The Popular Patch: Co-foraging behavior of *Bombus spp.* in a subalpine meadow

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Abstract

Bumble bees (*Bombus spp.*) exploiting patchy landscapes make strategic decisions to maximize energetic rewards. Previous evidence suggests that bumble bees use the presence of conspecifics as a cue for finding rewarding floral resources. However, co-foraging bumble bees also risk visiting depleted flowers. This suggests a trade-off between the benefits of exclusive resources and social information. Bumble bee foragers may shift from prioritizing social information to exclusive resources as they change from being naive to experienced. Here, I assess the frequency of co-foraging in flower patches for wild bumble bees in a natural subalpine meadow to determine whether foragers are prioritizing exclusive resources or social information and whether this changes as they gain experience throughout their lifetimes. I found that bees are not more or less likely to recruit to a patch with a co-forager than expected with random selection. However, bees stay longer at patches with co-foragers than without, even when controlling for flower density. Experience across days had no effect on the influence of co-forager presence on these indices of patch selection. These findings can inform our understanding of bumble bee foraging strategies and how their use of cues varies at differing scales and stages of floral resource selection.

Introduction

Members of the bee clade (Anthophila) vary widely in their level of sociality, from solitary carpenter bees to highly eusocial honeybees. Eusociality provides increased capacity for communication among closely related kin and in turn, greater fitness benefits (Frisch, 1967; Nieh, 2004). The most conspicuous example of eusocial communication is found in honeybees (*Apis mellifera*) whose complex dances give directions to rewarding resources (Frisch, 1967). Unlike the well known waggle dance of the honeybee, their relatives in the genus *Bombus* (bumble bees) are not known to actively transmit information to conspecifics (Michener, 1974). However, a vast amount of experimental data suggests that bumble bees transmit information via passive social cueing rather than active social signaling (Leadbeater & Chittka, 2005, 2007a, 2007b; Worden & Papaj, 2005; Bridges et al., 2024). Specifically, bumble bees learn how to recognize and access rewarding floral resources by watching conspecifics. (Worden & Papaj, 2005; Kawaguchi et al., 2007; Bridges et al., 2024; Kawaguchi et al., 2026). Social cueing has also been shown to allow a group of foragers to react faster to environmental changes which is critical given that a bumble bee worker's life spans longer than the flowering period of many plant species (Plowright & Laverty, 1984, P. Fraser et al., 2006; Kawaguchi et al., 2006).

Bumble bees must make strategic decisions when foraging and one of the markers of resource quality they may consider is the presence of other bumble bee foragers at a resource. Foraging alongside another bumble bee is risky because it increases the likelihood of visiting a flower depleted by co-foragers (Brosi, 2016; Valdovinos et al., 2016). Therefore, a forager using social cues must balance the benefits of social information and access to exclusive resources. A key predictor of whether a bee will be attracted to or avoid co-foragers is their familiarity with a location or flower species. (Kawaguchi et al., 2007). For naive foragers, information on rewarding flowers may be beneficial, allowing them to avoid making energetically costly mistakes. On the other hand, for more experienced foragers who are less likely to make mistakes, avoiding co-foragers may be more beneficial (Stout et al., 1998). Thus, the presence of

co-foragers may be a positive or negative cue to bumble bees seeking foraging resources depending on the context.

To my knowledge, all previous research on social cueing in bumble bees has been through experimental manipulation. The primary shortcoming of experimental trials is that they are limited to the smaller scale of flowers or inflorescences. In natural landscapes, floral resources are often distributed in patches and bumble bees must make strategic decisions about which patches to visit and for how long (Fragoso et al., 2021). One strategy bumble bees employ while foraging is maintaining a familiar route along a series of patches called a trapline (Anderson, 1983). However, foragers remain flexible within this framework, occasionally exploring, adding, or dropping patches from their traplines as new information is gained (Lihoreau et al., 2010, Ogilvie & Thomson, 2016). This information may be sourced through social cueing but has not been explored previously at the scale of flower patches. While bees may have access to different sensory cues at different ranges (Robert et al., 2018, Rands et al., 2023), there is not currently evidence that co-forager presence impacts resource selection variably at different scales.

In this study, I will follow bumble bees on their foraging bouts and note the presence of any co-foragers to to determine (1) How the presence of a co-forager affects patch recruitment, (2) How the presence of a co-forager affects the duration of a bee's stay in a patch, and (3) Whether either of these effects changes as a bumble bee gains experience foraging in a meadow.

Methods

Data Collection

I collected data for four weeks from June to August 2026 from 9:30 to 15:30. These were the dates and times in which bumble bee workers were most active. All field observations were performed in a single meadow at which the observational area is approximately 70 by 70 meters in size. Many animal pollinated plants bloomed in this meadow during the period of data collection. One of the most common was *Delphinium barbeyi*, which produces a purple zygomorphic flower and primarily provides insect pollinators with nectar. *D. barbeyi* presents flowers in raceme inflorescences and grows in a patchy distribution in the meadow. The flowers of *D. barbeyi* are visited by several long and medium tongued *Bombus spp.*. The most common visitors are *B. nevadensis* and *B. appositus*. *B. flavifrons* is also common and occasionally *B. californicus* and *B. occidentalis* are observed foraging on *D. barbeyi* flowers.

I repeatedly observed the behavior of bumble bee individuals over time by paint marking them. To do so, I caught bumblebees found foraging on *D. barbeyi* with a bug net and put them in a "bee-squeezer" (Kearns, 2001) which immobilizes bees for paint marking. The bee squeezer consists of a plastic vial with fine mesh glued between the lid and the tube and a plunger made from a wooden dowel with a circular piece of plastic sponge glued to one end. Once a bee is in the vial the plunger can be inserted to gently press the bee against the mesh. While the bee is immobilized with the center of its dorsal thorax pressed through a hole in the mesh, it can be marked with a unique code of three colors. These colors were carefully applied in a triangle with

oil based Sharpie® paint pens While a bee is in the bee squeezer it was identified to the species level and the time and date of capture will be recorded.

