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REVIEW ARTICLE

Behaviour genetics of *Drosophila*: Non-sexual behaviour

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Abstract

The analysis of genetic behaviour within and between species provides important clues about the forces shaping the evolution of behavioural genes. Genes can affect natural behavioural variation in different ways. Allelic variation causes alternative behavioural phenotypes, whereas changes in gene expression can influence the initiation of behaviour at different ages. Identifying the genes involved in polygenic traits has been difficult. Chromosomal analysis has been widely used as a first step in elucidating the genetic architecture of several behaviours of *Drosophila*. Behavioural genetic and molecular studies helped to reveal the genetic basis of circadian time keeping and rhythmic behaviours. In *Drosophila*, a number of key processes such as emergence from the pupal case, locomotor activity, feeding, olfaction and aspects of mating behaviour are under circadian regulation. Evolutionary biology considers migration behaviour as central in genetic structure of populations and speciation. Genetic loci that influence behaviour are often difficult to identify and localise in part due to the quantitative nature of behavioural phenotypes. Diapause is a hormonally mediated delayed response to future adverse conditions and can occur at any stage of development in an insect. Diapause-associated gene expression was studied in *Drosophila* using subtractive hybridisation. Several approaches have been made to unravel the genetic complexity of the behaviour, which have provided information that may be useful in different ways. There is evidence that species do differ in genetic architecture of photoresponse and this may be related to their natural environment. The classical experiments by Jerry Hirsh and Th. Dobzhansky to know the nature of genetic basis for extreme selected geotactic behaviour in fruit flies constituted the first attempt at the genetic dissection of a complex, polygenic behaviour. Understanding the genetic differences between these selected lines would provide an important point of entry into the study of genetic mechanisms of sensing and responding to gravity, as well as clues to the origins of genetic flexibility and plasticity in an organism's response.

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Introduction

Historically, the study of behaviour and the study of heredity have shared contradictory relationships. Behaviour genetic analysis is an approach to the study of organisms and their behaviour that combines the concepts and methods of behavioural analysis from psychology and ethology. The objective of genetic analysis is the discovery of chromosome and gene correlates of behaviour and of its components. In behaviour genetic analysis, behaviour is the phenotype providing access to genetic system through the breeding studies that constitute genetic analysis.

The experimental designs and methods of analysis of biometrical genetics have been used extensively in their study. Because of frequent difficulties in the separation of genotype from environment and hence in assessing the relative importance of the main effects of (and interaction between) genotype and environment, the study of the genetic control of behaviour habits has tended to lag compared with that of biochemical, physiological and morphological habits. An understanding of the relationship between genes and behaviour is aided by investigations of how genes influence development and neural function A large number of single gene mutations that affect the nervous system and behaviour have been isolated in *D.*

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melanogaster (for a review see Hall 1985). The scope and perspective of genetic analysis of behaviour and nervous system functions are rapidly expanding mostly due to the excellent tools for genetic analysis readily available through the *Drosophila* research community.

In neuroethology, the nervous system and behaviour are analysed in the context of the animal's natural habitat and evolutionary history. For the last several years the influence of genetics on neuroethology has steadily grown particularly in *Drosophila*. Genetic variants reveal new properties of neurons, they help to dissect neuronal circuits and complex behavioural systems; genetics provides new methods to visualise certain brain structures and to assign behavioural function to them and finally, genetic variants can be used to test ecological models.

The general framework of the relationship between genes and brain is not in dispute. Genes specify protein and other molecules; molecules determine the properties of cells; cells in turn, interact to promote developmental process, within the constraints of the environment, shapes the body including its neural circuitry in the brain, its hormonal and neuromodulatory outfit and its capacity to utilise experience. The relationship between genes and behaviour however is less straightforward. Although genes can influence behavioural functions at all these levels, they do not specify which behaviour occurs where, when and why. Behavioural phenotypes in *Drosophila* are associated with a large number of mutants belonging to more than 100 different genes. Many of them play a role during nervous system development and/or affect aspects of the functioning nervous system such as membrane excitability, synaptic transmission or muscle contraction. Many of these behavioural mutants have been generated in special screens for altered behaviour (Heisenberg 1997).

