Research article

Mortality rates of honey bees in the wild

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Abstract. Senescence, defined as an age-specific decrease in physiological performance accompanied by an increase in mortality rate, has been studied in a wide range of animals including social insects. It is not clear, however, whether honey bees in the wild live long enough to exhibit senescent decline. I tested for the effects of senescence on honey bees foraging in natural settings and documented the predicted pattern of exponential increase in mortality rate with forager age. These data indicate that, in spite of high rates of external mortality, senescence is an important factor determining the performance of insects such as honey bees in the wild.

Keywords: Honey bees, foraging, predation, mortality rate, life history.

Introduction

Honey bees (*Apis mellifera*) have served as a central model system in all branches of biology but we know little about bee senescence in the wild. In general, with few exceptions (e.g. Visscher and Seeley, 1982), research on honey bees (*Apis mellifera*) has been conducted in agricultural and urban settings and relatively little is known about relevant attributes of honey bees in natural settings. The literature on honey bee senescence is somewhat inconclusive. Laboratory data indicate cellular senescence in honey bees (Seehuus et al., 2006) and Remolina et al. (2007) documented lower resistance to starvation in older honey bees, which indicates effects of senescence. Rueppell et al. (2007b) documented increased mortality rates with age in bees collected from an outdoors hive and maintained in indoor cages until death. In the same study, however, Rueppell et al. (2007b) failed to document the predicted decline in cognitive and behavioural parameters with bee age. In the field, studies by Sakagami and Fukuda (1968) indicated increased mortality rate with honey bee age. Neukirch (1982) also examined honey bee life span in large cohorts of foragers, but did not explicitly examine patterns of senescence. Dukas and Visscher (1994) noted a dramatic reduction in foraging performance in the few bees that foraged for over two weeks. Similarly, Tofilski (2000) observed decline in foraging activity at the end of the lives of a few bees visiting a feeder adjacent to a hive.

As part of a long-term project quantifying the mechanisms underlying performance throughout the lifespan in honey bees in the wild (Dukas, 2008b; Schippers et al., 2006), I wished to examine the pattern of forager senescence, defined as an age-specific decrease in physiological performance accompanied by an increase in mortality rate (Finch, 1990; Rose, 1991). It is difficult to predict from theory the pattern of senescence in a given species (Abrams, 1993; Reznick et al., 2004; Williams et al., 2006) and it is not even clear whether wild insects live long enough to exhibit senescence (Kirkwood and Austad, 2000). That is, high mortality rates owing to predation could result in brief life spans and little senescence in wild insects. To date, only one study involving antler flies (*Protopiophila litigata*) has documented senescence in an insect in the wild (Bonduriansky and Brassil, 2002).

With few exceptions, the empirical data from a variety of vertebrates and insects in the laboratory indicate an exponential increase in mortality rate with age commencing at sexual maturity (Finch, 1990; Rose, 1991). The theoretical explanation for this pattern is that extrinsic mortality decreases the force of natural selection with age past sexual maturity (Kirkwood and Austad, 2000). For worker honey bees, which do not reproduce, one would expect senescence to commence with the behavioral switch from nurse to forager because nurse bees typically incur negligible mortality inside the hive whereas foragers are subjected to external mortality factors including

predation (Dukas, 2001b) and inclement weather (Visscher and Dukas, 1997). That is, one would predict that the decrease in the force of natural selection, which is responsible for senescence, would commence with the physiological and behavioral transition from nurse to forager. Hence I predicted an exponential increase in mortality rate with age in forager honey bees under natural settings.

