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The impact of body mass of colony-founding queens on the characteristics of reared bumblebee *Bombus lucorum* colonies

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Size has been shown to influence the individual performance of bumblebee queens, but effects of queen body mass on colony characteristics are not well known. We studied the effect of queen body mass on colony initiation, worker population size and the production of sexual offspring in laboratory-reared colonies of the bumblebee *Bombus lucorum*. Colonies with heavier queens had longer workers-only production period and they produced larger worker populations during the colony life cycle. Colonies with larger worker populations produced a higher number of reproductive offspring. Therefore, it seems that heavy queens increase pollination services through larger worker populations. The condition of colony-founding queens may be affected by resource availability in the previous summer, consumption of body energy reserves due to overwintering conditions, and/or exposure to pathogens. Decreasing condition of colony-founding queens may negatively impact pollination services on wildflowers and cultivated plants.

Introduction

Bumblebees are crucial pollinators of both wild and cultivated plants, making them important key species in both natural and agricultural ecosystems. However, the populations of many bumblebee species are declining due to habitat loss, climate change, pathogen transmission, the invasion of non-native species and the use of pesticides (Cameron & Sadd 2020, Ghisbain *et al*. 2024). The decline of bumblebees can have negative effects on biodiversity by altering plant communities, which in turn affects other species in the food web.

Recent predictions for climate change suggest highly variable climatic conditions, which are most pronounced in winter in boreal areas, where winter temperatures may increase up to 7 °C from current climate (Ruosteenoja & Jylhä 2021). There are several insects that need rather

cold conditions for hibernating and surviving through the winter without feeding, and bumblebees are among the largest of them. Bumblebee queens need an adequate body mass to be able to stay alive until spring; in *Bombus terrestris* (Linnaeus, 1758), the threshold mass is 0.6 g (Beekman *et al.* 1998), whereas *B. lucorum* (Linnaeus, 1761) can survive when their body mass exceeds 0.4 g (Vesterlund *et al.* 2014a). The mechanism behind body mass variation is mainly nutritional, through morphological growth (Plowright & Jay 1968, Sutcliffe & Plowright 1988, 1990) and accumulation of body fat. On the other hand, the body mass of overwintered colony-founding queens can vary according to the amount of remaining body fat reserves: body fat reserves were increasingly depleted in suboptimal overwintering temperatures in lighter queens but not so in heavier queens in *B. lucorum* (Vesterlund *et al.* 2014a).

Bumblebees are haplodiploid, which means that usually two types of eggs are produced. The foundress queen can lay both fertilized diploid eggs that develop normally as either workers or gynes (new queens), and haploid, male-producing eggs; the workers can only lay haploid male eggs. It is more beneficial for both the queen and the workers to rear their own sons, but only after the colony has reached its maturation point, because the males do not work and, once they emerge, the colony growth is bound to gradually decrease. In the bumblebee *Bombus terrestis*, competition between the queen and the workers on male production usually begins after the queen starts producing new gynes (van der Blom 1986, van Doorn & Heringa 1986, Duchateau & Velthuis 1988). The switching point from rearing workers to rearing reproductives varies between colonies (Duchateau & Velthuis 1988). *Bombus terrestris* has two alternative strategies: early-switching colonies producing mostly males, and late-switching colonies producing mostly gynes, both of which reach the competition point for the production of males about thirty days after the emergence of the first worker cohort (Duchateau & Velthuis 1988, Duchateau *et al.* 2004).

In *B. terrestris*, the foundress queen secretes a pheromone that induces diploid eggs to develop into workers (Röseler 1970, 1991), until it is in her best interests to start producing gynes (Bourke & Ratnieks 1999, 2001). Holland *et al*. (2013) suggest that the queen controls this key life-history event in at least *B. terrestris* bumblebees. Traditionally this is suggested to happen due to pheromonal control by the queen, but this is not proven and is highly doubted (Alaux *et al*. 2004, Amsalem *et al*. 2015, *but see* Holman 2014). The outcome of the conflict over male production depends on the relative power of the parties in each situation (Ratnieks & Reeve 1992, Beekman *et al*. 2003, Beekman & Ratnieks 2003).

