

# **RESEARCH PAPER**

# Persistence to Unrewarding Feeding Locations by Honeybee Foragers (*Apis mellifera*): the Effects of Experience, Resource Profitability and Season

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# Abstract

Honeybee foragers that find a profitable food source quickly establish spatiotemporal memories, which allow them to return to this foraging site on subsequent days. The aim of this study was to investigate how the previous experience of honeybee foragers at a feeding location affects their persistence at that location once food is no longer available. We hypothesised that persistence would be greater to locations that were more rewarding (closer to the hive, higher concentration of sucrose solution), for which a bee had greater prior experience (0.5-h vs. 2-h training access), and at times of the year of lower nectar availability in the environment. We studied individually marked worker bees from four colonies trained to sucrose-solution feeders. Our results support most of these predictions. Persistence, measured both in duration and number of visits, was greater to locations that previously offered sucrose solution of higher concentration (2 M vs. 1 M) or were closer to the hive (20 m vs. 450 m). Persistence was also greater in bees that had longer access at the feeder before the syrup was terminated (2 h vs. 0.5 h). However, contrary to our prediction, persistence was not higher in the season of the lowest nectar availability in the environment in the study year. In summary, honeybees show considerable persistence at foraging sites that ceased providing rewards. The decision to abandon a foraging site depends on the profitability the forager experienced when the foraging site was still rewarding.

#### Introduction

Animals forage in a dynamic environment in which food availability is neither entirely predictable nor random in space or time (Mobus & Fisher 1999). Animals normally revisit previously rewarding locations and give up on locations that are unrewarding (van Gils et al. 2003; Gende & Sigler 2006), and this may occur at various timescales. Bumble bees (*Bombus impatiens*), for example, abandon depleted food sources to search for alternatives and they do so more quickly than honeybees (*Apis mellifera*) (Townsend-Mehler et al. 2011; Townsend-Mehler & Dyer 2012). Great tits (*Parus major*) also abandon low-quality food sources if they have information about better alternatives, but the speed of abandoning a food source depends on the relative quality of the alternatives (Kerbs et al. 1978).

Honeybee foragers show a remarkable attachment to particular food patches and continue to visit the same patch for days or even weeks if the food patch continues to provide rewards (Butler et al. 1943; Butler 1945; Ribbands 1949; Moore 2001). Flower patches are usually rewarding only for relatively short periods of a few weeks (von Frisch 1967; Vogel 1983; Seeley 1995). At the group level, each honeybee colony faces the challenge of allocating its foragers to the best nectar and pollen sources in an area >100 km<sup>2</sup> (von Frisch 1967; Visscher & Seeley 1982; Seeley 1995; Beekman & Ratnieks 2000; Seeley et al. 2000). At the individual level, each forager has to decide whether to continue foraging at its patch, including whether or not to recruit additional foragers (von Frisch 1967; Seeley 1995), or, if the patch is deteriorating, whether to abandon it (Seeley 1995; Moore et al. 2011; Townsend-Mehler et al. 2011; Townsend-Mehler & Dyer 2012). Many factors determine the quality of a nectar patch, but an important currency is its energetic profitability (von Frisch 1967; Seeley 1995), which depends mainly on the sugar concentration (von Frisch 1967), the distance of the patch from the colony (Boch 1956) and the time it takes a forager to collect a load (Farina 1996).

In honeybees and many other social insects, decision-making concerning foraging is particularly complex because decisions made by individual foragers are influenced not only by their own private information about a food source but also by information from nestmates. Experienced honeybee foragers can choose between foraging location information from waggle dances and their own memory (von Frisch 1967; Seeley & Towne 1992; Gil & Farina 2002; Biesmeijer & Seeley 2005; Grüter et al. 2008, 2013; Grüter & Farina 2009; Grüter & Ratnieks 2011; Menzel et al. 2011; Wray et al. 2012) or can scout for new locations (Oettingen-Spielberg 1949; Seeley 1995; reviewed in Grüter et al. 2010). Foragers pay greater attention to social information when their own food source deteriorates in quality (Grüter & Ratnieks 2011).

