Determining the Evolutionary Effect that Head Width has on Task Association in Different Species of *Formica* Ants

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ABSTRACT

This paper specifically looks at the relationship between head width and task association in *Formica* ants. *Formica* ants lack discrete morphological subcastes and therefore do not follow a strict pattern for task specialization. Two different groups were tested: mound-building and subterranean. It was found that in the mound-building group’s ants with smaller head widths were more likely to be assigned to the honeydew collecting task rather than nest building or protein foraging. On the other hand, subterranean groups did not seem to have a strong association with head width to any of the tasks. This could indicate that in mound-building groups selection favors species with task specialization, so these species have a stronger size-task association leading them to have a stronger colony overall.

INTRODUCTION

Task association based on body size has been studied in multiple different animal societies. Some species have discrete morphological worker subcastes which are used to help divide labor to protect the colony. Social insects such as thrips, aphids, termites, stingless bees, and some ants break into size-based morphs (Richards 2020). This allows smaller workers to be tasked with the less intense jobs, while the bigger workers take on tasks with more physical requirements. Task specialization allows workers to learn their specific task and avoid the cost of task switching, which is thought to increase efficiency of the colony (Chittka and Muller 2009; West 2022). Some may assume that insects without discrete subcastes would have less efficient colonies; however, in some cases where there is a high variance in worker size, it has been shown that there is still an association between worker size and task specialization (Grüter et al. 2011). This suggests that even if there are not specific subcastes, that some species still determine tasks assignments based on size.

There are over 15,100 species of ants (Hymenoptera: Formicidae) in the world (Wong and Guenard 2017). Looking at ants specifically, the genus *Formica* have a high level of natural worker size variation while lacking discrete morphological worker subcastes. This genus is found in North America, Europe, and Asia and are usually found in sparse to medium-dense mature forests, along the edges of the forest, or in ephemeral open patches (Sundström et al. 2005). Within this genus there are two groups: mound-building and subterranean. Mound-building species are facultative social parasites that build mounds on top of their underground nests. Subterranean species are not socially parasitic and they can sometimes build loose dirt mounds above their nests, but are usually entirely underground (Goryunov 2015).

Using a genus of ants with a high level of variation and lacking discrete subcastes allows us to test whether there is an association between task specialization and worker size. A study performed by Tawdros, West, and Purcell tested the relationship between body size and task assignment found both linear allometric and some isometric scaling. They log-transformed measurements and used linear models to assess the associations using five different measurements (Tawdros et al. 2020). Taking this a step further, we test whether head width measurements have an impact on task assignment, rather than looking at body size as a whole. The main goal of this paper is to determine whether there is an association between head width size and task across species of *Formica* ants.

MATERIALS AND METHODS

*Collection*

Data was collected in June-August of 2017 throughout Alberta, Canada. Ten species of *Formica* ants were observed and collected at ten different locations. There were three tasks that were focused on while collecting: honeydew collectors (HC), nest builders (NB), and protein foragers (PF). Honeydew collectors tend to aphids or other plants and they were selected while performing this task. Nest builders carry the materials to build the nests (pine needles, wood chips, dirt, pebbles) and then were selected while building the nest. Protein foragers search for prey and can be found carrying other insects or spiders (Tawdros et al. 2020). The ants collected for this study were put into categories of “consistent” or “task switchers” depending on the tasks that they were observed performing. They found that 98.6% of the ants tested were in the category of “consistent” workers while 1.4% was in the “task switchers” group. This suggests that task switching was not observed often enough to make any reliable conclusions on the effect that it may have on task association (West 2022).

*Head Measurements*

A Leica S8AP0 microscope with Leica DMC2900 camera attached to imaging software was used to photograph the head in 25x magnification. Measurements of each specimen were taken to one-thousandth of a millimeter measuring the widest point across the eyes with the Leica Application Suite version 4.6.2 (Tawdros et al. 2020; West 2022).

