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Margaret J. Couvillon, Fiona C. Riddell Pearce, Christopher Accleton, Katherine A. Fensome, Shaun K. L. Quah, et al.. Honey bee foraging distance depends on month and forage type. *Apidologie*, Springer Verlag, 2015, 46 (1), pp.61-70. 10.1007/s13592-014-0302-5 . hal-01284422

HAL Id: hal-01284422

<https://hal.archives-ouvertes.fr/hal-01284422>

Submitted on 7 Mar 2016

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Honey bee foraging distance depends on month and forage type

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Received 26 February 2014 – Revised 11 May 2014 – Accepted 5 June 2014

Abstract – To investigate the distances at which honey bee foragers collect nectar and pollen, we analysed 5,484 decoded waggle dances made to natural forage sites to determine monthly foraging distance for each forage type. Firstly, we found significantly fewer overall dances made for pollen (16.8 %) than for non-pollen, presumably nectar (83.2 %; $P < 2.2 \times 10^{-23}$). When we analysed distance against month and forage type, there was a significant interaction between the two factors, which demonstrates that in some months, one forage type is collected at farther distances, but this would reverse in other months. Overall, these data suggest that distance, as a proxy for forage availability, is not significantly and consistently driven by need for one type of forage over the other.

forage availability / waggle dance / *Apis mellifera* / nectar / pollen

1. INTRODUCTION

Foraging is an essential, but costly, behaviour for most animals (Porter and Jorgensen 1981; Grubb and Greenwald 1982; Jeanne 1986; Hughes and Ward 1993; Visscher and Dukas 1997; Brown and Kotler 2004). Incurred costs such as time investment and energy consumed are especially relevant for animals that spend long periods collecting or range relatively far (Kacelnik et al. 1986; Krebs and Davies 2009). For ecologists, determining where an animal collects food is often challenging and becomes more so the farther afield they forage. This

difficulty has been partially mitigated in recent vertebrate studies with the advent of GPS tracking technology (Weimerskirch et al. 2002; Cagnacci et al. 2010), but what about animals, such as insects, that are too small to carry trackers?

Honey bees, *Apis mellifera*, present an ideal opportunity in foraging studies because it is the only animal that directly communicates where it has collected food with the waggle dance (von Frisch 1967; Couvillon 2012). A successful forager, upon returning to the hive, performs a stereotyped behaviour where the bee moves linearly on the comb while wagging her body from side to side. Dances are made to communicate sites where resources (e.g., nectar, pollen, water) can be collected, and during swarming, to communicate potential new nest sites (Lindauer 1955; Seeley and Buhrman 1999). The waggle runs, which form part of the waggle

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dance, encode a vector from the hive to the location where the forager has gathered food (von Frisch 1946, 1967) and can be decoded by researchers (Visscher and Seeley 1982; Waddington et al. 1994; Beekman and Ratnieks 2000; Steffan-Dewenter and Kuhn 2003; Couvillon 2012; Couvillon et al. 2014b).

Nectar and pollen are the main foods collected by honey bees. Nectar, which is converted into honey, is the major energy source, while pollen is the source of proteins and lipids and is fed to larvae and workers (Crailsheim 1992). Both are essential for individual and colony health. Although the same flowers often produce both pollen and nectar, this is not true for all plants (e.g., some wind-pollinated plants do not make nectar). Additionally, sometimes honey bee foragers will specialize on a type of forage, collecting either nectar or pollen from any given plant, even though both are available (Robinson and Page 1989; Pankiw and Page 2000). In other words, the locations at which a bee will forage for nectar is not necessarily where she or her nestmate may forage for pollen.

For honey bees, flight distance is one of the biggest costs in terms of time and energy that a worker must weigh against the gain of the food (Seeley 1994; Couvillon et al. 2014b). Therefore, bees will not collect food from far away unnecessarily, and forage distance can be used as a proxy for availability. In other words, the farther a bee must fly to forage, the less available that forage is closer by (Seeley 1994; Seeley 1995). Bees have evolved exceptional sensitivity to measuring relative energetic rewards and to discovering new forage sources in the landscape, so a forager will only dance for the “best” forage sites known at any given time (Schmid-Hempel 1987; Schmid-Hempel and Schmid-Hempel 1987; Seeley 1994; Barron et al. 2007; Grüter et al. 2011). Therefore, each observed dance has already passed a cost/benefit analysis and represents that bee’s economically smart advice for where the colony should direct foraging efforts.

