



# Life history of learning: performance curves of honeybees in settings that minimize the role of learning

REUVEN DUKAS

Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University

(Received 23 January 2007; initial acceptance 2 July 2007;  
final acceptance 22 August 2007; published online 28 January 2008; MS. number: A10678R)

Life history research has mostly neglected learning even though it is probably a major contributor to lifetime performance in a variety of animals. As part of an ongoing project evaluating the relative contribution of learning, physiology and effort to performance throughout the life span, I quantified lifetime performance of honeybees, *Apis mellifera*, foraging at a feeder. Unlike natural foraging, where bees may learn a variety of features that contribute to increased performance, food collection from a feeder requires little learning. Foragers showed no long-term change in the rate of food delivery, a pattern that was different from published data indicating a long-term gradual increase in foraging performance in honeybees under natural settings. The discrepancy between bees' lifetime performance in the artificial versus natural settings suggests that learning is the key component contributing to the increase in performance throughout a forager's life as observed in the field.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** *Apis mellifera*; effort; honeybees; learning; life history; physiology

Life history research has traditionally focused on the physical parameters of growth, survival and reproduction (Stearns 1992; Roff 2002). Whereas learning has been appreciated as a contributor to performance, it has not been well integrated within life history theory. In animals that reach terminal growth before sexual maturity, the three major contributors to reproductive success are effort, physiology and learning. Of these three factors, reproductive effort has been examined most extensively. Reproductive effort may be defined as investment in current reproduction that decreases future survival or reproduction. It is commonly assumed that effort should increase with age, although theoretical analyses emphasize that effort may also decrease with age under some conditions (Fagen 1972; Charlesworth & Leon 1976; Roff 2002). Taylor (1991) specifically mentioned effects of experience as a case in which changes in effort with age cannot readily be predicted. Empirical data are mixed, with some studies suggesting increased effort with age (Pugesek 1981; Clutton-Brock 1984; Candolin 1998; Poizat et al. 1999) and others documenting no change (Reid 1988).

Correspondence: R. Dukas, Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada (email: [dukas@mcmaster.ca](mailto:dukas@mcmaster.ca)).

Major physiological attributes such as muscle power and endurance may increase early in life. From sexual maturity onwards, physiology is subjected to senescence, typically described as an age-specific decrease in body condition associated with decreased fertility and survival rates (Rose 1991; Kirkwood & Austad 2000). As with reproductive effort, however, theory and data indicate that patterns of senescence may diverge from the predicted classical pattern (Abrams 1993; Williams et al. 2006; Reznick et al. 2004). We currently know little about lifetime patterns of physiology and their relation to performance in nonhuman animals.

To some extent, learning is similar to physical growth. Thus, in animals that rely on learning, investment in learning may be highest before sexual maturity. Unlike physical growth, however, some tasks are best learned by performing them, a feature referred to as 'learning by doing' in the economic literature (Arrow 1962). Hence learning may continue to increase performance throughout life as long as one's learning ability is not hindered by senescence. A few long-term studies on birds inferred a likely role for learning in the well-documented gradual increase in reproductive success throughout life (Nol & Smith 1987; Wooler et al. 1990; Black & Owen 1995; Rattiste 2004). Long-term effects of learning on performance have

also been extensively studied in humans (Stephan & Levin 1992; Ericsson et al. 2006). Overall, however, we know little about the relative contribution of learning to performance during the life span.