Weight variation is marked in both *B. terrestris* and *B. lucorum* queens (Beekman *et al*. 1998, Vesterlund *et al*. 2014a), and heavier queens of the latter species had stronger immune competence and larger body fat resources compared to smaller ones in an abnormally high (9 °C) overwintering temperature during a four-month artificial overwintering period (Vesterlund *et al*. 2014a). If the mean size of queens surviving the overwintering period were to increase due to rising hibernating temperatures, related changes in colony characteristics could lead to population-level effects in sex ratios and future population sizes. Queen size seems to have a bearing on individual performance, but in earlier studies, it has not been shown to affect colony characteristics (Duchateau *et al*. 2004). However, Duchateau *et al*. (2004) suggest that size (as a ratio of wing radial cell size and body mass) could be used as a life-expectancy measure. They discuss further that, theoretically, relatively light queens should start producing haploid eggs early in colony development and would consequently have male-biased colonies. On the other hand, relatively heavy queens should start producing haploid eggs later, and their colonies would be female-biased.

Our hypothesis is that, due to their greater body resources, heavier queens will begin laying eggs earlier and produce a greater number of female offspring, resulting in larger colonies (as workers are females). Our aim here is to test this hypothesis further by studying the effect of queen body mass on i) the timing of first eggs laid, ii) worker population size, and iii) the production of reproductive offspring (males and gynes) in the white-tailed bumblebee *B. lucorum*.

Materials and methods

Rearing of colonies

The white-tailed bumblebee (*B. lucorum*) is a widespread and common bumblebee species in Finland (Parkkinen *et al*. 2018). This cool-climate-adapted species has a distinctive yellow, black and white colouration and typically nests in underground burrows, such as those abandoned by rodents (Benton 2006, Parkkinen *et al*. 2018). Colony-founding queens are commonly seen flying in spring when the temperature exceeds 15 °C (Pekkarinen & Teräs 1997). Therefore, it is relatively easy to collect enough queens for the study. The queens used as foundresses (N = 140) were collected from the field in south-western Finland between the 15 and 28 April 2011. We identified the queens first by morphological characters and the timing of their emergence. Since pollen-collecting queens have already established their nest, we collected only those queens that had no pollen on their pollen basket and were seemingly collecting only nectar. Identification was verified after the rearing period using both sequencing and a PCR-RFLP method for short DNA-fragments (Vesterlund *et al*. 2014b).

The laboratory rearing was carried out to produce gynes for an overwintering experiment (Vesterlund *et al*. 2014a) where we aimed to measure threshold body mass for overwintering survival of young queens. For that study we measured body mass, but not morphological size measurements, as it was not needed for that study. Therefore, we here use queen body mass instead of morphological size as our measurement of queen size.

The queens were weighed with a precision scale to the nearest 0.01 mg and kept for one to a maximum of three days at +4 °C before they were transferred into small starter nest boxes. The boxes were made from round 250 ml clear plastic containers (10 cm diameter; 12 cm height); the lid worked as the bottom, and the container was held upside down. Holes were drilled into the bottom lid to help keep the box clean from faeces. A 2 mm stainless-steel wire mesh (5 × 5 cm) was installed on the top for feeding and ventilation. Holes were also drilled into the side of the box for additional ventilation. A piece of cardboard was taped onto the bottom to prevent excess moisture from gathering. Nectar (Biobest: BioGluc) was provided through a hole in the box with a 100 ml plastic water container commonly used in bird cages.

