectancy is in favor of the predictions of the model. © Inra/DIB/AGIB/Elsevier, Paris

division of labor / division of risk / life expectancy / *Apis mellifera* / *Nosema apis*

1. INTRODUCTION

Worker fitness depends on the reproductive success of the whole colony of related individuals, not only in the honey bee but also in other eusocial haplodiploids (Hamilton, 1964). Colony reproduction depends, however, on the total of nonreproductive labor carried out by workers. This demands that colony members undertake many tasks not associated with their direct reproduction, despite conflicting

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evolutionary interests between different castes and even particular nest members, manifested, for example, by worker–queen conflict over the sex ratio (Trivers and Hare, 1976; Sunström et al., 1996) or worker policing of the production of male eggs (Woyciechowski and Łomnicki, 1987; Ratnieks and Visscher, 1989).

There are suggestions that the division of nonreproductive labor influences colony survival and reproduction (Oster and Wilson, 1978; Robinson, 1992; Gordon, 1996). However, the decision on which individual in a colony undertakes which task necessitates a compromise among workers, as different tasks entail different mortality risks. Even the risk of the same task can change depending on weather conditions. External factors can lead to much higher mortality rates for tasks away from the nest than for tasks in the nest (Sakagami and Fukuda, 1968; Schmid-Hempel and Schmid-Hempel, 1984; Dukas and Visscher, 1994; but see also O'Donnell, 1996) and for tasks undertaken by foragers on a cold day as compared to a warm one. How workers reach this compromise in the division of nonreproductive labor is one of the most intriguing problems concerning insect societies.

Internal factors such as age, or more specifically life expectancy, can explain the compromise of workers in taking different risks. The fact that life expectancy differentiates workers results directly from the fact that in all eusocial colonies older individuals rear younger siblings. Although many authors have pointed out that the organization of work in the colony is influenced by internal and external factors [for a review see Robinson (1992); Gordon (1996)], only Jeanne (1986) and O'Donnell and Jeanne (1995a) showed that different levels of task risk and programmed senescence of workers create sufficient conditions for the evolution of a division of labor based on temporal polyetism. This is because task sequencing to avoid risky tasks at the beginning of life and to undertake risky tasks in old age prolongs the mean longevity of workers. On the other hand, it is well known that prolonging worker life increases the reproductive success of the colony (Schmid-Hempel, 1987; Schmid-Hempel and Wolf, 1988).

The hypothesis that the division of labor in foraging workers is a consequence of the division of risk among foragers with different life expectancies was tested using a dynamic programming model and confirmed experimentally. The model predicts that honey bee workers vary their foraging behavior with age or health status, foraging mainly under safe conditions when young or healthy and accepting risky foraging when old or sick. In the field experiment, workers collecting water on warm and cold days were examined. Their life expectancies were scored on the basis of wing wear and the presence of the *Nosema apis* Zander (Protista) parasite in the intestine.

2. THE MODEL

Let us consider bee workers choosing each day whether to stay in the nest (strategy $j = 0$) or to forage (strategy $j = 1$), depending on the weather. Weather is classified according to the risk of foraging in it, with the lowest risk for class $i = 1$ and the highest risk for $i = 160$ (the number of classes is arbitrary and adjusted to computer capacity). The probability of death during foraging one day under weather i is p_i, and the probability of weather i is c_i. Daily foraging yield is y_{ij} and always equals zero for $j = 0$, that is, for the workers staying in the nest.

Maximum worker lifespan is T, and it depends on health status. Physiological mortality (not dependent on foraging decisions) is $\mu(t)$, where t is age in days. Only workers older than 19 days are considered, because younger bees work in the nest. This cutoff age is close to the real value (Seeley, 1982).

The goal is to find the optimal strategy (stay in the nest or forage) for each age t, each weather class i and each health status (healthy or sick) to maximize the expected total yield toward the end of life T. This is a dynamic optimization problem, which will be solved here with dynamic programming (Bellman, 1957; Mangel and Clark, 1988). The discrete time unit is 1 day. Bellman's algorithm works backward. Let us consider first the last day T. It is always optimal to forage on this day, irrespective of the risk, because no more life is left. Thus the expected yield on this day is

$$F(i, T) = y_{i1} \qquad (1)$$

for all kinds of weather i. The decision whether to forage or not on day $T - 1$ depends not only on the day's weather but also on the residual yield of the last day which will be lost if the worker dies. Because the next day's weather is unknown, the residual yield for the last day under each weather multiplied by the probability that this weather will occur must be summed up across all weather classes k. Moreover, the expected residual yield must be multiplied by the age-dependent probability of surviving to age $T - 1$

$$\alpha(T-1) = \exp\left(-\mu(T-1)\right) \qquad (2)$$

for staying in the nest ($j = 0$), and for foraging ($j = 1$) also multiplied by the probability p_i of dying in weather i. Thus

$$F(i, T-1) = \alpha(T-1) \sum_{k=1}^{160} c_k F(k, T) \qquad (3)$$

for $j = 0$, that is, for staying in the nest, and

$$F(i, T-1) = y_{i1}(i) + \alpha(T-1) p_i \sum_{k=1}^{160} c_k F(k, T) \qquad (4)$$

for $j = 1$, that is, for foraging. Current yield is added only for $j = 1$, because y_{i0} equals zero. Now the value of equation (3) must be compared against equation (4), and the strategy giving higher $F(i,T - 1)$ is chosen. The procedure is repeated for all i, and optimal strategies and corresponding total yields are saved for further use.

