SMALLER BUMBLE BEE WORKERS ARE SAFEGUARDS AGAINST POOR RESOURCE ENVIRONMENTS

By

MICHAEL DAVID RIVERA

A Thesis Submitted to The Honors College
In Partial Fulfillment of the Bachelors degree
With Honors in
Ecology and Evolutionary Biology
THE UNIVERSITY OF ARIZONA
MAY 2015

Approved by:

Dr. Anna Dornhaus
Department of Ecology and Evolutionary Biology
Smaller bumble bee workers are safeguards against poor resource environments

Michael Rivera
Advised by Dr. Anna Dornhaus
Department of Ecology and Evolutionary Biology
May 6, 2016
Abstract

Bumble bees workers (*Bombus sp.*) exhibit a large variation in worker body size, with up to a ten fold weight difference between full genetic sisters. Stranger still is that there appears to be little adaptive benefit for producing them as smaller workers are worse at performing colony tasks. However smaller workers can survive starvation for longer than their larger sisters. We test the hypothesis that smaller workers are either adaptations to poor resource environments or highly variable resource environments. By raising colonies in the lab of different resource regimes we find that colonies in poor resource treatments show decreased average body size, but there appears to be no tradeoff in producing either larger or more workers.

Introduction

Variation within groups is seen across levels of organization, from multicellular organisms, where cells vary in function and morphology, to advanced eusocial societies, in which individuals play different roles. It is generally thought that this variation increases the performance of the group (Oster and Wilson 1978; Billick 2002; Bonner 2011; Fogarty et al. 2011). Social insects are perhaps the greatest example of this and are some of the most ecologically successful organisms on the planet. Ants, bees, wasps, and termites are species-rich groups and can constitute a significant proportion of the terrestrial biomass (Wilson, 1987; Hölldobler and Wilson, 1990). Their success is often attributed to a number of life history traits, unique among insects, such as advanced communication and division of labor. Perhaps most striking is morphological variation in the worker castes, which is thought to generally increase
the efficiency of the colony, and occurs in both termites and sparsely in termites (Fjerdingstad and Crozier, 2006).

When it does occur it is often the subject of great interest, particularly about the adaptive roles that castes may play (Hölldobler and Wilson. 1990; Wheeler 1986). For example the large head of a specialized Cephalotes caste enable them to defend nest entrances (Powell, 2008) or the division of labor between the larger foraging leaf cutting ants, Atta cephalotes and their smaller internidal sisters (Wetterer 1994). These provide clear examples of how morphological variation can increase colony fitness.

Bumble bees deviate from this straightforward trend by showing striking morphological variation (Cumber, 1949) 1 with little apparent adaptive value. Workers enclosing at the same time can have up to a ten-fold weight variation and up to a fivefold in thorax width or a ten fold weight. (Goulson et al., 2002; Peat et al., 2005) and there is little variation across the colony’s lifespan (Couvillon et al. 2010). Additionally, unlike in the ant examples above, there seems to be only weak specialization (Jandt et al., 2009; Jandt and Dornhaus, 2009), which is generally hypothesized to be a driver in the evolution of ant worker morphological variation. While non-specialized morphological variation (i.e. lacking features that greatly restrict behavior such as Cephalotes’s big headed workers) can contribute to a colony’s performance (Porter and Tschinkle, 1985; Billick and Carter, 2007) in the case of bumble bees, smaller workers seem to underperform compared to their larger sisters in almost every studied task despite all workers being able to perform every task. Larger bees are better at foraging (Gouldson et al., 2002;
Spaethe and Weidenmüller, 2002; Spaethe and Chittka, 2003), rearing brood (Cnaani and Hefetz, 1994; Dornhaus unpublished data) and undertaking (Ings et al., 2006).

The development of polymorphism in bumble bee workers can be linked to the developmental environment. As bumble bees spend their larval and pupal stages in wax cells, their natal environment (the most important components of which are nutrition and temperature) are controlled by the colony. Smaller workers are fed less and develop towards the edges of the nest structure (Couvillon and Dornhaus, 2009) and may experience more variable temperatures (Dornhaus and Bouchard unpublished data). Yet spatial variation is not enough to explain why small seemingly mal-adaptive workers are present during the entire colony’s lifespan, as honey bees, stingless bees and many ant species have naturally heterogeneous nests and yet still produce more consistently sized workers with less variation through thermoregulation or feeding regimes (Goulson et al., 2002; Toth and Robinson, 2005; Wilson, 1953). While the mechanism of varied body size has been worked out, there is no consensus on the ultimate cause of this variation.

