LARGER WORKERS ARE MORE LIKELY TO BE DRIFTERS IN THE BUMBLE BEE *B. IMPATIENS*

by

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As members of the Master's Committee, we certify that we have read the thesis prepared by Alaina Michaels, titled "Larger workers are more likely to drift in the bumble bee *B. impatiens*" and recommend that it be accepted as fulfilling the thesis requirement for the Master's Degree.

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Final approval and acceptance of this thesis is contingent upon the candidate's submission of the final copies of the thesis to the Graduate College.

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ABSTRACT

Worker drift, a behavior where individuals leave their natal colony to reside in another conspecific colony, has been given both adaptive and maladaptive explanations in social hymenopterans. This behavior is typically attributed to disorientation in commercially managed honey bees where it can increase disease transfer and negatively impact colony fitness. Alternatively, it has been shown that bumble bee and honey bee drifters are producing males in the foreign colony. This suggests individuals may be escaping policing in their natal colony in order to increase their own fitness. Drifters act as social parasites by not working in the foreign colony and reproducing despite potential retaliation. The mechanisms that allow drifters to go undetected in the foreign colony are still unclear. In this study, we further explore the hypothesis that drift is a reproductive strategy for individual workers in the bumble bee, *Bombus impatiens* Cresson, 1863, by looking at its relationship to worker size. We predict that larger workers' fertility will increase their propensity to drift. We found that larger workers are more likely to drift and those drifters are larger than both in-nest workers and foragers from their natal colony. This result provides further support that drifting in bumble bees functions as an alternate reproductive strategy.

Introduction

Cooperative groups often evolve cheaters that reap the benefits of living in cooperative groups without cooperating themselves (Dugatkin, 1997). Such freeloading is particularly interesting in eusocial groups where it often persists at low frequencies (Riehl & Frederickson, 2016) despite the fact that it may lead to retaliation against the freeloader: e.g. 'policing' in social Hymenopterans, where aggressive behaviors are directed at reproducing (and thus selfish) workers (Ratnieks & Visscher, 1989).

In this study, we examined a behavior that may represent a compromise between selfish behavior and reducing the risk of punishment in one's own group: worker drift. 'Drift' occurs when an individual worker enters another non-natal nest of the same species and resides there for part of or the remainder of her life (Birmingham et al., 2004; Free, 1958). Worker drift has been observed in many social bee species, from facultatively social halictids to the eusocial honey bees (Free, 1958; Goerzen et al., 1995; Oliveira et al., 2016; Stephens et al., 2017; Sumner et al., 2010; Ulrich et al., 2009).

Three explanations for drifting have been proposed. First, drifting may be a maladaptive consequence of high nest densities: this could occur, for example, if workers are disoriented and enter a non-natal nest by mistake. This has been argued to apply to commercially managed bee species (e.g. *Apis spp., Bombus spp., Megachile rotunda, Tetragonula carbonaria*), where unnaturally dense aggregations of visually-similar nests might lead to high rates of drift (Free, 1958; Goerzen et al., 1995; Stephens et al., 2017). In managed honey bees, drifting was reduced when hives were in different orientations and painted different colors (Free, 1958). However, studies in more natural distributions (i.e. less dense) also reported drifting, which suggests that this behavior extends beyond artificial aggregations in bumble bees (Zanette et al., 2014). Additionally, drifting still occurred in bumble bees housed in commercial greenhouses regardless of orientation cues (Birmingham & Winston, 2004).

Thus, the second proposed hypothesis for drifting is that workers reproduce in other colonies, thus effectively behaving like social parasites. There is evidence of successful reproduction by drifters in honey bees and bumble bees (Lopez-Vaamonde et al., 2004; Nanork et al., 2005), where workers escape the policing of worker reproduction in their natal colony. Third, if closely related colonies are in relatively dense aggregations, drifters might gain indirect fitness by tending brood from multiple colonies. This might be a particularly beneficial bet-hedging strategy if nest survival is stochastic because it spreads the worker's investments and thus reduces risk of total loss. For example, in polistine wasps where frequent whole-nest predation is common (Sumner et al., 2010).