Previous work demonstrated that foraging distance varies with month (Couvillon et al.

2014b). However, what is not known is if and how this variation differs between nectar and pollen. Specifically, we wanted to know if foraging distance, which reflects availability, was driven by one type of forage over another. Here, we analysed 5,484 waggle dances over 2 years. In agreement with previous studies, foraging distance was found to vary significantly with month for both nectar and pollen; however, we found that pollen and nectar distances varied differently per month, where during some months, one type of forage is collected significantly farther away, which would then reverse for another month. Overall, these data suggest that monthly forage availability is not significantly and consistently different for nectar versus pollen.

2. METHODS

2.1. Study organism and experimental set-up

Three colonies of honey bees of mixed European race, predominantly *Apis mellifera mellifera*, were used. They were housed in glass-walled observation hives located at our laboratory on the University of Sussex campus in East Sussex. Each colony contained approximately 5,000 workers on one deep and three medium Langstroth frames. Colonies were queen-right and maintained throughout the duration of the project for swarm prevention and to keep consistent the number of workers and quantity of stored honey (one medium frame) to control for foraging motivation. When supplemental feeding was needed, which was rare, colonies were given 2 M of sucrose solution on Friday afternoons. Data collection (videoing dances) was not done over the weekends, and the sugar solution was consumed by Monday morning. A 3-cm diameter×30-cm plastic tube gave foragers access to the outside so worker bees could visit natural forage sites.

2.2. Data collection

Data collection followed (Couvillon et al. 2012). Briefly, videos were made from 11 August 2009 to 31 August 2011 on most days when the bees were

foraging, March–October. Each observation hive was filmed for 1 h per study day using camcorders (Canon Legria HV40, HDV 1080i) and mini-DV tapes, adjusting the zoom of each camera so that a “dance floor” area c. 25 cm wide by 20 cm deep was recorded. Our goal was to film all three colonies simultaneously around the same time each day (10–11 a.m. GMT), although sometimes one of the colonies was inactive or bad weather prevented foraging. The tapes were uploaded to external hard drives connected to iMac computers running Final Cut Express (version 4.0.1). Videos were played until we observed a bee making a waggle dance, which consists of a wagging portion (waggle run) followed by a return phase, where the bee moves approximately to her start position before beginning another waggle run, all within the same dance bout. After we decoded all the bees on the screen at any given time, we fast-forwarded the video for 6 min, which was usually sufficient for a new group of dancers to enter the frame.

Previous work on waggle dance decoding used the duration of the entire circuit (waggle run+return phase) or several entire circuits that is then averaged (von Frisch 1946, 1967; Waddington et al. 1994; Beekman and Ratnieks 2000). However, the waggle run is the information-rich portion of the dance (Michelsen et al. 1992), while the return phase, or specifically, the quickness of the return phase, depends on resource quality (Seeley et al. 2000) and can be noisy. Therefore, we only used the waggle run, not the entire circuit, in our decoding.

To decode dances, it is usually necessary to extract two pieces of information per waggle run: the duration of the waggle run (von Frisch 1967; Seeley et al. 2000), which encodes the distance to the advertised forage location, and the direction of the waggle run relative to vertical, which gives the direction from the nest relative to the solar azimuth. For this project, we were only interested in foraging distance (waggle run duration), not direction. Duration was measured by noting the beginning and end of each waggle run, which was determined by the start and end of the blurring of the dancer’s body and wings, easily visible on a still frame of the video. Beginning and end times (hour, minute, second, frame) were taken from the timer of the video software, which provides a temporal resolution of

0.04 s (one frame). Thus, our maximum measurement error was approximately 0.08 s. Four mid-dance, consecutive waggle runs (Couvillon et al. 2012) were decoded, which repeat the same information multiple times within a dance. The four waggle runs were averaged to obtain a single duration per dance, which highly correlated to the duration that would be obtained if one decoded and averaged all the waggle runs within a dance (Couvillon et al. 2012). Duration was converted into distance (meters) using a linear calibration model built for our honey bee population and landscape (Schürch et al. 2013). Using our own calibration curve instead of relying on the curve of von Frisch (von Frisch 1967), as in previous studies, is important because the honey bee odometer is relative to the landscape over which they fly (Srinivasan et al. 2000; Esch et al. 2001) and may differ between strains (Boch 1957).