Heredity plays a major role in animal behaviour. This is quite obvious in the case of insects, because the majority of them had a solitary life in which they have no chance to be taught by their conspecifics how they should behave. Insect behaviour attracts the interest of many biologists, but the genetic basis of innate behaviour has been little explored because of lack of feasible approaches to identifying the genes responsible for behaviour in most cases. Explaining behaviour in genetic terms is no small task. The process is multilevel and draws on the activities of a wide range of genes acting at many different terms in the organisms' life. Our usual faith in the power of genetic analysis to identify key components and to suggest a scheme for their action is tampered by the realisation that behaviour draws on two distinct, complex networks for its realisation. One is the network of gene interactions that is normally enlisted during development; the other is the network of neurons, at least as complex as the gene network that produces the brain activity underlying behaviour. Moreover, behaviour is likely to be the most context-dependent of all phenotype and thus subject to many influences that are external to the individuals (Greenspan and Ferveur 2000).

The genetic analysis remains the best means to define mechanisms and to begin the process of assigning the contribution of genes to behaviour. The first publication to report use of *Drosophila* as an experimental organism dealt with the characterisation of its behavioural responses (Carpenter 1905). Two of the four life stages of *Drosophila* exhibit behaviour: larva and adult. There exists today a lot of information describing various aspects of *Drosophila* activities in both larvae and adults. Sexual and non-sexual behaviour of adults have been extensively studied (Grossfield 1978; Spieth and Ringo 1983). The non-sexual behaviour of adult, which has been studied in different species includes phototaxis, geotaxis, locomotion, oviposition, feeding behaviour, habitat selection etc that are affected by different environmental and genetic factors.

In the present review, we mainly focus on genetic control of non-sexual behaviour in different species of *Drosophila*.

Oviposition

Oviposition site preference is an important aspect of non-sexual behaviour of adult female *Drosophila* (Grossfield 1978). It is closely related to fitness since pre-adult *Drosophila* have low mobility due to which their survival depends largely on the choice of oviposition sites by their female parents. The capacity of organisms to discriminate and select suitable habitats undoubtedly has a profound effect on their survival within a species if the fitness of different genotypes vary in different habitats and if organisms select habitat in which their fitness is optimal, then genetic polymorphism can be maintained under conditions much less demanding than those of marginal over dominance (Taylor 1976). Due to the importance of oviposition site preference in determining the fitness and evolutionary potential of a species a number of investigations on this behaviour have been carried out in different species of *Drosophila*. Oviposition site preference (OSP) has been studied in different species of *Drosophila* and intra and interspecific variations with respect to OSP have been reported (Pyle 1976; Richmond and Gerking 1979). Oviposition behaviour is one of the key components of the evolutionary ecology of host and habitat specialisation in insects.

A diallele cross among four inbred strains of *D. melanogaster* carried out by Ruiz and del Solar (1993) confirmed the presence of additive genetic variance and dominance deviation for a high intensity of aggregation oviposition. The genetic organisation of this habit involves genes with additive and dominant effects. A substantial maternal effect may also be present. An analysis following Hayman (1954) revealed a high proportion of additive variation. These results confirm the supposition

of polygenic inheritance advanced by Ruiz and del Solar (1986) after observing the greater fluctuations in the intensity of aggregation of eggs in the lines under selective pressure. The genetic architecture of a behavioural habit may indicate the nature of the relationship between expression of the character and fitness. Characters closely associated with fitness usually show significant directional dominance (Broadhurst and Jinks 1974). Ruiz-Dubreuil and Kohler (1994) reported that the genes influencing gregarious oviposition behaviour in *D. melanogaster* is distributed over chromosome II and III. Interaction among the chromosomes was negligible. The differences in the gregarious oviposition performance of these two selected lines are due mainly to the accumulation of factor for low gregarious oviposition on Chromosome III. Chromosomes II and III play different roles in the control of this behavioural trait. *Drosophila* females exhibit gregarious oviposition. The choice of an oviposition site is important to our understanding of adaptation by *Drosophila* species. Carson (1971) pointed out that *Drosophila* females are generally more selective in choosing an oviposition site than a feeding site. De Jong (1982) has suggested that the ability of *Drosophila* females to select an appropriate oviposition site, which already contains eggs, is an important behaviour that could affect the viability of progeny increasing the probability of survival of their descendents.