In this study, we looked more closely at drifting in the eusocial bumble bee species, *Bombus impatiens*. Bumble bee workers within their natal colonies can produce males to increase their direct fitness, but the proportion of successful laying workers varies between species (Bourke, 1988). Bumble bee drifters found in non-natal colonies are more likely to have developed ovaries (Birmingham et al., 2004), supporting the idea that drifting may have evolved as a fitness-increasing behavior. Reproduction by workers is typically policed by other workers and the queen by either egg-eating or aggressive behavior towards laying workers (Ratnieks & Visscher, 1989). Drifting may be more likely towards queenless colonies, where policing would be diminished in some taxa (Chapman et al., 2009; Miller III & Ratnieks, 2001). Conversely, bumble bee drifters have been shown to move to colonies with higher worker and brood numbers, as well as more food stores (Birmingham et al., 2004).

It is unclear how drifters escape detection. Successful drifters may be behaviorally adapted to better infiltrate nests compared to other bees. For example, bumble bee drifters are more aggressive individuals and more fertile (Lopez-Vaamonde et al., 2004). Failure by the foreign colony to recognize drifters as non-nestmates must also play a role in drifter success. Drifting attempts have been shown to be less successful with increased distance from the natal colony in bumble bees, which suggests that colonies in close proximity are more prone to nestmate recognition error either by the drifter or the foreign colony (Zanette et al., 2014).

Worker size may also play a role in successful drifting. Bumble bee colonies exhibit a high and continuous size variation among workers (Alford 1975) --up to 10-fold by weight (Goulson 2003). Possible adaptive functions for bumble bee size variation are not fully understood, but it could increase colony efficiency through worker specialization via comparative advantage and size-specific costs (Kelemen and Dornhaus Submitted). In this eusocial system, smaller workers are more likely to perform within-nest tasks and larger workers are more likely to forage and are more efficient (Goulson et al. 2002). In bumble bees and wasps, larger workers have more developed ovaries (Holman, 2014; Jandt & Dornhaus, 2011; Röseler et al., 1984; Ross, 1985; Turillazzi & Pardi, 1977). In addition to larger ovaries, large bumble bee workers tend to display more aggressive behaviors (Ayasse et al., 1995) and lay eggs (Doorn, 1989). Workers that lay eggs tend to spend less time foraging (Honk et al., 1981) and more time inactive (Jandt & Dornhaus, 2011).

We tested if drifting in the bumble bee *Bombus impatiens* is linked to worker size by measuring workers and observing worker movement between colonies. The hypothesis that workers drift to reproduce in other colonies predicts that larger workers should be more likely to drift: this is because larger workers are more likely to be fertile, and may be more successful at dominance or aggressive behaviors. Alternatively, the hypothesis that drifters are disoriented and enter other colonies by mistake predicts that drifting bees will tend to be smaller individuals: smaller workers have smaller eyes, antennae, and brains, and this has been shown to have negative impacts on their orientation, stimulus recognition, and learning abilities (Mares et al., 2005; Spaethe & Chittka, 2003, 2003), thus potentially leading to a higher probability of orientation mistakes. These hypotheses were tested using paired colonies with access to a shared foraging space where all workers were tagged and measured in order to record drifter movement between the colonies.

Methods

Colonies and Maintenance

We obtained commercially produced bumble bee colonies (*Bombus impatiens*) from Koppert (MI) and housed them in nest boxes (22cm x 11cm x 11cm) lined with pine cat litter (Nature's Earth Products, Inc., West Palm Beach, FL, U.S.A) to reduce moisture, and with a clear plexiglass lid to view the colony. We maintained colonies on a 12h: 12h light: dark cycle at 23*C in the climate chamber experiment. In the greenhouse experiment, bees received natural light, i.e. light: dark cycles were under natural conditions for Arizona (September-November) and temperatures varied between 20-27°C. All colonies were allowed unrestricted foraging for pollen (from either tomato plants in the greenhouse or commercially purchased fresh-frozen obtained from Koppert Inc. in the climate chamber experiment) and 2M sucrose solution. Colonies were supplemented regularly with ground pollen and sucrose solution in the nest, particularly when large amounts of workers were removed to be tagged and measured.

Greenhouse Specifications

We used a 5,000 ft^2 greenhouse at the Controlled Environment Agriculture Center, University of Arizona. The greenhouse conditions were subject to some environmental disturbance, as it was a space also used for teaching. These include the application of neem oil, minor disturbances to colonies (e.g. movement of nest boxes to accommodate student workers), supplemental lighting changes, and variation in plants available to bees which included, tomato, bell pepper, and cucumber plants. Colonies were kept on a platform approximately 40 cm from the ground and entrances positioned parallel to one another and 35 cm apart. Nest box entrances were marked uniquely for each colony (yellow star, blue triangle). Sucrose feeders were kept on the same platform as the nest boxes near nest entrances.