Foraging theory predicts that the time taken to collect a certain amount of energy should play an important role in forager decisions to collect food at a particular location (Schoener 1971; Stephens & Krebs 1986; Fewell et al. 1992). Consequently, previous reward experiences affect later behaviour after the reward is removed (Bouton 2007; Moore et al. 2011; Townsend-Mehler & Dyer 2012). Given that honeybees return to familiar food locations even after these become unrewarding (von Frisch 1967; Moore 2001; Grüter & Ratnieks 2011; Moore et al. 2011), what factors influence the degree of persistence shown by honeybee foragers to feeding locations? Although short-term responses (≤60 min) have been quantified in foraging honeybees that have experienced low rewards (Seeley et al. 1991; Townsend-Mehler et al. 2011; Townsend-Mehler & Dyer 2012), this duration is likely to be too short to measure the actual degree of persistence because bees are known to return to empty food sources for days (Moore 2001; Grüter & Ratnieks 2011).

The aim of this study was to investigate how previous experience and reward at a feeding location affect the persistence of honeybee foragers to this location once food is no longer available. We hypothesised that several factors, which are likely to either affect the energetic efficiency of foraging (Seeley 1994) or information about the energetic efficiency of foraging would affect persistence. We predicted that persistence would be greater at locations that were more rewarding (closer, higher concentration of sucrose solution), for which a bee had greater prior experience, and at times of the year of lower nectar availability.

# **Material and Methods**

# Study Site and Organisms

Experiments were performed from Apr. to Oct. 2011. We used four honeybee colonies (C1–C4) of mixed European subspecies (but predominantly *Apis mellifera mellifera*) from the apiary of the Laboratory of Apiculture and Social Insects, University of Sussex. Colonies were kept in Langstroth hives with two medium-depth 10-frame boxes and always had space to store additional pollen and honey. Colony sizes change during the season, but were approximately 10 000–30 000 bees. Each colony was monitored weekly to confirm that it had a laying queen, brood, and was otherwise thriving.

# **Experimental Procedure**

We used standard procedures (von Frisch 1967, pp. 17-18) to train 10-30 foragers from each colony to a 1 м or 2 м sucrose solution feeder (Fig. 1). The feeders were similar to those of von Frisch (1967), fig. 18) and consisted of a small jar, 6 cm high and 4 cm in diameter, standing on a grooved base where worker bees could take syrup. To help trained bees learn the location, we placed each feeder on a sheet of blue A4paper on a small table. All training was conducted in the afternoon, usually between 12:30 and 15:30. We always trained bees of two colonies simultaneously (Fig. 1). Training started by placing a feeder at the hive entrance of two colonies. Then, when a large number of bees were feeding at the feeder of both colonies, we moved the feeders and the drinking bees to their designated feeder positions. We made sure that the foragers of a colony collected only at their designated feeder by monitoring whether fights took place at the feeder and later by using differently coloured number tags at the two feeders. The bees would then quickly learn the features of the new feeder location and return to it (von Frisch 1967). When foragers returned to the feeder for the first time after moving, we individually caught each bee gently using a standard (commercially available) queen marking cage



**Fig. 1:** Sequence of the experiments, treatments and hive combinations performed between 21 May and 12 Oct. (2011). Rectangles containing C1–C4 represent the four study colonies. Asterisks refer to trials that were also used to compare seasonal effects. In the last experimental period, there are two boxes missing (of C3 and C4) because these two colonies were already tested in the second experimental period with 2 M solution and 2 h access to the feeder. Boxes also show the sample size of a particular trial.

and marked them with plastic number tags (Opalithplättchen, manufactured by Chr. Graze, Endersbach, Germany). Unmarked bees that arrived shortly after the moving of the feeders (potential recruits) were also marked. Unmarked bees that arrived later during the training period were captured in plastic tubes and released at the end of the training period. We used different colours for the foragers of the two simultaneously trained colonies to be able to make sure that the foragers of one colony did not collect food at the feeder of the other colony. All marked bees that made less than two visits were excluded from the analysis. We considered a bee to have made two visits if the time between two landings was more than 2 min for the closer feeder (20 m) and more than 5 min for the further feeder (450 m). During each training session, we counted the number of visits to the feeder made by each marked bee during the whole access period, either 0.5 or 2 h.

