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Comparison of Flower Constancy and Foraging Performance in three Bumblebee species (Hymenoptera: Apidae: Bombus)

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Raine N E & Chittka L [Biol Sci, Queen Mary, London E1 4NS]: **Comparison of Flower Constancy and Foraging Performance in three Bumblebee species (Hymenoptera: Apidae: Bombus).** – Entomol Gener 28(2): 081–089; Stuttgart 2005-09.   – – –   [Article]

The three bumblebee species *Bombus terrestris* (Linnaeus 1758), *Bombus lapidarius* (Linnaeus 1758), and *Bombus pascuorum* (Scopoli 1763) showed consistent differences in their respective levels of flower constancy when foraging on three different pairs of flower species. *B terrestris* was always the most flower constant, followed by *B lapidarius*, with *B pascuorum* the least flower constant species. These interspecific differences in flower constancy were related to foraging performance under field conditions near Würzburg, Germany in 1999 and 2001. *B terrestris* was more flower constant, and predominantly outperformed *B lapidarius* at collecting nectar in both years. As *B terrestris* is also the larger of these species, these data also support the idea that larger bees are more efficient at nectar foraging, i.e. they bring home more nectar per unit time. However *B pascuorum*, the least flower constant of the three species tested, was the most efficient of them at collecting nectar, collecting 50% more nectar than *B terrestris* per hour. Therefore flower constancy appears to be a relatively poor predictor of species foraging performance, which is likely to be influenced simultaneously by many other factors including worker body size, tongue length, and foraging range.

Key words: *Bombus terrestris* (Linnaeus 1758) – *Bombus lapidarius* (Linnaeus 1758) – *Bombus pascuorum* (Scopoli 1763) – body size – flight duration – foraging strategy – nectar – pollination

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Die drei Hummel-Arten *Bombus terrestris* (Linnaeus 1758), *Bombus lapidarius* (Linnaeus 1758), und *Bombus pascuorum* (Scopoli 1763) zeigen gleichbleibende Unterschiede bezüglich ihrer Blütenstetigkeit beim Nektarsammeln an drei Paaren von Pflanzenarten. *B terrestris* hat den höchsten Grad von Blütenstetigkeit, gefolgt von *B lapidarius*, wohingegen *B pascuorum* die am wenigsten blütenstete Art ist. Diese artspezifischen Unterschiede wurden mit der Nektarsammelleistung dieser drei Arten in einem natürlichen Habitat in der Umgebung von Würzburg in den Jahren 1999 und 2001 korreliert. Die blütenstetere Art *B terrestris* hat in beiden Jahren durchschnittlich höhere Nektarsammelraten als *B lapidarius*. Da *B terrestris* außerdem die größere der beiden Arten ist, stützen diese Daten die These, daß größere Hummel-Arbeiterinnen mehr Nektar pro Sammelflugzeit einbringen. Allerdings hat *B pascuorum*, die am wenigsten blütenstete Art, die höchste Sammelrate: Arbeiterinnen trugen durchschnittlich 50% mehr Nektar pro Zeit ein als Sammlerinnen der Art *B terrestris*.

Daraus wird geschlossen, daß Blütenstetigkeit und Sammelleistung auf Artebene nicht streng korrelieren, da die Sammelleistung verschiedener Blütenbesucher gleichzeitig von mehreren Faktoren, wie Körpergröße, Länge des Rüssels sowie Flugdistanz beeinflußt werden.

Schlüsselbegriffe: *Bombus terrestris* (Linnaeus 1758) – *Bombus lapidarius* (Linnaeus 1758) – *Bombus pascuorum* (Scopoli 1763) – Bestäubung – Flugdauer – Körpergröße – Nektar – Sammelstrategie

1   Introduction

Flower constancy is a foraging strategy common amongst pollen or nectar collecting insects, including bees [eg: Waser 1986; Chittka et al 1999], butterflies [Lewis 1989; Goulson & Cory 1993], hoverflies [Goulson & Wright 1998], and potentially even beetles [De los Mozos Pascual & Domingo 1991]. An individual insect is flower constant if it visits only a restricted number of flower species, even if other species are available and equally rewarding, and if the insect has no innate predisposition to visit only flowers of a restricted plant taxon (this requires confirmation by observing that other conspecific insects visit other flower species within the same array: Waser 1986; Chittka et al 1999). But is flower constancy an optimal foraging behaviour?