When a marked bee was found foraging on *D. barbeyi* I followed it throughout its foraging bout while recording the exact time it arrives and departs each patch as well as whether any bumble bee co-foragers were present at the patch. These voice recordings were later transcribed to determine the duration of time spent at each patch. Co-foragers were noted as either heterospecifics or conspecifics to the focal bee and I also recorded the identity of any marked co-foragers. Because the team was marking and following bees in the site simultaneously, marking occurred far from following to reduce the likelihood of catching bees engaging in social interactions with the focal forager.

I determined a baseline of patch occupancy in the site and defined this value as control density. To do so, I revisited patches where focal bees foraged and recorded the occupancy status of each by scanning the patch for about ten seconds. If bees were present I recorded how many and their species identity. I performed these surveys immediately following the foraging bout of each bee which lasts between three and twenty minutes.

I conducted aerial drone flower surveys of the meadow from 11:00-11:30 each sampling day. The drone takes a photo every 0.7 seconds for a total of around 2,000 photos. We stitch the pictures together into an orthomosaic which is then analyzed by a convolutional neural network to evaluate flower density at each patch visited. We also ground-truthed the neural network every day of sampling by selecting three patches visited by bees that day and counting flowers by hand in a one by one meter quadrat centered on the middle of the patch where the GPS location was recorded.

Analyses

I analyzed the effect of co-forager presence on bumble bee recruitment to a patch with generalized linear mixed models using the glmer function from the lme4 package in R. To do so, I compared the density of co-foragers present in a patch when the focal bee was recruited and the density of bumble bees present in a patch when revisited (co-forager and control density, respectively). I then modelled bee density as the response variable and density type (control or co-forager) as the explanatory variable. I included date, time and flower density as fixed effects and bumble bee identity as a random effect. I intended to include bumble bee species as a random effect but the model could not estimate it.

I analyzed the effect of co-forager presence on bumble bee patch duration using a generalized linear model with patch duration as the response variable and co-forager density as the explanatory variable. I included date, time, and flower density as fixed effects and bumble bee species as a random effect.

I did not perform a formal analysis of the effect of experience on recruitment and duration, as the season yielded insufficient data. Instead, to analyse the effect of experience on these trends I visualized them across time using the ggplot function in R to plot individual patches or bouts as data points. I used the geom_smooth function to plot the linear relationships of duration and recruitment over the course of the sampling season (Fig. 3, 4).

I scaled the inflorescence counts measured by the neural network to flower density measured in the ground-truth using a generalized linear model with flower density as the response, offset log of the ground-truth flower density, days since first bloom and days since the first bloom squared as fixed effects and date and year as random effects.

Results

Of the 75 bees I observed, only 27 visited a patch with a co-forager. Bumble bees foraged alone at 96.9% of patches and 97.0% of patches sampled for null density were unoccupied. Within-patch density increased slightly throughout the season (Fig. 5). The model found no significant effect of co-forager presence on recruitment ($\chi^2 = 1.0$, $P = 0.31$) nor did it find any effect of time of day or travel time on bumble bee density ($\chi^2 = 0.11$, $P = 0.73$; $\chi^2 = 0.60$, $P = 0.44$). However, date and flower density did have a significant positive effect on bumble bee density ($\chi^2 = 9.8$, $P = 0.0017$; $\chi^2 = 21$, $P = 5.1e\text{-}6$) meaning bumble bee density at patches increasing throughout the season and with greater flower density (Fig. 1). The density of co-foragers at a patch had a significant positive effect (estimate = 0.50) on the duration of stay of the focal at the patch ($\chi^2 = 5.3$, $P = 0.022$). Date and time did not have any effect on patch duration ($\chi^2 = 2.1$, $P = 0.14$; $\chi^2 = 1.2$, $P = 0.27$). However, flower density was a significant positive predictor of patch duration ($\chi^2 = 130$, $P < 2e\text{-}16$) (Fig. 2). Visually analyzing these trends over time revealed no meaningful patterns indicative of social learning changing bumble bee foraging decisions (Fig. 3, 4).

Discussion

In this study, I found that bees forage for longer at patches with co-foragers even when accounting for the impact of flower density at those patches. This may be due to positive association with co-foragers by the focal bee or cryptic differences in patch quality. However, bumble bees did not recruit to patches with co-foragers more or less often than expected by random patch selection, contradicting the findings of previous studies. This contradiction could be attributed to differences in scale or bee density between my research and others. There is inconsistency in the effect of co-forager presence on my two indices of patch selection (recruitment and duration) which could be attributed to a difference in the use of cues in these independently made foraging decisions.

Duration

The positive correlation between the duration of time a bumble bee forages at a patch and co-forager presence suggests that bumble bees prefer to forage together despite increased resource depletion. This result concurs with previous research finding that bumble bees are attracted to floral resources with co-foragers present due to positive association (Leadbeater & Chittka, 2007). However, this result is in contrast with previous studies finding that bumble bees avoid flowers recently visited by co-foragers using scent marks as cues (Inouye, 1978, Stout et al., 1998). This contrast could be attributed to aspects of patch quality that are more cryptic, such as nectar concentration or quantity, that retain more bees at patches at once, increasing the

overall density of bees at that patch and allowing them to tolerate the presence of a co-forager for longer (Zhou et al., 2024).

Recruitment

The absence of correlation between recruitment of bumble bees to patches and co-forager presence does not align with previous studies that find that floral resource selection is significantly affected by the presence of another bee (Kawaguchi et al., 2007, Saleh & Chittka, 2006). There are a few explanations for the contradiction between the effects of co-foragers on recruitment in this study and others.

The first element to explain the differences in recruitment results between this study and others is the scale at which bumble bees are selecting resources. Different sensory cues become available to bumble bees as they approach a resource. At close range, bumble bees can sense temperature, humidity gradients and electrical fields. At far range, bees must rely on visual cues (Robert et al., 2018, Rands et al., 2023). This suggests that bumble bees may also use different cues to detect co-foragers at different scales and therefore interpret these cues differently. For example, when bees are selecting flowers at close range, as in previous studies, they may use a variety of cues to detect the presence of co-foragers, possibly allowing them to interpret these cues more clearly (either positively or negatively). In my study however, bees were selecting floral resources on the scale of patches from a greater distance and are likely only able to detect visual cues of a co-forager, which they may not be able to interpret as readily. This could explain the difference between my findings on recruitment and those of previous studies.

