

Life History of Learning: Performance Curves of Honeybees in the Wild

Reuven Dukas

Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada

Correspondence

Reuven Dukas, Animal Behaviour Group,
Department of Psychology, Neuroscience &
Behaviour, McMaster University, 1280 Main
Street West, Hamilton, ON L8S 4K1, Canada.
E-mail: dukas@mcmaster.ca

Received: June 3, 2008

Initial acceptance: July 5, 2008

Final acceptance: July 9, 2008

(S.A. Foster)

doi: 10.1111/j.1439-0310.2008.01565.x

Abstract

Learning is probably a major contributor to fitness in most animals yet it has not been well integrated into life history research. To quantify the role of learning in shaping lifetime patterns of performance, we must measure learning in natural settings as well as in controlled experimental conditions. As a part of a long-term project measuring the relative contributions of learning, physiology, and effort to observed patterns of lifetime performance, I quantified the foraging success of worker honeybees in the wild. Bees exhibited a four-fold increase in the net rate of food delivery to the colony over their first 4 d as foragers. The major contributors to that pattern were decreases in departure weights and increases in arrival weights. Combined with previous research, this study suggests that learning is the major contributor to the observed increases in lifetime performance, whereas age-specific changes in physiology and effort have a significant though lesser role.

Introduction

The lifetime pattern of performance in a wide variety of animals including humans is remarkably similar. Initial performance is quite low, gradually increasing to a peak at about midlife, followed by a steady decrease into old age (Dukas 1998, 2008c; Helton 2007). The universal nature of the inverted-U pattern of lifetime performance suggests that common mechanisms are involved across species. Indeed the three dominant factors that can determine lifetime performance in animals that reach maximal body size at reproductive maturity are learning, physiology, and effort. Whereas life history research has addressed the issue of effort (Charlesworth & Leon 1976; Clutton-Brock 1984; Taylor 1991; Poizat et al. 1999) and there has been extensive research on physiological deterioration with age, or senescence (Rose 1991; Williams et al. 2006), learning has not been well integrated into the life history literature. Furthermore, little research effort has been devoted to the important question of how learning, physiology, and effort combine to generate lifetime patterns of performance (Dukas 2008c).

To understand the evolutionary and ecological forces that have shaped the universal pattern of lifetime performance, we must quantify individual performance in natural settings. Honeybees (*Apis mellifera*) possess a few features that make them an ideal model system for such research. First, forager honeybees mostly focus on the single task of food collection, which contributes to colony survival and reproduction. Because bees deliver food to the hive, their foraging performance can readily be quantified (Dukas & Visscher 1994). Second, because honeybees have been used extensively in agriculture and science, a variety of techniques are available to facilitate research with this species (von Frisch 1967). Finally, although exploited extensively by humans, honeybees have retained their wild state, as indicated by the success of feral honeybees in North America (Seeley 1985, 1996). It should be noted, however, that with few exceptions (e.g., Visscher & Seeley 1982), foraging research on honeybees (*A. mellifera*) has been conducted in agricultural and urban settings and relatively little is known about patterns of honeybee foraging in natural settings.

The quantification of the effects of learning, physiology, and effort on performance requires a long-term project that examines the relative age-specific contribution of each factor and possible interactions between them.

My earlier attempt at establishing a field site for such a project (Schippers et al. 2006) has failed owing to a high abundance of flowers at an urban setting, which prevented me from using artificial feeders necessary in many of the experiments. I recently succeeded at setting up a field site in a natural forest low in flower density, where honeybees readily visit artificial feeders throughout the season (Dukas 2008c). It was thus crucial to investigate the lifetime patterns of foraging performance of honeybees in these specific natural settings.

Learning can cause a gradual increase in foraging performance owing to its effects on a variety of factors including improved rate of nectar and pollen extraction from individual flowers, increased efficiency at packing pollen on foragers' hind legs, better movement among flowers and plants, increased focus on flowers and plants offering higher rate of rewards, and enhanced navigation skills and travel between flowers and the hive (Dukas & Visscher 1994; Cartar 2004; Ohashi et al. 2007; Raine & Chittka 2007; Dukas 2008b). I thus predicted that natural foragers would exhibit a large increase in foraging performance over the first few days of their activity.