It is hard to see how such behaviour could be adaptive *per se*, since there is rarely only a single best food source, and specializing on one flower type while skipping other valuable ones encountered *en route*, would seem an unwise strategy to maximize energy intake per unit time [Waser 1986; Chittka 2002]. Thus, flower constancy can only be considered adaptive in the face of behavioural limitations that might make switching between species costly. Short term memory limitations represent a likely explanation [Chittka et al 1997; 1999]. While generalist bees are able to store both sensory cues and motor patterns for several flower species in long term memory, there appear to be delays in retrieving the sensory cues for flowers that have not been visited in the bee's immediate history [Greggers & Menzel 1993; Chittka & Thomson 1997; Bar-Shai et al 2004]. While such costs are often negligible for easily accessible flowers [Laverty 1994; Chittka et al 1997], they can be substantial when bees have to retrieve multiple, but drastically different motor patterns from memory [Woodward & Laverty 1992; Chittka & Thomson 1997]. Indeed, bees switching between plant species with very different floral morphologies show significantly increased flower handling times. Therefore, when flowers of the same and novel species are available at equal distances, foraging insects should be flower constant to minimize the costs of switching. Conversely, as travel time between flowers increases, or if all flowers are poorly rewarding, the costs of bypassing alternative species may exceed the costs of switching, which should favour inconstancy [Chittka et al 1999].

In reality, it is difficult to rigorously test these specific predictions in the economy of nature, because controlling the range of floral species, morphologies, and patterns of reward provision available to free foraging bees is virtually impossible. An alternative, and perhaps more direct, test of the adaptive benefits of flower constancy could be to examine bumblebee species that differ consistently in the extent to which they are flower constant, and to compare their relative foraging performance. Do more flower constant bumblebee species actually forage more effectively?

2 Material and methods

2.1 Flower choices

The floral choices of free foraging bees were monitored in the field using the bee interview technique [THOMSON 1981]. Foraging bees are "interviewed" when the observer offers them a choice of two flower species: a conspecific to the flower just visited by the bee, plus one other sympatric flower species. The "interviewer" records the bee's choice, i.e. which test flower species it lands on. Flower constant foragers would be expected to choose the same species they just visited when offered this experimental selection. Flowers for the experiment were picked at the field site (a 40m x 60m patch of meadow grassland near Würzburg, Germany) and each placed in a small vial of water. One flower was attached to each branch of a y-shaped fork at the end of a 1m long pole for each "interview". The observer presented the two flowers, attached to the y-shaped pole, so that they formed an equilateral triangle with the flower the test bee was currently visiting, and the distance to each of the test flower species was approximately 10cm. Each individual forager was "interviewed" once, and test flowers were replaced following each interview to prevent any scent marks left by previous foragers influencing subsequent bee choices. The floral constancy of three bumblebee species (*Bombus terrestris*, *Bombus lapidarius*, and *Bombus pascuorum*) was measured when they were foraging on four Fabaceous flower species: red clover (*Trifolium pratense* Linnaeus 1753), white clover (*Trifolium repens* Linnaeus 1753), bird's foot trefoil (*Lotus corniculatus* Linnaeus 1753) and cow vetch (*Vicia cracca* Linnaeus 1753) in the summer of 1999. At least 80 foraging choices per bumblebee species were recorded for each pair of test flower species (X & Y): i e a minimum of 40 choices from bees which had just visited flowers of species X, and a minimum of 40 choices from bees which had just visited flower species Y. Flower constancy indices were calculated (after CHITTKA et al 2001) using the formula: constancy $= 0.5[(A - B)/(A + B) + (C - D)/(C + D)]$. Here A represents the number of constant flights from X to X, B the flights from X to Y, C the flights from Y to Y, and D the flights from Y to X. Constancy calculated in this way can range from 1 (complete constancy), through 0 (random flights between species), to -1 (complete inconstancy). Flower constancy data were statistically analysed by two-sided Chi-square tests, with Yate's continuity correction (df = 1 in all cases).