Graphical user interface, application

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Figure : Example of head width

*Identifying Species*

Genetic sequencing (RADseq) was used to identify the species that had been captured. Two species in *F. rufa* group were unable to be identified so they are referred to as, ‘*F. rufa sp. #1*’ and ‘*F. rufa sp. #2*’. These species were separated into mound-building and subterranean groups. Mound-building groups included: *F. aserva, F. dakotensis, F. neorufibarbes, F. obscuricentris, F. ulkei,* and *F. rufa sp. #2.* The subterranean groups consisted of *F. glacialis, F. neoclara, F. podzolica,* and *F. rufa sp. #1* (West 2022) *.*

*Statistical Tests*

R Studio version 4.1.3 was used to evaluate data. A boxplot was made to demonstrate the relationship between head width and task for each species (Figures 1-11), as well as one with the total head widths and task assignments (Figure 12). A multinomial regression for head width and task association was performed under the assumptions that the model was specified correctly with no extraneous variables, the cases were independent of each other, and that there is no multicollinearity between the individual variables. The response level of each task was predicted using the ggeffects function in R. Another multinomial regression was used to test the effects of head width and species as a function of task. The *nnet* package in R was used to perform the multinom function. We specify that task be modeled as a function of head width. A logit model was made to demonstrate the ratio of the probability, or relative risk.

RESULTS

*Formica aserva, F. obscuriventris, F. ulkei, F. rufa sp. #1,* and *F. rufa sp. #2*, all show a statistically clear difference between ant head width of those selected for the honeydew collecting task when compared to the nest builders and protein foragers. *F. dakotensis* and *F. neorufibarbes* also demonstrate that there is a significant difference between honeydew collector head width and the other tasks. This difference is not as significant as *F. aserva*, but it follows the same trend. *F. glacialis, F. neoclara*, and *F. podzolica* do not show any indications that head width is a determinant of task association. Overall, there is a relationship between head width and task association in seven of the ten species that were tested with six of the seven belonging to the mound-building group (Figures 1-12).

Chart, box and whisker chart

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Figure : Boxplot depicting relationship between head width and task in F. aserva.

Chart, box and whisker chart

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Figure :Boxplot depicting relationship between head width and task in F. dakotensis.

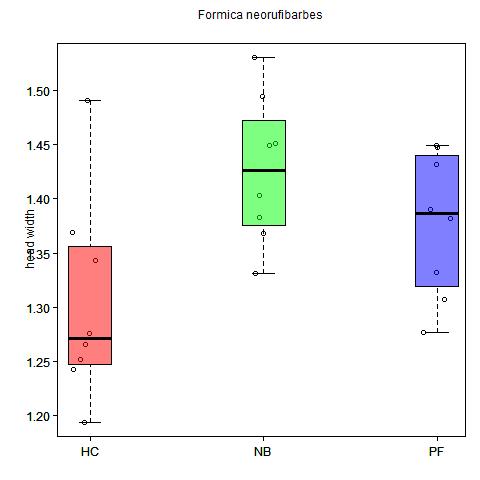


Figure : Boxplot depicting relationship between head width and task in F. neorufibarbes.

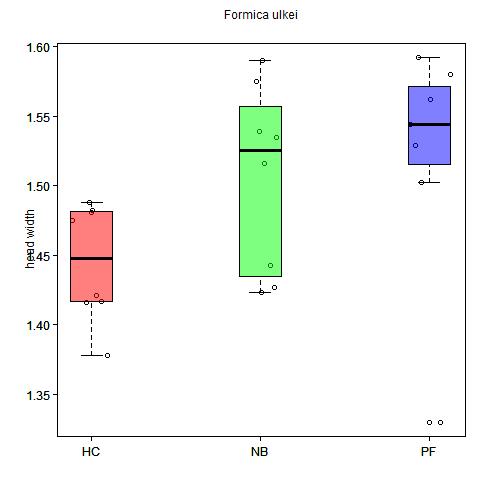


Figure :Boxplot depicting relationship between head width and task in F. ulkei.