To examine the relative importance of learning within the life history framework, one has to quantify its contribution to performance throughout the life span. However, neither the avian nor the mammalian systems cited above allow the proper experimentation necessary for evaluating the relative contribution of learning and other key factors to performance throughout the life span. For a few reasons, honeybees, *Apis mellifera*, are ideal models for research on the life history of learning. First, honeybees show excellent learning abilities and their waggle dance is one of the most sophisticated means of social learning in nonhuman species (von Frisch 1967; Seeley 1996; Gould & Gould 1988; Menzel & Giurfa 2001). Second, forager bees live only for several days, a time frame that allows one to acquire lifetime records for many individuals (Dukas & Visscher 1994). Third, although honeybees have been extensively used by humans for pollination and honey production, they have remained relatively close to their wild state, as indicated by the success of feral honeybee colonies throughout the world (Seeley 1996). Fourth, forager honeybees focus on the single task of food collection, which translates into fitness through its effect on colony survival and reproduction. Because the foragers themselves do not reproduce, their performance can readily be evaluated through quantifying their rate of food collection. That is, instead of measuring reproductive effort, one can measure a relevant surrogate, foraging effort, defined as investment in current foraging that decreases future survival or foraging performance. Finally, owing to the extensive use of honeybees in research, one can use a variety of established techniques for examining all aspects of honeybee life history.

My earlier work on honeybees indicated that the lifetime performance curve of foragers is remarkably similar to performance curves in other animals. That is, food delivery rates of novice foragers are very low, gradually increase, peak after several days and then drop in bees reaching old age (Dukas & Visscher 1994). A similar performance curve for forager honeybees was recently replicated in my laboratory (Schippers et al. 2006). Such inverted U-shape patterns of lifetime performance have been documented for reproductive success in birds (Wooler et al. 1990) and mammals (Clutton-Brock et al. 1982) as well as for scientific and athletic performance in humans (Stephan & Levin 1992; Starkes & Ericsson 2003).

In an experiment conducted within a long-term project examining the effects of effort, physiology and learning on lifetime performance, I aimed to evaluate the pattern of a foragers' lifetime performance when the effects of learning were minimized. That is, I aimed to assess the relative contribution of physiology and effort to lifetime performance. To this end, I allowed young honeybee foragers to visit a feeder containing sugar water and I monitored these bees until they died. Unlike the challenging foraging tasks encountered by bees in natural settings, there is little to learn about food collection from

the feeder. I thus predicted that bees would show short-term improvements in food-delivery rates during the first few trips to the feeder but no long-term increase in food-delivery rates over successive days of experience.

## METHODS

The research was carried out at the Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada in July 2006. The region 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. Weather information at the site was recorded every 10 min using a Davis Vantage Pro 2 station. During the experiment (0900 to 1700 hours between July 12 and July 28), the average  $\pm$  SE daily temperature was  $24.3 \pm 0.14^\circ\text{C}$  and the mean  $\pm$  SE wind speed was  $1.4 \pm 0.2$  m/s. There was no pattern of either an increase or decrease in weather parameters throughout that period.

Before the start of the experiment, I marked approximately 900 newly eclosed honeybees with individually numbered tags and added them into a two-frame observation hive containing about 2000 bees. I made two introductions of bees 2 weeks apart to have bees commencing foraging throughout the experiment. This allowed me to partially randomize day effects due to variation in weather, hive conditions and other external factors such as predator activity.

The observation hive was placed inside a research trailer and was connected to the outdoors through a Plexiglas tunnel. The trailer was equipped with an air conditioner so that the inside temperature did not exceed  $25^\circ\text{C}$ . Four days before the start of the experiment, an assistant began daily monitoring of all the active marked bees. The assistant, who had a few years of experience monitoring bee activity, classified each marked bee into one of the three categories of pollen foragers, nectar foragers and nonforagers. The monitoring of all marked bees continued until the end of the experiment. At the same time, I trained bees to visit a feeder located 400 m from the hive, which provided unlimited quantities of 2.5 M sugar water scented with anis. I removed excess bees visiting the feeder when necessary to avoid interference due to crowding.