A second explanation for differences in my studies findings on recruitment is low bumble bee density. It is well supported that experience of social cues drives bumble bees' interpretation of them and that competitive dynamics change with changing resource availability and bumble bee population size (Saleh & Chittka, 2006, Leadbeater & Chittka, 2009, Ye et al., 2025). If a bumble bee rarely sees a co-forager in a potential foraging patch, they likely will not develop behavioral patterns in response (Abts & Dunlap, 2022). To my knowledge, this is the first observational study of co-foraging behavior in bumble bees. Observing behavior in a resource rich environment yielded very low within-patch bee densities and thus few observations of social interactions. Later in the season, when fewer patches were blooming, we observed slightly more co-foraging interactions. When floral resources are limited as they were in the late season it is easier to observe social behavior. Therefore, future studies could focus on urban or similarly sparse environments like those used in Kawaguchi's (2007) wild bee experiment.

Experience

I could not assess my hypothesis on the effect of experience on co-forager interactions because of insufficient data. I was not able to repeatedly follow the same bee enough times throughout its lifetime, particularly during its first foraging bouts, to understand how its behavior changed with experience. Future studies could ensure that bees are followed during their very first foraging bouts by locating bumble bee nests and following newly emerging bees at the start of the season. Further, competition and co-foraging may have been co-occuring, diluting my results. To help distinguish interactions, future studies could characterize each both

quantitatively, by measuring the duration of the co-foraging interaction, and qualitatively by characterizing the nature of the interaction as neutral, facilitative, or competitive.

Conclusion

The difference I found between my two indices of patch selection may be due to mechanistic differences between the decisions regarding recruitment and duration. Pyke (1980) describes a sequence of four distinct decisions made when selecting a foraging resource: 1) whether to approach, 2) whether to land, 3) whether to probe, and 4) whether to stay in the patch. A bumble bee can choose to abandon the foraging attempt at any point in this sequence regardless of decisions made previously, suggesting that these decisions can be made somewhat independently of each other. Because of this bees may use cues independently to inform each one. In the case of co-foraging, bees may not use co-forager presence when making the first two decisions (whether to approach and land) but could begin to consider it as they make decisions three and four (whether to probe and stay in the patch). Future research should continue to analyze bumble bee social information use in the field, discerning the cues they use to make each of these decisions to strategically forage in a variety of environmental contexts. This research will help us understand bumble bees as a study system to develop our knowledge of animal social behavior and cognition and how it shapes the interactions between animals and the world.

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Tables & Figures

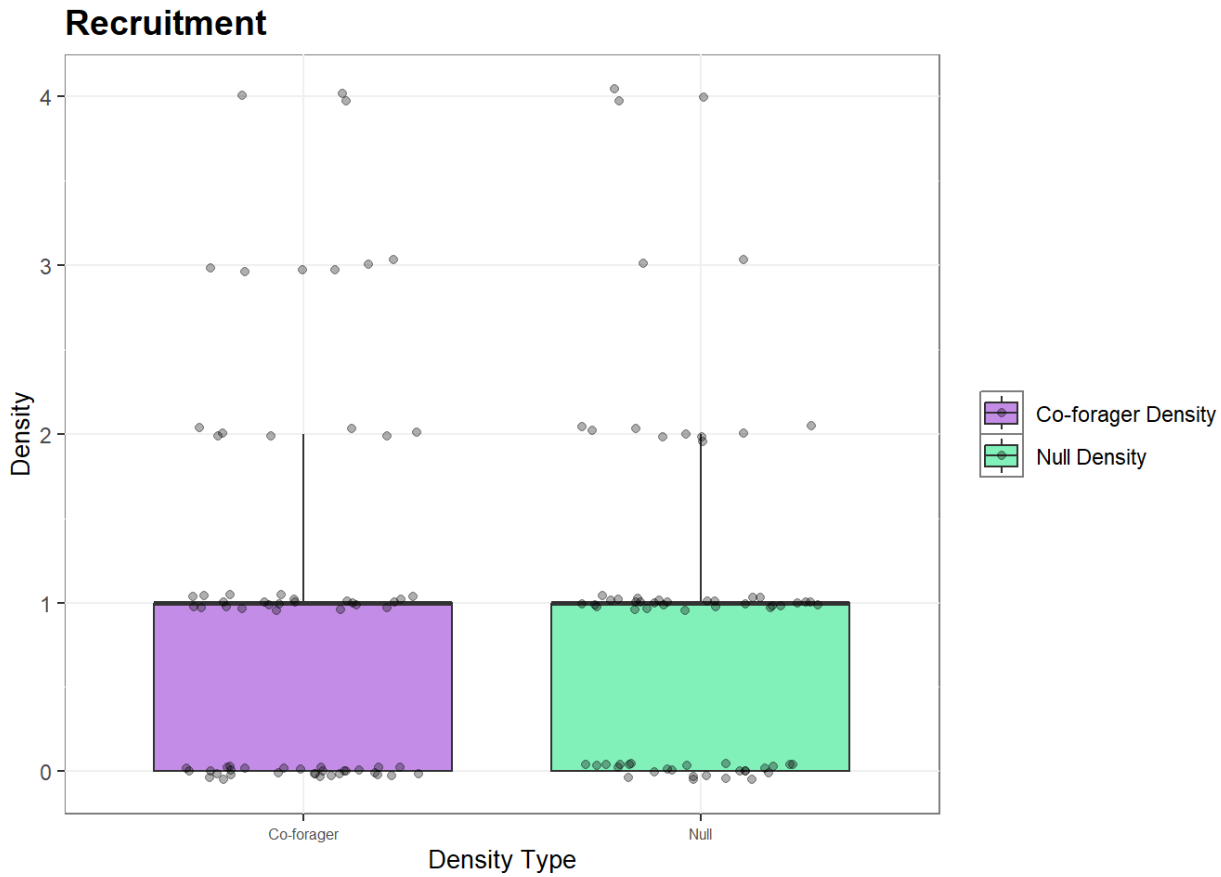

Fig. 1: The spread of densities of co-foragers per bout when a focal bee is recruited (purple) compared to the spread of densities of bumble bees per bout within the site (green), (co-forager density and null density respectively) for bouts where at least one bee was present either co-foraging or when null density was sampled. Box and whiskers plots display the median, first and third quartiles, and the upper and lower extremes. Each point represents a visit to a patch.