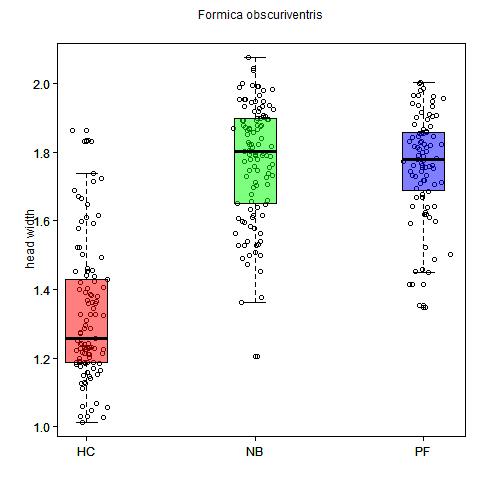


Figure :Boxplot depicting relationship between head width and task in F. obscuriventris.

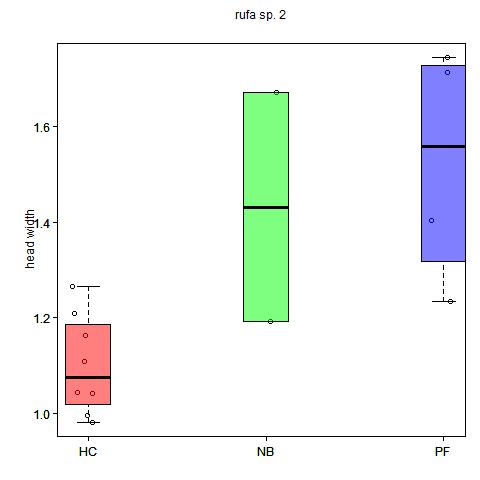


Figure :Boxplot depicting relationship between head width and task in F. rufa sp. #2.

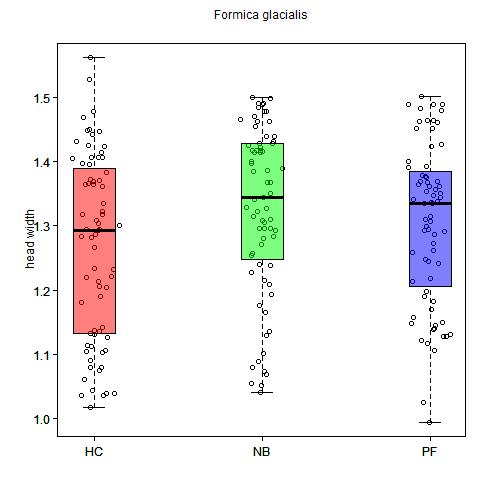


Figure : Boxplot depicting relationship between head width and task in F. glacialis.

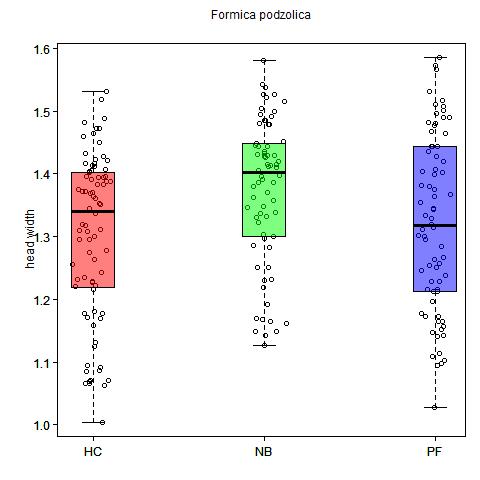


Figure : Boxplot depicting relationship between head width and task in F. podzolica.

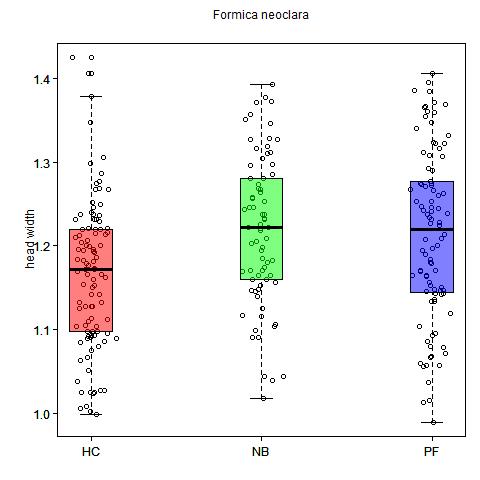


Figure : Boxplot depicting relationship between head width and task in F. neoclara.