A genetic basis for choice of substrate texture for oviposition has already been detected in *D. melanogaster* by Takamura and Fuyama (1980). Del Solar (1968) also found a genetic basis for aggregated oviposition by *D. pseudoobscura*. Ruiz and del-Solar (1986, 1991) observed a response to bi-directional selection for aggregated oviposition leading to populations of *D. melanogaster* with high or low indices of dispersion in a laboratory environment consisting of identical and discrete oviposition sites. Ruiz-Debruiel *et al*. (1994) compared the behaviour of females from lines selected for high (H) and low (L) aggregated oviposition in an environment consisting of discrete patches of resource available for larval development.

Bidirectional selection for choice of oviposition site on paper and medium was effective revealing the existence of genetic variation for this trait. Srivastava and Singh (1996) conducted bidirectional selection for choice of oviposition site in *D. ananassae*. Response to selection resulted in rapid divergence in paper and medium lines. Regression coefficients for both lines show significant deviation from control. Thus, bi-directional selection for oviposition site preference was effective which indicates that oviposition site preference in *D. ananassae* is under polygenic control with a substantial amount of additive genetic variation. Takamura and Fuyama (1980) detected a genetic basis for the choice of oviposition site in *D. melanogaster* either on medium or on a paper surface. Albornoz and Dominguez (1987) and Kamping and van Delden (1990) have described a quantitative genetic analysis of egg insertion behaviour of *D. melanogaster*. Choice of oviposition site has been studied in six species of *melanogaster* species subgroup by measuring the proportion of eggs deposited on paper placed on the medium (Takamura 1984). *D. melanogaster* has larger genetic variation for this habit. Interspecies variation with respect to oviposition site preference and pressure to insect eggs reflect niche differentiation among these species in natural environment (Takamura 1984). Gonzalez (1990) studied the genetic basis of insertion behaviour of laboratory strains of *D. melanogaster*. Examination of the effect of each chromosome revealed the greatest contribution to insertion tendency from the second and third chromosomes with significant effect of interaction or non-additivity of the insertion genes in these two chromosomes in the genotypes tested. In general, the insertion characteristics appear to be dominant over the non-insertion characteristics and are controlled by a polygenic system associated mostly with chromosomes 2 and 3. The X and fourth chromosomes appear to contribute a small effect in some strains. There was a strong tendency for oviposition on the ventral side (Van Delden and Kamping 1990). Richmond and Gerking (1979) analysed the OSP of 14 *Drosophila* species showing that this behaviour is not correlated with phylogenetic relationship OSP is an extremely labile behaviour in the laboratory, but a technique has been developed which minimises variation between replicates and allows the detection of OSP differences between semi-species of a single species.

Possidente *et al*. (1999) studied the quantitative genetic variation for oviposition preference with respect to phenylthiocarbamide in *D. melanogaster*. There was significant variation among strains for the percentage of eggs oviposited on each medium, ranging from $70 \pm 4\%$ preference for plain food to no significant preference. Reciprocal hybrids, backcross and F_2 generations derived from two extreme parent strains revealed significant additive and non-additive genetic variation but no evidence of maternal, paternal or sex-chromosome effects. The oviposition site preference of inseminated females must have great influence on pre-adult viability of the next generation. From an ecological point of view the oviposition site preference might have the key to adaptation to a new niche or widening habitat. Takamura (1980) studied genetics of choice of oviposition site in *D. melanogaster* isolated from natural populations. The results indicated that there is a large amount of genetic variation in natural populations of *D. melanogaster* and the flies actually choose the oviposition sites in natural fields according to their genetic variations. Allemand (1991) studied circadian oviposition behaviour in selected lines of *D. melanogaster* by chromosomal analysis. Mc Cabe and Birley (1998) compared the two behavioural rhythm pheno-

types, oviposition and locomotor activity in the four period genotypes (per^+, per^s, per^0 and per^1) of *D. melanogaster*. It is suggested that both rhythm phenotypes are determined by the period gene and estimates of the genetic penetrance of rhythmicity in oviposition and locomotor activity based on period and signal to noise ratios of the different strains are consistent with this hypothesis.