The nests were kept in constant darkness at 24–25 °C and 50–60% relative humidity. With these conditions we aimed to simulate ambient climatic conditions in Finnish summer. Red light invisible to bumblebees was used during monitoring and handling the bumblebees. Egg-laying was induced by providing the queen with a pea-sized ball formed from fresh frozen pollen and nectar. Most queens used this ball first for feeding and later laid eggs on top and started to incubate them. When the first workers emerged, the colonies were transferred to bigger nest boxes (30 × 25 × 30 cm) made of wood and stainless-steel wire mesh. The colonies were fed *ad libitum* with bee-collected pollen (fresh frozen) and nectar. Pollen was given through the mesh at least three times a week such that there was always a surplus of it in the nest at the time of the next feeding, and a nectar bottle was installed on the bottom of the nest box, from where the liquid could be consumed by sucking through a plastic tube filled with absorbent cotton.

From the 140 field-collected queens, 129 produced offspring and were transferred into bigger nest boxes. From these colonies, 98 managed to produce workers and reproductives, and were further used in this study. Males were produced in all 98 colonies, and 34 nests produced both males and gynes. The total number of produced reproductives was 2044 (1952 males; 92 gynes), and the number of workers at the end of rearing was 3074. The produced gynes were weighed with a precision scale to the nearest 0.01 mg at approximately seven days after emerging. The colonies were terminated by freezing when sexual offspring production ceased.

Statistical analysis

Egg-laying delay was calculated as the number of days between the initiation of rearing and the first laid egg. Colony maturation time was calculated as the number of days between the first laid

egg and the first emerged sexual offspring. All statistical analyses were carried out using SAS 9.4 statistical software using regression models in generalized linear models (GLM, GLIMMIX procedure in SAS). Analyses of count type variables (e.g., number of days, number of workers, gynes and males) were analysed using the Poisson or negative binomial regression (selected by better fit) with a log link function. The sex ratio was analysed with logistic regression using the number of gynes as the dependent variable with the total number of sexual offspring as the denominator with a binomial distribution and a logit link function. Normal (Gaussian) regression with an identity link function was used in the analyses concerning the association between gyne body mass and egg-laying delay, colony maturation time, and the number of reproductives. In addition, nest of origin was used as a random factor (with the Kenward-Roger approximation method for the degrees of freedom) in the analyses on gyne body mass because in several cases there were multiple new gynes from same nests.

Results

The fresh body mass of queens (N = 98) at the beginning of rearing varied broadly from 296.0 mg to 912.2 mg, average being 508.7 mg (± SD 122.1). The queens did not start laying eggs immediately after they were placed into the study nests; the egg-laying delay varied from five to 56 days (mean ± SD: 18.3 ± 9.2 days). Colony maturation time (from the first laid egg to the emerging of the first reproductives) varied from 27 to 121 days (mean ± SD: 61.5 ± 16.1 days). Worker population size at the time the reproductives emerged varied from three to 171 workers (mean ± SD: 21.4 ± 20.8). The colonies produced zero to eight gynes and one to 62 males.

Egg-laying delay was not associated with initial fresh body mass of the queens (Table 1). Colony maturation time increased with an increase in queen body mass, as did worker population size at the time the reproductives hatched and at the end of the rearing period (Table 1 and Fig. 1). Worker population size at the time the reproductives hatched increased