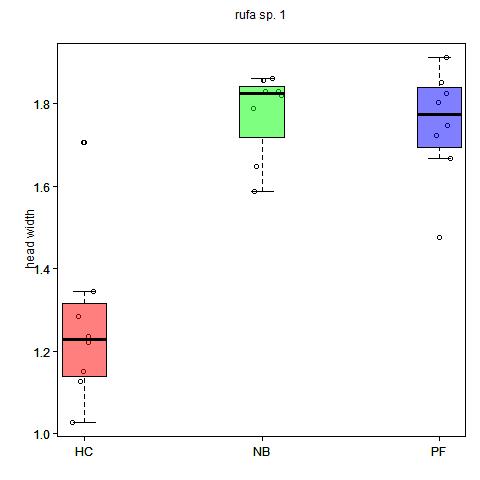


Figure : Boxplot depicting relationship between head width and task in F. rufa sp. #1.

Chart, box and whisker chart

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Figure : Boxplot depicting the relationship between all head widths and task assignment.

The multinomial logistic regression using task as a function of head width found that the coefficient for NB to HC to be 4.26 with a standard error of 0.35. The coefficient for PF to HC was 3.62 with a standard error of 0.35. The confidence intervals for NB was (3.57, 4.95), while PF was (2.94, 4.31). There was a total of 454 collections for HC, 515 for NB, and 515 for PF. Figure 13 was created to depict the predicted probability of each task with the ribbons showing the lower and upper confidence limits.

Table : Table showing data found via multinomial logistic regression using task as a function of head width.

|  |  |  |  |
| --- | --- | --- | --- |
| Task | Coefficient | Standard Error | Confidence Interval |
| NB-HC | 4.26 | 0.35 | (3.57, 4.95) |
| PF-HC | 3.62 | 0.35 | (2.94, 4.31) |

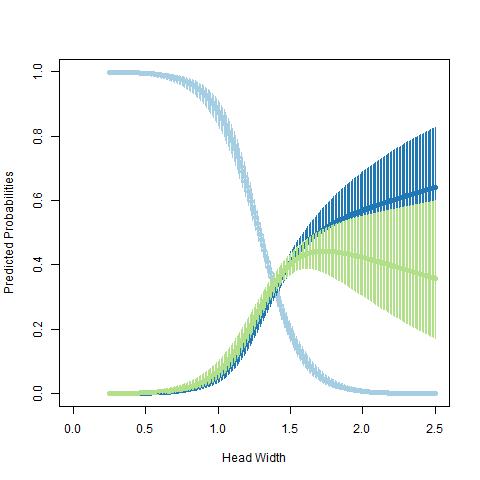


Figure : Graph showing the predicted values of which task will be selected depending on head width with ribbons showing the lower and upper confidence limits.

The AIC of the multinomial logistic regression that only used head width and task was 2621.004 with a residual deviance of 2613.004. The AIC of the regression including the group specifications was 2553.89 with a residual deviance of 2542.89, and the AIC of the regression that included species was 2522.92 with a residual deviance of 2478.92. The regression that included head width and species was the model of best fit. In that regression the coefficients for head width for NB was 7.16 with a standard error of 0.53. The coefficients for head width for PF was 6.59 with a standard error of 0.51. The following species had a slightly lower coefficient for PF than NB and a lower standard error: *F. glacialis, F. neorufibarbes*, and *F. podzolica.* The *F. dakotensis, F. obscurieventris,* and *F. ulkei* species all had lower coefficients, but had a higher standard error than PF. *F. neoclara, F. rufa p. #1,* and *F. rufa sp. #2* all had higher coefficients and lower standards of error than NB.