The oviposition behaviour in *Drosophila* is strongly influenced by light and dark conditions. Ohnishi (1977) found that *D. melanogaster*, *D. lutescens* and *D. virilis* females laid more eggs in light phase than in dark phase. It is suggested that light condition is favourable for oviposition in these species. Selection for high and low light intensity on oviposition has been done in *D. pseudoobscura* for several generations (Seiger and Sanner 1983). Additive genetic variability exists in preference for both high and low intensities. Light intensity as a factor in the choice of oviposition site by female has been studied in *D. pseudoobscura* and *D. persimilis*. The tendency of *D. pseudoobsura* females to lay eggs where other eggs have been laid is genetically conditioned and the degree to which the females will aggregate at oviposition site can be modified by selection (del Solar 1968). Jaenike (1982) tested the independent effects of larval and adult environments on oviposition in *D. melanogaster*, *D. pseudobscura*, *D. immigrans* and *D. recens*. In no case did the larval environments have a significant effect on subsequent oviposition behaviour, but if adults emerge in the vicinity of their larval environments, the processes of habituation and induced preference can promote local polyphagy, aid in the tracking of fluctuating resources and facilitate the spread of genes that adapt individuals to particular food resources.

Gross ablation experiments with insects have generally been done with a view towards partitioning the relative control of behaviour among portions of CNS of several species of *Drosophila* tested, only *D. melanogaster* was capable of oviposition after decapitation. Grossfield and Sakmi (1972) found divergence in the neural control of oviposition in *Drosophila*. The results suggest that two other species *D. tripunctata* and *D. pseudoobscura* were also capable of reflex oviposition during the operation but *D. virilis* and *D. paleestris* were not. These divergences of neural control mechanisms suggest the existence of at least two alternate circuits for the control of insect oviposition. Isofemale lines of the cactophilic species *D. buzzatii* exhibit genetic variation for their oviposition between yeast species in the laboratory. Barker *et al*. (1994) studied genotype-specific habitat selection for oviposition sets in the cactophilic species *D. buzzatii*. The analysis of the oviposition preference test showed significant line effects, which correlated with the laboratory results. Thus, a genetic component for oviposition preference under laboratory and field conditions was demonstrated and this strengthens the evidence for genotype-specific habitat selection in *D. buzzatii*. Jaenike (1987) studied the genetics of oviposition site preference in *D. tripunctata*. Crosses among several strains revealed the existence of autosomal genes with dominance and interaction effects having substantial influence on oviposition-site preference.

Habitat selection expressed as oviposition site preference (OSP) is one component of the complex of behaviors of females seeking a place to oviposit. Barker and Starmer (1999) studied the environmental effects and the genetics of oviposition site preference for natural yeast substrates in *D. buzzatii*. They reported that OSP of *D. buzzatii* females is heritable, with evidence from variation among isofemale lines, direct estimation of heritability, generation means analysis and short term selection. Further, this genetic variation appears to be ubiquitous, polygenic and largely non-additive for all yeast species combinations. OSP for yeast species would seem to be a powerful force for the maintenance of genetic variation and not only at loci affecting the choice of oviposition sites.

Imamura *et al*. (1998) reported that ovulation responses of *D. biarmipes* females to an injection of methanolic extract from conspecific males vary with the strains of females. This strain differences seems to be controlled by a small number of autosomal genes, with low responsiveness being recessive. The oviposition behaviour of the four species in the *D. melanogaster* complex (*D. melanogaster*, *D. simulans*, *D. mauritiana* and *D. sechellia*) was investigated from natural morinda fruit (the normal resource of *D. sechellia*) and the two major aliphatic acids of this fruit (hexanoic acid, C6 and octanoic acid C8); significant behavioural differences were observed with major effects due to genotype, concentration and their interaction. Hybrid behaviour was intermediate between those of their parents. In F_1 flies, a dominance reversal was observed with increasing C8 concentration (Amlou *et al*. 1998).