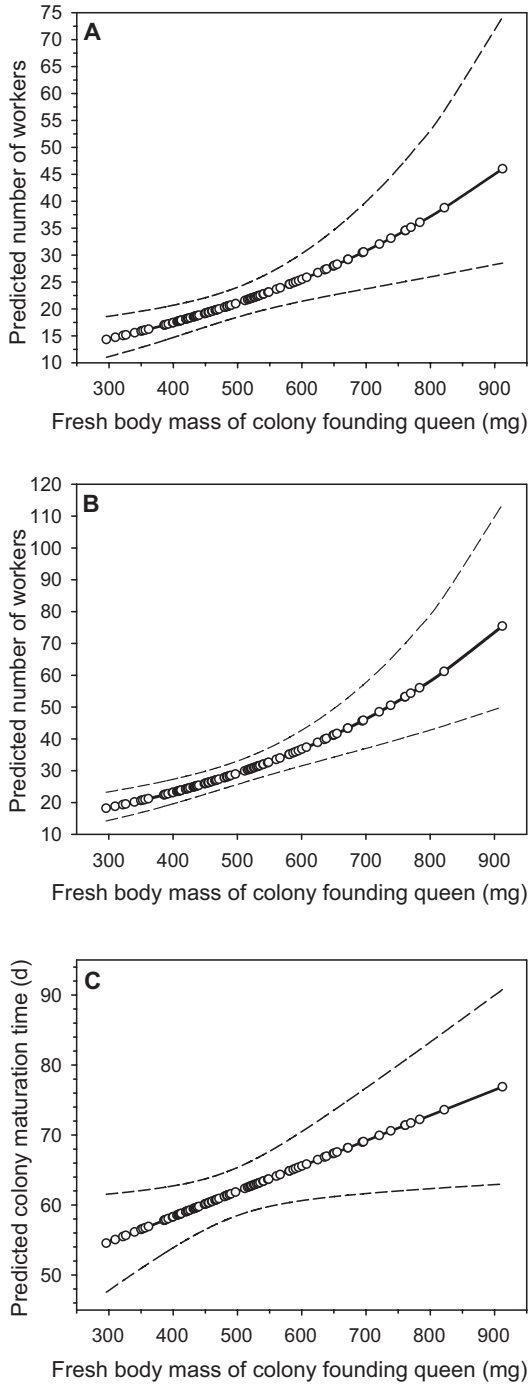

Fig. 1. Association of initial fresh body mass of the queen with the number of workers in the colony when — **A**: reproductives hatch and — **B**: production of reproductives ceased (GLM_{NEGBIN} ± 95% confidence limits). — **C**: Association of initial fresh body mass of the queen with colony maturation time, i.e., days from the first eggs laid to hatching of the first sexual offspring ($GLM_{GAUSSIAN}$ ± 95% confidence limits).

with an increased colony maturation time (GLM_{NEGBIN}: $F_{1, 85} = 19.52$, $p < 0.0001$; Fig. 2).

Body mass of the foundress queen had no direct effect on the number of gynes and males or the proportion of gynes in the reproductive offspring (Table 1). The total number of sexual offspring increased with an increasing number of workers at the time the first reproductives hatched ($GLM_{POISSON}$ $F_{1, 90} = 40.47$, $p < 0.0001$; Fig. 3A). The number of workers did not affect the number of produced gynes, but it increased the number of produced males ($GLM_{POISSON}$, gynes: $F_{1, 90} = 1.35$, $p = 0.25$; males: $F_{1, 91} = 45.77$, $p < 0.0001$; Fig. 3B); thus, it decreased the proportion of gynes in the reproductive offspring ($GLM_{BINOMIAL}$: $F_{1, 90} = 11.87$, $p = 0.0009$; Fig. 4).

There was no association between the body mass of the foundress queen and the weight of gynes it produced (Table 1). An increase in the number of males did not affect the fresh body mass of their sister gynes ($GLM_{GAUSSIAN}$, male number: $F_{1, 31} = 0.13$, $p = 0.72$). Worker population size when the reproductives hatched did not affect the fresh body mass of gynes ($GLM_{GAUSSIAN}$, $F_{1, 31} = 1.58$, $p = 0.22$).

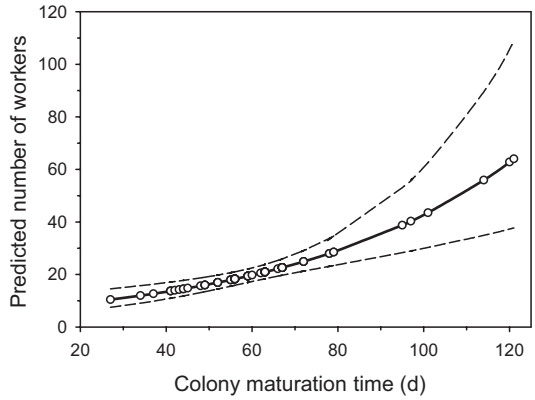

Fig. 2. Predicted number of workers at colony maturation time (GLM_{NEGBIN} ± 95% confidence limits) associated with colony maturation time.

