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Original article

Risky robbing is a job for short-lived and infected worker honeybees

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Abstract – Researchers in many fields would like to understand the determinants of risk-taking. Social insects are an excellent model for examining them since the tasks they perform bear different risks. Some honeybee (*Apis mellifera*) workers do not forage for nectar or pollen; instead, they take on the extreme risk of robbing honey from other bee nests. In this paper, we show that robbers live shorter lives than foragers under the same cage conditions, and that they are more often and more heavily infected with the intestinal parasite *Nosema* than foragers are. This finding supports the theoretical prediction that risky tasks should be undertaken by shorter-lived individuals.

Apis mellifera / division of labour by division of risk / life expectancy / robber bees / *Nosema*

1. INTRODUCTION

The factors that affect risk-taking are addressed in many fields of study. Economists and psychologists focus on revealing the mechanisms of risk-taking and the consequences of those choices (Sanfey et al. 2003; Paulus 2007; Lawrence et al. 2008). Evolutionary biologists want to understand how animals maximize their fitness by undertaking risks related to different benefits (Kacelnik and Bateson 1997). Social insects give us an excellent model for analysing risk-taking, since the individual workers' decision depends on the behaviour of other group members, affects the productivity of the colony, and thus can benefit or harm the inclusive fitness of all colony members. Most insect communities have an age-related division of labour: younger adult workers execute safe tasks inside the nest; later in life they

undertake riskier outside-nest tasks like foraging (Winston 1987; Schmid-Hempel and Schmid-Hempel 1984; Visscher and Dukas 1997). Risk-taking by social insects is not limited to a choice between inside- or outside-nest tasks. Tasks performed by workers outside the nest can also differ in the risk level. Ant (*Cataglyphis* sp.) foragers are safer at optimal temperature than under thermal stress (Cedrá and Retana 2000; Clémencet et al. 2010). Among honeybee (*Apis mellifera*) foragers, collecting water is more risky than collecting nectar (Woyciechowski 2007), and foraging is riskier during inclement weather than during fair weather (Woyciechowski and Kozłowski 1998). Robbing the provisions stored in foreign bee nests is a task associated with extremely high risk. Individuals undertaking robbery are vulnerable to direct attack by nest defenders and can have their wings damaged or they can even be killed during their mission (Free 1954; Winston 1987).

Many proximate factors influence workers' movement from inside-nest task to outside-nest foraging. It is well-known that the time for

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onset of foraging is related to the genotype of the workers (Page et al. 2000), the hormone titre in hemolymph (Pankiw 2004), colony demography (Robinson 1992), and environmental components (Robinson 1992; Gordon 1996). Considerably seldom discussed, however, are the ultimate factors in the evolution of the division of labour based on age polyethism. Jeanne (1986) and Tofilski (2002) explored the evolutionary factors of age polyethism. They showed that executing risky tasks later in the workers' life can prolong their mean longevity. Such a choice increases the colony's reproductive success (Schmid-Hempel and Wolf 1988). Based on similar assumptions, the 'division of labour by division of risk' hypothesis (Woyciechowski and Kozłowski 1998) suggests that the decision as to which individual undertakes a certain task in a colony arises from the division of risk among workers differing in their life expectancy: individuals with a longer life expectancy, which is to say the young and/or healthy, should undertake less risky tasks than should workers with a shorter life expectancy, namely those older and/or infected with pathogens.

There are experimental results that show a relationship between the life expectancy of workers and the onset of their foraging. As predicted, workers with a longer life expectancy initiated risky foraging later in life than did same-age workers whose life expectancy was experimentally shortened. This has been observed in the ant, *Myrmica scabrinodis* (Moroń et al. 2008), and the honeybee (Woyciechowski and Moroń 2009). The converse was confirmed in a study of behavioural reversion in honeybee colonies: foragers with experimentally shortened life expectancy reverted to a safe inside-nest task less frequently than did same-age foragers from the control groups (Kuszewska and Woyciechowski 2013). In another recent study, *M. scabrinodis* foragers with experimentally shortened life expectancy undertook foraging under higher risk (farther from the nest; higher temperature; presence of competitors) than those from the control group (Moroń et al. 2012).

In all of those cited studies testing the 'division of labour by division of risk' hypothesis, the life

expectancy of individuals was artificially manipulated. Little is known about whether risk-taking depends directly on worker life expectancy in natural field conditions. Here, we compared the life expectancy and levels of infection with the intestinal parasite *Nosema* sp. between honeybee workers performing outside-nest tasks associated with different risks—foraging for nectar and pollen (lower risk) and robbing the provisions stored in foreign bee nests (higher risk). We expected the robbers to have a shorter lifespan and to be infected more frequently and with a larger number of spores than the bees foraging for nectar and pollen.