Foraging behaviour

Most quantitative habits are influenced by many genes (polygenic inheritance); however, the actual number of genes involved and the magnitude of their individual effects is a subject of controversy (Falconer 1981). The classical view is that hundred of genes with small equal and additive effects are involved. While more recently it has been proposed that quantitative habits are controlled by relatively few major genes modified by minor genes (Thoday and Thompson 1976). Rover/sitter is a naturally occurring behavioural polymorphism in *Drosophila* larvae. The phenotype is measured as the distance (path-length) a larva travels while foraging in a yeast coated petiridish. Rovers have significantly longer paths than sitters. Rovers/sitters is a quantitative trait influenced by one major gene with rover dominant to sitter and modified by minor

genes (De Belle and Sokolowski 1987). Anderson (1986) tested the two hypotheses, which are parts of the "optimal foraging theory" that animals are able to choose between different types of food and that diet choice is heritable. *D. melanogaster* larvae were allowed to choose between two different kinds of food. Thus there is genetic influence on foraging behaviour in *D. melanogaster* larvae.

Whole chromosome analysis of both established laboratory (Sokalowski 1980) and recently field-derived strains (Bauer and Sokolowski 1985) revealed a predominantly second chromosomes genetic basis for rover/sitter. Compound autosome analysis localized the major gene to the left arm of chromosome-2 (De Belle and Sokolowski 1989). De Belle *et al*. (1989) have localized the lethal tagged forging (*for* 2–10) gene by deficiency mapping to 24 A3–C5 on the polytene chromosome map. Sokolowski (1980) identified a behavioural polymorphism in *D. melanogaster* larval foraging strategies, which was attributed to differences in a single pair of chromosome. Sokolowki (1982) studied the temporal patterning of foraging behaviour in *D. melanogaster* larvae. The results suggested that rover larvae traverse a large area whereas sitter larvae covers a small area while foraging on a yeasted petri dish. Genetic analysis using chromosome substitution revealed that both the second and third chromosomes affect differences in larval feeding rate. Crosses between rovers and sitters support that the polymorphism is under relatively simple genetic control with the rover phenotype showing complete dominance over the sitter and no significant sex-linked or maternal effects. Foraging behaviour can be defined on the relative amount of feeding (shoveling) and locomotion (crawling movements) performed during a test period (Sokolowki 1980).

Sokolowski and Hansell (1992) used *D. melanogaster* larvae with different alleles at the foraging (*for*) locus in a variety of behavioural tests to evaluate normal muscle usage of rover and sitter phenotypes. The results show that sitter and lethal sitter alleles of *for* do not affect larval behaviour through a mutation, which affects larval muscle usage. Little is known about how genes affect an animal's behaviour throughout development. A single gene can have multiple but similar behavioural effects in very different life history stage. The behaviour and ecology of larval and adult *Drosophila* show little similarity. De Belle *et al*. (1989) after mutagenesis isolated two new sitter larval mutant strains, *for s*♀*/for s*♀ and *for* s^2*/for* s^2 from for^R/for^R larval laboratory strain. If mutagenesis resulted in a change in both larval and adult foraging behaviour, this could only be due to a charge in alleles at *for*. The adult behaviour of the sitter mutant provides strong evidence that *for*, originally defined through its effect on larval behaviour also influenced adult behaviour. Pereira and Sokolowski (1993) have reported that mutation in the larval foraging gene affects adult locomotors behaviour after feeding in *D. melanogaster*. Larvaes with the rover allele (for^R) move significantly more while eating during a set time period than those homozygous for the sitter allele (for^s). In *Drosophila* a genetic approach was fundamental to the identification of components of the phototransduction pathway underlying adult photobehaviour (Zuker *et al*. 1985). Traditionally, *Drosophila* genetic screens using behavioural paradigms have been conducted using adult flies. A few recent examples include the isolation of mutations that disrupt associative learning (Boynton and Tully 1992), circadian rhythms (Sehgal *et al*. 1992) and hydro-and/or thermosensation (Sayeed and Benzer 1996). Genetic screens using the third instar larva proved that this developmental stage is also a good model for the identification of novel behavioural genes (Kernan *et al*. 1994). Iyengar *et al*. (1999) designed a genetic screen to identify mutations that disrupt the response of foraging third instar larva to light.