Discussion

We found a marked body mass variation among overwintered field-collected *B. lucorum* queens, and queen body mass affected several variables in colony development. Heavier queens had a longer worker-production period preceding colony maturation time, had a larger worker population at the colony maturation point, and produced more workers before production of sexuals ceased. Large colonies produced all in all more sexual offspring than smaller ones; however, the increase in quantity of sexual offspring was due to increased production of males. As suggested by Duchateau *et al*. (2004), heavier queens also started to produce reproductives later than the smaller queens but, contrary to what was expected, their colonies were more male biased and produced proportionally and numerically fewer gynes.

Duchateau *et al*. (2004) reported a numerical proportion of 0.326 gynes among sexual offspring in their laboratory colonies of *B. terrestris*. However, caution should be exercised when interpreting the sex ratios of laboratory-reared bumblebees, since laboratory conditions can introduce artefacts. For example, the length of hibernation may affect the results obtained from laboratory studies. Furthermore, data on bumblebee sex ratios in natural environments are lacking (Goulson 2010). Unlike in natural conditions, in our laboratory conditions the bumblebee nest boxes with steel-wire walls were almost side by side, thus possible queen pheromones or other signals such as vibration from neighbouring colonies may have affected the production of gynes and possibly males as well. In addition, the humidity in climate room (50–60% relative

Table 1. Effect of queen fresh weight at the beginning of the nesting season on different colony parameters. Results of GLM regression models are shown with distribution parameters of best fit.

	Distribution	df	*F*	*p*
Egg laying delay	Gaussian	1, 96	1.89	0.17
Colony maturation time	Gaussian	1, 84	5.15	0.026
Number of workers[a]	Negbin	1, 89	11.48	0.001
Number of workers[b]	Negbin	1, 96	22.09	<0.0001
Number of gynes	Poisson	1, 96	0.05	0.82
Number of males	Poisson	1, 96	0.09	0.76
Proportion of gynes	binomial	1, 96	0.03	0.87

[a]At the time of emergence of the first reproductive.
[b]At the time production of reproductives ceased.

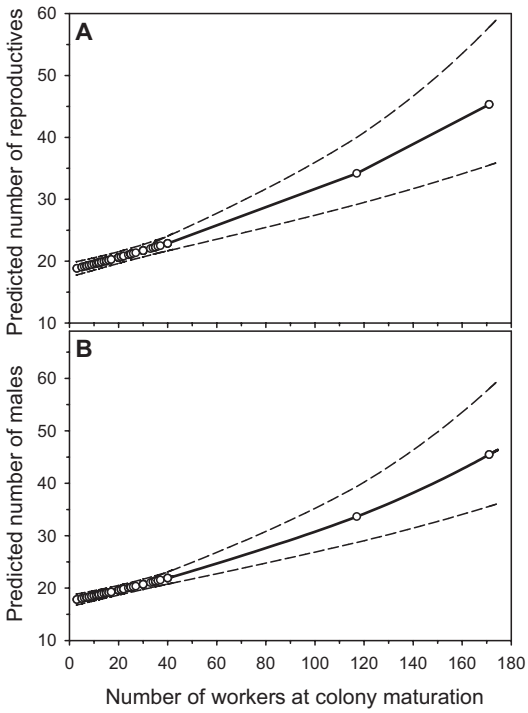

Fig. 3. Predicted number of produced — **A**: total reproductives and — **B**: males ($GLM_{POISSON}$ ± 95% confidence limits) associated with number of workers at colony maturation time.

humidity) may have been suboptimal. Due to the possible artefact effect caused laboratory setup, we cannot draw strong conclusions on sex allocation between gynes and males along worker-population-size and queen-body-mass gradients. However, we suggest that the decrease in proportional allocation to gynes with a greater number of workers is due to female larvae tending to develop into workers rather than gynes in suboptimal laboratory conditions. Beyond this possible gyne-to-worker shift, we cannot consider mechanisms that could have produced laboratory artefacts affecting our main result of the association between queen body mass and worker population size. In addition, there were no nutritional differences among colonies due to constant feeding with identical diet.