Exactly the same procedure is repeated for $T - 2$, yielding the expressions

$$F(i, T-2) = \alpha(T-2) \sum_{k} c_k F(k, T-1) \qquad \text{for } j = 0$$

$$F(i, T-2) = y_{i1} + \alpha(T-2) p_i \sum_{k} c_k F(k, T-1) \qquad \text{for } j = 1$$

For any $t < T$, this recursive procedure is represented by

$$F(i, t) = \max_{j} \left\{ y_{ij} + \alpha(t) p_i \sum_{k} c_k F(k, t+1) \right\} \qquad (5)$$

where max means that the strategy j which maximizes the functional (5) should be chosen. Solving this problem backward to age 20 days gives the best strategy for any foraging risk at each age. In other words, for each age we find the level of risk taking that maximizes the expected yield of the whole life.

To illustrate the problem with a numerical example, we will assume that maximum longevity T equals 100 days for healthy workers and 80 for infected ones (referred to as sick hereafter). We also assume that physiological mortality is

$$\mu(t) = q\frac{T}{T-t} \qquad (6)$$

Mortality approaches infinity when t tends toward T, and parameter $q = 0.002$ defines how early in life aging has a pronounced effect on mortality. We also assume that the probability of surviving foraging is constant at 0.98 for the first 50 weather classes, then decreases with i linearly to 0.036 for $i = 160$. We assume that all weather classes are equally likely, and that yield does not depend on weather. These assumptions are not very realistic, but we shall show that they do not affect, or very weakly affect, the results we are interested in: the proportions of old or sick workers under good and poor weather. The last assumption (yield independent of weather) was used because water collection was studied here; for nectar or pollen collection, decreased yield on days with risky foraging (wind, rain, cold) would be more realistic.

The probability of surviving to a given age (l_t) under physiological mortality for healthy and sick workers is represented by the thin lines in *figure 1.* Risk taking for workers depends on health status as shown in *figure 2.* The lines on this graph represent the maximum tolerable risk of foraging for healthy and sick workers at a given age, which means that they forage at a risk lower or equal to the value at the line and stay in the nest if the risk is higher. All workers older than 19 days (all foragers in the model) should leave the nest when the daily risk of foraging is equal to or lower than 0.05, although sick workers also forage at a 0.06 probability of death. Higher risk is taken differentially, depending on health status. For example, at a risk of 0.07, healthy workers younger than 43 days should stay in the nest, and sick workers should stay if younger than 26 days. At a risk of 0.13, healthy workers should forage if older than 78 days, and sick ones if older than 60 days.

We are interested not only in age- and health-dependent risk taking, but also in the proportions of healthy and sick workers foraging under different weather conditions. These proportions can be used to test the hypothesis that workers adjust their decisions optimally.

Because we know maximal risk taking *(figure 2),* we can calculate the average probability of surviving to a given age (l_t) for workers, taking into account both physiological mortality and mortality from foraging (thick lines in *figure 1*; we must remember, however, that short-term weather anomalies may change l_t). After 19 days, when workers start to forage, the thick lines go down much faster than the thin lines do, and converge at the end of life.

The probability of surviving to a given age for healthy workers is repeated in *figure 3A.* This probability also means 'the expected number of workers at a given age' assuming a stable age structure and a stable total number of workers. The values on this graph are standardized so that the number of hatched individuals equals one ($t = 1$). To obtain the number of workers 20 or more days old we have to integrate l_t from 19 (because age 19 denotes the end of the 19th day) to infinity, and the integral is represented by the sum of the two hatched areas under this graph. The second hatched area, starting at age 42, represents the number of workers 43 days old and older. We can calculate such areas for any age. Their values are represented in *figure 3B.* Using this graph together with the information about optimal risk taking represented in *figure 2,* we can predict the number of healthy and sick bees foraging at a given risk. These numbers are marked with squares for good weather when all workers older than 19 days forage (risk $r \leq 0.05$), triangles for intermediate weather ($r = 0.07$), and asterisks for harsh weather ($r = 0.13$). Assuming a stable age distribution, a stable total worker number,