Ruiz Dubreuil *et al*. (1996) studied larval foraging behaviour and competition in *D. melanogaster*. Their findings demonstrate that larval feeding rate in the precritical period of larval development is the principal component of fitness for the scramble-type competitor. Individual differences in larval feeding rate are genetically determined and affect larval growth rate, survival and competitive ability (Sewell *et al*. 1975; Burnet *et al*. 1977). The studies of ecological genetics and behaviour of *D. melanogaster* larvae demonstrated a direct relationship between laboratory and field phenotypes, thereby linking the ecology behaviour and genetics of *D. melanogaster* (Sokolowsky 1980; Sokolowsky *et al*. 1986). Larval foraging behaviour in *Drosophila* is of interest since adult emergence is dependent on the success of the larva in utilizing available resources and choosing a suitable site for pupation (Ohnishi 1979).

Sokolowski *et al*. (1997) examined the effect of high and low animal rearing densities on the larval foraging path length phenotype and show that density dependent natural selection produces changes in this trait. Density dependent mechanisms may be sufficient to maintain variation in rover and sitter behaviour in laboratory population. Godoy-Herrera *et al*. (1994) studied larval foraging behaviour in two sibling species, *D. pavani* and *D. gaucha* belonging to the *mesophragmatica* species group. Their results suggest that inter specific hybrid larvae derived from both reciprocal crosses to the parent species show disruption in the organisation of their behaviour leading to lower mean feeding rate. This together with interactions involving biotic residues is likely, under competitive conditions, to contribute to reducing the fitness of the hybrids relative to their parent species.

The foraging (*for*) locus represents one of the few genes isolated by studying larval behaviour of *D. melanogaster*. Ball *et al*. (1985) tested the behaviour of larvae of the lethal (2) thin mutation, a mutation that affects larval muscle development in *D. melanogaster*. They

found that crawling (locomotary contraction) and shoveling (number of feeding movements) were reduced in mutant larvae. The central complex (CC) is a prominent component of the adult insect brain. Vernam *et al*. (1996) described altered larval behaviour resulting form mutation in six CC structural genes. Central body defect 1 (Cbd1), central complex deranged (1) (CCd1), central brain deranged 1 (Ceb1) and central complex 1 (acex1) larvae all had general defects in locomotion. Both ellipsoid bodies open 2 (*ebo2*) and no bridge1 (*nob1*) had larval foraging behaviour defects. Genetic analysis suggested that *nob 1* interacts additively with two other genes influencing larval foraging behaviour, foraging (*for*) and chaser (*Csr*). *for* also had influence on adult foraging. Besides the change in behaviour seen in all of the mutants generated, the lethal alleles also exhibit a central nervous system phenotype. *for* was subsequently locoalized to 24A3–5 on the polytene chromosome map. This is the same position on *dg2*, the gene encoding a cyclic GMP dependent protien kinase (PKG)[4] several pieces of evidence indicate that *for* and *dg2* are synonymous, the most convincing of these is the change in behaviour from sitter to rover in lines transgenic for the T2 transcript of *dg2*.

Genetic loci that influence behaviour are often difficult to identify and localise in part due to the quantitative nature of behavioural phenotypes. Shaver *et al*. (2000) identified and localised new mutants that influenced larval foraging (movement in the presence of food) and general locomotion (movement in the absence of food) behaviour. When the lethal mutation segregated with the behavioural alteration this permitted the mapping of the behavioural locus. Nine new loci on the second chromosome were found to affect larval behaviour. Of these, seven loci affected forging and two affected locomotion. Analysis of these new loci will lead to further understanding of the mechanistic basis of larval behaviour.

Pupation site preference

Drosophila larvae spend most of their lives foraging for food. When larvae have reached their minimum weight for pupation (late third instar), they begin to search for a pupation site. The effects of a variety of physical and biological factor on pupation site choice were tested in a study of Sokal *et al*. (1960). They concluded that there were significant developmental, as well as gene environment interactions, affecting pupation site choice. Pupation site preference is an important step in *Drosophila* preadult development because the place selected by larvae can have a decisive influence on their subsequent survival (Sameoto and Miller 1968). Thus, total fitness is heavily influenced at the larval stage, and pupation site preference is an important component of fitness (Markow 1979). Genetic variability for pupation behaviour may be maintained through habitat selection in heterogeneous environments (Rodriguez *et al*. 1992). Singh and Pandey (1993a) conducted bidirectional artificial selection experiments for high and low pupation height in *D. ananassae*. Their findings suggest that pupation height in *D. ananassae* is under polygenic control, with a substantial amount of additive genetic variation. Sokolowski and Hansell (1983) found positive correlation between pupation height and larval foraging behaviour in *D. melanagaster*.