2. METHODS

The study, conducted from 4 to 18 September, used 16 colonies of honeybees (*A. m. carnica*) in the experimental apiary of the Institute of Environmental Sciences (Krakow, southern Poland). All colonies were regularly inspected and never showed symptoms of *Nosema* infection. The experiment was done during a period when robbing is often observed. Foragers and robbers were collected in the early afternoon. Bees that collected nectar or pollen from flowers no more than 50 m from the apiary were considered foragers; workers that performed characteristic swaying flight (Free 1954) and tried to get into hives by means other than through the entrance (Muszyńska 1993) were considered robbers.

The two groups of captured bees, robbers and foragers, were marked with different colours and caged in order to assess their lifespan independently of external mortality. These bees were randomly placed in four cages (15×14×6 cm, wood-framed, with glass in one side and steel mesh in the other side) and provided with a small piece of bee comb. There were 27–33 workers per group (robbers and foragers) in each of the four test cages. The cages were incubated at 36 °C and 60 % RH and provided with sucrose syrup (50 % w/v, *ad libitum*). The cages were checked every day, and dead bees were counted and removed.

Separately, foraging bees (60 workers) and robbers (70 workers) were collected, frozen immediately, and then dissected in order to detect and count *Nosema* sp. spores in their intestines. To do this, the digestive tract

(without crop) of each bee was homogenised in 300 μL distilled water. The *Nosema* spores were counted in a Bürker haemocytometer in a total solution volume of 1.25×10^{-2} μL . If the number of spores counted per sample was less than 10, the total solution volume per sample was increased to 8×10^{-2} μL . The total number of spores per bee was determined according to the following formula: number of spores per bee = number of spores per sample $\times 300$ μL / total solution volume of sample.

The difference in survival between robbers and foraging workers was analysed using a generalized linear/nonlinear model (GLZ) module in Statistica 9.0 (StatSoft 2012) with Poisson distribution and the Link function of LOG, which is a semiparametric statistical test (Härdle et al. 1996). Cage was a random effect, and group (robbers or foragers) was a fixed effect. If the effect of a factor was statistically significant, GLZ was followed by multiple comparisons using the post-hoc Tukey HSD test with 0.05 taken as indicating significance. The proportions of infected and uninfected workers was compared between foragers and robbers using the G-test with William's correction, and the significance of differences in levels of infection between foragers and robbers was tested using the nonparametric Mann–Whitney *U* test. All calculations were conducted with two-tailed statistical test and were performed with STATISTICA 9.0.

3. RESULTS

In our laboratory experiment with caged workers, the lifespan of the robbers was significantly shorter than that of the nectar or pollen foragers (GLZ, Wald's $\chi^2=60.541$, $P<0.001$; Figure 1). Lifespan was also affected by the cage in which the bees were kept (GLZ, Wald's $\chi^2=64.390$, $P<0.001$); the post-hoc Tukey HSD test showed that this difference in longevity was between the bees kept in cage 3 and the ones in cages 1 and 4 (Tukey HSD, $P<0.05$). The interaction between group and cage did not influence the longevity of the robbers or foragers (GLZ, Wald's $\chi^2=1.116$, $P=0.773$).

Among the bees collected straight from the field, *Nosema* spores were more prevalent and

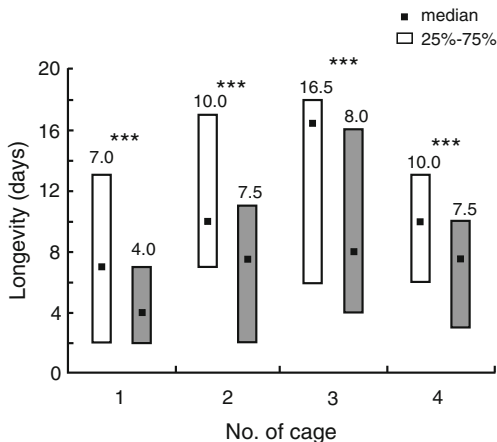


Figure 1. Longevity (median and quartiles) of foragers (empty bars) and robbers (grey bars) in the cage experiment. Numbers indicate the median of longevity (in days) in each group. The stars indicate significant differences ($P<0.001$) between robbers and foragers in each cage

abundant in robbers than in foragers. Among the 60 nectar- or pollen-foraging workers, 53 (88 %) were infected with *Nosema* spores; 69 (98.5 %) of the 70 robbers were infected. The difference in prevalence was significant (*G*-test: $G=6.323$, $df=1$, $P<0.0120$). *Nosema* spores were also more abundant in robber workers (median 4.080×10^5) than in foragers (median 0.169×10^5); the difference was significant (Mann–Whitney *U* test: $U=623$, $Z=-6.89$, $N_1=70$, $N_2=80$, $P<0.02$; Figure 2).