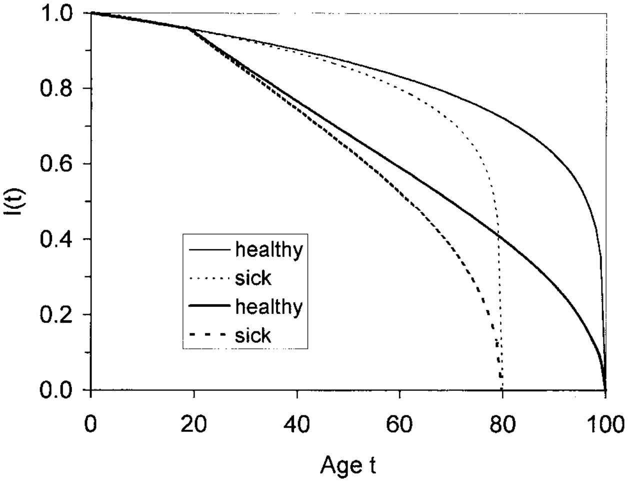

Figure 1. Probability of surviving to a given age for healthy (solid lines) and infected (broken lines) workers. Thin lines reflect physiological mortality only; thick lines also include mortality during foraging, assuming that bees behave optimally.

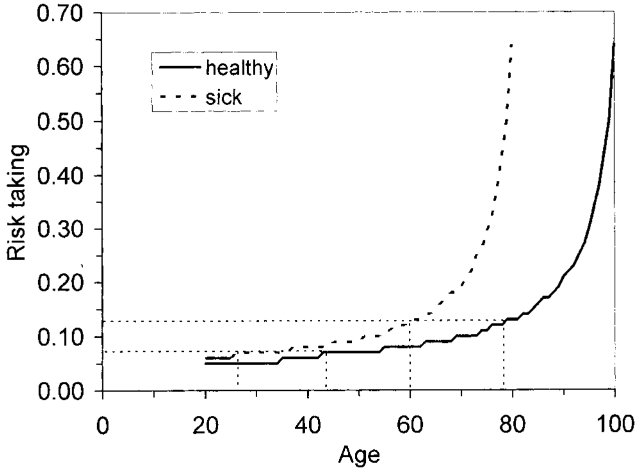

Figure 2. Risk taking for healthy (solid line) and infected (broken line) workers. Risk taking means that workers will forage if the probability of death is lower or equal to the one shown on the graph. The graph shows the ages of sick and healthy workers accepting two arbitrary risks of 0.07 and 0.13.

and 50% *N. apis* infection in 20-day-old bees in the nest, we can expect 45 % sick foragers in good weather, 54 % in intermediate weather and 56 % in harsh weather. Thus the proportion changes markedly between good weather and intermediate weather, but only slightly between intermediate and harsh weather. Although the proportion does not change, the number of foraging bees decreases significantly when the weather worsens, as can be seen from *figure 2* and *figure 3B* together.