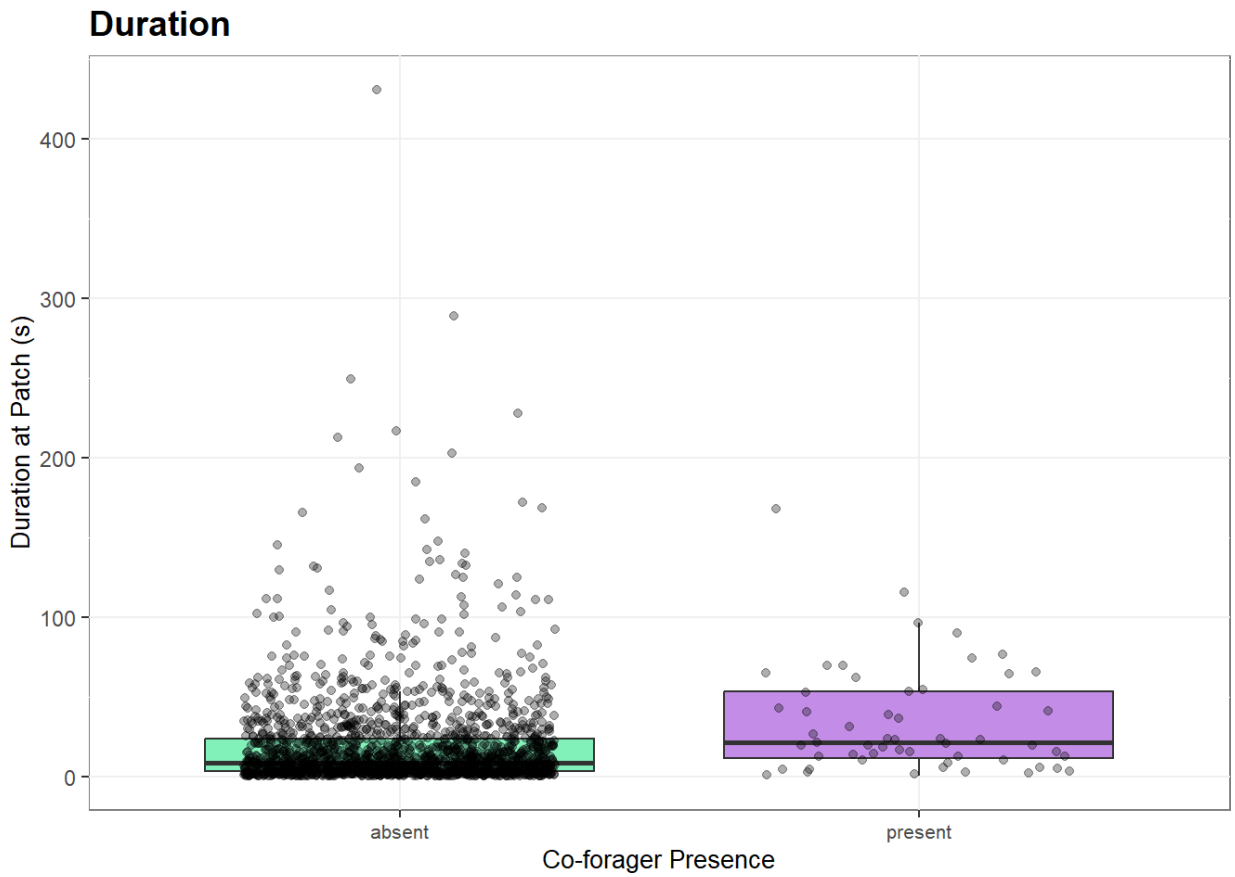

Fig. 2: The spread of data for length of stay at patches in seconds with co-foragers (purple) and without (green). Box and whiskers plots display the median, first and third quartiles, and upper and lower extremes excluding outliers. Each point represents a visit to a patch.