Climate Chamber Specifications:

A climate controlled chamber was used to better control and monitor colonies in a smaller space. We divided the climate chamber with a mesh curtain, which allowed for a partition between the nest boxes and foraging space (2.8m x 1.7m x 1.8m). Nest boxes were kept outside the foraging space so we could access and observe them (Fig. 1). Bees were allowed access to the foraging space via plastic tubing with nest entrances 1 m apart. Colonies were size matched so that each colony had approximately 135 workers during the initial tagging and measuring period by randomly selecting bees to cull. Colonies were kept on a platform approximately 40 cm from the ground and pollen and sucrose feeders were set up at an equal height inside the foraging space.

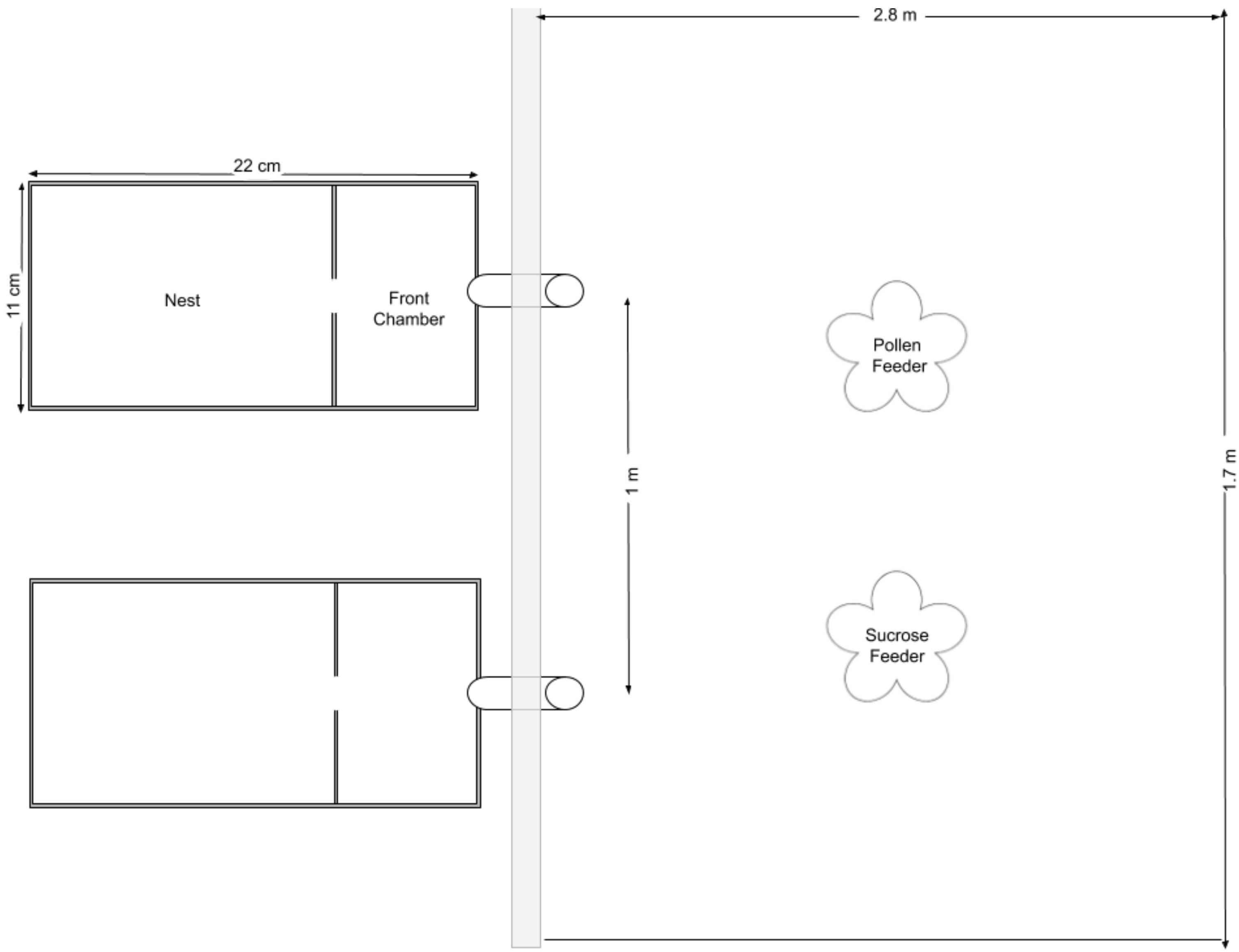

Fig 1: Climate chamber specifications

Drifting Experiment

We measured thorax width, a standard measurement of body size for bumble bees (Goulson 2003), with digital calipers to the nearest 0.1 mm (Neiko Tools, USA) and tagged all workers with numbered plastic tags with colony-specific colors. Colonies were allowed access to smaller foraging arenas (75cm x 60cm x 40cm) for sucrose and pollen during the initial tagging and measuring period. After the tagging period, paired colonies were allowed unrestricted access to either 1) a greenhouse or 2) a climate controlled chamber both with *ad libitum* food. In total, two colonies from each foraging space are included in the analyses. We tagged and measured new workers on a weekly basis and males were removed. We observed colonies for 10 minutes each day and recorded new drifters by looking for non-matching color tags on bees in each colony. Bees found dead in the nest were