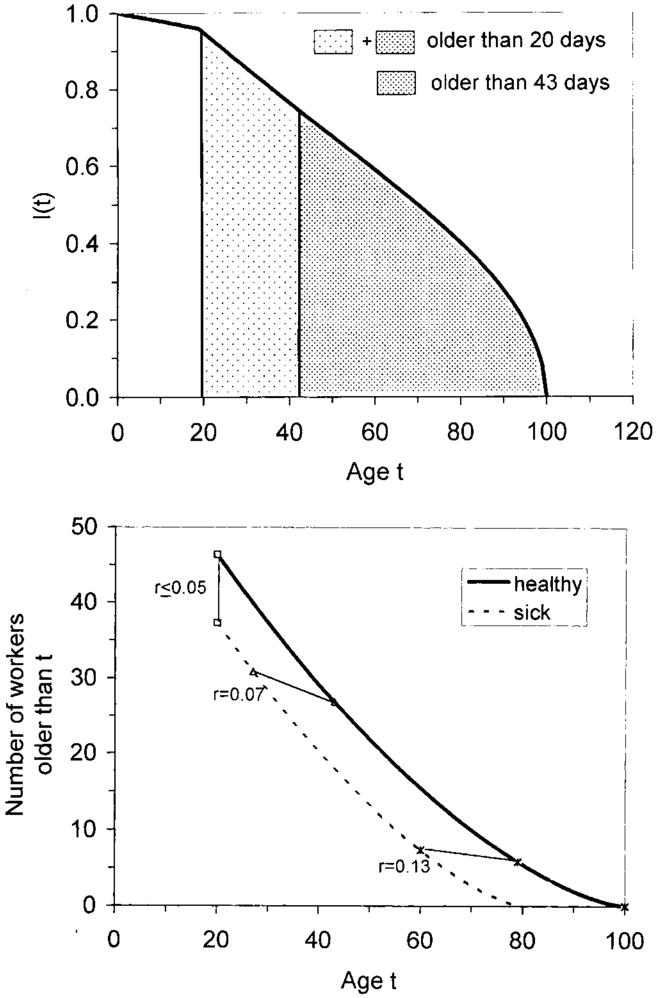

Figure 3. (A) Number of workers at age *t*, which under the assumption of stable age distribution and stable worker number is proportional to the probability of surviving to age *t*. The number of workers 20 days old and older is equal to the area under the *l*(*t*) curve up to *t* = 19, because the age at the axis represents the end of each day. (B) Number of workers at a given age and older. Squares show the numbers of healthy and sick workers foraging at not greater than 0.05 risk, triangles at 0.07 risk, and asterisks at 0.13 risk. Worker numbers are standardized so that the number of 1-day-old individuals equals one.

Although failure to satisfy the assumptions of a stable age distribution and an equal number of sick and healthy bees early in life may change the proportions, we can still expect a greater percentage of sick workers under poor than under good weather conditions.

To test the robustness of the model, we changed different parameters. After doubling or halving parameter q in the equation for physiological age-dependent mortality [equation (6)], the fraction of sick foragers in good weather was still 44–45 %, and 54 and 59 % under intermediate and harsh weather. Similarly, increasing the mortality risk in good weather to 0.05 per day had only a small effect on the proportions (46 % for good weather, 59 and 60 % for intermediate and harsh weather). Other changes in the distribution of risk also had very weak effects. One parameter, however, was very important to the expected proportion of sick foragers in good weather: the difference between the maximum lifespans of sick and healthy workers. Decreasing this parameter for sick workers from 80 to 70 days changed the proportion from 45 to 41 %, and a further decrease to 60 days reduced it to 36 %; increasing maximum lifespan to 90 days yielded 48 % sick foragers in good weather. Interestingly, the proportion of sick foragers in bad weather is still in a narrow range: 54–58 %. It seems, therefore, that the proportion of sick foragers is much more sensitive to shortening lifespan in good weather than it is in bad weather. Thus, the qualitative result that the proportion of sick foragers should become much higher in poor than in good weather seems robust.

3. MATERIAL AND METHODS FOR FIELD EXPERIMENT

Honey bee workers collecting water were captured from a watering trough (not more than 50 m from the farthest hive) in an apiary of about 60 hives near Krakow (southern Poland) in spring and summer 1995, on three pairs of cold-and-cloudy and warm-and-sunny days, between 11 a.m. and 2 p.m. During the capture of bees on cold days the maximum mean temperature was 15.7 °C and there was a strong wind. On the warm days the minimum mean temperature was 20.4 °C and there was no wind. The time gap between the days in each pair was not longer than 3 days. The foraging activity of workers on the pairs of compared days differed significantly, being significantly lower on the cold days. This could be easily observed because of the small number of workers that left the hives and also because the number of bees gathering water from the watering trough was several times lower on the cold days than on the warm days.

The presence of the parasite *N. apis* spore was checked with a hematocytometer in 1/40 mm^3 samples of individual worker abdomens macerated in 1 mL distilled water. If there were spores in a sample the individual was classified as infected; if no spores were found it was classified as uninfected.

The wear of each of the front wings of the captured workers was evaluated using a scale from 0 to 3. Zero meant that the outer wing margin was not damaged; 1 meant that the outer margin was slightly damaged; 2 meant that the wing was damaged one third of the distance to the ends of the medial veins (M1, M2); 3 indicated damage two thirds of the distance to the ends of the medial veins, or farther. The sum of two values, for the two front wings, characterized each worker. If this sum was ≤ 3 it was assumed that the individual's wings were in good condition; a sum > 3 was taken to mean worn wings.

The proportions of uninfected/infected individuals and also of individuals with wings in good/worn condition were compared for each pair of cold and warm days. For all individuals, the proportions of workers with good/worn wings in the infected and uninfected groups were compared. For this analysis the *G*-test with $df = 1$ and William's correction were used (Sokal and Rohlf, 1981).

4. EXPERIMENTAL RESULTS

Individuals infected with *N. apis* spores were significantly over-represented on cold days in April ($G = 8.903$, $P = 0.0028$) and June ($G = 10.156$, $P = 0.0014$), when the total proportions of infected workers were high on cold as well as on warm days (*figure 4*). The overall infection level was low in July, as is usual in summer (Furgala and Mussen, 1978; Pickard and El-Shemy, 1989), which made the sample size of sick workers too small (five infected workers on cold and three on warm days) to obtain a significant over-representation of infected bees on the cold day ($G = 0.193$, $P = 0.6608$).