2.2 Foraging performance

Colonies of the same three bumblebee species were placed in the field (near Würzburg) to measure species nectar foraging performance. An area of typical central European bumblebee habitat was chosen as the field site, giving colonies access to multiple flower species in bloom in dry grassland, deciduous forest and farmland. This area included the patch of grassland in which the flower choice experiments were conducted. Test colonies of *B lapidarius* (2 colonies in 1999, 3 colonies in 2001) and *B terrestris* (2 colonies in 1999, 5 colonies in 2001) were reared in the laboratory from wild-caught queens. These queens, and subsequently the developing colonies, were kept in controlled temperature and humidity conditions (27°C, 60% RH) and fed pollen-honey paste *ad libitum* prior to field tests. We were unsuccessful at rearing *B pascuorum* from wild-caught queens, but found a small colony in the wild, which was raised to a relatively large size in the laboratory (where it was kept under identical conditions to colonies of the other two test species) before placing it in the field, alongside two colonies each of *B terrestris* and *B lapidarius*. A Plexiglas tunnel with a system of shutters, attached to the entrance of each colony, allowed the observer to control the movements of bees into and out of the nest. All workers were marked with individually numbered tags (*Opalith-Plättchen*, Christian Graze KG, Weinstadt-Endersbach, Germany) so they could be accurately identified. Hence the observer could monitor the flow of forager traffic, and record the time and weight of each individual forager when it departed, and returned to, the nest from each foraging bout. The foraging rate of individual workers was determined by dividing the difference in body mass (i e return minus outgoing weight) by the duration of the foraging trip [SPAETHE & WEIDENMÜLLER 2002; CHITTKA et al 2004].

Only trips longer than 10 minutes were considered foraging trips in an effort to exclude orientation and defecation flights [Capaldi & Dyer 1999; Spaethe & Weidenmüller 2002]. 2.6% (22/845) of all trips were excluded on this basis: 21 of the trips shorter than 10 minutes were likely defecation flights because bees returned lighter than when they left the nest. The foraging performance of all three species was compared with a Kruskal-Wallis test using the 1999 data. Colony data were pooled within species after confirming that there were no significant intercolony differences in foraging rate (B terrestris: Mann Whitney U = 314, p = 0.073; B lapidarius: U = 127.5, p = 0.93).