marked as in-nest workers. Deceased bees found in the foraging space and bees observed foraging were recorded as foragers. Since most bees die outside the nest, deceased bees were not recorded as foragers if they were found in the front chamber of the nest box (Fig. 1). Colonies were frozen when worker production ceased. Additional drifters and in-nest workers were recovered from nest boxes and recorded.

Statistical Analyses

We used linear models (lm(Thorax.Width ~ workertype + Colony, data=alldata) in R) with body size (thorax width) as the response variable and worker type (either drifter vs. non-drifter or three levels, drifter, in-nest worker, and forager) as the main factor, with colony ID as a random factor. To compare the median size of drifters to other workers in each colony, we used Mann-Whitney-U-Tests separately for each colony (e.g.

wilcox.test(Colony1$Thorax.Width..mm.~Colony1types) in R). We used R version 3.6.1 (*R: The R Project for Statistical Computing*, n.d.).

Results

Does body size affect the likelihood of drifting?:

Larger bees were more likely to be drifters (LM, r^2=0.053, p<0.001, n=1067) with a colony level effect (p<.005 (all), n=4). Colonies 1 and 4 had significantly larger drifters compared to workers from their natal colony (Mann-Whitney-U, Colony 1: p=0.01, n=307; Colony 2: p=0.2751, n=216; Colony 3: p=0.7924,n=301; Colony 4: p<0.01, n=243) (Fig. 2). Additionally, drifters in the climate chamber experiment are larger than both in-nest workers (operationally defined as workers found dead in the nest) and foragers (defined as workers found dead outside the nest, i.e. in the climate chamber) (Fig. 3) (LM, r^2=0.052, p<0.0001 (both), n=387) with no significant colony-level effect (p<0.05 (both), n=2).