Comparing the wings of the same workers on each pair of days (*figure 5*), we found that there were significantly more workers with worn wings collecting water on the cold day in April ($G = 4.187$, $P = 0.0407$) and July ($G = 5.014$, $P = 0.0251$). Only in June, when the proportion of workers with worn wings was very low,

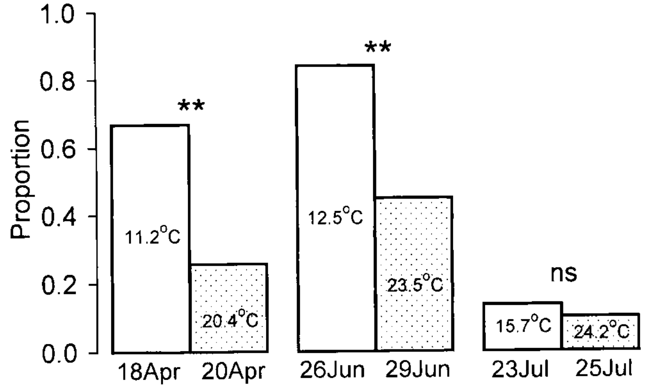

Figure 4. Proportion of workers infected with *N. apis* on cold days (unshaded bars) and warm days (shaded bars). The numbers of tested workers on cold and on warm days was 27 and 35 in April, 31 and 29 in June, and 37 and 30 in July. Mean temperature at the time of capture is marked in the bars. G-test: * – $0.05 \geq P > 0.01$, ** – $0.01 \geq P > 0.001$, ns – $P > 0.05$.

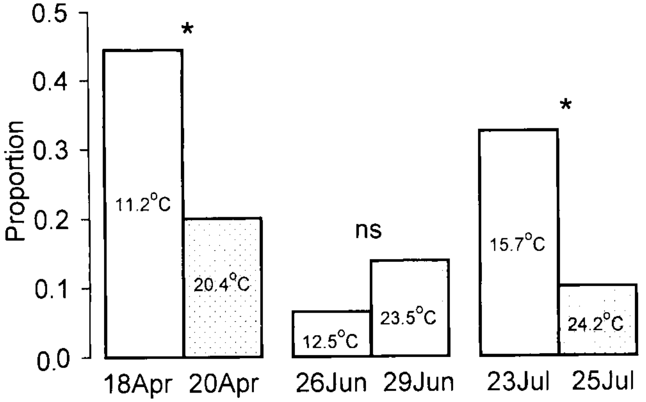

Figure 5. Proportion of workers with worn wings on cold days (unshaded bars) and warm days (shaded bars). Number of tested individuals and other indicators as in *figure 4*.

over-representation of workers with badly worn wings was not found ($G = 0.887$, $P = 0.3462$; two and four workers with worn wings on cold and warm days).

Analyzing the health status and wing condition of the workers, we observed that infected individuals more often had worn wings in each of the three pairs of days. Totaling the data for all workers captured during the experiment, worn wings were found almost twice as often among infected (29.3 %) than among uninfected (15.8 %) workers. This difference was significant ($G = 4.844$, $N = 189$, $P = 0.0277$).

5. DISCUSSION

Most of the model results seem to conform to intuition, our field experiment and many well-known results of early observations. It is obvious that the probability of worker survival must drop abruptly when foraging starts *(figure 1)*. High mortality in workers undertaking tasks outside the nest was observed by Sakagami and Fukuda (1968) and recently by Visscher and Dukas (1997). It is also patently true that the risk connected with foraging affects both healthy and sick foragers. The model also predicts that, independent of age and health status, all foragers (in the model, workers older than 19 days) are ready to undertake tasks if their risks are relatively low (lower than 0.05 for numerical example; *figure 2*). Depending on the expected life span corresponding to health status and age, foragers can maximize the expected total life foraging yield by undertaking different maximal risks of foraging *(figure 2)*. Thus, sick workers undertake higher risks earlier in life than healthy workers do. This result is consistent with O'Donnell and Jeanne's (1995a) predictions. Not so obvious is the result that even at the beginning of the workers' foraging life the difference in the ages of sick and healthy foragers undertaking the same risk is only slightly less than the difference between the maximal longevities of healthy and sick workers *(figure 2)*.

Not only physiological mortality, different for healthy and sick workers, but also the level of risk taking, dependent on life expectancy, affects the age structure and health statistics among foragers in the nest. All foragers forage when the risk of it is very low ($r \leq 0.05$; *figure 3B*). The model predicts, however, that some of the foragers will remain in the nest while others leave it when the risk of foraging increases. Such risky foraging ($r = 0.07$ or $r = 0.13$) is not undertaken by the youngest and the healthy workers *(figure 3B)*. This is why sick and old workers are over-represented among foragers compared to the ratio under safe conditions.

Our field experiment confirms the model predictions of the age structure and health of foragers. Among water collecting workers, the proportions of both diseased individuals *(figure 4)* and workers with significantly damaged wings *(figure 5)* show an over-representation of sick and old workers (presumably with shorter life expectancy) during risky weather conditions compared to their proportions under safe conditions. This does not mean that these individuals prefer to work under more risky conditions, but only that they decide to undertake more risky tasks than workers with longer life expectancies do.