For experiments with a feeder at 450 m, we trained bees in two steps: first, we moved a feeder with 20–30 foragers on it to a location 350 m from the hive. To avoid disturbing the drinking bees during the transport, the feeder was placed inside a cardboard box with 15 cm side length (the same box was used throughout the experiment). After bees were accustomed to this location and repeatedly visited the feeder, we performed the second step by moving it another 100 m to its designated final location by carrying it quickly without shaking the box. Both steps were performed on the same day. We tested the effect of four different factors on persistence: the number and duration of rewarded visits (i.e. training visits made during the 2 or 0.5 h access period), sucrose concentration (1, 2 M), distance from hive to feeder (20, 450 m) and time of the year. We used two measures of forager persistence: the total number of visits made by a marked bee after the feeder ceased to be rewarding (visit-persistence) (visit: landing on feeder) and the maximum duration, number of days, that a marked bee returned to the empty feeder (duration-persistence).

The experiments were carried out at different times in 2011 during the foraging season, and data were analysed over different periods (see Fig. 1 for details). During Period 1, from 21 May to 20 Jul. (spring-early summer), we tested the effect of access duration and the number of rewarded visits. To create the necessary variation in the number of visits at the feeder between colonies and individuals, we allowed foragers from one colony 2-h access vs. 0.5 h for the other colony. Subsequently, the access and training locations were switched (Fig. 1). Each colony's feeder had 2 м sucrose. During Period 2, from 25 Jul. to 9 Sep., we tested the effect of sucrose concentration. The feeders were both at 20 m distance from the two colonies; both colonies had 2-h access with one colony receiving 1 м sucrose and the other 2 м. Subsequently, the treatment and training locations were switched. During Period 3, from 17 Aug. to 12 Oct., we tested the effect of distance with one hive being trained to a feeder at 20 m and the other at 450 m, with the treatment and training locations switched subsequently. Training to the 450-m feeder location was conducted on the same day as training to the 20-m location. Both feeders had 2 M sucrose and 2-h access.

At the end of the training phase, we removed and emptied the feeders. Over the following days, the empty and cleaned feeders were recorded at their respective training location from 10.00 to 16.00 using video cameras (Sony HDR-XR550VE). We stopped recording at a feeder when it had not been visited by any trained bees for 2 d of good foraging weather. From the videos, we were able to determine how often and for how many days the marked bees returned to the empty feeders. Bee mortality could potentially have affected our measures of persistence. However, it is likely that bee mortality would reduce any treatment effects on persistence as it reduces overall persistence and, therefore, is likely to affect our findings in a conservative direction.

# Statistical Analyses

We analysed the data using ANOVA in Minitab (version 14). We first tested whether colonies (including colony as an explanatory variable) differed in our two measures of persistence, duration and visits. If not, we pooled the data from the four colonies to increase statistical power. If colonies did differ, we included colonies as an explanatory variable in the model. We transformed the response variables by using log10 or square root transformations whether this was necessary to meet the assumptions of ANOVA (Grafan & Hails 2002). To this aim, we inspected the distribution of the residuals of the models. Nonsignificant interactions between explanatory variables (p > 0.05) were removed from the model. All tests are two-tailed and a significance level of  $\alpha = 0.05$  was used. A Tukey's post hoc test was used to compare seasons and colonies. Descriptive statistics are given as arithmetic mean  $\pm$  standard deviation.

# Results

We studied 361 marked bees (Fig. 2a). Across all treatments, the average number of training visits to a feeder was  $14.41 \pm 10.02$  (range: 2–46, N = 361). After training, the average number of visits (6 h video per day) to the empty feeder (visit-persistence) was  $4.29 \pm 4.47$  (range: 0–25; N = 361) with the trained bees returning for an average of  $1.89 \pm 1.56$  d (duration-persistence; range: 0–7; N = 361). Figure 2 shows the distribution of visits and number of bees' persistence per day after training.

In total, we observed 1548 visits to the unrewarding feeders (N = 361 bees) (Fig. 2b). Bees visited the unrewarding feeder across the full 6 h of video





**Fig. 2:** The persistence on days 1–7 after training to a feeder on day 0 decreases over time. (a) The data show that every day, a substantial proportion of bees give up visiting the empty feeder. (b) The number of visits per individual bee per day after the training day. Data of all treatments and all colonies combined are shown in this figure. Mean and standard errors are shown.

recording, and the video period included the period of peak visiting activity.