An understanding of the genetic basis of differences in *Drosophila* larval pupation behaviours is emerging through laboratory and field studies. Sokolowski and Bauer (1989) investigated the inheritance of *D. melanogaster* larval pupation behaviour in sixteen reciprocal crosses between field-collected lines. A chromosomal analysis showed that the second and third chromosomes act additively on pupation distance and that the third pair of chromosomes had a much larger effect than the second. In general, genetic analyses have shown that genetic variation for differences in *D. melanogaster* larval pupation behaviour exists in many natural populations and that the trait can be selected for, by artificial selection. The genetic basis to differences in pupation behaviour in all of these assays is autosomal with little or no dominance. The relative contributions of the second as compared to the third pair of autosome is however dependent on the pupation behaviour of interest. Pupation height in vials has a greater second chromosome contribution (Bauer and Sokolowski 1985) whereas pupation distance in dishes (Sokolowski and Bauer 1989) and in a field assay has a greater third chromosome contribution. This difference in chromosomal contribution may result from the third chromosome making a greater contribution to pupation behaviours with horizontal as opposed to vertical locomotory movement (i.e. the pupation height measure may have a geotactic component that is influenced by second chromosome genes.)

Path length and pupation height should both be measured on the same larva to further determine whether behavioural correlation reflects linkage and (or) pleiotrophy. Bauer and Sokolowski (1985) reported that genes controlling path length and pupation height are in the same linkage group (the second chromosomes). Preliminary data indicates that the second-chromosome genes controlling these behaviours are located on opposite arms. It is also known that genes on the third chromosomes influence pupation height.

The choice of pupation sites is an important step in *Drosophila* preadult development because the place selected by the larvae can have a decisive influence on their subsequent survival. (Sameoto and Miller 1968; Wallace 1974; Casares and Rubio 1984). Garcia-Florez *et al*. (1989) found divergent directional selection for high and low pupation height in *D. melanogaster*. A quick response was observed in the two directions of selection and the selection for increasing and decreasing pupation

height proves the existence of additive genetic variation for *D. melangaster*. Behaviours related with habitat selection may be of great importance in determining the genetic structure of populations (Taylor 1976). Casares and Carracedo (1986a) studied genetic variation in pupation height in a population of *D. simulans*. Preadult mortality of *D. simulans* in the laboratory is influenced by larval behaviour during pupation site choice. Casares *et al*. (1997) studied the larval behaviours underlying the pupation height phenotype in *D. simulans* and *D. melanogaster*. In both species, the high pupation lines showed greater mobility than the corresponding controls. Selection for high pupation height diminished the digging behaviour in *D. simulans* but not in *D. melanogaster*, whereas selection for low sites augmented the percentage of digging in *D. melanogaster*. In *D. simulans*, low lines were geopositive and high lines were neutral, while low lines were neutral and high lines were geonegative in *D. melanogaster*. The results indicate that pupation height is a complex trait determined by other simpler behaviours, so that a given phenotype can be produced by different genetic systems.

Singh and Pandey (1993b) studied the mode of inheritance of pupation height in *D. ananassae*. The findings provide evidence that the inheritance of pupation height fits a classical additive polygenic model and suggested that there is substantial amount of additive genetic variation in natural populations of *D. ananassae*. Furthermore, the analysis of reciprocal backcrosses shows significant maternal effect. In *D. willistoni*, it was found that allelic variation at a single locus determined whether larvae pupated in food cups or on the bottom of the population cage, which demonstrates the importance of genetically determined pupation site choice (De Souza *et al*. 1970). Bauer and Sokolowski (1985, 1988) demonstrated the genetic control of larval pupation behaviour by making crosses between high and low pupating strains of *D. melanogaster*. A transient maternal effect on pupation behaviour was also detected which was confined to only F_1 back crosses (Bauer and Sokolowski 1988). Singh and Pandey (1991) found intra and inter species variations in pupation height in three species, *D. ananassae*, *D. bipectinata* and *D. malerkotliana*. A significant variation was found among the three species. Significant variations among different strains of the same species were also found in *D. ananassae* and *D. bipectinata*. These observations provide evidence for intra and interspecies variations in pupation height in *Drosophila*. Variations among different strains of the same species in pupation height can be attributed to genetic heterogeneity among strains.