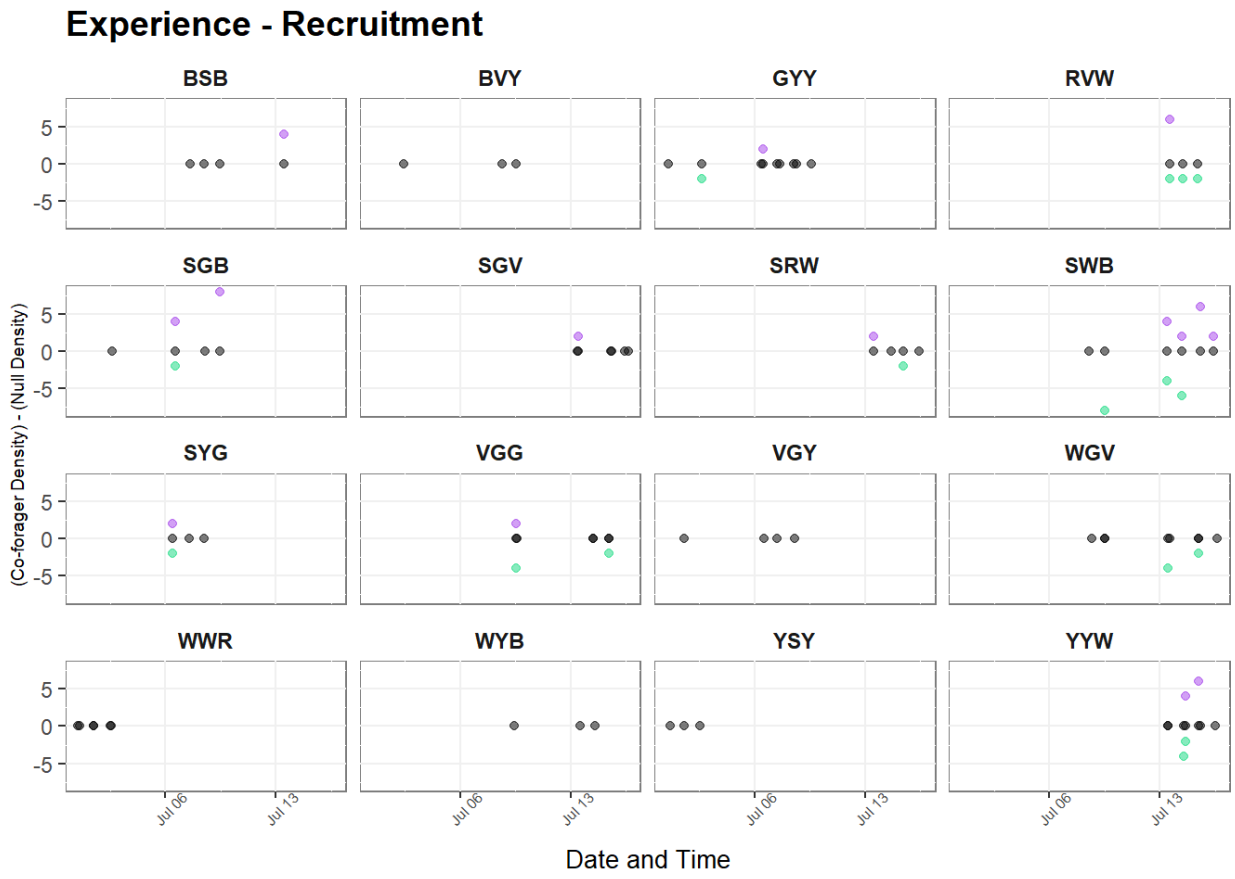

Fig. 3: The difference in the density of co-foragers with the focal bee and the density of bees in each patch when revisited later (co-forager density and null density respectively) by day and time for each bee followed for three or more bouts. Each point represents one foraging bout with the difference in co-forager and null density in each patch summed for each bout and date and time averaged for each bout. Green points indicate a positive difference, purple points indicate a negative difference, and black points indicate no difference. Each facet shows a unique bee's behavior with the bee's three letter code displayed at the top. Each letter represents a color (Pi = pink, R = red, Y = yellow, G = green, B = blue, V = violet, W = white, S = silver).

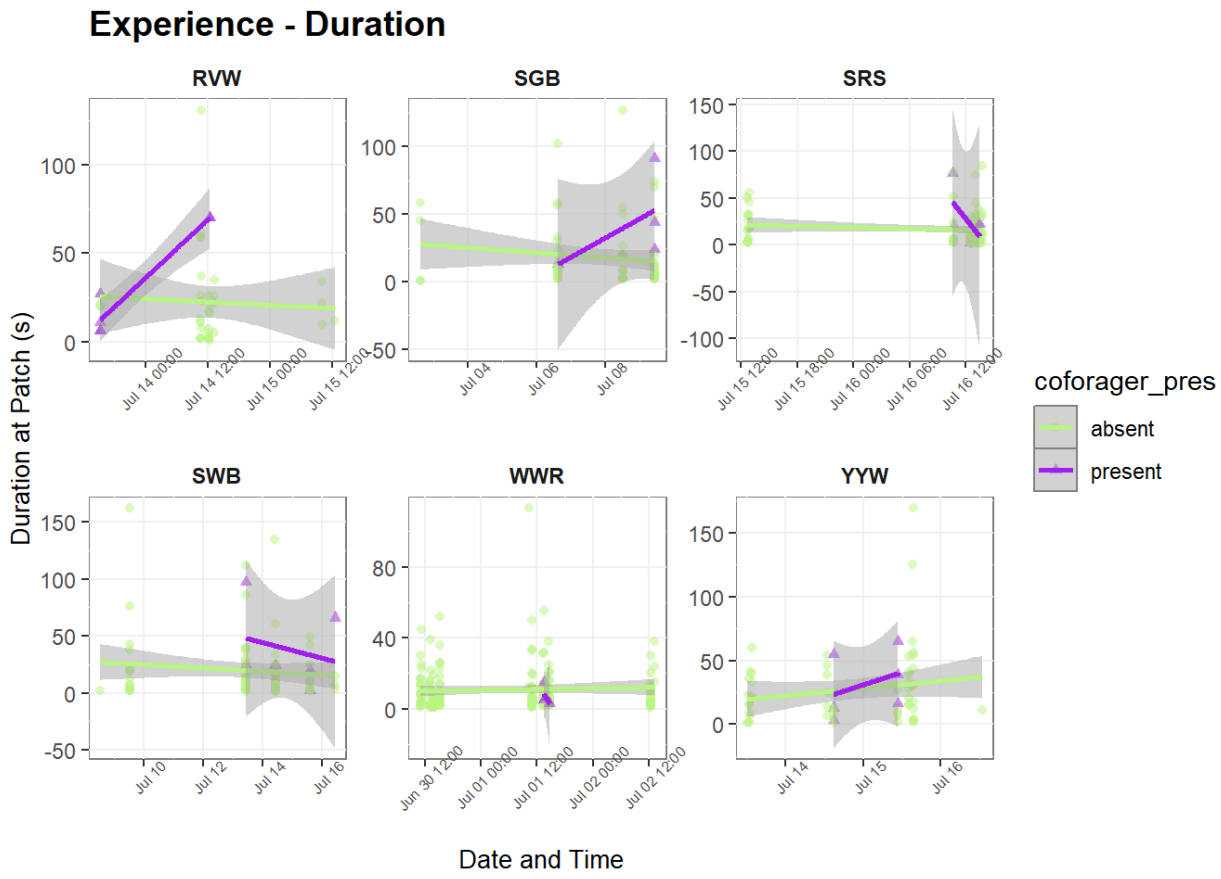

Fig. 4: The length of stay at patches in seconds with co-foragers (purple triangles), and without co-foragers (green points) by day and time for each bee which visited a patch with a co-forager more than three times. Each point represents a visit to a single patch during a bout. Lines are fitted using linear models to show the trend of the data, grey bands show 95% confidence intervals for lines of best fit. Each facet shows the spread of data for a unique bee with the bee's three letter code displayed at the top. Each letter represents a color (Pi = pink, R = red, Y = yellow, G = green, B = blue, V = violet, W = white, S = silver).