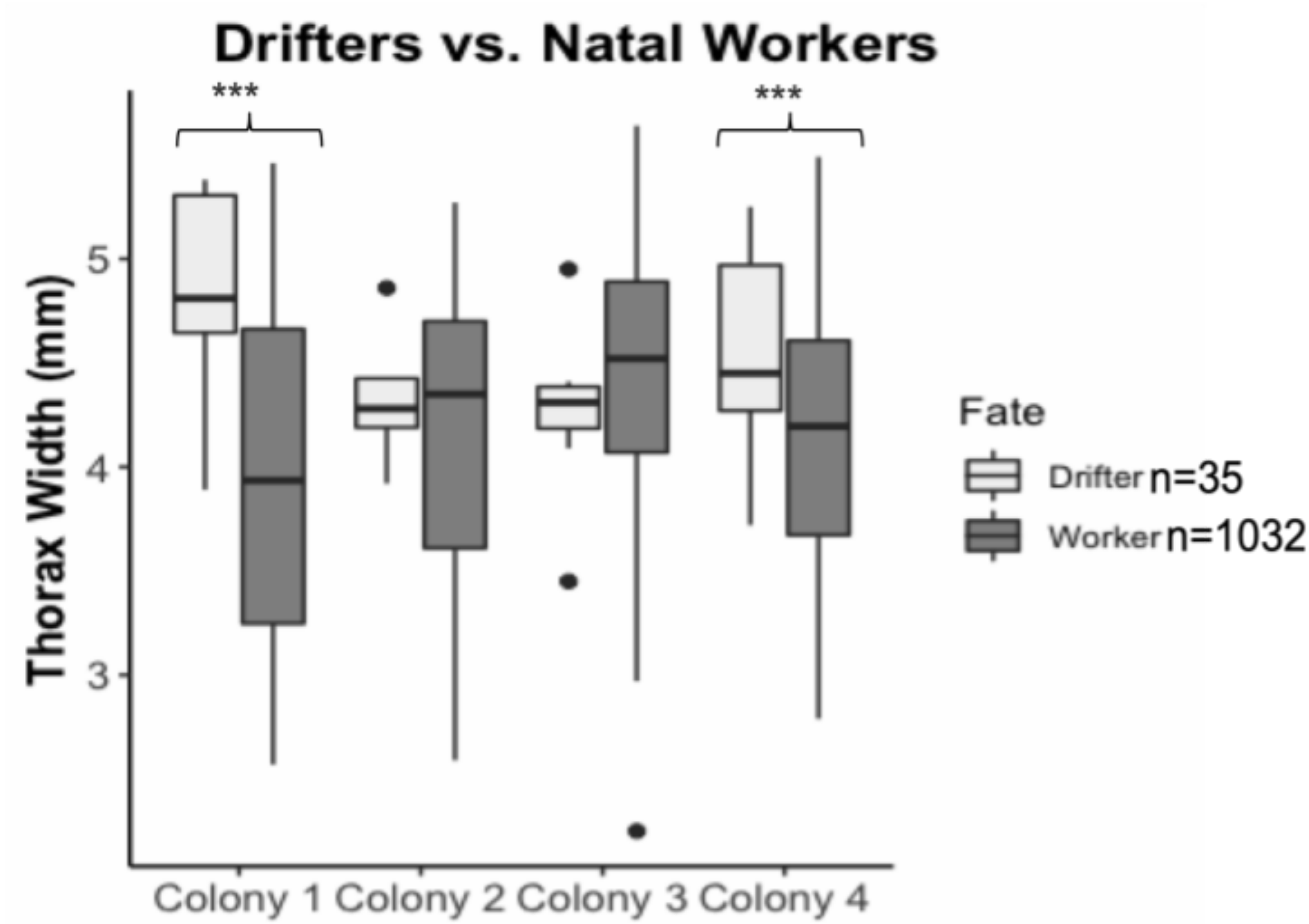

Fig. 2: Drifter sizes compared to all workers from their natal colony. Greenhouse: Colony 1 (worker n=290, drifter n=17) Colony 2 (worker n=209, drifter n=7), Climate Chamber: Colony 3 (worker n=297, drifter n=4), Colony 4 (worker n=236, drifter n=7).