Methods

The research was carried out at the Wildlife Research Station in Algonquin Provincial Park, ON, Canada in July–August 2007. Established in 1893, this large park (7 630 km²) is characterized by rolling hills covered with mature forest and numerous lakes and rivers. Flower density is low and limited to small flower patches in forest openings and lake shores. Occasional weighing of the hive indicated a loss of 0.75 kg in the first 2 wk of the experiment and an increase of 1.4 kg in the last 2 wk of the study. Weather information at the site was recorded every 10 min using a Davis Vantage Pro 2 station (Davis, Hayward, California). During the experiment (9 am–5 pm between July 2 and August 10), the average (\pm SE) daily temperature was $23.8 \pm 0.5^\circ\text{C}$ and the mean wind speed was 1.4 ± 0.15 m/s. Whereas daily temperatures and wind speeds fluctuated, there was no consistent pattern of either increase or decrease in weather parameters throughout that period.

For the experiment, I marked a total of 250 newly enclosed honeybees with individually numbered tags and added them into a two-frame observation hive containing about 2500 bees. I made three introductions of bees each about 10 d apart to have bees commencing foraging throughout the experiment. The first and last bee cohorts consisted of 100 bees each and the middle cohort had 50 bees. The segregation of bee introduction allowed me to partially randomize day effects owing to variation in weather, hive conditions and other external factors such as predator activity and competitors.

The observation hive was placed inside a research trailer and connected to the outdoors through a transparent Plexiglas tunnel. The trailer was equipped with an air conditioner so that the inside temperature did not exceed 25°C . On the first day of the experiment, a few marked bees that had started foraging earlier were removed. All other marked bees were monitored until the end of the experiment. A random sample of the marked bees was chosen for detailed recording of their lifetime performance. New randomly chosen bees that were about to initiate foraging replaced dead foragers throughout the experiment. The final sample size consisted of 26 bees that commenced foraging between day 1 and day 27 (median = day 17). When the selected marked bees left and returned to the hive, they were diverted into a side tunnel, caged, and weighed on an analytical balance with precision of 0.1 mg. The balance reported the bees' weights and time of day to the computer, and an observer recorded the bees' identities, travel directions, and whether they carried pollen.

I recorded bee activity from 10 am until 4 pm EST on a total of 34 successive days excluding a few rainy periods. At the end of the experiment, I edited the data set to include only trips longer than 5 min. I omitted all shorter trips assuming they were short orientation trips by bees about to initiate foraging (Ribbands 1953; Dukas & Visscher 1994; Capaldi et al. 2000). For each bee and day of foraging activity, I calculated the average trip duration in minutes, the average weight of forage in milligram (arrival weight minus departure weight), and the average food delivery rate, defined as the weight of forage over trip duration.

It was essential to compare the behavior of the same individual bees throughout their life to control for the possibility of a positive correlation between foraging performance and lifespan. Hence, following Dukas & Visscher (1994), the main statistical analyses involved repeated measures ANOVA on the data

set consisting of the first 7 d of the 12 bees that foraged for at least 7 d. Only three of these bees did not collect pollen, precluding separate analyses for each of the three forager types (pure nectar, pure pollen, and nectar + pollen). With few exceptions, bees belonged to a single forager type and pollen source throughout their foraging life. The difference between these forager categories was effectively added to the between-individual variation. To substantiate the results for the 12 bees, an additional analysis included the 21 bees that foraged for at least 4 d. Only five bees foraged for at least 12 d and preliminary analyses indicated that this sample size was insufficient for examining senescence. All statistical comparisons involved repeated measures ANOVA with Huynh–Feldt corrections in all cases in which sphericity assumptions were violated. In total, I conducted two detailed analyses including (1) 7 d for 12 bees and (2) 4 d for 21 bees (the 12 bees in the first analysis plus nine bees).

Results

Bees exhibited a large increase in food delivery rate over their first 4 d of foraging, followed by a decline through day 7 (repeated measures ANOVA, $F_{5,51} = 2.9$, $p < 0.05$ for the overall within subject effect representing a change over time within individuals, $F_{1,11} = 9.5$, $p < 0.01$ for the quadratic contrast, indicating that the within individual change fits a quadratic function, Fig. 1). Contributing to this pattern was an inverted U-shape pattern of the net weight of food delivery (repeated measures ANOVA, $F_{5,50} = 5.5$, $p < 0.01$ for the overall within subject