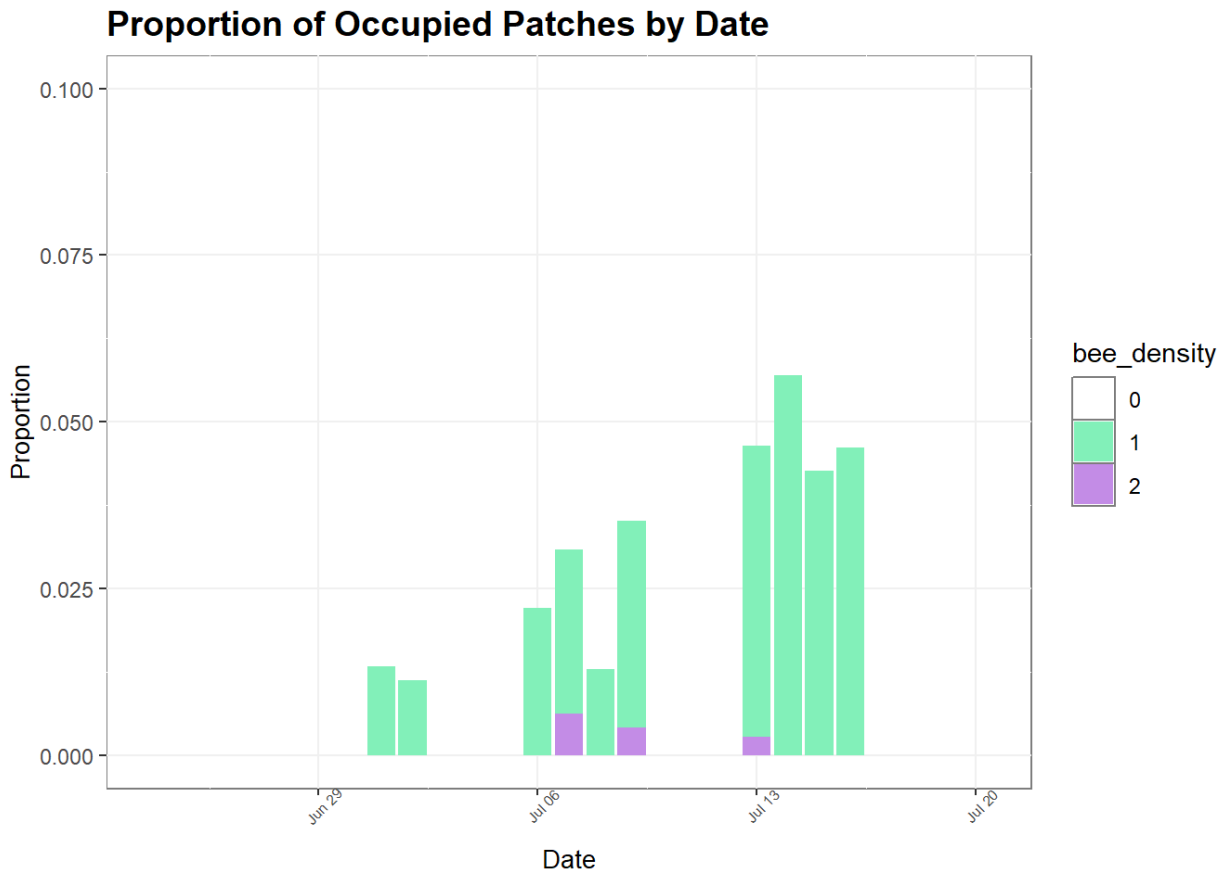

Fig. 5: The proportion of patches sampled, both for co-forager and control density, with one or two bees by day. Green bars represent patches with one bee, purple bars represent patches with two bees. The rest of the data was empty patches.