Lastly, for each dance, whether or not the bee carried pollen in her pollen baskets was noted. This is easily seen on the video. Any bee without a pollen load was classified as a nectar forager. It is possible, during the summer months, for bees also to dance for water; however, there is no easy way to distinguish nectar from water foragers without removing the bee from the colony, which would disturb her dance, and testing the liquid in her crop. Additionally, water feeders were routinely provided in our apiary, so water foragers usually collected from nearby and performed “round” dances (Gardner et al. 2008), which we did not analyse in this project. Lastly, we know from another project that even during the high summer, less than 2 % of returning foragers are carrying water in their crop (Couvillon et al. 2014b). England is not overly warm, so there will most likely be more water foragers in other, warmer locations.

2.3. Data analysis

Dances had been decoded for another project where we did not distinguish between nectar and pollen foragers (Couvillon et al. 2014b). This amounted to 5,484 decoded dances over 2 years, which we analysed here separately for the two types of forage. Overall, we saw 922 from pollen foragers

and 4,562 from nectar foragers. Analysis was done using Minitab (version 16.2.3) and SPSS (version 20). We began with some descriptive statistics to determine the mean and distribution for the two types of forage and whether or not these differ for nectar and for pollen. Then we square-root transformed the response variable (foraging distance) so the model would meet the modelling assumptions. Next, we tested foraging distance against foraging month for both nectar and pollen dancers using a one-way ANOVA to determine overall, separate patterns of monthly variation. Then what factors may influence distance [month, forage type (nectar versus pollen), and month \times forage type] were explored using a general linear model (GLM). Lastly, Spearman's rank correlation was used to determine if there is a correlation between monthly foraging distance for the two types of forage (nectar and pollen).

3. RESULTS

3.1. Foraging means and distributions significantly differ between nectar and pollen

Overall, the mean distance foragers travelled for pollen was 1,074 m, whereas the overall mean distance foragers travelled for nectar was 1,408 m. These means differed significantly from each other (square-root transformed data, two-sample t (1,379)=10.08, $P<0.001$). Additionally, the two distributions also significantly differed (two-sample Kolmogorov-Smirnov, $P<0.001$, Figure 1). Pollen was more positively skewed, with a kurtosis_{pollen}=3.85 versus kurtosis_{nectar}=1.75 (Figure 1).

3.2. Significantly more nectar than pollen dances were performed by honey bees

Overall, 83.2 % of all the dances we decoded to natural forage site were non-pollen dances, presumably for nectar. The number of decoded waggle dances for nectar (4,562) out of our data set (5,484) is significantly more than half (binomial two-tailed test, $P<2.2\times 10^{-23}$).

3.3. Foraging distance varies with month for both nectar and pollen, but it varies differently

The mean foraging distances communicated by the dances varies significantly with month for both nectar and pollen (distances were square-root transformed to obtain normality of residuals; one-way ANOVA for nectar, $n=4,562$, $F_{16,4,476}=143$, $P<0.001$; one-way ANOVA for pollen, $n=922$, $F_{16,871}=22.3$, $P<0.001$; Table 1; Figure 2). A general pattern is shown for both nectar and pollen in the variation with significantly greater distances in summers (defined as pre-autumnal bloom, August 09; July 2010; July 2011) than in early springs (March 2010; March 2011) and autumns (defined as during autumnal bloom, Sep–Oct 2009; Sep–Oct 2010).

When foraging distance is analysed against the fixed factors of forage type (nectar versus pollen), month, and an interaction of the two (forage type \times month), the variation by month also varies depending on if the forage is nectar or pollen, as demonstrated by the significant interaction of the two factors (GLM; month: $F=55.8$, $P<0.001$; forage type: $F=2.16$, $P=0.14$; forage type \times month: $F=7.0$, $P<0.001$; $R^2=34.1$ %). In other words, for some months, nectar collection is done at farther distances, but at other months, pollen collection is done at farther distances (Table 1, Figure 3a).