Neither the number of males in the colony nor the body mass of the foundress queen affected the fresh body mass of produced gynes in *B. lucorum*. The latter result seems to imply that body-mass variation will persist in the progeny of both large and small queens. Cnaani and Hefetz (1994) found that colonies where the workers in the first cohort were large, produced more and larger workers in the following cohorts. This difference was linked to nutrition of larvae, because poor nutrition lengthens development time and results in small workers, and this effect cascades into the following worker cohorts. Since worker number did not affect gyne size, and because gyne size did not vary between colonies with variable male numbers, we assume that the overall nutritional status in the nests to feed both male and gyne larvae was sufficient. The colonies were fed abundantly, and it is not likely that they were under nutritional stress during rearing. Unlike in nature, all forager workers were constantly inside the nest which could add stress to colonies with large worker numbers, but if there had been some additional, unknown stress factors involved, there should not have been any significant differences in stress levels between the colonies. It is unclear, however, whether the gynes continue gaining body mass until they mate and go into hibernation, which would probably change the outcome to some degree. In our study, the gynes were weighed at the expected time of maturation in laboratory conditions (seven days after hatching from pupa), using the closely related *B. terrestris* as a reference (e.g., Duchateau 1985, Kwon *et al*. 2006).

Vesterlund *et al*. (2014a) showed that heavier-than-average *B. lucorum* queens perform

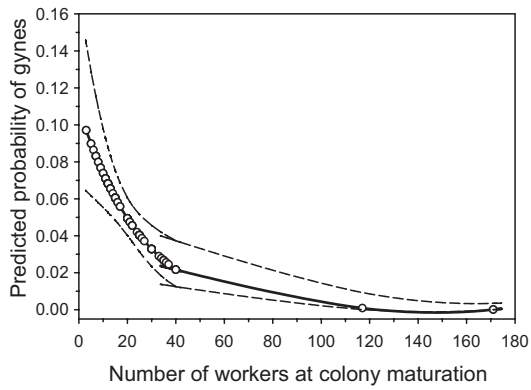

Fig. 4. Predicted probability of gynes among sexual offspring associated with number of workers at colony maturation time ($GLM_{BINOMIAL}$ ± 95% confidence limits).

better after hibernation in mild temperatures; they have more fat left in the abdomen and, consequently, significantly more resources left for their immune functions than in the smaller queens. Queen's body mass and physiological condition during the colony-founding period may be affected by nutrition in the previous summer and later by the rate of consumption of body-energy reserves (fat). Body-energy reserves can be depleted due to suboptimal overwintering conditions (Vesterlund *et al*. 2014a) or by infections of parasites such as *Apicystis bombi* and *Crithidia bombi* (Brown *et al*. 2003, Rutrecht & Brown 2008, Jones & Brown 2014, Fauser *et al*. 2017). As the original setup of the present study was intended for rearing new queens for another experiment, we did not measure morphological size of the colony queens. Had we done so, we would have obtained the queen condition variable (body mass relative to morphological size), which would have enabled us to discuss post-overwintering conditions in relation to colony demography in more detail.

Although made in laboratory conditions, our results suggest possible queen-body-mass-related cascadic effects in bumblebee populations if the queens' body mass is decreasing, for example due to elevated overwintering temperatures or other climatic reasons such as a possible phenological mismatch caused by an early heatwave or drought events (Vesterlund & Sorvari 2014, Korten & Steffan-Dewenter 2026).

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