# Experiment 1: Effect of Training Access Duration and Number of Training Visits

We tested 122 bees in total, 46 bees (details in Fig. 1) with 0.5 h access to the feeder (average number of training visits  $4.24 \pm 1.84$ ) and 76 bees (details in Fig. 1) with 2-h access (15.66  $\pm$  10.87 visits).

There was no difference among colonies in visitpersistence ( $F_{3,118} = 2.12$ ,  $R^2[adj] = 2.70\%$ , p = 0.102). Overall, visit-persistence was 23% greater for 2 h vs. 0.5 h of training access (1.69 vs. 1.3, average number of visits per bee). As bees in the 2-h treatment made on average 3.69 times as many training visits as bees in the 0.5-h treatment ( $F_{1,120} = 49.75$ ,  $R^2[adj] = 28.72\%$ , p < 0.001), we performed a new model that included both the number of training visits and training duration as explanatory variables and found that both access duration and number of training visits had a significant positive effect on visitpersistence (training duration:  $F_{1,118} = 8.74$ ,  $R^2$ [adj] = 14.28%, p = 0.004; Fig. 3a; number of training visits:  $F_{1,118} = 15.53$ ,  $R^2$ [adj] = 14.28%, p < 0.001). A significant interaction between the two explanatory variables ( $F_{1,118} = 11.11$ ,  $R^2$ [adj] = 14.28%, p = 0.001) suggests that the number of training visits has a decreasing effect on visit-persistence as total training duration increases (the direction of the interaction was interpreted based on visual representations of the interaction).

There were significant differences between hives in duration-persistence ( $F_{3,118} = 5.51$ ,  $R^2$ [adj] = 10.07%, p = 0.001). Hence, we included hive in the model with training duration and number of training visits. We found a significant effect of hive ( $F_{3,115} = 7.66$ ,



**Fig. 3:** Both visit-persistence (a) and duration-persistence (b) are greater for 2 h vs. 0.5 h of training access if the number of training visits is taken into account. Both feeders were at 20 m distance from the hive. Means and standard errors are shown. The letters A and B above bars indicate a statistically significant difference (p < 0.05) between the two access durations. Numbers inside bars show the sample sizes.

 $R^2$ [adj] = 29.81%, p < 0.001), a positive effect of training duration (F<sub>1,115</sub> = 6.13,  $R^2$ [adj] = 29.81%, p = 0.015; Fig. 3b) and a positive effect of the number of training visits (F<sub>1,115</sub> = 12.25,  $R^2$ [adj] = 29.81%, p = 0.001). Additionally, we again found a significant interaction between access duration and number of training visits (F<sub>1,115</sub> = 5.86,  $R^2$ [adj] = 29.81%, p = 0.017).

#### **Experiment 2: Effect of Sucrose Concentration**

We trained 86 bees (see Figs 1 and 4for details) with 2 м (number of training visits:  $19.21 \pm 9.09$  visits) and 60 bees (see Figs 1 and 4 for details) with 1 м sucrose (17.22  $\pm$  10.26 visits). There was a difference between hives in visit-persistence ( $F_{3,142} = 5.10$ ,  $R^{2}$ [adj] = 7.81%, p = 0.002) and duration-persistence  $(F_{3,142} = 4.83, R^2[adj] = 7.34\%, p = 0.003)$ . There was no statistically significant effect of molarity on the number of training visits  $(F_{1,144} = 1.53, R^2[adj])$ = 0.36%, p = 0.219). Therefore, we ran a model with molarity and hive as explanatory variables and found that the two factors interacted  $(F_{3,138} = 3.70)$ ,  $R^{2}$ [adj] = 18.52%, p = 0.013). The two main effects had a significant positive effect on visit-persistence (Hives:  $F_{3,138} = 5.88$ ,  $R^2[adj] = 18.52\%$ , p = 0.001; molarities:  $F_{1,138} = 12.98$ ,  $R^2[adj] = 18.52\%$ , p < 0.001; Fig. 4a). When analysing the data on durationpersistence, we again found significant effects of hive  $(F_{3,141} = 4.24, R^2[adj] = 11.74\%, p = 0.007)$  and a positive effect of molarity  $(F_{1,141} = 8.08, R^2[adj] =$ 11.74%, p = 0.005; Fig. 4b).