Methods

The research was carried out at the Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada from July to August 2007. Established in 1893, this large park (7,630 km^2), is characterized by rolling hills covered with mature forest and numerous lakes and rivers. During the study, I closely monitored plants in bloom within a few km from the hives. The flower density was low and mostly restricted to small flower patches in forest openings and lake shores. I spotted forager bees from the observation hives at 13 flower patches. The median distance and range of these flower patches were 450 m and 150–1350 m respectively. Occasional weighing of the two observation hives used in the study indicated an average loss of 0.615 kg in the first 2 weeks of the experiment and an average increase of 1.26 kg in the last 2 weeks of the study. Weather information at the site was recorded every 10 min using a Davis Vantage Pro 2 station. During the study, the average (± SE) daily temperature (9 AM to 5 PM) was 23.8 ± 0.5 °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.

The main experiment involved a two-frame observation hive containing about 2500 bees. A second similar observation hive was used primarily for another study, but the marked bees in that hive were also monitored and are included in the data set. I made 3 introductions of newly eclosed honey bees with individually numbered plastic tags each about 10 days apart. The first hive received 250 marked bees at each introduction and the second hive received 100, 50 and 100 bees in the first, second and third introductions respectively. The successive introductions resulted in bees commencing foraging over a long period of time. This made it easier to monitor the bees and also decoupled effects of age and day effects owing to variation in hive conditions, weather and other external factors such as predator activity and competitors. Overall, bees initiated foraging at an average age of 12.8 ± 0.28 days, and foragers from the two hives had nearly identical mean lifespans (6.6 ± 0.3 and 6.8 ± 0.2; $F_{1,609}$=0.2, P>0.6).

The observation hives were placed inside a research trailer and connected to the outdoors through transparent Plexiglas tunnels. 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 before that day were removed. All other marked bees were monitored until the end of the experiment. Two observers recorded all bee departures and arrivals daily between 11 AM to 5 pm for 6 weeks excluding a few rainy days. Bees were identified as foragers once they started to take trips longer than 5 min (Capaldi et al., 2000; Dukas and Visscher, 1994; Ribbands, 1953). In addition, the observers noted individuals carrying pollen loads and returning foragers transferring nectar.

Out of the total of 852 marked bees observed throughout the study, 611 bees were recorded as foragers. Only these 611 bees were included in the analysis. I calculated the instantaneous mortality rate (force of mortality), μ_x and fitted it with the Gompertz-Makeham model, $ae^{bx}+m$ where a is the initial mortality rate, b is the exponential rate of increase in mortality rate, x is age and m is the age independent mortality rate (Carey, 2001; Finch, 1990) using the nonlinear regression analysis in SPSS. I chose the Gompertz-Makeham model a-priori based on preliminary data (see Dukas, 2008b), which suggested a high age-independent mortality rate. I chose a priori to focus on the main

prediction of exponential increase in mortality rate because I did not expect the sample size to allow me a sensible comparison of distinct models and exact parameter estimates. The precise pattern of mortality rate in the field is likely to vary in time and space and a generalization of this pattern would require enormous research effort involving numerous bees and many replications.

Results

The mortality rate of forager bees increased exponentially with age (Gompertz-Makeham model, r^2=0.93, P<0.001; Fig. 1). The estimates (± SE) for b (0.369 ± 0.06), the exponential rate of increase in mortality rate, and m (0.134 ± 0.025), the age independent mortality rate, were significantly different from zero (P<0.05) whereas the low value of a, the initial mortality rate (0.001 ± 0.001), was not significantly different from 0. The expected life span of bees initiating foraging (e_x) was 6.3 days and the average life span of foragers was 6.76 ± 0.19 days.
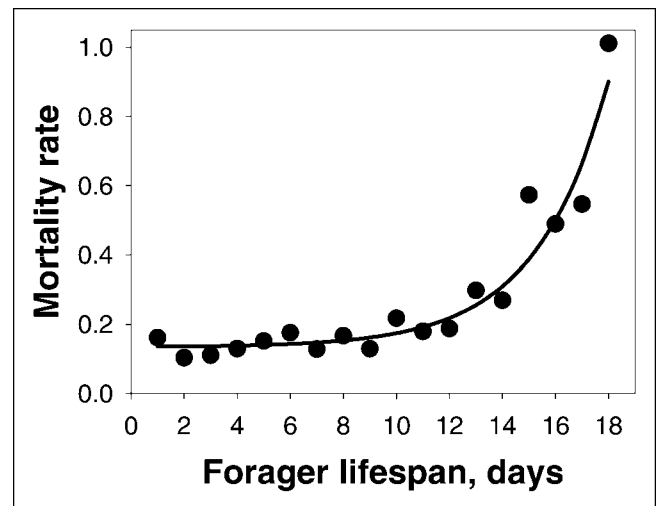