The experiment commenced when the first marked bee started visiting the feeder and ended 18 days afterwards. Overall, I recorded the behaviour of 32 marked bees but had insufficient data for four bees with brief life spans. I thus had at least 1 day of data for 28 bees, at least 3 days for 26 bees, and at least 8 days for nine bees. The median foraging span of the 32 bees was 4.5 days but almost half of the bees were still alive at the end of the experiment. Bees initiated visiting the feeder on most days between day 1 and day 16, allowing partial randomization of day effects. When I observed a new marked bee at the feeder, I checked the extensive data set to verify that she was a new forager. Only new foragers were allowed to continue visiting the feeder. With three exceptions of bees initiating foraging late in the day, I closely monitored new foragers from their very first foraging trip to the feeder.

The observations included monitoring of the net weight of sugar water delivered by bees and their trip durations. Each day, on a sample of foraging trips, marked feeder bees departing from and arriving at the hive were diverted into a side tunnel, caged and weighed on an analytical balance with precision of 0.1 mg. The balance reported the bee weight to a computer, and an assistant added the bee identity and travel direction. In addition, the assistant reported to me via a two-way radio the identity of each departing and arriving marked feeder bee. I recorded this information, as well as the arrivals and departures of the bees at the feeder, into a hand-held computer. Overall, I attempted to have a full record of the first few foraging trips by each new forager, at least three daily departure weights and six daily arrival weights for each bee and as much duration data as possible. The variation in sample sizes was based on preliminary data indicating that, within a given day, there was little variation in departure weight, moderate variation in arrival weight and large variation in duration data. I also attempted to record all feeder trips by all marked bees during the periods of observation to allow calculation of the number of feeder visits per hour by each bee (visit rate).

For the main statistical analyses examining effects of experience over days, I calculated for each bee and day of foraging experience the food-delivery rate, defined as the average weight of sugar water over average trip duration, and the hourly visit rate to the feeder, which served as a measure of effort. I also examined each of the components determining food-delivery rate, which were departure weight, arrival weight, flight duration from the hive to the feeder, feeding duration and flight duration from the feeder to the hive. All statistical comparisons involved repeated measures ANOVA with Huynh–Feldt corrections in the two cases in which sphericity assumptions were violated.

It was essential to compare the behaviour of the same individual bees throughout their life to control for the possibility of a positive correlation between foraging performance and life span. Hence, the main statistical analyses involved repeated measures ANOVA on the data set of food-delivery rates over the first 8 days of foraging experience by the nine bees that foraged for at least 8 days. I used 8 rather than 7 days as in my previous studies (Dukas & Visscher 1994; Schippers et al. 2006) because no bee died after 7 days of foraging. To evaluate the effect of experience early in a foragers' life, I also analysed the performance of the 26 bees that foraged for at least 3 days. Because sample sizes were insufficient for analyses beyond 10 days of foraging experience, I could not critically evaluate my earlier observations suggesting senescence (Dukas & Visscher 1994).

Finally, I also examined performance over the first few visits to the feeder by each new bee. Because a new bee was always spotted at the feeder, I did not know the first flight duration from the hive to the feeder. Thus I also did not know the overall duration of the first trip. Hence I analysed the above parameters for the second through sixth initial trips. The analyses for feeding duration and flight duration from the feeder to the hive included trips one through six. Limited sample sizes allowed me to

include in the weight analyses only the initial second to fourth departure weights and the first three arrival weights. Because of the variation in sample sizes and trips included, I analysed only separate weight and duration data and did not calculate the net rate of food delivery per trip. Again, statistical analyses involved repeated measures ANOVAs with sample sizes slightly varying between tests because of missing data.