#### Experiment 3: Effect of Distance to Feeder

We trained 82 bees (details in Fig. 1) at 20 m (number of training visits to feeder:  $18.44 \pm 8.91$ ) and 66 bees (details in Fig. 1) at 450 m (10.14  $\pm$  4.04 visits). As there was no difference between colonies in visit-persistence ( $F_{3,144} = 1.60, R^2[adj] = 1.20\%, p =$ 0.193) or duration-persistence ( $F_{3,144} = 1.49$ ,  $R^2$ [adj] = 0.98%, p = 0.221), we pooled the data across colonies. Overall, visit-persistence was 13% greater for 20 m vs. 450 m (2.4 vs. 2.09, average number of visits per bee,  $F_{1,146} = 4.73$ ,  $R^2[adj] = 2.47\%$ , p = 0.031; Fig. 5a). However, as bees also made more training visits to the 20-m feeder than the 450-m feeder  $(F_{1,146} = 49.08, R^2[adj] = 24.65\%, p < 0.001)$ , we ran an additional model that included the number of training visits as a predictor variable. This showed that the difference in persistence is affected by the number of training visits ( $F_{1,145} = 10.67$ ,  $R^2[adj] = 8.53\%$ , p = 0.001) rather than by distance itself (F<sub>1.145</sub>)



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Fig. 4: (a) Bees of the colonies C2 and C3 made significantly more visits to the empty feeder (visit-persistence) and b) bees of the colonies C1 and C2 visited the feeder for more days (duration-persistence) when they were trained on 2 M vs. 1 M of the sucrose solution during the training period. Figure shows means and standard errors over the black and white bars of the data for 1 M vs. 2 M, respectively. The letters A and B above bars indicate a statistically significant difference (p < 0.05) between the two different molarities. Numbers inside bars show the sample sizes.

 $= 0.09, R^{2}$ [adj] = 8.53%, p = 0.762). When analysing duration-persistence, we again found significant differences between bees trained to feeders at 20 m vs. 450 m. Overall, duration-persistence was 11% greater 1.68 vs. 1.49, average number of days per bee for 20 m vs. 450 m ( $F_{1,146} = 5.98$ ,  $R^2[adj] = 3.27\%$ , p = 0.016; Fig. 5b). When we again included the number of training visits in the model, we found that foraging distance was had a significant positive effect  $(F_{1,145} = 4.07, R^2[adj] = 2.63\%, p = 0.046)$ , but that the number of training visits was not significant  $(F_{1.145} = 0.03, R^2[adj] = 2.63\%, p = 0.856).$ 

# **Experiment 4: Effect of Different Seasons**

Here, we compared persistence only in colonies C1 and C2 (marked with asterisks in Fig. 1) for which data were available at three different periods of the year: Season (spring) = May–Jun. (36 bees, details in Fig. 6); Season (summer) = Jul.–Aug. (46 bees, details in Fig. 6); Season (autumn) = Sept.–Oct. (27 bees, details in Fig. 6). For colonies C1 and C2, the

respectively.

visits as explanatory variables. We found significant differences among  $(F_{2,102} = 3.99,$ seasons  $R^{2}$ [adj] = 25.45%, p = 0.021; Fig. 6a) and a significant effect of the number of training visits  $(F_{1,102} = 25.16, R^2[adj] = 25.45\%, p < 0.001)$ , but no significant effect of colonies  $(F_{1,102} = 3.77,$  $R^{2}$ [adj] = 25.45%, p = 0.055; Fig. 6a). In addition, there was a significant interaction between season  $(F_{2,102} = 4.24,$  $R^{2}[adj] = 25.45\%,$ and colony p = 0.017, Fig 6a). Tukey's post hoc analysis showed that persistence was higher in autumn than in summer (p = 0.038), while there was no difference between spring and autumn (p = 0.066) and between spring and summer (p = 0.989).

