Breeding: Selection on Genetics

Introduction

Line breeding is a common breeding design used by small-scale breeders selecting and breeding from within a small closed population (the line). Small operations, such as the West Wales Bee Breeding Program (WWBBP), can generally only resource a single line, within which a limited number of individual queen lines will be maintained. Within-family selection has been recommended when working with relatively small populations such as this (Moritz, 1986). It is considered as the best approach for small-scale operators wanting to improve stock quality while concurrently trying to maintain genetic diversity across generations. The basic approach is to each year select and breed from the best performing colony in each breeder family. In conjunction with queen selection, one can also simultaneously manipulate male mediated contributions by using the drones produced by sister queen cohorts that had been raised from strong and vigorous colonies the previous summer. These drones would mediate the transfer of promising grandmother colony characteristics through the male line. This approach has been loosely applied by the WWBBP to date.

4.1.1 Avoiding inbreeding

Charles Darwin (1876) was the first to formally describe the detrimental effects of inbreeding. He demonstrated this by comparing the fitness effects of cross and self-fertilization in numerous plant species. Since then, innumerable studies on both wild and captive populations have demonstrated similar effects in sexually producing organisms. Crnokrak and Roff (1999) subsequently published a significant work suggesting that wild inbred individuals will on average suffer seven times more from the effects of inbreeding depression than similarly inbred captive individuals. Inbreeding depression appeared to be expressed to a greater extent under stressful circumstances. The increased rates of colony losses observed in the Northern hemisphere over recent years indicate that honeybees are experiencing a period of increased stress. It is possible that the multifaceted nature of these challenges could render bees more susceptible to the expression of detrimental inbreeding effects.

Inbreeding is an inevitable consequence of line-breeding (Harbo and Rinderer, 1980) since selection constricts the transfer of genetic material across generations. Inbreeding will eventually be detrimental to breeding efforts since enhancing the expression of desired characteristics becomes more difficult with each passing generation as selecting for desirable traits will be far less effective in inbred populations. Colonies with inbred bees might also express reduced vigor and may have spotty brood pattern (glossary) due to homozygosity at the sex determination locus. It is commonly argued that the social hymenoptera are particularly susceptible to inbreeding depression due to genetic load on the sex determination locus (*csd)* and to their usually low effective population sizes (Zayed and Packer, 2005) In reality, little is known about the effects of inbreeding in haplodiploid insects (Liautard and Sundström, 2005) and there seems to be limited evidence that it is a problem in large managed commercial beekeeping operations that use open mating (Oldroyd, 2012).

Two hypotheses (dominance and over-dominance) are frequently evoked to explain the expression of inbreeding depression (Zayed, 2009). Firstly, diploid individuals randomly mating in a large population carrying lethal and non-lethal alleles at low frequency will be protected from the deleterious effects of rare maladapted alleles by the masking effect of dominant non-deleterious homologs (dominance). The expression of inbreeding depression becomes more likely in small closed populations due to the increased likelihood that maladaptive alleles become paired due to mating between relatives. In addition, random genetic drift in small populations reduces genetic diversity (since alleles are more likely to be lost in small populations) leading to increased homozygosity and increased likelihood of inbreeding depression (Lande, 1988). The accumulated effect of numerous homozygous loci carrying maladapted genes results in general loss of vigor. This in effect is inbreeding depression. The second hypothesis relating to inbreeding is over-dominance, which suggests that inbreeding is caused by the tendency of homozygotes to have lower overall fitness than heterozygotes.

4.1.2. Genetic variation in honeybee populations

Honeybees have been managed by humans for thousands of years and extensively so in Europe and North America since the middle of the nineteenth century. Domestication in general usually results in loss of genetic diversity (Wright et al., 2005; Zeder et al., 2006) and low levels of genetic diversity have been observed in several European and North American populations (Delaney, et al., 2009; Jaffé et al., 2010; Meixner et al., 2010). In light of the very poor health of many contemporary managed populations (Cobey et al., 2012; vanEngelsdorp and Meixner, 2009) these observations have raised concern that historical bee management and breeding practices may have resulted in a depleted contemporary genetic pool. Many studies have correlated increased diversity with superior colony robustness and vitality hence the maintenance of variation is important.

However, honeybees are not strictly 'domesticated' and recent work by Harpur, et al. (2012) indicates that managed admixed populations of honeybees in Europe have more genetic diversity than either of their two progenitor populations, i.e., the Western (*M*) and the Eastern (*C*) lineages (Franck et al., 1998; Garnery et al., 1992; Whitfield et al., 2006). Genetic and morphological methods indicate that honeybees spread out of Africa during two separate expansion events and that they were historically geographically isolated into North West and South East Europe. The translocation of bees between these regions was begun by beekeepers and breeders during the middle of the nineteenth century and continues to this day (Meixner et al., 2010). It appears that the constant input of imported stock and the somewhat novel mating biology of honeybees may have allowed diversity to be maintained despite the selection pressures that are applied due to management practices (Harpur et al., 2012; Oldroyd, 2012). There is also evidence from large breeding operations using open mating that neutral genetic diversity is maintained (Oldroyd, 2012).