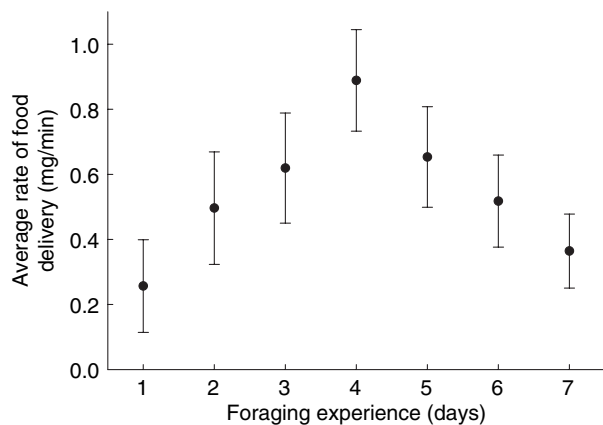


Fig. 1: The average (\pm SE) rate of food delivery as a function of foraging experience of forager honeybees. Data points are for the 12 foragers that were active for at least 7 d.

effect, $F_{1,11} = 14.5$, $p < 0.01$ for the quadratic contrast, Fig. 2a) and a continuous increase in foraging trip duration through day 7 (repeated measures ANOVA, $F_{3,36} = 4.2$, $p < 0.01$ for the within subject effect, Fig. 3). The pattern of net weight of food delivery was generated by a sharp decrease in departure weight, especially on the first 4 d (repeated

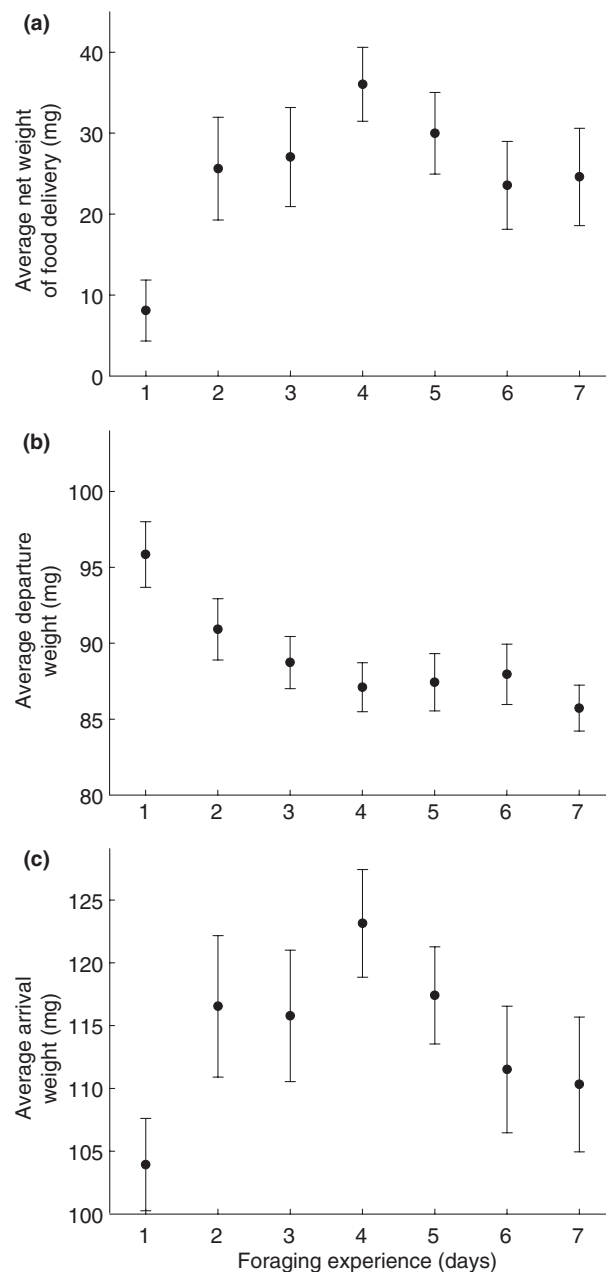


Fig. 2: The average (\pm SE) (a) net weight of food delivery, (b) departure weight, and (c) arrival weight as a function of foraging experience of forager honeybees. Note the different scales of the Y-axes. Data points are for the 12 foragers that were active for at least 7 d.

