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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

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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.

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).

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

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).

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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 ± SE daily temperature was 24.3 ± 0.14°C and the mean ± SE wind speed was 1.4 ± 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°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.