## RESULTS

### Long-term Experience

Bees' rate of food delivery was not significantly associated with experience (repeated measures ANOVA:  $F_{7,56} = 0.8$ ,  $P = 0.5$ ; Fig. 1). Neither the departure weight ( $P = 0.09$ ) nor the arrival weight ( $P = 0.7$ ) showed significant change with experience. Whereas neither feeding duration ( $P = 0.18$ ) nor flight duration from the feeder to the hive ( $P = 0.7$ ) showed significant change with experience, flight duration from the hive to the feeder significantly decreased with experience. Bees with 8 days of foraging experience flew to the feeder almost 20% faster than first-day foragers ( $F_{7,56} = 5$ ,  $P < 0.001$ ; Fig. 2). The overall rate of food delivery was unaffected by this decrease, however, because of the nonsignificant increase in feeding duration and flight duration from the feeder to the hive (Fig. 2). Similar results were obtained with the data including the 26 bees that foraged for at least 3 days. That is, with the 26 bees, there was no significant increase in the rate of food delivery over the first 3 days of foraging experience ( $F_{2,48} = 0.3$ ,  $P = 0.7$ ) and all the components of foraging performance except flight duration from the hive to the feeder showed no change with experience. The mean  $\pm$  SE flight duration from the hive to the feeder decreased by 18%, from  $77.1 \pm 2.2$  s on the first day to  $63.3 \pm 1.6$  s on the third day ( $F_{2,49} = 17.9$ ,  $P < 0.001$ ).

The hourly visit rate to the feeder was highly variable both within and between bees, but there was a significant trend of increased rates of visits over the 8 days ( $F_{6,47} = 2.5$ ,  $P < 0.05$ ; Fig. 3). On average, the bees visited

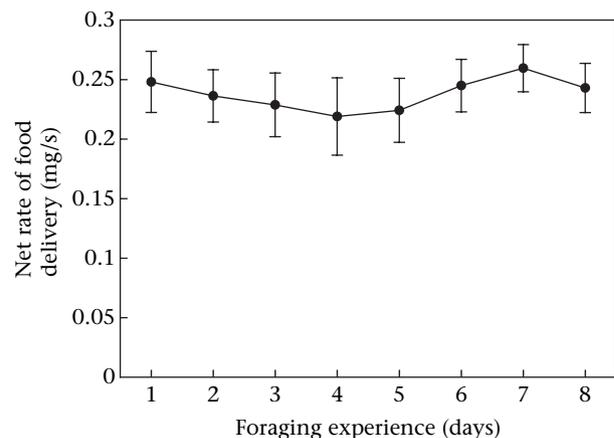
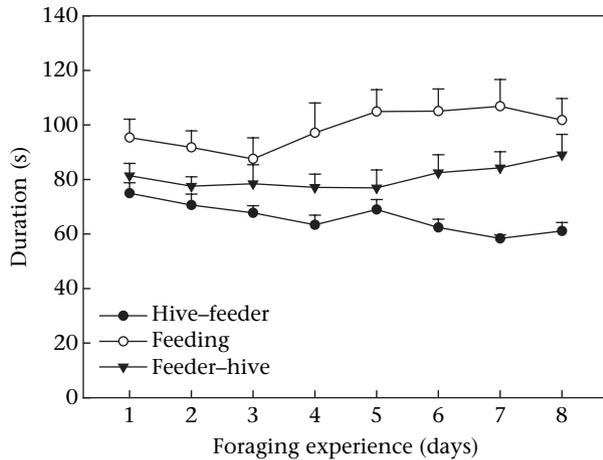


Figure 1. Mean  $\pm$  SE rate of food delivery as a function of experience of honeybees foraging at a feeder providing 2.5 M sugar water. Means are based on individual averages of the nine bees that were active on each of the 8 days.

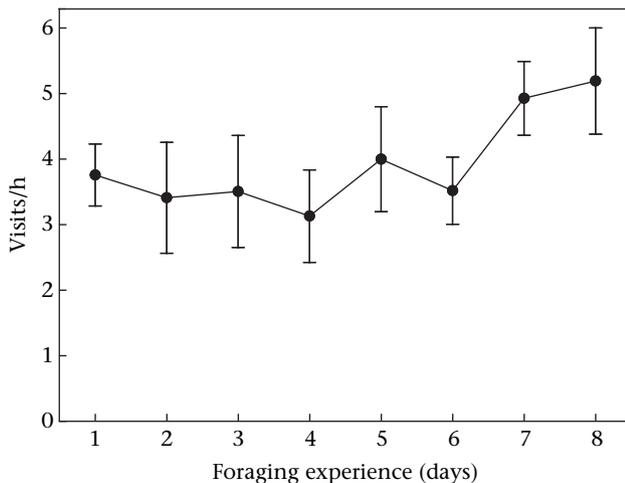


**Figure 2.** Mean  $\pm$  SE durations of three foraging trip components as a function of long-term experience ( $N = 9$  bees).