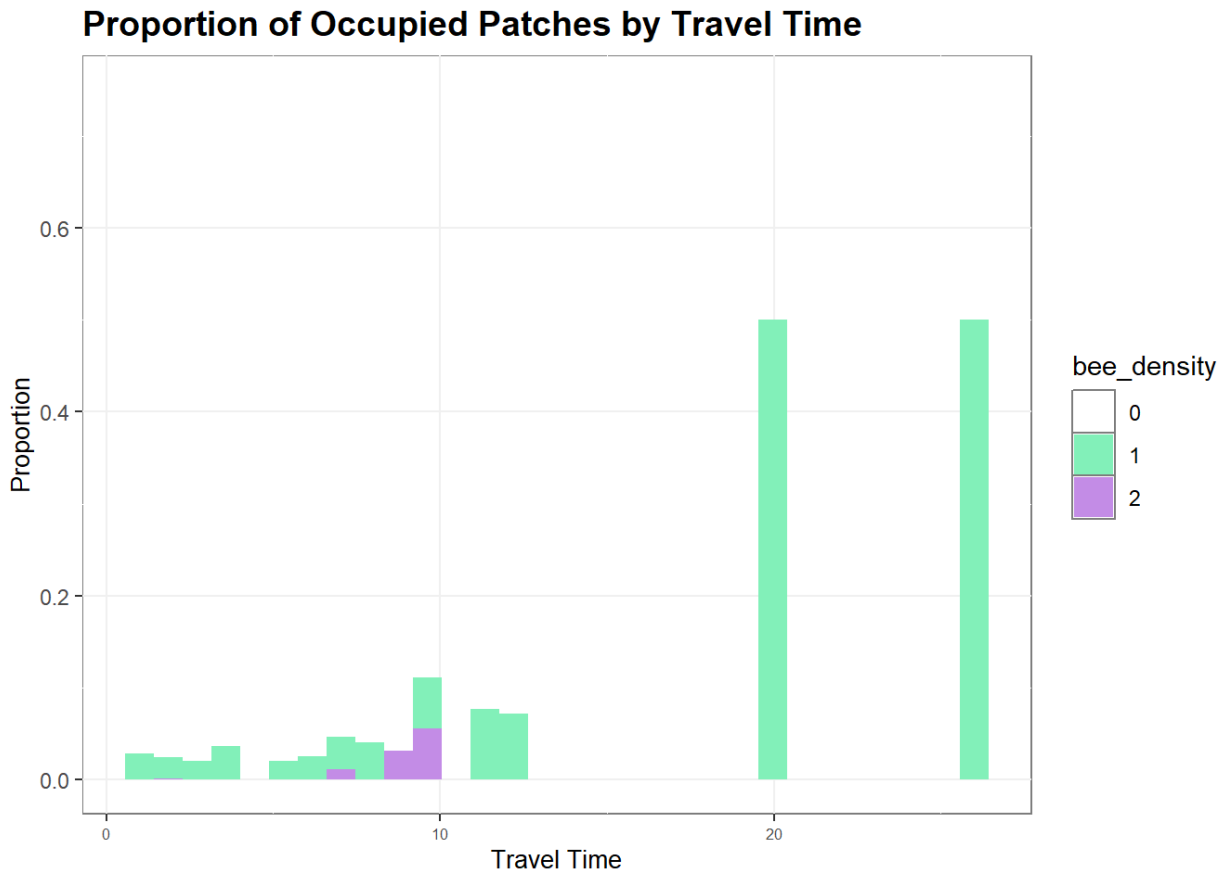

Fig. 6: The proportion of occupied patches sampled with one or two bees by travel time. Green bars represent patches with one bee, purple bars represent patches with two bees. The rest of the data was empty patches.

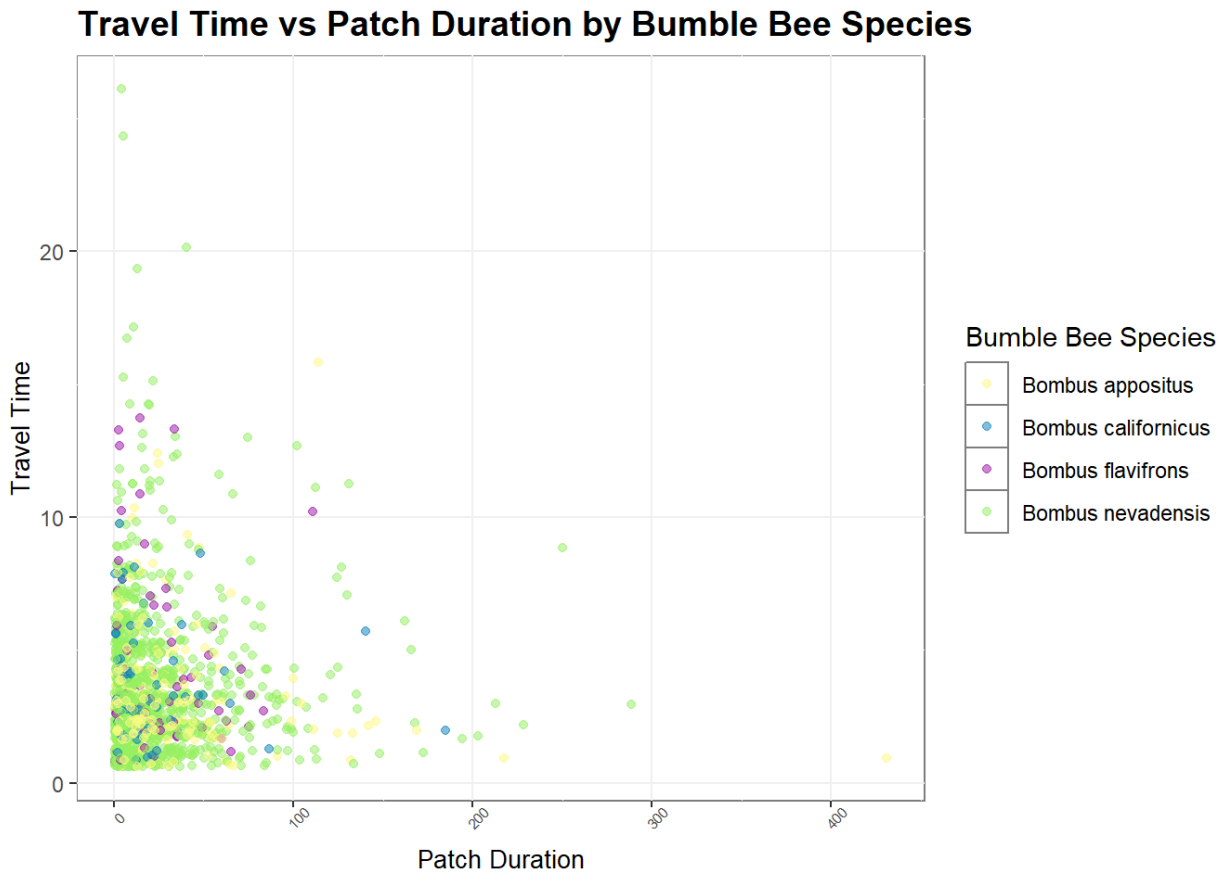

Fig. 7: The travel time compared to the length of stay at a patch by bumble bee species. Each point represents a visit to a patch. Each bumble bee species is represented by a different colored point (yellow = B. appositus, blue = B. californicus, purple = B. flavifrons, green = B. nevadensis).