average number of training visits for the three periods

was  $12.03 \pm 8.50$ ,  $20.35 \pm 10.21$  and  $17.11 \pm 9.74$ ,

There were significant differences between colonies

in visit-persistence ( $F_{1,107} = 4.12$ ,  $R^2[adj] = 2.81\%$ ,

p = 0.045). As bees also made different numbers of

training visits at different seasons, we ran a model

that included colony, season and number of training



**Fig. 5:** The data show that both visit-persistence and duration-persistence are significantly greater for the closer food source (20 m vs. 450 m). Both feeders offered that same molarity (2  $_{\rm M}$ ) and for the same duration (2 h). Figure shows means and standard errors. A and B above bars indicate a statistically significant difference (p < 0.05) between the two different distances. Tukey's *post hoc* test was used to compare colonies. Numbers inside bars show sample sizes.

There was no difference between the two colonies in duration-persistence  $(F_{1,107} = 0.20,$  $R^{2}$ [adj] = 0.00%, p = 0.658; Fig. 6b). Hence, we ran a model including the number of training visits and season as explanatory variables. We found significant effects of both the season  $(F_{2,103} = 7.38, R^2[adj] = 20.76\%$ , p = 0.001) and the number of training visits  $(F_{1,103} = 8.63, R^2[adj] = 20.76\%, p = 0.004)$ . Additionally, we found a significant interaction between season and the number of visits  $(F_{2,103} = 6.62)$ ,  $R^{2}$ [adj] = 20.76%, p = 0.002), suggesting that the effect of experience with a particular food source on persistence depends on the season. A post hoc test showed that persistence was greater in autumn than in summer (p = 0.018), and that there was no difference between spring and summer (p = 0.062) or between spring and autumn (p = 0.767).

# Discussion

Our results clearly show that the persistence of honeybee foragers to an unrewarding feeding location that was previously rewarding is significantly affected by their prior experience of that location and its profitability in ways that match predictions. Prolonged access (training access of 2 h vs. 0.5 h) and greater profitability (closer to the nest, 20 m vs. 450 m; more concentrated artificial nectar, 2 m vs. 1 m sucrose) increased persistence, both in the number of visits made and in their overall duration. Season seemed to have an effect, with persistence being greatest in autumn in our study year.

Bees continued to visit an empty feeder for up to 7 d after only a short period of training access (Fig. 2a). In nature, a bee would likely have foraged for longer at a patch, maybe days or even a week (Butler et al. 1943; Butler 1945; Ribbands 1949). This persistence is considerably longer than reported in a previous study (Moore et al. 2011; up to 4 d). Interestingly, some bees interrupted visiting the empty feeder for 1-4 d before being recorded again at the feeder. This shows that foragers may check a location even after a long gap in visiting. Why should bees continue to visit unrewarding food source locations? Food sources often become unavailable temporarily, such as due to bad weather or natural rhythms in food production (Kleber 1935). Thanks to persistence, profitable food sources do not need to be rediscovered each day by scouts (von Frisch 1967; Moore et al. 2011).

Long-term persistence was positively affected by the number of training visits made by an individual bee, while the feeder offered food. Similarly, Moore et al. (2011) found that the number of training days had a positive effect on long-term persistence. Nearly a century ago, von Frisch (1923) realised that reward amount is an important factor for food quality. A larger number of training visits means more learning trials, which increases the predictability of the reward and has been shown to positively affect the retention of memory in honeybees (Menzel 1999) and shortterm persistence in flower constancy (Grüter et al. 2011).

When we trained bees to two different sucrose molarities, three of four colonies showed a positive effect of molarity on persistence (Fig. 4a) with one colony showing no effect. The reason for this difference is unknown. Previous work has shown that foragers respond to the quality of a food source during the training period by making more visits to the more concentrated feeder (Seeley 1986). However, how differently colonies respond to 1 M vs. 2 M might



**Fig. 6:** The data show significant differences in persistence between seasons (spring, summer and autumn) of the year 2011. The figure shows means and standard errors for colonies C1 and C2. A and B indicate a statistically significant difference (p < 0.05) between the different seasons within 2011. Tukey's *post hoc* test was used to compare seasons. Numbers inside bars show sample sizes.

depend on factors such as the availability of alternative food sources or the amount of stored honey and, therefore, will vary between colonies and seasons (Lindauer 1948; Seeley 1989). Sucrose molarity has been shown to affect many other foraging-related behaviours including crop filling at the food source (Núñez 1966), memory formation (Bitterman et al. 1983; Scheiner et al. 1999), flying speed (von Frisch & Lindauer 1955), forager body temperature (Stabentheiner 1996), the probability to perform waggle dances (von Frisch 1967; Seeley 1995), trophallactic behaviour inside the colony (Farina & Grüter 2009) and flower constancy (Grüter et al. 2011). As a consequence of these changes, a feeder offering a highly concentrated sucrose solution will attract many more bees than a feeder with diluted sucrose solution (von Frisch 1967; Seeley 1995).