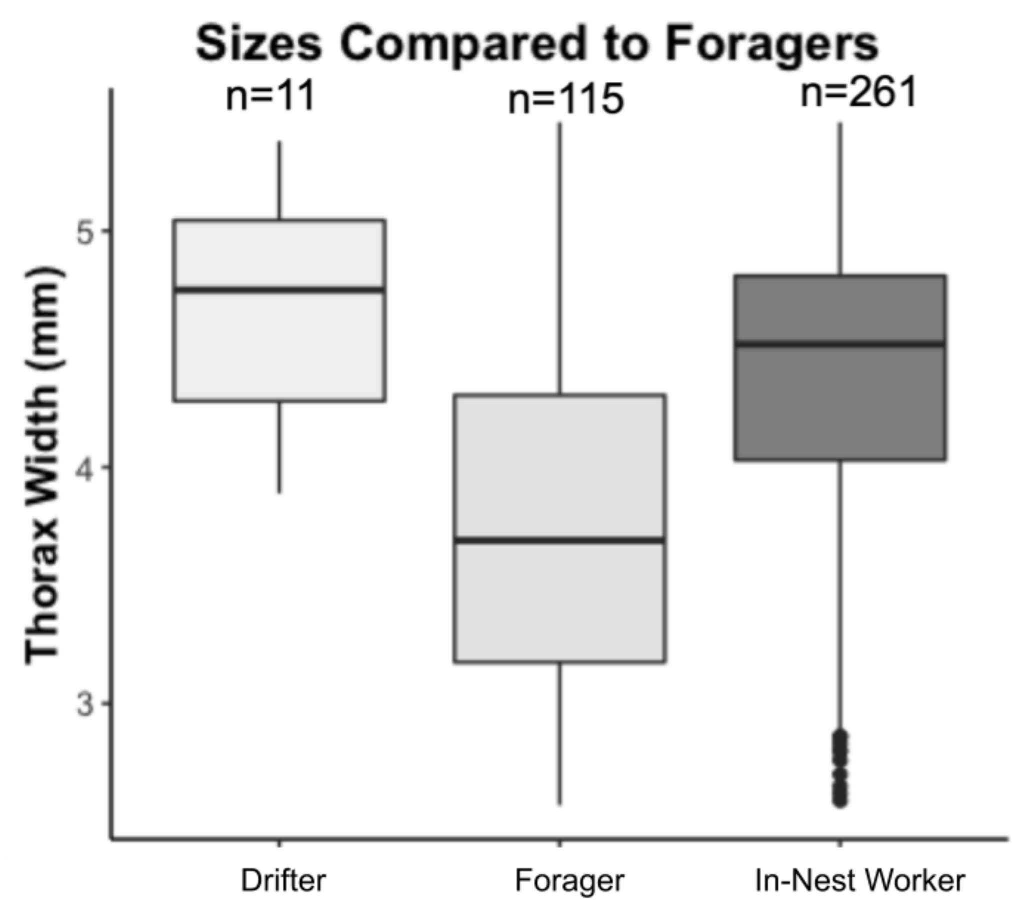

Fig. 3: Drifters compared to foragers (defined as workers found dead outside the nest, i.e. in the climate chamber) and in-nest workers (operationally defined as workers found dead in the nest) from climate chamber colonies. Drifters are larger than both in-nest workers and foragers.Typically, we expect foragers to be the largest workers in the colony. However, foragers are the smallest in size of the three groups in this experiment.

Discussion

We found that drifters were larger than workers of their natal colony in two of four colonies. We also found that drifters were larger than foragers and in-nest workers in the climate chamber experiment. The fact that drifters are larger in two colonies suggests that drifting in bumble bees is not due to disorientation. Instead, it is more likely to be an alternate reproductive strategy by which individuals are able to increase their own fitness by increasing their chance of reproducing in a foreign colony. Drifters may also be behaviorally adapted to infiltrate and successfully reproduce in a foreign colony as some studies have shown increased aggression in drifters (Lopez-Vaamonde et al., 2004). There may be other underlying mechanisms to drifter success besides individual aggression. First, the lack of a colony-wide alarm in bumble bees along with increased drifter aggression may allow drifting to persist at low frequencies. Once a drifter has invaded, it may be costly for the foreign colony to remove them. Additionally, the propensity to produce selfish workers could be linked to a more aggressive colony-level personality. Indeed, there was a colony-level effect in our linear model predicting size by drifter and colony, which suggests that individuals are more likely to drift depending on which colony they came from. We accounted for colony size being linked to increased colony aggression (Birmingham et al., 2004) by size-matching worker populations for the climate chamber experiment. It is likely that many factors we've described, including colony and individual aggression, contribute to drifter success.

Although the rates of successful drifting attempts aren't well known, reproductive gains achieved by drifting seems to be one of a few explanations for why social insects attempt to enter non-natal colonies. For example, when foraging resources are scarce, commercially managed honey bees will enter other colonies to steal honey and then return to their natal colony (Fries & Camazine, 2001). Other attempts to enter non-natal colonies fall under social parasitism. Some ant species will steal brood from neighboring colonies of either their own species (e.g. brood raiding) or a host species (e.g. slave-making) and raise them in their natal colony (Pollock & Rissing, 1989). Additionally, social bumble bees are parasitized by the closely related subgenus, *Psithryus* Lepeletier, 1833, which are effectively workerless queens that parasitize social bumble bee species by laying male and queen eggs in the foreign colony. Aggressive behaviors range from killing the natal queen to seemingly coexisting within the colony (Free & Butler, 1959; Küpper & Schwammberger, 1995). The latter behavior of social parasites is surprisingly similar to that of drifters and it has been suggested that drifters may be an evolutionary step towards obligate parasitism that is seen in this subgenus.

Regardless of the potential adaptiveness of drift for individuals, there is evidence that it decreases natal colony fitness (Goodwin et al., 1994; Jay, 1968). Aggressive interactions between the drifter and the foreign colony workers also may decrease the foreign colony's fitness. One of the means by which drifting can reduce foreign colony fitness is by increasing disease transfer between colonies (Bordier et al., 2017) and increased mortality (Fries & Camazine, 2001).