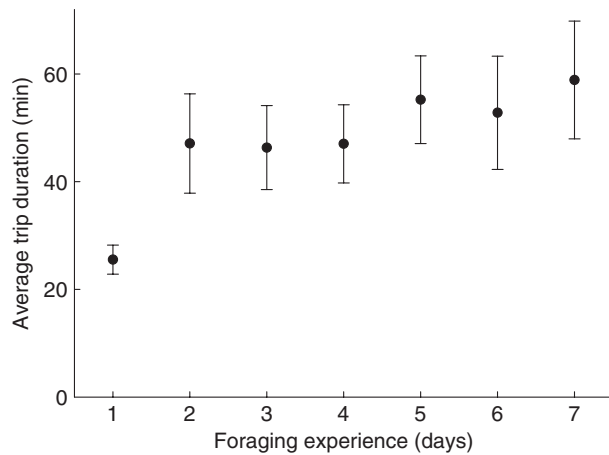


Fig. 3: The average (\pm SE) trip duration as a function of foraging experience of forager honeybees. Data points are for the 12 foragers that were active for at least 7 d.

measures ANOVA, $F_{4,48} = 11.8$, $p < 0.001$ for the within subject effect, Fig. 2b) and an inverted U-shape pattern of arrival weight (repeated measures ANOVA, $F_{6,66} = 3.6$, $p < 0.01$ for the overall within subject effect, $F_{1,11} = 11.2$, $p < 0.01$ for the quadratic contrast, Fig. 2c). Analyses of the 21 bees that foraged for at least 4 d revealed a pattern similar to the one detailed above, with the net rate of food delivery rising sharply over the first 4 d of foraging (repeated measures ANOVA, $F_{3,60} = 9.6$, $p < 0.001$ for the within subject effect, Fig. 4).

All the analyses revealed a large between-bee variation ($p < 0.001$). My direct observations of bees also indicated a wide range of pollen colors, trip durations, and food delivery rates (Fig. 5). For example,

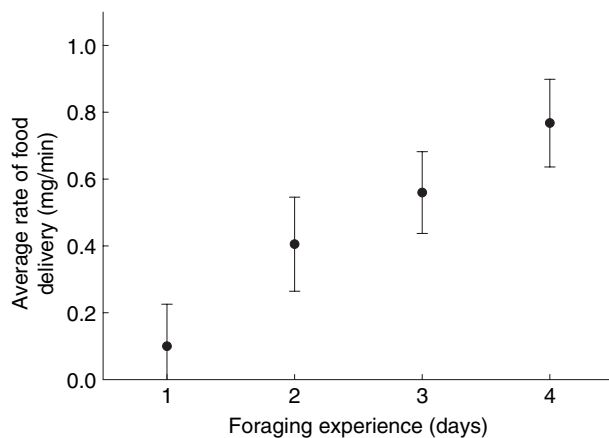


Fig. 4: The average (\pm SE) rate of food delivery as a function of foraging experience of forager honeybees. Data points are for the 21 foragers that were active for at least 4 d.

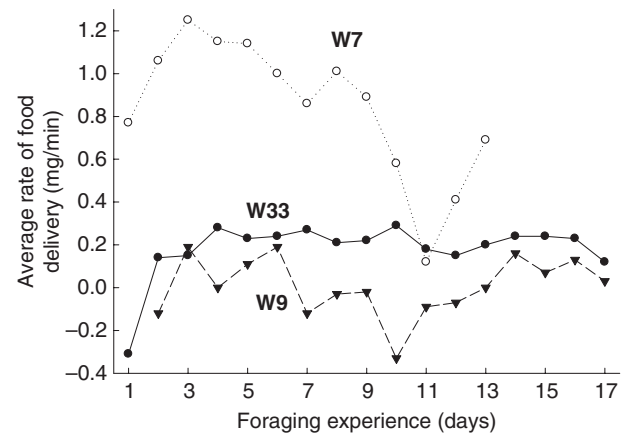


Fig. 5: The average daily rate of food delivery as a function of foraging experience in the three oldest forager honeybees in the study. (Data are missing for day 1 of W9).

the two longest lived foragers (17 d) exhibited sharply distinct foraging patterns. W9 apparently foraged on a nearby patch, collecting orange pollen loads and probably no nectar (mean net weight \pm SE of 0.07 ± 0.4 mg per trip), with a very short average trip duration of 11.7 ± 0.5 min. W33, on the contrary, collected an average net weight of 18.1 ± 1.9 mg nectar and brown pollen per trip, with a relatively long average trip duration of 90.1 ± 5.2 min.

Overall, I recorded the behavior of 26 bees. They commenced foraging at a median age of 19 d (range of 7–29 d) and their median foraging life span was 6 d (range of 1–17 d).