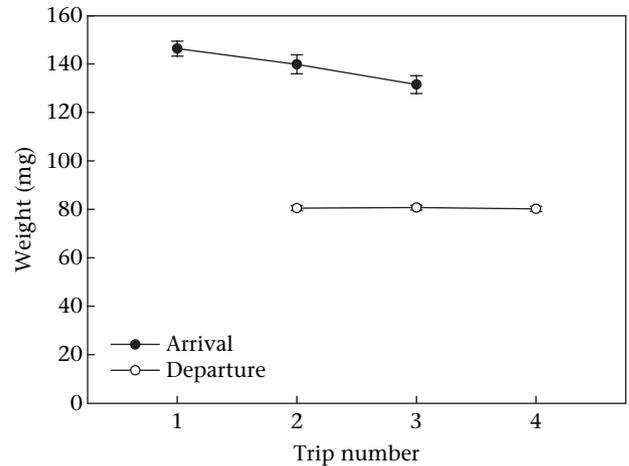
the feeder  $3.9 \pm 0.25$  times per hour and delivered  $58.5 \pm 2.1$  mg sugar water per trip. Assuming 10 h of daily activity, each bee flew an average distance of 31.2 km and delivered 2281.5 mg sugar water per day, which is approximately 28 times a bee's weight.

### Short-term Experience

Experience had strong effects on bee performance over the first few feeder visits. First, bees showed an unexpected, clear and consistent pattern of reducing the weight of food delivered per trip ( $F_{2,48} = 13.7$ ,  $P < 0.001$ ; Fig. 4), but showed no change in departure weights ( $F_{2,41} = 1.9$ ,  $P = 0.16$ ; Fig. 4). Second, the overall trip duration declined with short-term experience ( $F_{4,50} = 2.9$ ,  $P < 0.05$ ). This resulted from shorter flight durations to and from the feeder ( $F_{4,57} = 4.7$ ,  $P < 0.005$  and  $F_{5,86} = 6.5$ ,  $P < 0.001$ , respectively; Fig. 5) but not from a change in Feeding duration, which showed only a nonsignificant reduction ( $F_{5,80} = 1.9$ ,  $P = 0.1$ ; Fig. 5).