Figure 1. The instantaneous mortality rate of forager honey bees (circles) fitted with the Gomertz-Makeham model (curve).

Discussion

The results indicate an exponential increase in mortality rate with age in forager honey bees under natural settings. This is in spite of the relatively high value (~13.4%) of the age-independent mortality rate. It is likely that both the age-independent and age dependent mortality rates are caused primarily by predation (Dukas, 2001b), with the age-dependent factor increasing exponentially owing to physiological and mechanical deterioration. Limited data indeed suggest that forager honey bees slow down with advanced age (Dukas and Visscher, 1994) and that there is a positive correlation between forager honey bee age and the degree of wing damage (Higginson and Barnard, 2004). Furthermore, experimental evidence in bumble-bees (*B. melanopygus*) indicates that wing damage

increases mortality rate (Cartar, 1992). Future research should critically examine the effects of senescence on the highly demanding tasks involved in long flights and predator avoidance.

Honey bees belong to the large group of species in which the life stage is more relevant than chronological age (Caswell, 2001). Nurse bees are mostly protected from external mortality whereas foragers are exposed to numerous hazards such as predators and inclement weather. Thus one would expect senescence to commence with the switch from nurse bees to foragers because the force of natural selection would start declining rapidly with forager age (Kirkwood and Austad, 2000). Indeed oxidative stress-induced damage in the honey bee brain occurs in foragers but not hive bees regardless of chronological age (Seehuus et al., 2006). Forager bumblebees (*Bombus terrestris*) also exhibit reduced immunocompetence compared to hive workers of similar ages (Konig and Schmid-Hempel, 1995) suggesting differential effects of senescence on foragers and hive bees. Nevertheless, the few published life tables for honey bees and bumblebees in the field have used chronological age rather than the biologically relevant forager age (Goldblatt and Fell, 1987; Rodd et al., 1980; Sakagami and Fukuda, 1968). Still, chronological age does have some effects on worker honey bees as indicated by the positive correlation between worker age and mortality rate in fed (Rueppell et al., 2007b) and starved bees in the laboratory (Remolina et al., 2007) and by the negative correlation between the age of foraging onset and worker lifespan (Guzman-novoa et al., 1994; Rueppell et al., 2007a).

Whereas the current study provides the first clear evidence for honey bee senescence in the wild, it should be noted that honey bees are not native in North America. Nevertheless, feral honey bees have thrived in North America for over 200 years, and the availability of vast undisturbed forests provide a unique opportunity for research on honey bees in the wild (Seeley, 1996). A few previous studies from either urban or agricultural settings provided some relevant data. Rueppell et al. (2005) documented an increase in mortality rate with age in drone honey bees. Drone life history is unique because it includes death after copulation and expulsion from the hive, which results in death (Sammataro, 1998). Hence drones cannot readily be compared to foragers. Visscher and Dukas (1997) reported a constant mortality rate in forager honey bees but relied on a very small sample size. Recently, Rueppell et al. (2007a) documented an increase in mortality rate with worker age, which was mainly caused by the transition from the low mortality nurse stage to the high mortality forager stage. Finally, Neukirch (1982) speculated that the total flight performance of honeybees is fixed but presented no data in support of this assertion, which is not in agreement with evolutionary theory of senescence (Kirkwood and Austad, 2000; Rose, 1991).