3.4. Overall, foraging distance is not predicted by forage type

The non-significance of forage type ($P=0.14$) in the above model demonstrates that distance does not significantly depend on what food type, nectar, or pollen, the bee collected. This is further supported by a strong correlation between average monthly nectar foraging distance and average monthly pollen foraging distance (Spearman correlation, $r_s=0.82$, $P<0.001$; Figure 3b). The months when bees are travelling far for one type of forage also tend to be the months when bees are travelling far for the

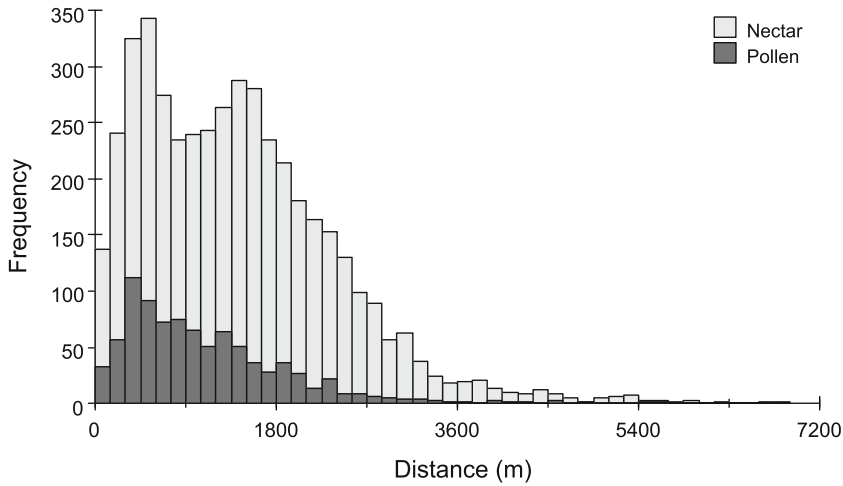


Figure 1. Frequency distributions and overall means for the foraging distances for nectar (=1,408 m) and pollen (=1,074 m) significantly differed ($P < 0.001$ for both). The pollen distribution is more positively skewed (kurtosis=3.85) than the nectar distribution (kurtosis=1.75).

Table I. Number of decoded dances, percent of dance type compared to total, average foraging distance, and standard error of the mean (SEM) communicated by dances per foraging month August 2009–August 2011, for nectar and pollen forage.

	Pollen				Nectar			
	<i>n</i>	Percent of dances	Ave. dist. (m)	SEM.	<i>n</i>	Percent of dances	Ave. dist. (m)	SEM
Aug 2009	10	2	3,089.2	437.0	429	98	2,512.7	54.0
Sep 2009	61	13	1,277.1	67.4	406	87	1,393.2	36.1
Oct 2009	43	11	2,022.5	204.1	358	89	1,434.2	47.5
Mar 2010	27	24	511.4	46.3	87	76	509.3	26.9
Apr 2010	27	16	1,252.9	138.7	141	84	710.7	49.6
May 2010	24	14	858.1	184.7	150	86	1,051.5	56.2
Jun 2010	46	19	904.5	103.8	202	81	1,531.6	58.0
Jul 2010	27	8	1,738.8	122.8	313	92	2,292.1	57.7
Aug 2010	78	22	1,294.8	87.5	269	78	1,553.2	48.5
Sep 2010	85	30	1,316.6	55.8	197	70	1,377.7	43.4
Oct 2010	71	31	720.5	51.8	160	69	686.1	30.9
Mar 2011	79	41	599.2	34.9	116	59	403.9	27.9
Apr 2011	98	21	655.8	46.7	362	79	663.2	28.0
May 2011	91	25	1,046.4	76.8	271	75	1,047.6	51.4
Jun 2011	43	10	722.4	104.2	369	90	1,253.8	48.4
Jul 2011	34	10	1,597.0	109.9	319	90	1,608.6	37.5
Aug 2011	44	11	1,025.6	85.0	344	89	1,438.4	39.2