**Figure 3.** Mean  $\pm$  SE visit rates to the feeder as a function of long-term experience ( $N = 9$  bees).

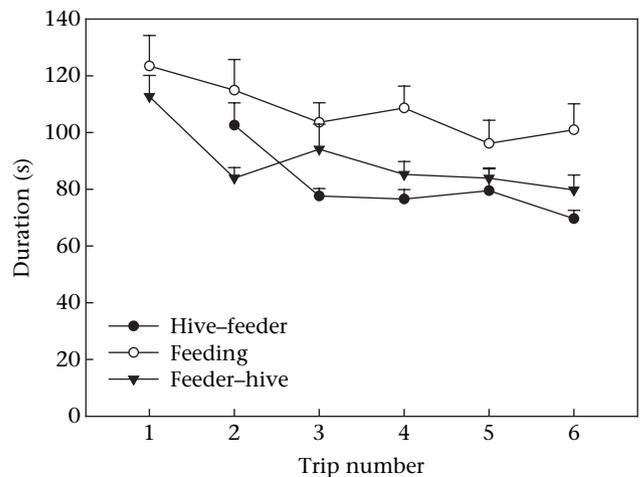


**Figure 4.** Mean  $\pm$  SE departure and arrival weights of bees on their first recorded trips ( $N = 26$  bees).

## DISCUSSION

### Long-term Experience

The most important result of this study is that, under settings requiring little learning, bees' foraging performance did not increase with foraging experience (Fig. 1). This is in sharp contrast to field data, which indicated a large, long-term improvement in foraging performance with experience (Figure 2 in Dukas & Visscher 1994; Figure 1 in Schippers et al. 2006). The simplest way of explaining the difference between the current feeder data and the previous field data is that learning is the major contributor to the observed increased performance in the field. By experimentally eliminating the need for long-term learning in the feeder experiment, I abolished the long-term increase in performance observed in the field. This result suggests that physiology and effort may be only relatively minor contributors to the observed increase in performance in the field. The effects of physiology and effort, however, may not be negligible and will be closely examined in further experiments (see below).



**Figure 5.** Mean  $\pm$  SE trip-leg durations over bees' first six visits to the feeder ( $N = 26$  bees).

There were two long-term patterns that I did not predict and cannot currently explain. First, the average flight duration from the hive to the feeder significantly decreased over 8 days of experience (Fig. 2). It is very unlikely that changes in either physiology or effort could explain this pattern because there was not a parallel change in either flight duration from the feeder to the hive (Fig. 2) or the weight of food delivered. Second, visit rates to the feeder showed a slight but significant increase over 8 days of experience (Fig. 3). This result might indicate increased effort late in life. Further experiments may help clarify these issues.

### Short-term Experience

As expected, bees improved their foraging performance over the first few visits to the feeder. Because these changes typically occurred within less than 2 h, it is unlikely that they were caused by changes in either physiology or effort. Intriguingly, bees reduced the weight of sugar water carried per trip (Fig. 4). This most likely reflected learning to adjust to the unusually high food quality. The nectar concentration was about 85% (weight/weight) sugar compared to typical natural sugar concentrations in wildflowers of about 30%. And it took a bee only about 1.5 min to collect the nectar compared to over 30 min in natural settings. Perhaps bees initially overfilled their honey crop, which decreased their flight performance. Bees then may have learned to take slightly smaller volumes of the rich sugar water. Note that the short-term improvement in flight performance (Fig. 5) had a negligible effect on the long-term flight performance (Fig. 2) because the improvement occurred within a few trips constituting only a small fraction of the trips on the first day.

The short-term reduction in flight parameters most likely reflected spatial learning. Indeed, the steepest reductions in flight durations occurred between the first and the second flights recorded for both the hive-to-feeder and feeder-to-hive legs (Fig. 5). It is well known that bees visiting a new food source spend time learning its surroundings (von Frisch 1967; Lehrer 1993). Unlike the decrease in flight durations, there was no significant change in feeding duration (Fig. 5), reflecting the ease of sipping sugar water from the feeder.

### Contribution of Learning to Lifetime Performance

In an experiment eliminating much of the need to learn about foraging, I observed no long-term increase in foraging performance. This result agrees with the proposition that learning is the major contributor to the large, long-term increase in foraging performance observed in honeybees in the field (Dukas & Visscher 1994; Schippers et al. 2006). Unlike learning, which requires experience, bees could be well prepared physiologically before initiating foraging. That is, the hormonal changes underlying the behavioural transition from hive bee to forager (Sullivan et al. 2000) could also cause changes in flight muscle physiology. Indeed, physiological measurements

replicated over 3 years indicate that there is a large increase in the concentration of key enzymes determining flight muscle output in hive bees before they initiate foraging but little change over foragers' life span (Schippers et al. 2006, unpublished data). A similar phenomenon of adaptive physiological preparations prior to a major life event is well known from birds, in which changes in daylength trigger the neuroendocrine system to initiate fattening and increased flight muscle size and performance in preparation for migration (e.g. Pant & Chandolasaklani 1993; Deviche 1995).