Our results overall support the hypothesis that drifting may be part of a worker reproductive strategy in bumble bees; the hypothesis that it is caused by disorientation is not supported. Whether this is entirely selfish from the workers' point of view, or contributes indirectly to colony fitness is unknown. The distribution of worker sizes in bumble bee colonies may thus, in part, be under selection to produce very large, aggressive workers as a semi-parasitic strategy.

References

Ayasse, M., Marlovits, T., Tengö, J., Taghizadeh, T., & Francke, W. (1995). Are there pheromonal dominance signals in the bumblebee Bombus hypnorum L (Hymenoptera, Apidae)? *Apidologie*, *26*(3), 163–180. https://doi.org/10.1051/apido:19950301

Birmingham, A. L., Hoover, S. E., Winston, M. L., & Ydenberg, R. C. (2004). Drifting bumble bee (Hymenoptera: Apidae) workers in commercial greenhouses may be social parasites. *Canadian Journal of Zoology*, *82*(12), 1843–1853. https://doi.org/10.1139/z04-181

Birmingham, A. L., & Winston, M. L. (2004). Orientation and drifting behaviour of bumblebees (Hymenoptera: Apidae) in commercial tomato greenhouses. *Canadian Journal of Zoology*, *82*(1), 52–59. https://doi.org/10.1139/z03-201

Bourke, A. F. G. (1988). Worker Reproduction in the Higher Eusocial Hymenoptera. *The Quarterly Review of Biology*, *63*(3), 291–311. JSTOR.

Chapman, N. C., Nanork, P., Gloag, R. S., Wattanachaiyingcharoen, W., Beekman, M., & Oldroyd, B. P. (2009). Queenless colonies of the Asian red dwarf honey bee (Apis florea) are infiltrated by workers from other queenless colonies. *Behavioral Ecology*, *20*(4), 817–820. https://doi.org/10.1093/beheco/arp065

Doorn, A. V. (1989). Factors influencing dominance behaviour in queenless bumblebee workers (Bombus terrestris). *Physiological Entomology*, *14*(2), 211–221. https://doi.org/10.1111/j.1365-3032.1989.tb00954.x

Dugatkin, L. A. (1997). *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press.

Free, J. B. (1958). The drifting of honey-bees. *The Journal of Agricultural Science*, *51*(3), 294–306. https://doi.org/10.1017/S0021859600035103

Free, J. B., & Butler, C. G. (1959). *Bumblebees*. http://agris.fao.org/agris-search/search.do?recordID=XE2012200603

Fries, I., & Camazine, S. (2001). Implications of horizontal and vertical pathogen transmission for honey bee epidemiology. *Apidologie*, *32*(3), 199–214. https://doi.org/10.1051/apido:2001122

Goerzen, D. W., Richards, K. W., & Rank, G. H. (1995). Drifting in populations of the alfalfa leafcutting bee, Megachile rotundata (Fab.) (Hym., Megachilidae). *Journal of Applied Entomology*, *119*(1–5), 575–579. https://doi.org/10.1111/j.1439-0418.1995.tb01338.x

Goodwin, R. M., Perry, J. H., & Houten, A. T. (1994). The effect of drifting honey bees on the spread of American foulbrood infections. *Journal of Apicultural Research*, *33*(4), 209–212. https://doi.org/10.1080/00218839.1994.11100873

Holman, L. (2014). Bumblebee size polymorphism and worker response to queen pheromone. *PeerJ*, *2*, e604. https://doi.org/10.7717/peerj.604

Honk, C. G. J. van, Röseler, P.-F., Velthuis, H. H. W., & Hoogeveen, J. C. (1981). Factors Influencing the Egg Laying of Workers in a Captive Bombus terrestris Colony. *Behavioral Ecology and Sociobiology*, *9*(1), 9–14. JSTOR.

Jandt, J. M., & Dornhaus, A. (2011). Competition and cooperation: bumblebee spatial organization and division of labor may affect worker reproduction late in life. *Behavioral Ecology and Sociobiology*, *65*(12), 2341–2349. https://doi.org/10.1007/s00265-011-1244-9

Jay, S. C. (1968). Drifting of Honeybees in Commercial Apiaries. IV. Further Studies of the

Effect of Apiary Layout. *Journal of Apicultural Research*, *7*(1), 37–44. https://doi.org/10.1080/00218839.1968.11100185