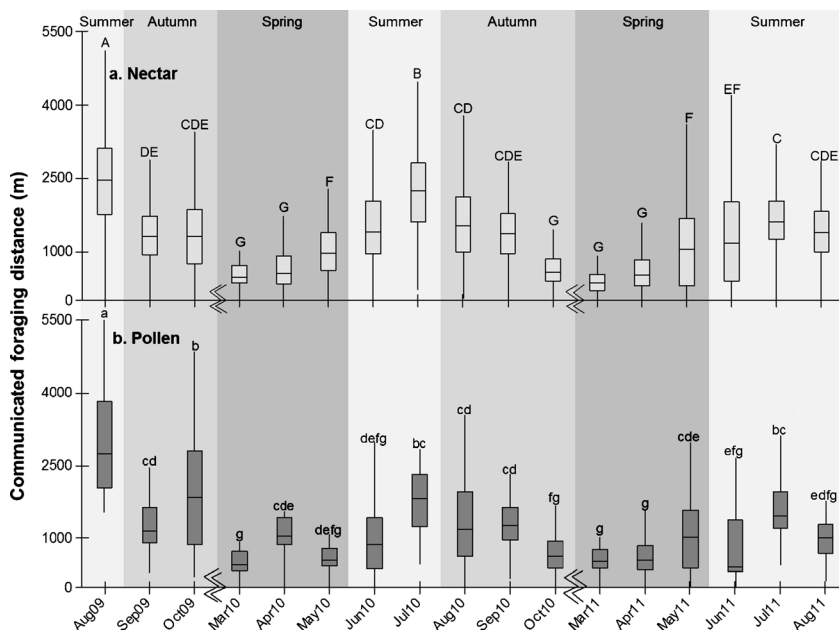


Figure 2. Foraging distance, as communicated by waggle dances, significantly varies with month for both nectar (**a**, $n=4562$) and pollen (**b**, $n=922$). Letters (capital=nectar and lower case=pollen) display post hoc results, where months that share letters do not significantly differ. Box lines report medians, and whiskers extend to either maximum and minimum data points or to 1.5 times the interquartile range. Breaks in the x-axis indicate winter, when there is little or no foraging. Median foraging distances tended to be greater in summers (defined as pre-autumnal bloom; Aug 2009, July 2010, July 2011, see (Couvillon et al. 2014b)) than springs (March 2009, 2010) or autumns (defined as during autumnal bloom; September and October 2009 and 2010, see (Couvillon et al. 2014b)).

other type of forage. Lastly, when mean foraging distance per month for nectar and pollen is compared (Table I), we see that in 11 of the 17 months, bees fly farther for nectar than for pollen. This (11/17) is not significantly different from the null expectation of 8.5/17 months (binomial two-tailed test, $P=0.3$).

As mentioned in materials and methods, care was taken for dance decoding to be done on individual bees (i.e., independent sampling). Additionally, as all our results were highly significant, multiple testing should not be an issue (García 2004).

4. DISCUSSION

Here, we have shown that monthly foraging distance is not significantly predicted by forage

type. The overall average nectar distance and distance distribution significantly differed from the overall average pollen distance and distribution, most likely because in the summer, when bees must fly farther anyway (Couvillon et al. 2014b), the bees are less likely to be collecting pollen because there is less brood rearing. Crucially, foraging distance varies with month differently for the two forage types, when during some months, distance is greater for one forage type, but this reverses in other months. Overall, this suggests that the distance that foraging honey bees must fly is not significantly driven by one type of forage over another, with summer in general being the season where bees must fly farthest to collect forage compared to spring or autumn.