The confirmation of the model prediction by field observations can be accepted if certain assumptions are satisfied. Neither of the two parameters, that is, the presence of the parasite *N. apis* and wing wear, were expected to determine the exact age of the tested honey bee workers. Each of these parameters was used only to divide the workers into two groups differing in life expectancy, following earlier observations that both sickness and wing condition are good predictors of life expectancy. Lifetime is significantly reduced in honey bees infected with *N.*

apis (Wang and Moller, 1969, 1970; Moffet and Lawson, 1975). The relationship between age and infection level has been demonstrated (El-Shemy and Pickard, 1989); it seems to be a general rule in workers infected with other parasites also (Schmid-Hempel and Schmid-Hempel, 1993). Moreover, it has been proved that age and duration of foraging affect worker wing wear not only in honey bees (Visscher and Dukas, 1997) but also in bumble bees (Alford, 1975) and solitary bees (Michener, 1969). In our experiment the relation between the presence of parasites and wing wear confirms the correctness of the choice of these parameters, which probably both correlate with worker life expectancy.

There are no exact data on how senescence influences mortality in workers with limited maximum longevity *(figure 1).* An experiment with a small sample of workers has been interpreted to mean that long-living foragers undergo senescence (Dukas and Visscher, 1994) and that their probability of death is not age-dependent (Visscher and Dukas, 1997). However, life tables of honey bees (Sakagami and Fukuda, 1968), and other work [for a review see O'Donnell and Jeanne (1995a)] support our assumption that senescence influences mortality.

Survival curves represented in *figure 1* may look not very realistic: they are not smooth at the beginning of foraging (20 days), and they go abruptly down at the end of life. Real survival curves for bee workers, although concave downward for some time, have a concave up 'tail' at the end (Sakagami and Fukuda, 1968; Visscher and Dukas, 1997). We must remember, however, that our curves are not conventional curves representing probabilities of survival of an average individual. They represent survival curves for two 'clean' strategies, healthy and sick, and when foraging starts exactly at the 20th day if weather is not too harsh. If foraging of different workers starts at a different time, for example between 20th and 40th day, the survival curve becomes smooth at the beginning. Moreover, if health status is treated as a continuous variable, which means in the model that lifespan can take any value between, say, 60 and 100 days, the concave upward 'tail' appears toward the end of life (Woyciechowski and Kozłowski, unpublished data). This is because workers in the poorest state die earlier and those in a better state survive longer. A similar phenomenon has been described in a nematode *Caenorhabdities elegans* for which, unlike the honey bee, genes for senescence are well known. In the mixture of genotypes, the survival curve is strongly elongated, whereas in strains developed from either short- or long-lived individuals the curves end more abruptly (Brooks et al., 1994). A close look at the Sakagami and Fukuda (1968) paper supports our view: mortality rates increase rapidly toward the end of life up to some age, then remain constant or even decrease slightly, and further increase at a slower rate. It is difficult to explain this result on a physiological ground, but such an effect is straightforward if the data represent a mixture of workers with different genotypes and different health status. Milne (1980) and Guzmán-Novoa and Gary (1993) demonstrated probable genetic variability for longevity in worker honey bees.

We assumed that weather conditions determine honey bee workers' foraging decisions and we ignored the potential role of the distance to water sources. This distance was relatively short in our experiment. Gathering water probably has been a greater risk on cold days throughout honey bee evolution; workers returning to the hive with water are more likely to die of starvation than those engaged in gathering nectar (Visscher et al., 1996). By testing workers collecting only water at about the same distance from their hives, we eliminated other factors connected with distance to resources in the worker life strategy (Schmid-Hempel, 1987) or to their genetic predisposition to undertake one task (Robinson and Page, 1988).

Our field experiment results can be interpreted in several different ways. It is possible that on cold days less water is needed and therefore new (young) bees are not recruited to collect it. It can also be suggested that only more experienced workers undertake foraging during cold weather conditions. These alternative explanations should be studied. In any case both the model predictions and the field results are in agreement with the contention that worker task sequencing based on temporal polyethism is a result of the varying risk levels of the tasks to be undertaken. It is generally known that safe work in the nest precedes dangerous foraging in all eusocial insect groups that do not have polymorphic workers [ants: for a review see Hölldobler and Wilson (1990); bees: Seeley and Kolmes (1991); wasps: Jeanne (1991), but see O'Donnell (1996); termites: Gerber et al. (1988)]. This basic division of tasks is probably the main reason for (O'Donnell and Jeanne, 1995b) and not a result of (Fénéron et al., 1996) morphological and physiological changes during the ontogenesis of adult individuals. As a consequence of these changes, sequences of safe duties inside the hive are most likely driven by physiology. This is why the division of these risk-independent tasks is so difficult to distinguish (Seeley, 1982) that its existence is even questioned (Kolmes, 1986).