Discussion

The first ever detailed analyses of the performance of individual honeybee foragers in natural settings indicate a sharp, four-fold increase in the average food delivery rate over the first 4 d of foragers' activity (Figs 1 and 4). It is likely that learning is the major factor contributing to the dramatic increase in performance observed in the current study as well as previous research conducted in urban settings (Dukas & Visscher 1994; Schippers et al. 2006). Such learning has been associated with changes in the mushroom body of the bee brain with experience (Fahrbach & Dobrin in press). Although I cannot directly compare this study to previous ones, it is worth noting that an experiment at exactly the same location in July 2006 documented a flat performance curve over the life of foragers visiting a feeder providing unlimited volumes of 'nectar' (Dukas 2008c).

The major difference between the previous feeder experiment and the current natural study is that only the latter provides for numerous learning opportunities (see below).

Inspection of the individual components contributing to the gradual increase in performance with experience indicates a decrease of about 10% in departure weight over the first 4 d and an increase of about 20% in arrival weight over the same period (Fig. 2b, c). Intriguingly, no such patterns were observed with feeder foragers (Dukas 2008c). The most likely explanation for the initially heavy departure weight of natural foragers is that they leave with extra honey to sustain long periods of orientation and searching for flowers. The combination of low arrival weight and short trip duration (Fig. 3) on day 1 indeed suggests that bees took orientation trips and attempted to locate food sources based on either observing dances or scouting. Both tasks are known to be challenging in urban and rural settings (Seeley 1983) and were probably even more demanding in the natural surroundings of homogeneous forest in the current study.

The gradual improvement in performance over the first few days of foraging activity is similar to the pattern of expertise development extensively studied in humans (Ericsson et al. 2006; Helton 2007). Quantifying the multiple factors contributing to the increase in performance of forager bees in the wild, however, may be a daunting task. One can readily measure relatively simple aspects such as flower handling time (Lavery 1980) and rate of pollen collection (Raine & Chittka 2007). However, as expertise research in humans indicates (Ericsson et al. 2006) long-term experience allows for a variety of small improvements on subtle tasks, which may be difficult to quantify in bees under realistic field settings. Examples include improved patterns of movement between flowers and plants (Ohashi et al. 2007), selective visits to individual flowers and plants providing relatively higher rates of reward (Dukas 1987; Cartar 2004) and improved routes of travel between the hive and flowers.

Whereas learning may be the major contributor to the observed increase in performance with forager experience in natural settings, it would be premature to dismiss a role for effort and physiology. First, in my previous feeder experiment, bees exhibited a significant increase in the hourly number of foraging trips to the feeder over 8 d (Fig. 3 in Dukas 2008c). This could indicate effects of increased effort. Quantifying possible changes in effort by natural foragers is not as obvious. Nevertheless, in the present study,

I found no increase in the rate of foraging trips per day over 7 d ($p > 0.3$). The possible role of effort, defined as investment in current foraging that decreases future survival or foraging performance, will be critically examined in a future experiment.

As for physiological changes, levels of the major thorax-muscle enzymes crucial for flight reach a peak before bees commence foraging. However, proteomic analyses suggest that mature foragers have increased concentrations of troponin T 10A, a major regulatory muscle protein, which may contribute to some increase in flight and thus foraging performance (Schippers et al. 2006). This issue is currently under investigation.

A major unexpected result of the study was the decline in foraging performance from day 4 onward. Such pattern was not observed in two previous urban studies (Dukas & Visscher 1994; Schippers et al. 2006). Perhaps the major difference between the current natural study and the previous urban work is a rapid dynamic change in the availability of food sources in nature versus relative stability in urban gardens. Indeed Visscher & Seeley (1982) documented large daily changes in forager distributions among flower patches in a rural setting. It could be that older foragers tended to stay in their current patches despite decreases in food collection rates, whereas young recruits initiating foraging were directed through dances to richer patches. Given that foragers in natural settings have a brief expected life span of about 6 d (Dukas 2008a), it may be optimal for bees that have foraged for a few days to keep on doing what they already know best rather than switch to new sources. The possibility of an age-specific decrease in the inclination to switch to and learn about new food resources will be tested in a future experiment.

In total, data presented here and in recent papers from the same long-term project indicate that learning is the major contributor to the dramatic increase in performance of young forager honeybees in the wild. Future studies will critically follow up on the data suggesting smaller but significant effects of effort and physiological changes. I also intend to investigate the complex interactions between learning, physiology, and effort, which ultimately shape lifetime performance curves in all animals.

Acknowledgements

I thank Lauren Dukas for patiently watching and weighing the bees, Kevin Abbott, Lauren Dukas, Susan Foster, Deak Helton and anonymous referees

for helpful comments on the manuscript, Les Simoffy for providing the bees, staff of the Wildlife Research Station, Algonquin Park for help throughout the experiment, and Algonquin Provincial Park Service for permits to work in the park. This study was supported by the Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation, and Ontario Innovation Trust.