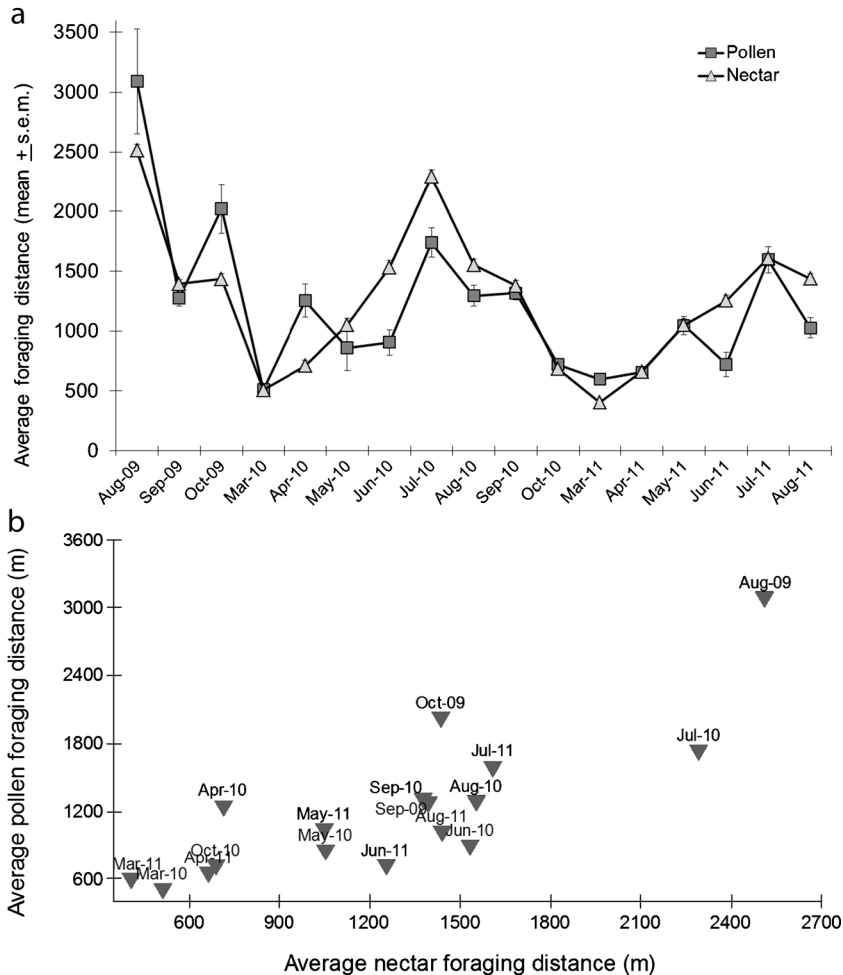


Figure 3. Foraging distance is not significantly and consistently driven by forage type. **a** Mean foraging distance varies differently for the two types of forage (forage type \times month, $P < 0.001$); however, one type of forage is not collected consistently at farther distances than the other type ($P = 0.14$). **b** Monthly foraging distances for the two types of forage strongly correlate ($r_s = 0.82$, $P < 0.001$), such that the months that bees tend to forage at farther distances for one type of forage are the same months that the bees will forage at farther distances for the other type of forage. Note that there is a break from October to March for each year: bees overwinter and typically do not forage in November–February.

This does not necessarily mean that the bees dancing for nectar or pollen were visiting the same flowers. In addition to the fact that not all flowers produce both nectar and pollen, we see in our own data a crossing over in foraging distances, where in some months, the foragers have to fly farther for nectar, and in other

months, the foragers have to fly farther for pollen. Additionally, the distance distributions significantly differ, which demonstrates that the two distributions are drawn from different populations. Overall, this strongly suggests that the two forage types are, in many months, coming from differently located patches.

Not all returning foragers perform waggle dances (von Frisch 1967; Seeley 1994, 1995). A foraging honey bee takes into account many factors, such as forage quality, distance to forage, wait time to unload forage (nectar only), reliability of forage, and prevalence of competitors on the forage, in her decision first to return to a forage location and secondly to recruit to that patch with the dance (Seeley 1989; Seeley et al. 1991; Seeley 1995). Additionally, individual bees vary in their propensity to dance for the same resource. Therefore, dance decoding does not give information about all the foraging sites currently being used by a honey bee colony. Rather, waggle dances are filtered information (Seeley 1995; Grüter et al. 2010) that already integrate the above factors to communicate the locations of the most profitable feeding locations known to a colony at that time.

The fact that waggle dances in the summer, as demonstrated by the post hoc analysis in Figure 2, advertise nectar and pollen patches at greater distances indicates that summer is the most challenging season to find food in the landscape (Couvillon et al. 2014a, 2014b). However, the non-significance of forage type in the model shows that whether the dance is for nectar or pollen does not consistently predict monthly distance. Rather, the same months when one type of forage is relatively less available, as shown by higher foraging distance, the other type of forage is also likely to be less available (Figure 3).

The overall proportion of pollen dances (17 %) was less than previously reported in another study (31 %) that examined honey bee foraging over a shorter time period (Visscher and Seeley 1982; Schneider 1989). Indeed, during some months, our bees foraged for pollen at or greater than 31 % proportion of all dances. Interestingly, African and Africanized honey bees consistently allocate more foragers (approximately 60 %) to pollen collection than European honey bees (Danka et al. 1987; Pesante et al. 1987; Schneider 1989; Schneider and McNally 1992). This difference in forage priority most likely reflects the contrasting ecological landscapes of temperate versus tropical:

temperate honey bees, like those found in parts of Europe and North America, must create enough carbohydrate stores (honey) to survive overwintering (Seeley 1985; Winston 1987) and therefore prioritize nectar collection unless brood is actively being reared. In contrast, African and Africanized colonies experiencing no prolonged winter season, store significantly less honey (Winston 1987; Rinderer 1988; Schneider and Blyther 1988), and can devote more energy to brood production, which necessitates more pollen collection, as pollen is the food source for developing brood. It would be interesting to examine any potential differences in honey bee foraging distance for African and Africanized bees, especially in regards to their pollen collection.