The data on honey bee mortality rate in the wild (Fig. 1) help us understand the lifetime patterns of performance observed in bees and other animals. Foragers experienced a high value (~13.4%) of age-independent mortality rate, which was similar to that observed in the only other study of insect senescence in the wild (Bonduriansky and Brassil, 2002). Given the short time horizon available to young foragers as well as many other short lived species, they would benefit from optimizing their physiological preparations for flight before initiating foraging. Indeed physiological measurements replicated over three 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). Furthermore, given the relatively high probability of daily mortality, foragers should probably maximize their effort from the outset. This is different from large mammals such as red deer (*Cervus elaphus*) in which the age independent mortality rate is relatively low and hence increasing effort with age may be optimal (Clutton-Brock, 1984).

In contrast to the effects of physiology and effort on performance, learning, by definition, implies a relatively low initial success. Specifically, a variety of environmental features are unique to a certain time and place and thus must be learned by each forager (Dukas, 2008a). That is, unlike physiology, which can peak before the start of foraging, learning would result in a gradual increase in performance with forager age. Indeed other studies within my long-term project examining lifetime performance suggest that much of the observed increase in performance with forager age can be attributed to learning (Dukas, 2008b; Schippers et al., 2006). To some extent, learning could reduce bee mortality because experience can decrease disorientation and exposure to inclement weather and predators. Bees indeed can learn to avoid locations with increased predation risk (Dukas, 2001a; Dukas and Morse, 2003; Reader et al., 2006). Although it is likely that learning contributes to some decrease in age specific mortality rate, the overall lifetime pattern in bees and other animals is ultimately dominated by senescence.

In spite of the broad interest in the evolutionary biology of senescence, many basic issues remain unresolved (Williams et al., 2006). Honey bees possess a variety of features that make them an ideal experimental model system for studying life history in natural settings (Dukas, 2008b; Dukas and Visscher, 1994; Schippers et al., 2006). Documenting the classical pattern of senescence in forager honey bees in natural settings opens up new opportunities for using honey bees in research on senescence and its interactions with the other mechanisms that determine performance throughout the life span in the wild.

Acknowledgements

References

Abrams P.A. 1993. Does increased mortality favor the evolution of more rapid senescence. *Evolution* **47:** 877–887

Bonduriansky R. and Brassil C.E. 2002. Rapid and costly ageing in wild male flies. *Nature* **420:** 377

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. and Riley J.R. 2000. Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature* **403:** 537–540

Carey J.R. 2001. Insect biodemography. *Annu. Rev. Entomol.* **46:** 79–110

Cartar R.V. 1992. Morphological senescence and longevity: an experiment relating wing wear and life span in foraging wild bumblebees. *J. Anim. Ecol.* **61:** 224–231

Caswell H., 2001. *Matrix population models : construction, analysis, and interpretation.* Sinauer Associates, Sunderland, Mass. 722 pp

Clutton-Brock T.H. 1984. Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123:** 212–229

Dukas R. 2001a. Effects of perceived danger on flower choice by bees. *Ecol. Lett.* **4:** 327–333

Dukas R. 2001b. Effects of predation risk on pollinators and plants. In: *Cognitive Ecology of Pollination* (Chittka L. and Thomson J., Eds). Cambridge University Press, Cambridge. pp 214–236.