Küpper, G., & Schwammberger, K. H. (1995). Social parasitism in bumble bees (Hymenoptera, Apidae): observations of Psithyrus sylvestris in Bombus pratorum nests. *Apidologie*, *26*(3), 245–254. https://doi.org/10.1051/apido:19950306

Lopez-Vaamonde, C., Koning, J. W., Brown, R. M., Jordan, W. C., & Bourke, A. F. G. (2004). Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature*, *430*(6999), 557–560. https://doi.org/10.1038/nature02769

Mares, S., Ash, L., & Gronenberg, W. (2005). Brain Allometry in Bumblebee and Honey Bee Workers. *Brain, Behavior and Evolution*, *66*(1), 50–61. https://doi.org/10.1159/000085047

Miller III, D. G., & Ratnieks, F. L. W. (2001). The timing of worker reproduction and breakdown of policing behaviour in queenless honey bee (Apis mellifera L.) societies. *Insectes Sociaux*, *48*(2), 178–184. https://doi.org/10.1007/PL00001762

Nanork, P., Paar, J., Chapman, N. C., Wongsiri, S., & Oldroyd, B. P. (2005). Asian honeybees parasitize the future dead. *Nature*, *437*(7060), 829–829. https://doi.org/10.1038/437829a

Oliveira, R. C., Oi, C. A., Vollet-Neto, A., & Wenseleers, T. (2016). Intraspecific worker parasitism in the common wasp, Vespula vulgaris. *Animal Behaviour*, *113*, 79–85. https://doi.org/10.1016/j.anbehav.2015.12.025

Pollock, G. B., & Rissing, S. W. (1989). Intraspecific Brood Raiding, Territoriality, and Slavery in Ants. *The American Naturalist*, *133*(1), 61–70. https://doi.org/10.1086/284901

R: The R Project for Statistical Computing. (n.d.). Retrieved May 1, 2020, from https://www.r-project.org/

Ratnieks, F. L. W., & Visscher, P. K. (1989). Worker policing in the honeybee. *Nature*, *342*(6251), 796–797. https://doi.org/10.1038/342796a0

Riehl, C., & Frederickson, M. E. (2016). Cheating and punishment in cooperative animal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1687), 20150090. https://doi.org/10.1098/rstb.2015.0090

Röseler, P.-F., Röseler, I., Strambi, A., & Augier, R. (1984). Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, Polistes gallicus. *Behavioral Ecology and Sociobiology*, *15*(2), 133–142. https://doi.org/10.1007/BF00299381

Ross, K. G. (1985). Aspects of worker reproduction in four social wasp species (Insecta: Hymenoptera: Vespidae). *Journal of Zoology*, *205*(3), 411–424. https://doi.org/10.1111/j.1469-7998.1985.tb05626.x

Spaethe, J., & Chittka, L. (2003). Interindividual variation of eye optics and single object resolution in bumblebees. *Journal of Experimental Biology*, *206*(19), 3447–3453. https://doi.org/10.1242/jeb.00570

Stephens, R. E., Beekman, M., & Gloag, R. (2017). The upside of recognition error? Artificially aggregated colonies of the stingless bee Tetragonula carbonaria tolerate high rates of worker drift. *Biological Journal of the Linnean Society*, *121*(2), 258–266. https://doi.org/10.1093/biolinnean/blw048

Sumner, S., Kelstrup, H., & Fanelli, D. (2010). Reproductive constraints, direct fitness and indirect fitness benefits explain helping behaviour in the primitively eusocial wasp, *Polistes canadensis*. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1688), 1721–1728. https://doi.org/10.1098/rspb.2009.2289

Turillazzi, S., & Pardi, L. (1977). Body Size and Hierarchy in Polygynic Nests of Polistes Gallicus (l.) (hymenoptera Vespidae). *Monitore Zoologico Italiano - Italian Journal of Zoology*, *11*(1–2), 101–112. https://doi.org/10.1080/00269786.1977.10736294

Ulrich, Y., Perrin, N., & Chapuisat, M. (2009). Flexible social organization and high incidence of drifting in the sweat bee, Halictus scabiosae. *Molecular Ecology*, *18*(8), 1791–1800. https://doi.org/10.1111/j.1365-294X.2009.04154.x

Zanette, L. R. S., Miller, S. D. L., Faria, C. M. A., Lopez‐Vaamonde, C., & Bourke, A. F. G. (2014). Bumble bee workers drift to conspecific nests at field scales. *Ecological Entomology*, *39*(3), 347–354. https://doi.org/10.1111/een.12109