Literature Cited

- Capaldi, E. A., Smith, A. D., Osborne, J. L., Fahrbach, S. E., Farris, S. M., Reynolds, D. R., Edwards, A. S., Martin, A., Robinson, G. E., Poppy, G. M. & Riley, J. R. 2000: Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature* **403**, 537–540.
- Cartar, R. V. 2004: Resource-tracking by bumble bees: responses to plant-level differences in quality. *Ecology* **85**, 2764–2771.
- Charlesworth, B. & Leon, J. A. 1976: The relation of reproductive effort to age. *Am. Nat.* **110**, 449–459.
- Clutton-Brock, T. H. 1984: Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**, 212–229.
- Dukas, R. 1987: Foraging behavior of three bee species in a natural mimicry system: female flowers which mimic male flowers in *Echallium elaterium*. *Oecologia* **74**, 256–263.
- Dukas, R. 1998: Evolutionary ecology of learning. In: *Cognitive Ecology* (Dukas, R., ed.). Univ. of Chicago Press, Chicago, pp. 129–174.
- Dukas, R. 2008a: Bee senescence in the wild. *Insectes Soc.* **55**. In press. DOI: 10.1007/s00040-008-0995-4.
- Dukas, R. 2008b: Evolutionary biology of insect learning. *Annu. Rev. Entomol.* **53**, 145–160.
- Dukas, R. 2008c: Life history of learning – short and long term performance curves of honeybees in settings that minimize the role of learning. *Anim. Behav.* **75**, 1125–1130.
- Dukas, R. & Visscher, P. K. 1994: Lifetime learning by foraging honey bees. *Anim. Behav.* **48**, 1007–1012.
- Ericsson, K. A., Charness, N., Feltovich, P. J. & Hoffman, R. R. 2006: *The Cambridge Handbook of Expertise and Expert Performance*. Cambridge Univ. Press, Cambridge.
- Fahrbach, S. E. & Dobrin, S. (in press): The how and why of structural plasticity in the adult honey bee brain. In: *Cognitive Ecology II* (Dukas, R. & Ratcliffe, J., eds). Univ. of Chicago Press, Chicago, in press.
- von Frisch, K. 1967: *The Dance Language and Orientation of Bees*. Harvard Univ. Press, Cambridge.
- Helton, W. S. 2008: Expertise acquisition as sustained learning in humans and other animals: commonalities across species. *Anim. Cogn.* **11**, 99–107.
- Laverty, T. M. 1980: The flower visiting behaviour of bumble bees: floral complexity and learning. *Can. J. Zool.* **58**, 1324–1335.
- Ohashi, K., Thomson, J. D. & D'Souza, D. 2007: Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. *Behav. Ecol.* **18**, 1–11.
- Poizat, G., Roscchi, E. & Crivelli, A. J. 1999: Empirical evidence of a trade-off between reproductive effort and expectation of future reproduction in female three-spined sticklebacks. *Proc. R. Soc. B Biol. Sci.* **266**, 1543–1548.
- Raine, N. E. & Chittka, L. 2007: Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). *Naturwissenschaften* **94**, 459–464.
- Ribbands, C. R. 1953: *The Behavior and Social Life of Honeybees*. Bee Research Association, London.
- Rose, M. R. 1991: *Evolutionary Biology of Aging*. Oxford Univ. Press, New York.
- Schippers, M. -P., Dukas, R., Smith, R. W., Wang, J., Smolen, K. & McClelland, G. B. 2006: Lifetime performance in foraging honeybees: behaviour and physiology. *J. Exp. Biol.* **209**, 3828–3836.
- Seeley, T. D. 1983: Division of labor between scouts and recruits in honeybee foraging. *Behav. Ecol. Sociobiol.* **12**, 253–259.
- Seeley, T. D. 1985: *Honeybee Ecology*. Princeton Univ. Press, Princeton.
- Seeley, T. D. 1996: *The Wisdom of the Hive*. Harvard Univ. Press, Cambridge.
- Taylor, P. 1991: Optimal life histories with age dependent tradeoff curves. *J. Theor. Biol.* **148**, 33–48.
- Visscher, P. K. & Seeley, T. D. 1982: Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* **63**, 1790–1801.
- Williams, P. D., Day, T., Fletcher, Q. & Rowe, L. 2006: The shaping of senescence in the wild. *Trends Ecol. Evol.* **21**, 458–463.