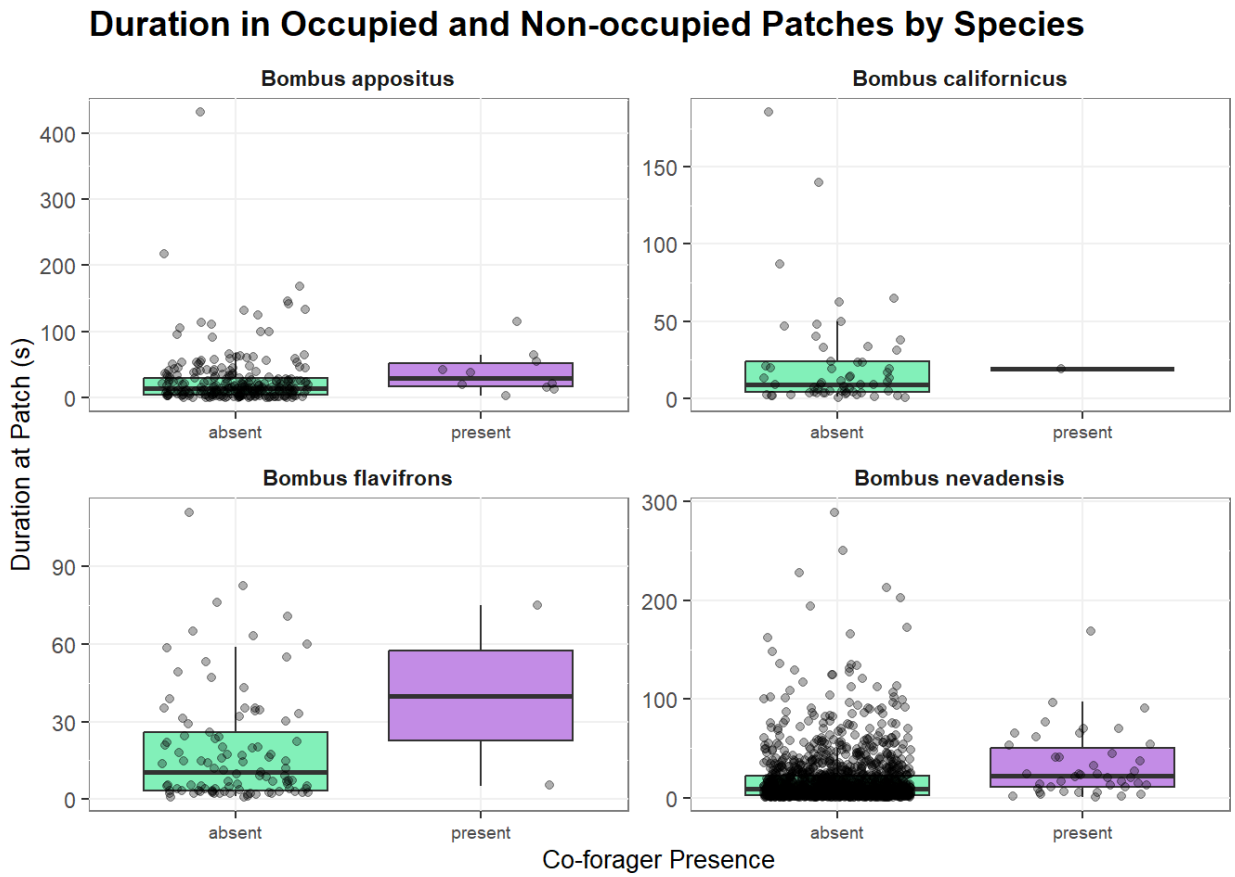

Fig. 8: The spread of data for length of stay at patches in seconds with co-foragers (purple), and without co-foragers (green) for bees who foraged alongside a co-forager. Box and whiskers plots display the median, first and third quartiles, and the upper and lower extremes excluding outliers. Each point represents a visit to a patch. Each facet shows the spread of data for a different Bombus species.

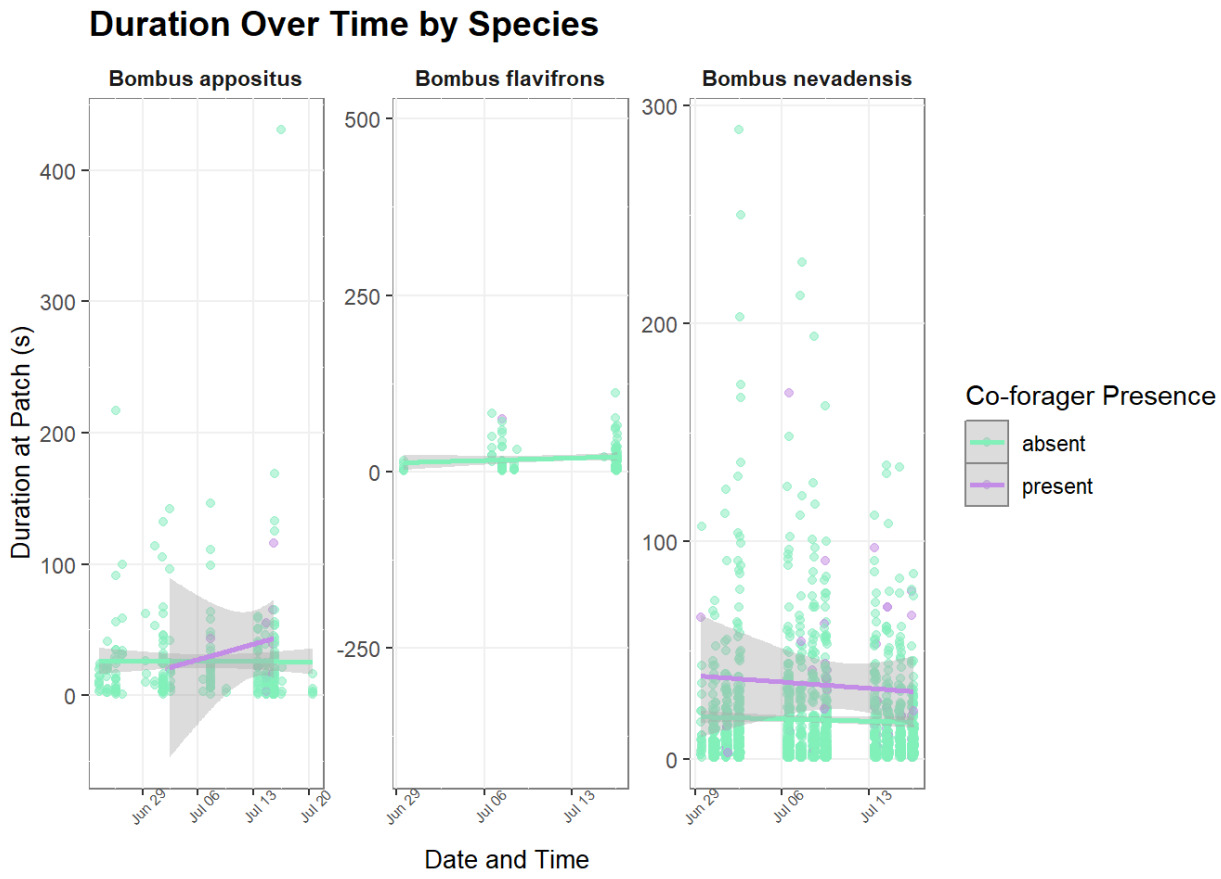

Fig. 9: The spread of data for length of stay at patches in seconds with co-foragers (purple), and without co-foragers (green). Each point represents a visit to a patch. Each facet shows the spread of data for a Bombus species which was seen co-foraging more than three times.