The increase of outside duties observed in workers infected with *N. apis* (Hassanein, 1953; Wang and Moeller, 1970) is not caused directly by the parasite. Nor does it have to be an adaptation by which diseased workers avoid tasks which increase the chance of parasite spread among colony members as suggested by Wang and Moeller (1970) and Schmid-Hempel (1995). More likely, sick workers undertake risky duties at an early age because of their shortened life expectancy. Consequently, the same strategy should be anticipated not only in sick individuals but in all workers receiving cues of shortened life expectancy.

Although it is known that safe tasks in the nest usually are undertaken prior to risky tasks outside the nest in many insect societies, there are only preliminary results on the age dependence of foraging tasks sequenced according to risk (Woyciechowski and Łomnicki 1995; Woyciechowski et al., 1996). So far as we know, our findings are the first to be in favor of the hypothesis that in the honey bee and possibly also in other eusocial insects the division of labor results from the division of risks among workers with different life expectancies.

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Résumé – La division du travail par la répartition des risques en fonction de l'espérance de vie des ouvrières chez l'abeille (*Apis mellifera* L.). Chez l'abeille mellifère, ainsi que chez d'autres Hyménoptères eusociaux, la reproduction de la colonie dépend en totalité du travail non destiné à la reproduction qu'accomplissent les ouvrières. Cela implique que les membres de la colonie entreprennent de nombreuses tâches qui ne sont pas en relation directe avec leur reproduction. Pourtant décider quel individu dans une colonie va accomplir quelle tâche nécessite un compromis entre les ouvrières, car les diverses tâches occasionnent des risques de mortalité différents. C'est une règle que les facteurs externes conduisent à des taux de mortalité beaucoup plus élevés pour les tâches accomplies hors du nid que pour celles accomplies dans le nid. Le risque d'une tâche extérieure donnée peut varier lui-même selon les conditions météorologiques.

L'hypothèse, selon laquelle la division du travail chez les ouvrières qui butinent est une conséquence de la répartition du risque parmi les butineuses ayant des espérances de vies différentes, a été testée à l'aide d'un programme de modélisation dynamique et confirmée expérimentalement. Dans le modèle seules les ouvrières de plus de 19 j ont été prises en compte, car nous estimons que les ouvrières plus jeunes travaillent dans le nid. Nous estimons aussi que le vieillissement influence la mortalité des ouvrières et délimite une longévité maximale qui est de 100 j pour les ouvrières en bonne santé et de 80 j pour les ouvrières infectées *(figure 1)*.

Le modèle prédit que, indépendamment de l'âge et de l'état de santé, toutes les butineuses sont prêtes à entreprendre des tâches si les risques sont relativement faibles *(figure 2)*. En fonction de l'espérance de vie correspondant à l'état de santé et à l'âge, les butineuses peuvent maximiser la production du butinage sur l'ensemble de leur espérance de vie en prenant des risques maximaux plus ou moins élevés au cours du butinage *(figure 2)*. Les ouvrières modifient ainsi leur comportement de butinage avec l'âge et l'état de santé, butinant surtout dans des conditions sûres lorsqu'elles sont jeunes ou en bonne santé et acceptant un butinage plus risqué lorsqu'elles sont vieilles ou malades. C'est pourquoi les ouvrières malades et vieilles sont sur-représentées parmi les butineuses lors de conditions météorologiques risquées en comparaison avec des conditions météorologiques sûres *(figure 3B)*.

Dans l'expérience en champ, les ouvrières récoltant de l'eau ont été capturées à un abreuvoir dans un rucher d'environ 60 ruches, au printemps et en été, au cours de trois jours froids et nuageux et de trois jours chauds et ensoleillés. Leur espérance de vie a été évaluée d'après l'usure des ailes et la présence du parasite *Nosema apis* dans les intestins. Les résultats confirment les prédictions du modèle quant à la structure de l'âge et la santé des butineuses. Parmi les récolteuses d'eau, la proportion à la fois d'individus malades et d'ouvrières avec des ailes significativement endommagées *(figure 5)* est sur-représentée dans les conditions météorologiques à risques en comparaison avec des conditions météorologiques sûres.

Il est bien connu que, dans de nombreuses sociétés, les tâches sans danger dans le nid sont généralement accomplies avant les tâches à risques hors du nid, mais nos résultats sont les premiers, à notre connnaissance, à confirmer l'hypothèse selon laquelle, chez les abeilles et peut-être aussi chez les autres insectes sociaux, la division du travail pourrait découler de la répartition des risques parmi les ouvrières ayant différentes espérances de vie.