One line of evidence suggests that the ability to produce small workers may be linked to the colony’s resource environment. While larger bees may contribute more to the colony’s workforce, smaller workers require fewer resources to be produced and can survive starvation for longer periods of time (Couvillon and Dornhaus, 2009). Thus the ability to produce smaller workers can be a safeguard for the colony against poor or variable resource environments by increasing its robustness.
One way this could come about is if colonies with limited resources produce smaller workers, which are better adapted to low resource environments. This would predict that overall colony resource levels should dictate the body sizes of workers produced. However if shorter-term fluctuations in resource are highly influential on colony success, then colonies may produce smaller workers in a highly variable environment compared to more stable environments.

We sought to test the hypotheses that colonies of the bumble bee *Bombus impatiens* produce smaller workers 1) in poor resource environments (as a potential adaptive safeguard against colony mortality) and/or 2) an adaptation to increase the robustness of the colony in a variable environment. These predict that 1) when the resource environment declines in quality, colonies able to produce smaller workers may experience a decline in overall colony efficiency, but will still have a workforce ready when the environment improves, instead of losing all workers to starvation or 2) colonies in highly variable environments would benefit from producing a wide range of worker sizes, to increase the robustness of the colony. To test these hypotheses, we reared lab colonies in different resource environments and measured changes in colony worker production.

**Methods**

**Bees**

Twenty-one colonies of the common eastern bumble bee (*Bombus impatiens*) were obtained from a commercial supplier (Koppert, MI) early in their life cycle (~30 workers). There were maintained in a wooden nest box (dimensions?) with a clear Plexiglas lid. This was attached to a foraging arena (.5m x .75m x .5m). Sucrose solution (2M) was provided in this foraging arena
from a multi-well feeder, and pollen (fresh-frozen, commercially obtained from Koppert) was
ground in a coffee bean grinder and placed in a petri dish adjacent to the nest structure inside the
nest box. Initial colony size measurements (worker counts) were taken within 48 hours of arrival
in lab. Colonies were then given a week prior to treatments with ad libitum sucrose solution and
pollen.

_Treatments_

Twenty-one colonies were placed under one of three food regimes for four weeks (initiated the
week after they arrived into the lab). The ad libitum colony was given large amounts of sucrose
solution and pollen every 2 days. If an ad lib. colony ever got close to finishing the amounts
given, the diet was increased in the next feeding period. By measuring the amount of food
consumed and remaining we calculated the weight of pollen per bee per day consumed by in the
ad lib colony. Restricted colonies were given half the pollen per bee per day as the ad lib.
colonies. Due to the inaccuracies in measuring “consumed” solution from feeders (due to excess
sucrose solution stored in honey pots, many of which are not visible) restricted colonies were
given a set 50ml of 2M sucrose solution for each 2-day period. This was always completely
consumed before the end of the 2-day period. Variable colonies were given ad lib. access to
pollen and nectar three days a week, with nothing else the remaining four days. Pollen and
sucrose solution remaining in the feeders were removed, although any sucrose solution stored in
honeypots was left.
Measurements

The volume of nectar and weight of pollen consumed were measured every 2-3 days. Weekly measurements of thorax width were made of all newly enclosed bees, by briefly anesthetizing them in a freezer then measuring the thorax. After which the bees were marked on their thorax with paint and returned to the colony. Thorax measurements were taken horizontally at the widest part, just behind the wings (as this heavy sclerotized body part does not change throughout the life span). All comparisons of body sizes and counts analyzed were made after the third week under the treatment, as the typical development time from egg to adult in *B. impatiens* is 21 days, so all bees analyzed were raised from egg to adult within the food regime.

Results

Effect of treatment on worker body size

Colonies under a restricted food regime produced on average smaller workers than both colonies in the ad lib. and variable treatments. (Body size~treatment, Kruskal-Wallis $x^2 = 9.79$ p = 0.0074, Mann-Whitney U Test, ad lib~restricted p = 0.0052, restricted~variable p = 0.045). There was no significant difference in the average worker body size produced by ad lib. or variable colonies (Mann-Whitney U Test, ad lib~variable p = 0.103). See Figure 1A.