4. DISCUSSION

Here, we demonstrated that workers undertaking to rob nests, a risky task, were shorter-lived than nectar and pollen foragers (Figure 1). These results are in line with the expectations of the ‘division of labour by division of risk’ hypothesis (Woyciechowski and Kozłowski 1998) and strongly suggest that individuals with a shorter life expectancy undertake riskier tasks than do longer-lived workers (Tofilski 2009). In eusocial insects, it is a rule that workers undertake safe inside-nest tasks earlier in life

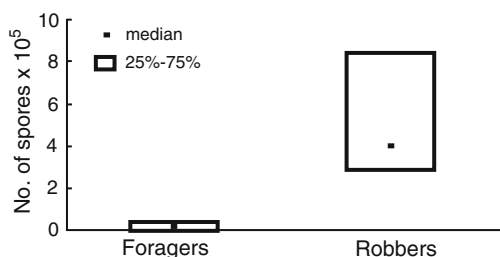


Figure 2. Number of *Nosema* sp. spores in foraging and robbing workers

than risky foraging, and according to our knowledge, there are only two exceptions from this rule, one found in a species of termite (*Zootermopsis angusticollis*) and another in a species of ant (*Amblyopone pallipes*) by Traniello and Rosengaus (1997). There are even examples of task partitioning in which the task consists of two subtasks differing in the associated risk. In the honeybee, nectar is collected by foragers under more dangerous conditions, but is stored in comb cells by inside-nest younger workers in much safer conditions. Another example is from the leaf cutting ant, *Atta cephalotes*: younger workers remove waste from the fungus garden and transfer it to the garbage chamber, which is staffed by older workers performing the last task of their lives; they never will leave that chamber (Bot et al. 2001). The workers living in the garbage chamber are exposed to potentially pathogenic waste material and usually live only a few days after starting on this job (Hart and Ratnieks 2001). Both of these examples of task partitioning show the association between worker life expectancy and the risk involved in the task undertaken.

Our data demonstrate that honeybee robbers not only lived shorter lives but were infected with *Nosema* spores more frequently and more heavily than the foragers were (Figure 2). This result doubly confirms our predictions since previous studies have shown that individuals infected with *N. apis* have a shorter lifespan (Woyciechowski and Moroń 2009) and more often than healthy foragers collect nectar during unfavourable

weather conditions (Woyciechowski and Kozłowski 1998). Higher levels of *N. apis* infection often are associated with worker age (Malone and Giacomini 1996). Older workers generally are more heavily infected than younger bees (Smart and Sheppard 2012), a finding attributable to their longer exposure to the parasite (El-Shemy and Pickard 1989) or to the 6-day developmental life cycle of *Nosema*, relatively long in relation to the workers' lifetime (Fries 1988). Wang and Moeller (1970) even suggested that *Nosema*-infected workers are physiologically older than the same-age healthy bees and therefore carry out some activities at an earlier age (Woyciechowski and Moroń 2009; Goblirsch et al. 2013). This means that regardless of the reason, be it age or disease, the robbers had a shorter life expectancy and had therefore undertaken a task involving a greater risk.

The mortality rate is higher outside the nest than inside, due not only to greater exposure to external hazards (e.g. predators, accidents, disorientation) but also to internal resource depletion (Neukirch 1982, Woyciechowski 2007). Honeybee workers have a limited energy reserve in their flight muscles and when this is used up, they cannot fly and return to the colony. This results in their death (Neukirch 1982; Page and Peng 2001). Rueppell et al. (2007) showed that internal resource depletion has a greater impact on the longevity of bees than external hazards because workers foraging for longer periods had shorter lifespans than those with a limited amount of time for foraging. In our experiment, we compared two groups of free-flying bees performing, respectively, low- or high-risk tasks. We have no reason to suspect that robbers and foragers differed in length of flying time and thus in internal resource depletion.

Our main conclusion does not challenge the idea that the energetic state affects the decision to start foraging by honeybee workers (Mayack and Naug 2011). *Nosema* imposes an energetic stress on infected bees, which have an elevated appetite and hunger level (Mayack and Naug 2009, 2010). Kaatz et al. (1994) showed that starved workers had higher juvenile hormone

titres, while Alaux et al. (2010) suggested that the energetic stress associated with malnutrition probably is one of the causes of immunodeficiency in honeybee colonies. Interestingly, old workers are more sensitive than younger bees to starvation stress, which causes increased mortality (Remolina et al. 2007). These examples seem to support the idea that the energetic shortfall is a cause of shorter life expectancy; that would explain why workers are slotted to safer or riskier tasks.