3 Results

3.1 Flower constancy

The degree to which bees were flower constant was highly significant for all bumblebee species on all pairs of flower species examined (Tab 1). There were consistent differences in the levels of flower constancy exhibited by the three bumblebee species tested, irrespective of the pairs of flower species compared. B terrestris was always the most flower constant species, followed by B lapidarius, with B pascuorum the least flower constant (Fig 1). B terrestris and B pascuorum were both extremely consistent in their respective levels of flower constancy across all flower species pairs tested (floral constancy index
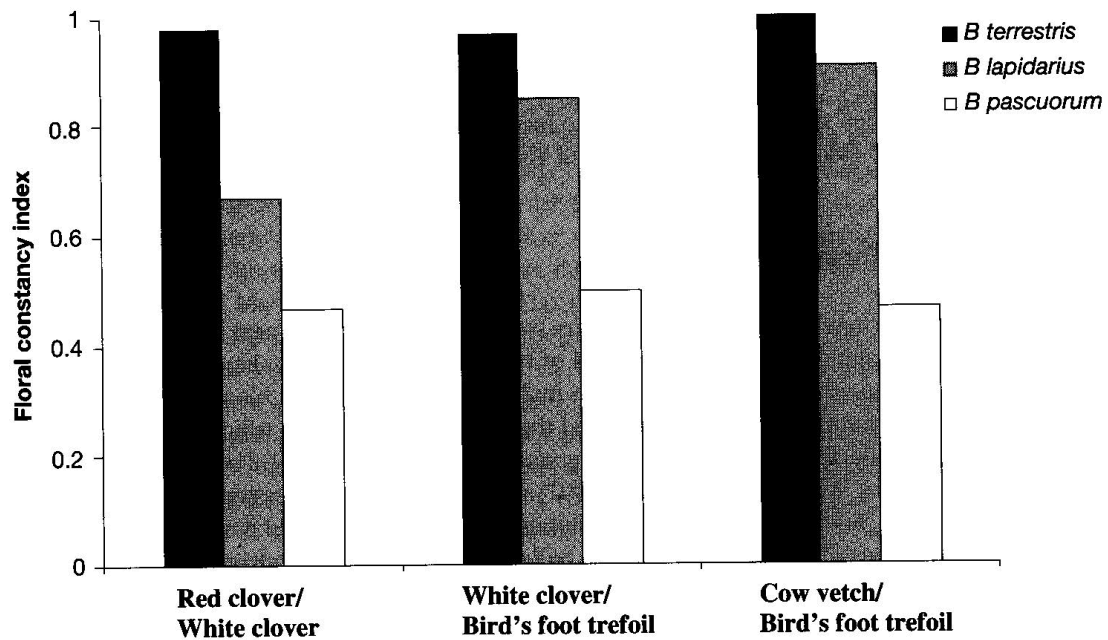
Fig 1: Consistent differences in flower constancy across three bumblebee species [Hymenoptera: Apidae: Bombus]. Bees were tested using the bee interview technique [Thomson 1981] using three pairs of plant species: red clover (Trifolium pratense), white clover (Trifolium repens), bird's foot trefoil (Lotus corniculatus) and cow vetch (Vicia cracca). Common plant names are given on the x-axis labels. Higher values of the flower constancy index indicate bees are more likely to move between flowers of the same species when foraging. Constancy indices were calculated according to Chittka et al [2001] and can vary from 1 (complete constancy), through 0 (random flights between species), to -1 (complete inconstancy).

ranges: 0.97 – 1 and 0.47 – 0.5), whilst *B lapidarius* showed appreciably more variation in constancy, dependent on which flower species combination they were offered (index range 0.67 – 0.91). *B terrestris* was significantly more flower constant than both *B lapidarius* (χ^2 = 19.3, p<0.0001) and *B pascuorum* (χ^2 = 69.9, p<0.0001), and *B lapidarius* was significantly more constant than *B pascuorum* (χ^2 = 27.4, p<0.0001).

3.2 Foraging performance

The more flower constant *B terrestris* foragers predominantly outperformed *B lapidarius* at collecting nectar (**Fig 2a**). In 1999, *B terrestris* colonies brought in nectar 1.3 – 2.5 times faster than *B lapidarius* colonies; and in 2001, three of the five *B terrestris* colonies tested collected nectar at measurably faster rates than all three *B lapidarius* colonies. From this one might conclude that a higher degree of floral constancy enhances foraging performance in the grassland habitat in which these bees were tested. However *B pascuorum*, consistently the least flower constant of the three bumblebee species tested, collected nectar 1.3 – 2.1 times faster than *B terrestris*, and 2.8 – 3.3 times faster than *B lapidarius* colonies in 1999. These interspecific differences in foraging performance in 1999 were highly significant (Kruskal-Wallis test, p = 0.001). Direct species comparisons show *B pascuorum* had a significantly higher foraging rate than either *B terrestris* (Mann Whitney U = 214, p = 0.005) or *B lapidarius* (U = 51, p < 0.005). However, although *B terrestris* collected nectar at a markedly higher rate than *B lapidarius* (means ($\pm$ 1 SE) = 41.7 $\pm$ 7.0 vs. 22.4 $\pm$ 2.5) this difference was not statistically significant (U = 899.5, p = 0.213). There were also interspecies differences in the duration of foraging flights (**Fig 2b**). The mean ($\pm$ 1 SE) duration of foraging flights for *B terrestris* and *B lapidarius* colonies in 1999 was similar, ranging from 67 ($\pm$12) to 97 ($\pm$10) minutes, however *B pascuorum* foraging bouts were much shorter: lasting an average of 45 ($\pm$ 5) minutes.