Table : Table showing data found via multinomial logistic regression using task as a function of head width and species, specifically focused on head width as well as using task as a function of head width and group.

|  |  |  |  |
| --- | --- | --- | --- |
| Task | Coefficient | Standard Error | Confidence Interval |
| NB-HC | 7.16 | 0.53 | (6.13, 8.19) |
| PF-HC | 6.59 | 0.51 | (5.58, 7.60) |
| Group NB-HC | 5.65 | 0.43 | (4.81, 6.49) |
| Group PF-HC | 5.09 | 0.42 | (4.27, 5.92) |

DISCUSSION

The outliers in the head widths within each task makes it difficult to accurately assess the size-task association of the *Formica* ants on the boxplots, but by looking at the interquartile range it is easier to see the differences in size-task association. If the error bars do not overlap then there is a significant difference between the tasks. The values depicted in the boxplots seem to follow the trend that mound-building species have a stronger association between the ants with smaller head widths being assigned to the honeydew collecting task (Figures 1-12). Since mound-building requires carrying larger loads to build the mounds, the ants with larger heads could be assigned to the more physically demanding jobs to make them more efficient. Whereas, in the subterranean groups this would not be necessary. The association in *F. Dakotensis* and *F. Neorufibarbes* were not as strong as the relationship found in the other mound-building species. This could be due to the variance in sampling size impacting the quality of data necessary to draw conclusions. Another possibility would be that these species did not build as big of mounds as the other species, so ants with smaller heads could still complete the task. Likely the most possible explanation would be that head width specifically may not be the determinate of task assignment in those species or in the subterranean groups.

The coefficients for the relative risk of task and head width found that PF to HC was more accurate than NB to HC. Since they both have a standard error of 0.35, the smaller coefficient in the PF makes it the more precise measurement. This means that with each additional increase in head width the log odds of choosing NB is 3.62 chances higher, while the log odds of choosing PF is 4.26 chances higher than choosing HC. Figure 13 shows the predicted values of a certain task being selected based on head width with upper and lower confidence levels. This shows that HC has a much higher chance of being assigned if the head width is small compared to NB or PF. As the head width increases, the chances of getting assigned either NB or PF increases, while the likelihood of HC decreases. In both of the other regressions performed it also showed that NB was more likely to be chosen as the head width increased. Due to the difference in sample sizes the graphs make it seem that there is a more significant difference between the mound-building and subterranean groups, but the results show that there is a stronger association when accounting for the species rather than the groups. It can be concluded that in most cases there is an association between head width and task assignment suggesting selection would favor species that have task specialization because it would lead to colonies being more strongly protected.

To further consider the impact that species may have on this relationship we performed a multinomial logistic regression using both head width and species as a function of task. By looking at the AIC values between this multinomial logistic regression and the one that only uses task and head width, it shows that this model is a better fit for the data. The AIC of this model is 2522.92 with residual deviance of 2478.92 which is lower and therefore more accurate than the previous model which had an AIC of 2621.004 with residual deviance of 2613.004. *F. Glacialis, F. Neorufibarbes*, and *F. Podzolica* had the lowest coefficient as well as the lowest standard error suggesting that they were the most precise. *F. Glacialis* and *F. Podzolica* are both subterranean species, but *F. Neorufibarbes* is a mound-building species. These are all species that had smaller sampling sizes, which could be why the results are showing that they are more precise. Further research would warrant larger sample sizes to see if the results match on larger populations.

There is some variation in the results, but most of them followed the trend that subterranean groups did not have as strong of a relationship between head width and task association. In all of the mound-building groups it was found that ants with smaller head widths were more commonly assigned to the honeydew collecting task rather than nest building or protein foraging. There are some cases where ants with smaller head widths are assigned to other tasks, but it seems that there are relatively few with larger heads that are assigned to honeydew collecting. This suggests that smaller ants may be able to step up to larger tasks, but most of the larger headed ants are needed for the physically demanding tasks and would not be assigned to the honeydew collecting task. These results support that head width could be an evolutionary change that has evolved in multiple species of Formica ants, even those that do not have specific morphological subcastes, in order to strengthen their colonies, and in turn produce more offspring.

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