Effect of food regime on variation in worker size

Colonies in the restricted regime also experienced an increase in the variation of worker body sizes being produced compared to the ad lib colonies (standard deviation~treatment, Kruskal-Wallis $x^2 = 8.80$ p = 0.012, Mann-Whitney U Test, ad lib~restricted p = 0.002) but not to the variable colonies (Mann-Whitney U Test, restricted~variable p = 0.147). See Figure 1B.
Effect of treatment on number of workers produced

None of the treatments varied significantly in the number of workers being produced in relation to colony size (Kruskal-Wallis $x^2 = 3.08 \ p=0.213$) or in the total number of workers produced over the span of the experiment (Kruskal-Wallis $x^2 = 8.80 \ p=0.643$). See Figure 1C and 1D respectively.

Is there a tradeoff between worker size and number of workers produced?

Both overall and within treatment there is no significant correlation between producing more or larger workers, although the combined treatments are trending towards significance. (Treatments combined Spearman’s rank correlation $p=0.058$, rho=0.418, within ad lib Spearman’s rank correlation $p=0.556$, rho=0.285, restricted Spearman’s rank correlation $p=0.212$, rho=0.466, variable Spearman’s rank correlation $p=0.321$, rho=-0.564). See Figure 2.

Discussion

We sought to see if bumble bee colonies produce smaller, less-efficient workers as 1) as response to a general decline in the resource environment 2) to increase the robustness in a highly variable resource environment. Colonies produced smaller workers in response to a decline in the amount of resources; yet do not show a corresponding decline in the number of workers produced. Additionally colonies under resource stress still produce a few large workers, albeit in smaller numbers.
It appears that the ability to produce small workers is an adaption to poor resource environments in that it allows colonies to maximize worker number in poor resource environments. Even in ad libitum resource conditions small workers were produced, in restricted conditions the average body size was significantly smaller. The benefits to the colony are two-fold. The colony spends fewer resources producing the small workers and once emerged they are hardier against starvation (Couvillon and Dornhaus, 2010). This is not common among social insects, where starvation usually results in decreased worker production. In ants larvae are often used as food sources replete (Wilson, 1987; Wetterer, 1994). In these restricted colonies relativity large workers are still being produced albeit in smaller numbers. Inversely to the smaller workers the large workers require higher resource investment and are more sensitive to food shortages. The continued production of these large workers may represent a tradeoff between producing resource-poor adapted small workers and maintaining an efficient large worker workforce. Future work investigating how workload is spread across individuals across these treatments will provide more insight into this tradeoff. If small workers continually have poor performance and activity even in resource poor environments, then the continued presence of these large workers makes adaptive sense.

We also tested the idea that variable sized workers may be produced to increase robustness of the colony, producing anticipatory small workers to account for fluctuations in resources. Colonies produce smaller workers in response to fewer resources and small workers are continually present in the colony, but there is no increase in body size variation on a variable diet. While variation in social insect workers has been shown to increase robustness to a novel environment, it has not been shown over these shorter highly fluctuating environments (Fogarty et al, 2011).
Perhaps the variation present normally in a colony is enough to ensure the colony’s survival across a varied environment, as Couvillion et al. showed that small workers are present at all times during colony development (Couvillion et al., 2010).

Perhaps most interestingly we see no tradeoff in producing more or larger workers. This is surprising given the importance of this size/number tradeoff in the reproductive efforts of a number of genera (Reznick, 1983; Walker et al., 2008). If resource poor colonies are producing smaller but not fewer workers, this suggests that maintaining colony size is an important feature in trying environments. Stranger is that within the restricted colonies there is a positive trend between the number of workers produced and their size. Some colonies were able to produce more and larger workers while under the same restricted diet as others. There are genetic features known to affect the ways in which social insects allocate resources and this could be playing a role in the restricted colonies (Toth and Robinson, 2005). Future studies will show if this is also playing a role here.
Figure 1 – Effects of food regime treatments on the A. average worker size, B. standard deviation, C. bees produced corrected for colony size, and D. total colony size. The number of colonies in each treatment were ad lib n=7, restricted n-9, and variable n=5.
Figure 2 – There appears to be no tradeoff between producing more workers or larger workers across or within colonies.
References
Alford AV (1975) Bumblebees, London


Couvillon MJ, Dornhaus A (2010) Small worker bumble bees (*Bombus impatiens*) are harder against starvation than their larger sisters. Insectes sociaux 57: 193-197