4 Discussion

The order of flower constancy found amongst these three bumblebee species in this study (*B terrestris* > *B lapidarius* > *B pascuorum*) is consistent with previous studies. CHITTKA et al [1997] studying the same bee species foraging in a meadow (near Berlin, Germany) found *B terrestris* remained constant in 85%, *B lapidarius* in 82%, and *B pascuorum* in 74% of observed transitions between plants. Likewise, in a study near Southampton, England, *B terrestris* foragers were observed to be more constant than *B pascuorum* [STOUT et al 1998]. As both these studies included flower species, and plant families, not used in this study, it is concluded that *B terrestris* is consistently more flower constant than both *B lapidarius* and *B pascuorum*. To what extent, then, is this consistent difference in foraging strategy mirrored in the foraging performance of these bee species? At first inspection, the more flower constant *B terrestris* foragers performed consistently better (both in 1999 and 2001) than the less constant *B lapidarius* (**Fig 2a**). However, flower constancy alone appears to be a relatively poor predictor of species foraging performance: indeed it is found that *B pascuorum*, the least flower constant of the three bee species tested, performed considerably better than *B terrestris*. This suggests that factors besides flower constancy may be decisive in determining foraging performance. Forager body mass might be one such factor, as larger bees appear to bring home more nectar per unit time [GOULSON et al 2002; SPAETHE & WEIDENMÜLLER 2002; CHITTKA et al 2004; INGS et al, in press].
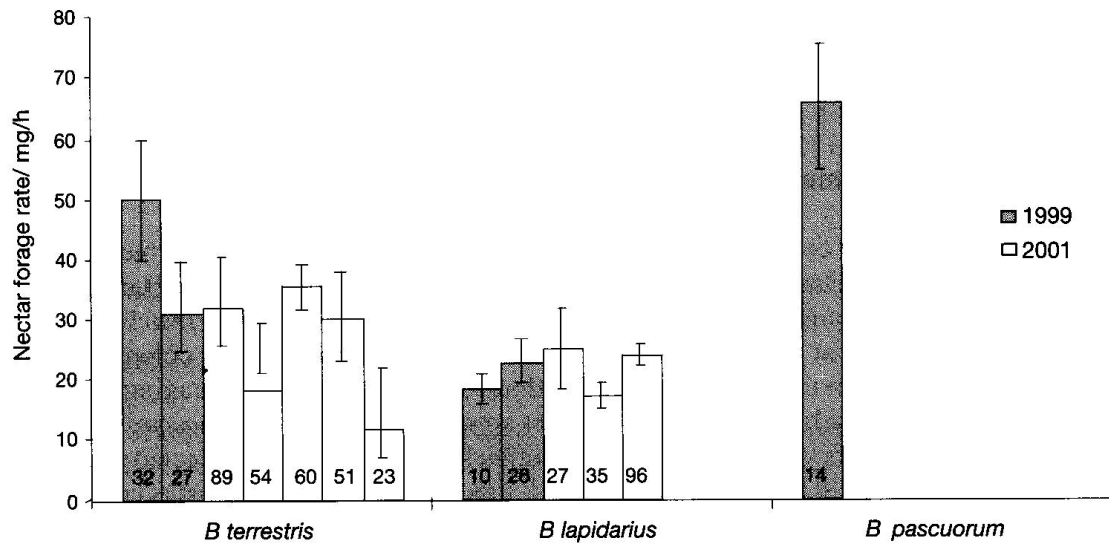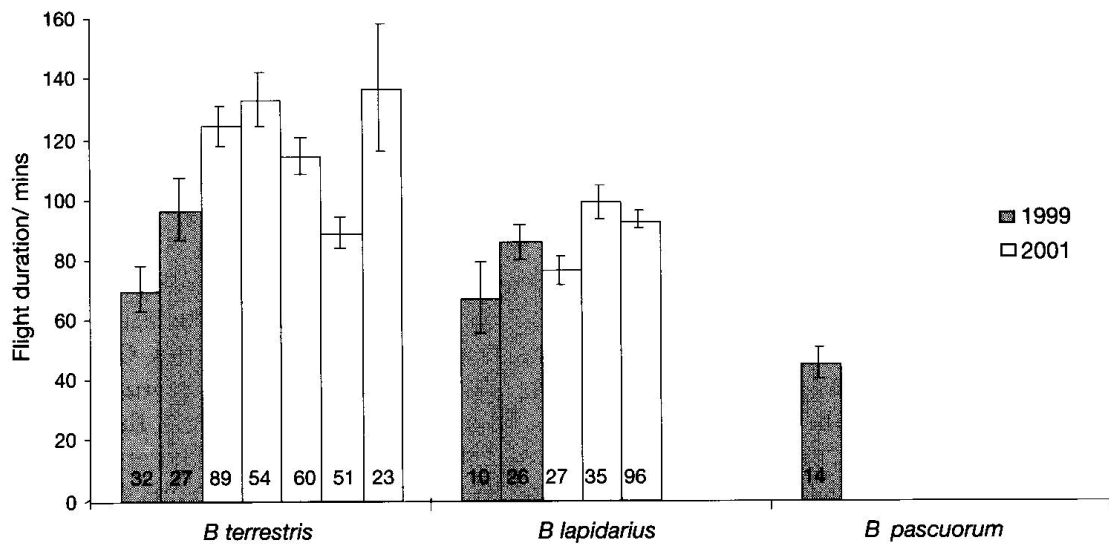
Figure 2a