For central place foragers (i.e. animals that must return with the food to a particular place such as a nest), such as a honeybee, increased foraging distance may result in greater exposure to predators and environmental risks and can reduce the rate at which food is collected per time unit or per unit of energy expended. The latter is the energy currency maxi-

mised by honeybees (Seeley 1994). As a consequence, foraging distance is known to affect foraging decisions in honeybees (Seeley 1995) and other bees. In agreement with these predictions, in the giant tropical ant Paraponera clavata, the giving-up time depends on travel time (Breed et al. 1996). In our experiments, there was a significant difference in both persistence measures between the two different foraging distances (20, 450 m). As expected, persistence was greater for the closer food source: visit-persistence was 13% greater for 20 m vs. 450 m and durationpersistence was 11% greater for 20 m vs. 450 m. Our results are to some degree ambiguous as to whether this is caused by a different number of rewarded visits during training to the closer feeder or the distance itself. To disentangle these two factors, a third treatment would have been necessary that allowed bees to make the same number of training visits at a 450 m feeder as they did at the 20-m feeder. The maximum distance in the experiment was only approx. 0.45 km, but honeybees will forage at up to approx. 13 km in nature. However, average foraging distances are usually much shorter (Visscher & Seeley 1982; Ratnieks 2000; Steffan-Dewenter & Kuhn 2003) and vary between months or seasons (Waddington et al. 1994; Beekman & Ratnieks 2000). An important factor affecting food source profitability is the nectar production rate of flowers. Nectar flow rate has been shown to affect dancing and food-sharing behaviour in honeybees (Núñez 1970; Farina 1996; Farina & Grüter 2009), and its effect on persistence should be addressed in future studies.

Long-term persistence also differed between seasons, being highest in autumn and lowest in summer. These results are to some degree puzzling because we expected forager persistence to correlate negatively with natural food abundance and food abundance is higher in autumn than in summer in the study area. In autumn, colonies gained more weight (data not shown) and foragers forage at shorter distances compared to summer, due to the availability of ivy, Hedera spp., in autumn (Couvillon et al. 2012; Garbuzov & Ratnieks, in preparation). On the other hand, seasonal effects were tested with only two colonies, which were tested only during a few days in one study year. It is likely that day-to-day weather conditions are not always typical for a season and, therefore, can cause considerable unaccounted variation or depend on the colonies situation. Honeybee researchers are well aware of seasonal differences in acceptance thresholds of sucrose solution (Scheiner et al. 2003; Martinez & Farina 2008), learning performance (Scheiner et al. 2003) and dance thresholds (Lindauer 1948). This manifests itself, for example, in the difficulty to train bees to forage from a feeder in months of food abundance (Lindauer 1948; von Frisch 1967, p. 18). Furthermore, forager lifetimes might be longer in autumn than summer (Winston 1987; partly due to differences in the amount of brood raised, Smedal et al. 2009), which could bias the data to suggest longer persistence in autumn. Clearly, more research is needed to better understand the role of season on foraging persistence.

In summary, our results are in line with previous studies showing that if the conditions are suitable for foraging, foragers will revisit favourable areas for several days (Butler 1945; Ribbands 1949; Moore 2001). Additionally, our study shows that foragers continue to visit an unrewarding feeding site, sometimes for several days, after only a short training period. Persistence to food source locations is not only known in honeybee foragers, but also ants are known to return to food locations for weeks or even months by using their route memory (Collett et al. 2003). However, honeybees take the profitability of a food source into account when deciding to abandon an unrewarding food source. This ability to abandon unrewarding food sources according to their prior profitability is likely to contribute to a colony's ability to re-allocate its foragers in a changing environment.

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