Dukas R. 2008a. Evolutionary biology of insect learning. *Ann. Rev. Entomol.* **53:** 145–160

Dukas R. 2008b. 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. and Morse D.H. 2003. Crab spiders affect patch visitation by bees. *Oikos* **101:** 157–163

Dukas R. and Visscher P.K. 1994. Lifetime learning by foraging honey bees. *Anim. Behav.* **48:** 1007–1012

Finch C.E., 1990. *Longevity, senescence, and the genome.* University of Chicago Press, Chicago. 922 pp

Goldblatt J.W. and Fell R.D. 1987. Adult longevity of workers of the bumble bees *Bombus fervidus* (F.) and *Bombus pennsylvanicus* (De Geer) (Hymenoptera: Apidae). *Can. J. Zool.* **65:** 2349–2353

Guzman-novoa E., Page R.E. and Gary N.E. 1994. Behavioral and life - history components of division-of-labor in honey-bees (*Apis mellifera* L). *Behav. Ecol. Soc.* **34:** 409–417

Higginson A.D. and Barnard C.J. 2004. Accumulating wing damage affects foraging decisions in honeybees (*Apis mellifera* L.). *Ecol. Entomol.* **29:** 52–59

Kirkwood T.B.L. and Austad S.N. 2000. Why do we age? *Nature* **408:** 233–238

Konig C. and Schmid-Hempel P. 1995. Foraging activity and immuno-competence in workers of the bumble bee, *Bombus-terrestris* L. *Proc. R. Soc. Lond. B.* **260:** 225–227

Neukirch A. 1982. Dependence of the life span of the honeybee (*Apis mellifica*) upon flight performance and energy consumption. *J. Comp. Physiol. A* **146:** 35–40

Reader T., Higginson A.D., Barnard C.J. and Gilbert F.S. 2006. The effects of predation risk from crab spiders on bee foraging behavior. *Behav. Ecol.* **17:** 933–939

Remolina S.C., Hafez D.M., Robinson G.E. and Hughes K.A. 2007. Senescence in the worker honey bee *Apis mellifera. J. Insect Physiol.* **53:** 1027–1033

Reznick D.N., Bryant M.J., Roff D., Ghalambor C.K. and Ghalambor D.E. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431:** 1095–1099

Ribbands C.R., 1953. *The Behavior and Social Life of Honeybees.* Bee Research Association, London. 352 pp

Rodd F.H., Plowright R.C. and Owen R.E. 1980. Mortality rates of adult bumble bee workers (Hymenoptera: Apidae). *Can. J. Zool.* **58:** 1718–1721

Rose M.R., 1991. *Evolutionary Biology of Aging.* Oxford University Press, New York. 221 pp

Rueppell O., Bachelier C., Fondrk M.K. and Page R.E. 2007a. Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). *Exp. Gerontol.* **42:** 1020–1032

Rueppell O., Christine S., Mulcrone C. and Groves L. 2007b. Aging without functional senescence in honey bee workers. *Curr. Biol.* **17:** R274-R275

Rueppell O., Fondrk M.K. and Page R.E. 2005. Biodemographic analysis of male honey bee mortality. *Aging Cell* **4:** 13–19

Sakagami S.F. and Fukuda H. 1968. Life tables for worker honeybees. *Res. Popul. Ecol.* **10:** 127–139

Sammataro D., 1998. *The Beekeepers Handbook.* Cornell University, Ithaca. 190 pp

Schippers M.-P., Dukas R., Smith R.W., Wang J., Smolen K. and McClelland G.B. 2006. Lifetime performance in foraging honey-bees: behaviour and physiology. *J. Exp. Biol.* **209:** 3828–3836

Seehuus S.C., Krekling T. and Amdam G.V. 2006. Cellular senescence in honey bee brain is largely independent of chronological age. *Exp. Gerontol.* **41:** 1117–1125

Seeley T.D., 1996. *The Wisdom of the Hive.* Harvard University Press, Cambridge, MA. 295 pp

Tofilski A. 2000. Senescence and learning in honeybee (*Apis mellifera*) workers. *Acta. Neurobiol. Exp.* **60:** 35–39

Visscher P.K. and Dukas R. 1997. Survivorship of foraging honey bees. *Insect. Soc.* **44:** 1–5

Visscher P.K. and 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. and Rowe L. 2006. The shaping of senescence in the wild. *Trends Ecol. Evol.* **21:** 458–463