Apis mellifera* / division du travail / répartition risques / espérance de vie / *Nosema apis

Zusammenfassung – Arbeitsteilung durch eine der Lebenserwartung entsprechende Risikoverteilung bei Honigbienen (*Apis mellifera* L.). Bei Honigbienen, aber auch bei anderen eusozialen Hymenopteren hängt die Vermehrung von Kolonien von der insgesamt durch die Arbeiterinnen verrichteten nichtreproduktiven Arbeit ab. Dies bedingt, daß die Koloniemitglieder viele Arbeiten verrichten, die nicht mit ihrer direkten Reproduktion im Zusammenhang stehen. Da unterschiedliche Arbeiten mit unterschiedlichem Überlebensrisiko behaftet sind, erfordert die Entscheidung, welches Einzeltier in einem Volk welche Arbeit ausführt, einen Kompromiß zwischen den Arbeiterinnen. Es ist ein Regelfall, daß äußere Einwirkungen wesentlich mehr zur Sterblichkeit beitragen, sobald die Tätigkeiten abseits vom Nest ausgeführt werden, als bei Arbeiten innerhalb des Nestes. Bei Tätigkeiten ausserhalb des Nestes kann das Risiko sich hierbei in Abhängigkeit von Wetterbedingungen ändern.

Die Hypothese, daß die Verteilung der Arbeit bei Sammlerinnen eine Folge der Verteilung des Risikos zwischen Arbeiterinnen mit unterschiedlicher Lebenserwartung ist, wurde unter Verwendung eines dynamischen Modellprogramms untersucht und durch Experimente gestützt. In diesem Modell wurden unter der Annahme, dass jüngere Arbeiterinnen Arbeiten innerhalb des Nestes verrichten, nur Arbeiterinnen mit einem Alter von mehr als 19 Tagen berücksichtigt. Ebenso nahmen wir an, daß das Altern die Sterblichkeit der Arbeiterinnen beeinflußt, wobei von einer begrenzten maximalen Lebensdauer von 100 Tagen bei gesunden und 80 Tagen bei infizierten Arbeiterinnen ausgegangen wurde *(Abb. 1)*.

Das Rechenmodell sagt voraus, daß bei verhältnismäßig geringem Risiko alle Arbeiterinnen unabhängig von ihrem Alter oder Gesundheitszustand zur Übernahme von Arbeiten bereit sein sollten *(Abb. 2)*. In Abhängigkeit von der entsprechend dem Gesundheitszustand und dem Alter zu erwartetenden Lebensdauer, können die Sammlerinnen ihren Lebens-Gesamteintrag dadurch maximieren, daß sie unterschiedlich hohe Maximalrisiken während des Sammelns eingehen *(Abb. 2)*. Daher würden Arbeiterinnen ihr Sammelverhalten nach ihrem Alter oder Gesundheitszustand richten. Solange sie jung sind, würden sie hauptsächlich unter sicheren Bedingungen sammeln, wenn sie alt oder krank sind aber auch riskantes Sammeln akzeptieren. Als Folge wären kranke und alte Arbeiterinnen unter risikoreichen Wetterbedingungen im Vergleich zu sicheren Bedingungen überrepräsentiert *(Abb. 3B)*.

In einem Freilandversuch wurden an drei gepaarten Beobachtungen mit kaltbewölkten oder warm-sonnigen Tagen im Frühjahr und Sommer wassersammelnde Honigbienen von einer Wasserstelle an einem Bienenstand mit etwa 60 Völkern abgefangen. Ihre zu erwartende Lebensdauer wurde anhand der Flügelabnutzung und dem Befall mit dem Parasiten *Nosema apis* im Mitteldarm bewertet. Das Ergebnis dieses Freilandversuchs bestätigt die Vorhersage aus dem Modell über die Altersstruktur und den Gesundheitszustand der Sammlerinnen. Bei den wassersammelnden Arbeiterinnen zeigte der Anteil sowohl von befallenen als auch von Arbeiterinnen mit deutlich beschädigten Flügeln eine Überrepräsentation alter und kranker Bienen bei risikoreichen Wetterbedingungen im Vergleich zu den sicheren Bedingungen.

Obwohl allgemein bekannt ist, daß bei vielen Insektensozietäten die sicheren Aufgaben innerhalb des Nests gewöhnlich in jüngerem Alter ausgeführt werden als die riskanten Arbeiten außerhalb des Nestes, sind diese Befunde unseres Wissens die ersten, die die Hypothese unterstützen, daß bei Honigbienen und möglicherweise auch bei anderen eusozialen Insekten die Arbeitsteilung auf die Risikoverteilung zwischen Arbeiterinnen unterschiedlicher Lebenserwartung zurückzuführen sein könnte.

Apis mellifera* / Arbeitsteilung / Risikoverteilung / Lebenserwartung / *Nosema apis

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