Figure 2b

Fig 2: Interspecific comparison of foraging performance in three bumblebee species [Hymenoptera: Apidae: *Bombus*]: (a) nectar foraging rate, (b) foraging flight duration. The foraging rate of individual workers from each colony was determined by dividing the difference in body mass (i e: incoming minus outgoing weight) by the duration of their foraging trip. Colony foraging performance was evaluated by averaging each bee's performance across all foraging bouts, then averaging across the all bees tested. Column heights are colony mean (± 1 SE) foraging rates/ flight durations in each year tested, and the number of foragers evaluated per colony is indicated at the foot of each column. For two species (*B terrestris* and *B lapidarius*), the experiment was performed in two different years (1999 and 2001), while for *B pascuorum* it was only performed in 1999.

Tab 1: Statistical data for the flower constancy tests for three species of bumblebees [Hymenoptera: Apidae: *Bombus*] and three pairs of flower species.

	Bombus terrestris	*Bombus lapidarius*	*Bombus pascuorum*
Trifolium repens – Trifolium pratense	n = 90 $\chi^2 = 54$ p < 0.0001	n = 107 $\chi^2 = 25.1$ p < 0.0001	n = 93 $\chi^2 = 10.5$ p = 0.0012
Trifolium repens Lotus corniculatus	n = 80 $\chi^2 = 47.3$ p < 0.0001	n = 113 $\chi^2 = 48.8$ p < 0.0001	n = 80 $\chi^2 = 9.6$ p < 0.0019
Vicia cracca Lotus corniculatus	n = 95 $\chi^2 = 60.3$ p < 0.0001	n = 111 $\chi^2 = 55.8$ p < 0.0001	n = 95 $\chi^2 = 10.4$ p < 0.0013