Alternative explanations of our results are possible. One is that robbers potentially are more exposed to *Nosema* infection than foragers if they rob honey from heavily infected colonies (Fries and Camazine 2001). A high level of infection produces yellow or yellowish brown excrement stains inside the hive. In the colonies where the *Nosema* infection is mild, if any excrement is laid on the comb, it is quickly removed by resident workers, so the chance of infecting robbers is very low. No colonies in our experimental apiary were so heavily infected during the study (i.e. no excrements were visible on frames) that the parasite would have been transmitted horizontally by robbing workers, so it is reasonable to conclude that the *Nosema* infection that shortened the life expectancy of our honeybee workers is better explained as a cause rather than a consequence of robbery. We also realise that robbers had already suffered some damage while fighting in the course of robbery, and this could influence their longevity in our cage experiment. It is difficult to distinguish whether longevity determines the type of performed task, or whether the performed task influences longevity. There are many papers showing that both of these explanations are possible and that neither of them excludes the other (Neukirch 1982; Amdam and Omholt 2002; Rueppell et al. 2007). However, according to our observations, robbing workers can be stung and die immediately or can suffer from destruction of their wings, which has no impact on their life expectancy if they are caged. Therefore, we believe that our results show clearly enough that more prevalent and abundant *Nosema* spores in

robber bees were the cause of their higher mortality relative to foraging bees.

An alternative explanation is that the infected workers' tendency to rob may be caused by the parasite manipulating the behaviour of its host and provoking it to visit other colonies. This would be a way of increasing horizontal transmission of *Nosema*. Parasites have been suggested to affect the behaviour of host social insects. Honeybee workers infected with *Nosema ceranae* tend to remain in places where the temperature is higher (Campbell et al. 2010), which increases the reproductive potential of the parasite (Martín-Hernández et al. 2009). Workers infested with *Varroa destructor* or *Nosema* have a reduced spatial orientation capacity (Kralj and Fuchs 2006; Kralj and Fuchs 2010), which increases the chances of infecting bees from other colonies. As suggested by those authors, however, such a response in infected individuals probably is the result of the overall reaction to the presence of the parasite. If the parasite had indeed manipulated the workers' behaviour in our study, we should have seen robbing being done throughout the season, as well as in the spring when the first increase of infected workers occurs (Mattila and Otis 2006). Robbing is observed almost exclusively later in the summer when resources are not readily available in the field (Free 1954; Winston 1987). It is unlikely that the parasites would manipulate the host's behaviour only during the part of the season when the host's food resources are least. The much more probable explanation is simply that the bees tend to rob when pollen and nectar are in short supply.

Another possible hypothesis is that more heavily infected robber workers have taken the route of altruistic suicide because their presence is harmful to their native colony members. Such behaviour has been observed in ants (*Temnothorax unifasciatus*) (Heinze and Walter 2010) and has been suggested as an explanation for the experimental results Rueppell and colleagues (2010) obtained in the honeybee. In both of those studies, moribund workers removed themselves, abandoning the nest and

their social role, leading to complete or almost complete cessation of all active and passive contact with their nestmates. Robbing workers behave in quite a different way: having successfully gained entry to a foreign colony, they ingest a load of honey and return to the native colony, where they then recruit other workers to rob (Winston 1987; Moritz and Neumann 2004). Active contact such as this on the part of robbers with members of both their own and the robbed colony cannot be linked to altruistic suicide but possibly rather to the parasite manipulation discussed above.

Our results are consistent with the prediction that tasks, or more precisely the risks associated with specific tasks, are divided between colony members depending on their life expectancy. One of the riskiest tasks—robbing—is performed by the less valuable members of the colony: the oldest and/or disease-infected. Therefore, it can be supposed that differentiation in worker life expectancy and the different risk related to each task are sufficient factors for the evolution of division of labour in honeybee and probably in all eusocial insects.

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Prendre le risque de voler du miel est une tâche pour les ouvrières à durée de vie courte et fortement infectées par *Nosema*

Apis mellifera / division du travail / prise de risque / espérance de vie / vol de miel

Riskantes Räuberei ist ein Job für kurzlebige und infizierte Arbeiterinnen

Apis mellifera / Arbeitsteilung / Risikoteilung / Lebenserwartung / Räuberbienen

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