Proteomic analyses, however, suggest that changes in protein composition of flight muscles in mature foragers could contribute to their improved foraging performance. Most notably, compared to hive bees, mature foragers have much higher concentrations of troponin T 10A, a key regulatory muscle protein (Schippers et al. 2006). Variation in troponin T isoforms has been linked to flight performance in dragonflies (Marden et al. 1999) and might have similar effects in honeybees. This possibility is currently under investigation.

As with physiology, the data do not indicate a dramatic increase in effort throughout a forager's life span. Hence the published field data indicating a gradual increase in foraging performance over the first 7 days of a forager's life (Dukas & Visscher 1994; Schippers et al. 2006) probably cannot be attributed to increased effort. Still, there may be some age-related increase in effort, suggested by the increase in visit rate over 8 days (Fig. 3) and perhaps later in life. This issue will be critically examined in further experiments.

One can readily imagine how learning would cause a gradual increase in foraging performance over several days under field conditions, which are typically very challenging. Honeybees can improve at navigation, gradually learning to take faster, more direct routes between the hive and the flowers. They may learn to bias their visits to locations, plants or flower morphs that offer higher reward rates (Dukas 1987; Cartar 2004). Bees may improve at manipulating flowers, increasing the rate of reward collection (Free 1970; Laverty 1980). And, finally, foragers may become more efficient at moving between flowers and plants (Ohashi et al. 2007). In other words, the bees may gradually acquire expertise as foragers in a process similar to the development of expertise in humans (Ericsson et al. 2006). This topic is currently under investigation.

In summary, honeybees foraging at a feeder providing unlimited amounts of food and little need to learn did not show the typical gradual increase in performance observed under field settings. These results suggest that learning is the primary factor responsible for the observed increase in foraging performance over foragers' lives. Whereas this and a recent study (Schippers et al. 2006) suggest that effort and physiology, respectively, may also contribute significantly to increased performance, their relative contribution is probably smaller than that of learning.

### Acknowledgments

I thank Lauren Taylor for superb assistance, helpful comments on the manuscript and sustaining a few stings,

Les Simonffy for providing the bees, two anonymous referees for thoughtful comments, the 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.