In this study, the larger *B terrestris* foragers (mean body mass ± 1SD = 166 ± 43mg) appear to have a foraging advantage over the smaller *B lapidarius* workers (114 ± 35mg). But once again, body size cannot explain the observed superior foraging performance of *B pascuorum* (138 ± 18mg), which is much smaller than *B terrestris*. Tongue length and foraging range could be other important factors. *B pascuorum* has a longer proboscis than both *B terrestris* and *B lapidarius* [PRYS-JONES & CORBET 1991; GOULSON & DARVILL 2004], which allows them to collect nectar from flowers with long corolla tubes which might not be accessible to the other two species [BARROW & PICKARD 1984]. The foraging ranges of bumblebees have also been shown to vary, often considerably, across species, with *B terrestris* regularly the most long range forager [WALTHER-HELLWIG & FRANKL 2000; DARVILL et al 2004]. *B pascuorum* foragers appear to fly much shorter distances to foraging patches than other species, possibly even half the distance of *B terrestris* [DARVILL et al 2004]. The present data clearly show that *B pascuorum* foragers make distinctly shorter foraging flights than those from both other species, which is consistent with this species foraging closer to its nest. Whilst it would be simplistic to assume the higher foraging efficiency of *B pascuorum* is solely due to a reduction in flight distance to a foraging patch, it does raise the interesting question why the other species don't forage closer to home. In terms of foraging economics, the nearer of two equally rewarding forage patches should be favoured. But if flight speeds whilst travelling to foraging patches are high relative to time spent foraging within patches, then the reward differential need not be very large before the more distant patch becomes more profitable overall [CRESSWELL et al 2000].

DRAMSTAD [1996] suggested foraging further from the nest might act to minimise intracolony competition for limited local floral resources, leading to the prediction that species with larger colonies should forage more widely. In principle, the present data support this prediction because *B terrestris* and *B lapidarius* foragers (colony size 100–400 workers) spent much longer on each foraging trip than *B pascuorum* foragers (20–100 workers [ALFORD 1975]). However, whilst minimising intracolony competition might potentially explain why bees from larger colonies forage further from their nest at low nest densities, CHAPMAN et al [2003] demonstrated that workers from a very large number of colonies of both *B pascuorum* and *B terrestris* were found within foraging patches; suggesting that intercolony and interspecific competition will be more important determinants of foraging range and performance.

Hence, although flower constancy is an important factor in determining foraging performance, each bee species might effectively choose micro-habitats with a plant species composition that best suits its own particular foraging strategies [CHITTKA et al 1999; THOMSON & CHITTKA 2001]. It is concluded that using species comparisons to determine the adaptive significance of foraging strategies in the field is difficult because species will typically differ with respect to multiple foraging related traits. This is an important general lesson about the evolution of foraging behaviour: animals will typically be able to proceed along multiple alternative evolutionary pathways to optimize foraging behaviour, and constraints imposed by one foraging related trait might be easily compensated for by alterations of another trait.

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TURILAZZI J & WEST-EBERHARD M J (Eds): **Natural History and Evolution of Paper-Wasps.** – In Oxford Science Publications. – [XIV+400 pp, var fig + tab, 155 x 235 mm, hardcover]. – **Publ:** Oxford University Press, Oxford–NewYork–Tokyo; **ISBN:** 0-19-854947-4; **Pr:** Brit £ 35.--.

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The diversity of social behaviour among birds and primates is surpassed only by members of the Hymenoptera (bees, ants, wasps). This volume contains 18 contributions by various authors which were subjects of several symposia. They consist of in-depth survey of most major areas of research on paper-wasps (Polistini) which have played a keyrole in studies and theories of social evolution. Synthetic reviews and new unpublished data are combined with original ideas reaching far beyond this particular group to topics of general interest to evolutionary biologists and ethologists. Most major areas of research on the paper-wasps are covered – from syntheses of taxonomy and phylogeny, natural history (nesting behaviour, social organization, orientation, and natural enemies) to topics of general theoretical interest such as the evolution of cooperation, social parasitism, kin recognition, and the division of labor. This volume is still timely, even many years after it was published, and it will ever be a basis for further research on paper-wasps.