ACKNOWLEDGMENTS

We would like to thank Ellie Blows and Sarah Hudson for being volunteer dance decoders. MJC is funded by a donation from The Nineveh Charitable Trust, UK. Waitrose Ltd. provided funds for a research MSc (to FCRP) and summer undergraduate research bursaries (to CA, KAF, SKLQ, and ET). Additional research funding was provided by Burt's Bees, The Body Shop Foundation, and Rowse Honey Ltd.

La distance de butinage de l'abeille varie en fonction du mois et du type de substance récoltée

Disponibilité de l'approvisionnement / danse de recrutement / *Apis mellifera* / nectar / pollen

Die Sammeldistanz bei Honigbienen hängt vom Monat und Art des Sammelns ab

Trachtvorkommen / Schwänzeltanz / *Apis mellifera* / nektar / pollen

REFERENCES

- Barron, A.B., Maleszka, R., Vander Meer, R.K., Robinson, G.E. (2007) Octopamine modulates honey bee dance behavior. *Proc. Natl. Acad. Sci. U. S. A.* **104**(5), 1703–1707

- Beekman, M., Ratnieks, F.L.W. (2000) Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* **14**(4), 490–496
- Boch, R. (1957) Rassenmässige Unterschiede bei den Tänzen der Honigbiene (*Apis mellifica* L.). *Z. Vgl. Physiol* **40**(3), 289–320
- Brown, J.S., Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**(10), 999–1014
- Cagnacci, F., Boitani, L., Powell, R.A., Boyce, M.S. (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**(1550), 2157–2162
- Couvillon, M.J. (2012) The dance legacy of Karl von Frisch. *Insect. Soc.* **59**(3), 297–306
- Couvillon, M.J., Riddell Pearce, F.C., Harris-Jones, E.L., Kuepfer, A.M., Mackenzie-Smith, S.J., et al. (2012) Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding. *Biol. Open* **1**(5), 467–472
- Couvillon, M.J., Fensome, K.A., Quah, S.K.L., Schürch, R. (2014a) Summertime blues: August foraging leaves honey bees empty-handed. *Comm. Integr. Biol.* **7**(1), e28821
- Couvillon, M.J., Schürch, R., Ratnieks, F.L.W. (2014b) Waggle dance distances as integrative indicators of seasonal foraging challenges. *PLoS ONE* **9**(4), e93495
- Crailsheim, K. (1992) The flow of jelly within a honeybee colony. *J. Comp. Physiol. B.* **162**(8), 681–689
- Danka, R.G., Hellmich II, R.L., Rinderer, T.E., Collins, A.M. (1987) Diet-selection ecology of tropically and temperately adapted honey bees. *Anim. Behav.* **35**(6), 1858–1863
- Esch, H.E., Zhang, S., Srinivasan, M.V., Tautz, J. (2001) Honeybee dances communicate distances measured by optic flow. *Nature* **411**(6837), 581–583
- García, L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**(3), 657–663
- Gardner, K.E., Seeley, T.D., Calderone, N.W. (2008) Do honeybees have two discrete dances to advertise food sources? *Anim. Behav.* **75**(4), 1291–1300
- Grubb Jr., T.C., Greenwald, L. (1982) Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.* **30**(3), 637–640
- Grüter, C., Leadbeater, E., Ratnieks, F.L.W. (2010) Social learning: the importance of copying others. *Curr. Biol.* **20**(16), R683–R685
- Grüter, C., Moore, H., Firmin, N., Helanterä, H., Ratnieks, F.L.W. (2011) Flower constancy in honey bee workers (*Apis mellifera*) depends on ecologically realistic rewards. *J. Exp. Biol.* **214**(8), 1397–1402
- Hughes, J.J., Ward, D. (1993) Predation risk and distance to cover affect foraging behaviour in Namib Desert gerbils. *Anim. Behav.* **46**(6), 1243–1245
- Jeanne, R.L. (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav. Ecol. Sociobiol.* **19**(5), 333–341
- Kacelnik, A., Houston, A.I., Schmid-Hempel, P. (1986) Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. *Behav. Ecol. Sociobiol.* **19**(1), 19–24
- Krebs J.R., N.B. Davies. (2009) Behavioural ecology: an evolutionary approach. Wiley-Blackwell.
- Lindauer, M. (1955) Schwarmbienen auf wohnungssuche. *Z. Vgl. Physiol* **37**(4), 263–324
- Michelsen, A., Andersen, B.B., Storm, J., Kirchner, W.H., Lindauer, M. (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behav. Ecol. Sociobiol.* **30**(3/4), 143–150
- Pankiw, T., Page Jr., R.E. (2000) Response thresholds to sucrose predict foraging division of labor in honeybees. *Behav. Ecol. Sociobiol.* **47**(4), 265–267
- Pesante, D., Rinderer, T.E., Collins, A.M. (1987) Differential pollen collection by Africanized and European honeybees in Venezuela. *J. Apic. Res.* **26**, 24–29
- Porter, S.D., Jorgensen, C.D. (1981) Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste. *Behav. Ecol. Sociobiol.* **9**(4), 247–256
- Rinderer, T.E. (1988) Evolutionary aspects of the Africanization of honey-bee populations in the Americas. In: Needham, G.R., Page, R.E., Definado-Baker, M., Bowman, C. (eds.) *Africanized honey bees and bee mites*, pp. 13–28. Westview Press, Boulder
- Robinson, G., Page Jr., R. (1989) Genetic determination of nectar foraging, pollen foraging, and nest-site scouting in honey bee colonies. *Behav. Ecol. Sociobiol.* **24**(5), 317–323
- Schmid-Hempel, P. (1987) Efficient nectar-collecting by honeybees I. Economic models. *J. Anim. Ecol.* **56**(1), 209–218
- Schmid-Hempel, P., Schmid-Hempel, R. (1987) Efficient nectar-collecting by honeybees II. Response to factors determining nectar availability. *J. Anim. Ecol.* **56**(1), 219–227
- Schneider, S.S. (1989) Spatial foraging patterns of the African honey bee, *Apis mellifera scutellata*. *J. Insect Behav.* **2**(4), 505–521
- Schneider, S.S., Blyther, R. (1988) The habitat and nesting biology of the African honey bee *Apis mellifera scutellata* in the Okavango River Delta, Botswana, Africa. *Insect. Soc.* **35**(2), 167–181