## References

- Abrams, P. A. 1993. Does increased mortality favor the evolution of more rapid senescence? *Evolution*, **47**, 877–887.
- Arrow, K. J. 1962. The economic implication of learning by doing. *Review of Economic Studies*, **29**, 155–173.
- Black, J. M. & Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *Journal of Animal Ecology*, **64**, 234–244.
- Candolin, U. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proceedings of the Royal Society of London, Series B*, **265**, 1171–1175.
- 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. *American Naturalist*, **110**, 449–459.
- Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Deviche, P. 1995. Androgen regulation of avian premigratory hyperphagia and fattening: from eco-physiology to neuroendocrinology. *American Zoologist*, **35**, 234–245.
- Dukas, R. 1987. Foraging behavior of three bee species in a natural mimicry system: female flowers which mimic male flowers in *Echium elaterium*. *Oecologia*, **74**, 256–263.
- Dukas, R. & Visscher, P. K. 1994. Lifetime learning by foraging honey bees. *Animal Behaviour*, **48**, 1007–1012.
- Ericsson, K. A., Charness, N., Feltovich, P. J. & Hoffman, R. R. 2006. *The Cambridge Handbook of Expertise and Expert Performance*. Cambridge: Cambridge University Press.
- Fagen, R. M. 1972. An optimal life history strategy in which reproductive effort decreases with age. *American Naturalist*, **106**, 258–261.
- Free, J. B. 1970. *Insect Pollination of Crops*. London: Academic Press.
- von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Cambridge: Massachusetts Harvard University Press.
- Gould, J. L. & Gould, C. G. 1988. *The Honey Bee*. New York: Scientific American.
- Kirkwood, T. B. L. & Austad, S. N. 2000. Why do we age? *Nature*, **408**, 233–238.
- Laverty, T. M. 1980. The flower visiting behaviour of bumble bees: floral complexity and learning. *Canadian Journal of Zoology*, **58**, 1324–1335.
- Lehrer, M. 1993. Why do bees turn back and look? *Journal of Comparative Physiology A Neuroethology Sensory Neural and Behavioral Physiology*, **172**, 549–563.
- Marden, J. H., Fitzhugh, G. H., Wolf, M. R., Arnold, K. D. & Rowan, B. 1999. Alternative splicing, muscle calcium sensitivity, and the modulation of dragonfly flight performance. *Proceedings of the National Academy of Sciences, U.S.A.*, **96**, 15304–15309.
- Menzel, R. & Giurfa, M. 2001. Cognitive architecture of a mini brain: the honeybee. *Trends in Cognitive Sciences*, **5**, 62–71.
- Nol, E. & Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology*, **56**, 301–313.
- Ohashi, K., Thomson, J. D. & D'Souza, D. 2007. Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. *Behavioral Ecology*, **18**, 1–11.
- Pant, K. & Chandolasaklani, A. 1993. A role for thyroid hormones in the development of migratory disposition in redheaded bunting, *Emberiza bruniceps*. *Journal of Comparative Physiology B, Biochemical Systemic and Environmental Physiology*, **163**, 389–394.
- Poizat, G., Rosecchi, E. & Crivelli, A. J. 1999. Empirical evidence of a trade-off between reproductive effort and expectation of future reproduction in female three-spined sticklebacks. *Proceedings of the Royal Society of London, Series B*, **266**, 1543–1548.
- Pugesek, B. H. 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). *Science*, **212**, 822–823.
- Rattiste, K. 2004. Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proceedings of the Royal Society of London, Series B*, **271**, 2059–2064.
- Reid, W. V. 1988. Age-specific patterns of reproduction in the glaucous-winged gull: increased effort with age? *Ecology*, **69**, 1454–1465.
- Reznick, D. N., Bryant, M. J., Roff, D., Ghalambor, C. K. & Ghalambor, D. E. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature*, **431**, 1095–1099.
- Roff, D. 2002. *Life History Evolution*. Sunderland, Massachusetts: Sinauer.
- Rose, M. R. 1991. *Evolutionary Biology of Aging*. New York: Oxford University Press.
- Schippers, M.-P., Dukas, R., Smith, R. W., Wang, J., Smolen, K. & McClelland, G. B. 2006. Lifetime performance in foraging honeybees: behaviour and physiology. *Journal of Experimental Biology*, **209**, 3828–3836.
- Seeley, T. D. 1996. *The Wisdom of the Hive*. Cambridge, Massachusetts: Harvard University Press.
- Starkes, J. L. & Ericsson, K. A. (Eds) 2003. *Expert Performance in Sports: Advances in Research on Sports Expertise*. Champaign, Illinois: Human Kinetics.
- Stearns, S. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stephan, P. E. & Levin, S. G. 1992. *Striking the Mother Lode in Science: the Importance of Age, Place, and Time*. New York: Oxford University Press.
- Sullivan, J. P., Jassim, O., Fahrback, S. E. & Robinson, G. E. 2000. Juvenile hormone paces behavioral development in the adult worker honey bee. *Hormones and Behavior*, **37**, 1–14.
- Taylor, P. 1991. Optimal life histories with age dependent tradeoff curves. *Journal of Theoretical Biology*, **148**, 33–48.
- Williams, P. D., Day, T., Fletcher, Q. & Rowe, L. 2006. The shaping of senescence in the wild. *Trends in Ecology & Evolution*, **21**, 458–463.
- Wooler, R. D., Bradley, J. S., Skira, I. J. & Serventy, D. L. 1990. Reproductive success of short-tailed shearwater *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology*, **59**, 161–170.