- Schneider, S.S., McNally, L.C. (1992) Seasonal patterns of foraging activity in colonies of the African honey bee, *Apis mellifera scutellata*, in Africa. *Insect. Soc.* **39**(2), 181–193
- Schürch, R., Couvillon, M.J., Burns, D.D.R., Tasman, K., Waxman, D., et al. (2013) Incorporating variability in honey bee waggle dance decoding improves the mapping of communicated resource locations. *J. Comp. Physiol. A. Neuroethol. Sens. Neural. Behav. Physiol.* **199**(12), 1143–1152
- Seeley, T.D. (1985) Honeybee ecology. Princeton University Press, Princeton
- Seeley, T. (1989) Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. *Behav. Ecol. Sociobiol.* **24**(3), 181–199
- Seeley, T.D. (1994) Honey bee foragers as sensory units of their colonies. *Behav. Ecol. Sociobiol.* **34**(1), 51–62
- Seeley, T.D. (1995) The wisdom of the hive. Harvard University Press, Cambridge
- Seeley, T.D., Buhrman, S.C. (1999) Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**(1), 19–31
- Seeley, T., Camazine, S., Sneyd, J. (1991) Collective decision-making in honey bees: how colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* **28**(4), 277–290
- Seeley, T.D., Mikheyev, A.S., Pagano, G.J. (2000) Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *J. Comp. Physiol. A.* **186**(9), 813–819
- Srinivasan, M.V., Zhang, S., Altwein, M., Tautz, J. (2000) Honeybee navigation: nature and calibration of the "odometer". *Science* **287**(5454), 851–853
- Steffan-Dewenter, I., Kuhn, A. (2003) Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. B Biol. Sci.* **270**(1515), 569–575
- Visscher, P., Dukas, R. (1997) Survivorship of foraging honey bees. *Insect. Soc.* **44**(1), 1–5
- Visscher, P.K., Seeley, T.D. (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* **63**(6), 1790–1801
- von Frisch, K. (1946) Die Tänze der Bienen. *Österr. Zool. Z.* **1**, 1–148
- von Frisch, K. (1967) The dance language and orientation of bees. Harvard University Press, Cambridge
- Waddington, K.D., Herbert, T.J., Visscher, P.K., Richter, M.R. (1994) Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behav. Ecol. Sociobiol.* **35**(6), 423–429
- Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabile, G., Dell'Omo, G., et al. (2002) GPS tracking of foraging albatrosses. *Science* **295**(5558), 1259
- Winston, M.L. (1987) The biology of the honey bee. Harvard University Press, Cambridge