Demerec (1950) gave a detailed account of formation of pupa and then adult in *Drosophila*. Many of the Hawaiian *Drosophila* routinely pupate several inches deep in the ground (Carson *et al*. 1970) and the adult must work their way back up through the soil. Although the results of different studies on the effect of light on pupation site preference vary, selection for dark pupation site has been considered advantageous to avoid light areas where desiccation and exposure to predation might occur (Markow 1979). According to Manning and Markow (1981) *D. melanogaster* prefers to pupate in dark while its sibling species *D. simulans* prefers light. Pupation site preference has been studied in F_1 hybrids obtained by making reciprocal crosses between these two species. The F_1 progeny from cross between *D. melanogaster* females and *D. simulans* males selected pupation sites intermediate between two parental species while the F_1 progeny of the opposite cross preferred to pupate in light. Manning and Markow (1981) concluded that genes controlling light dependent pupation site selections are sex linked. Hutter (1986) reported genetic variation in the preference for pupation sites under conditions of varying white light intensity in *D. melanogaster* and *D. simulans*. It was observed that *D. simulans* responded only to selection for negative larval photo preference while *D. melanogaster* responded strongly to selection for positive but weakly to selection for negative photo preferences.

Casares and Carracedo (1986b) studied geneotpe-environment interaction for pupation height in *D. simulans*. A genetic component for pupation height was revealed in the population. The results suggest that pupation site choice has a genetic component in three treatments, whether measured by the pupation height, the wall height, or the wall percentage parameters. The change in the relative performance of several genotypes from one environment to another can also be explained if the trait measured is being determined by other simpler traits. Casares and Carracedo (1986c) conducted selection experiment for high and low pupation height in *D. simulans*. Only the selection for increased pupation height was successful. Casares *et al*. (1997) studied the larval behaviours underlying the pupation height phenotype in *D. simulans* and *D. melanogaster*. The results indicate that pupation height is a complex trait determined by other simpler behaviours, so that a given phenotype can be produced by different genetic systems. Ringo and Wood (1983) carried out selection experiment for increased pupation height for 17 generations in two lines of *D. simulans*. The realised habitability for mean pupation height in each line, calculated over the 17 generations did not differ significantly from zero. Both selected lines tended to pupate away from the center of the culture medium to a greater extent than the control in the latter generations of the experiment but not in earlier generations. *Drosophila* larvae are suitable organisms for studies of habitat selection.

Locomotor activity

The central complex is one of the most prominent yet functionally enigmatic structures of the insect brain. Re-

cently, behavioural, neuroanatomical and molecular approaches in *Drosophila* have joined focus to disclose specific components of higher locomotion control in larvae and adult flies such as those that guarantee the optimal length and across body symmetry of strides and an appropriate activity. The locomotor activity of adult *Drosophila* is an important factor affecting dispersal, the search for feeding and breeding sites and avoidance of predation. It is an important determinant of mating success. That individual differences in activity are substantially under genetic control is already well established (Ewing 1963; Connolly 1967). No distinction has been made between the amount and speed of locomotor activity. The responses of selection observed by Connolly (1967) demonstrate that spontaneous activity and reactivity are probably controlled by different genetic systems. Burnet *et al*. (1988) observed that there is significant genetic variation in the amount of locomotor activity in courtship. Genes controlling the amount of movement in the open field, as well as those controlling the speed of locomtion may also influence the amount of locomotion in courtship. Burnet *et al*. (1988) reported that Oregon and Formosa strains show difference at gene loci affecting the amount, or the speed of locomotion within individuals of the Sierra Leone population may be a consequence of linkage relations between gene loci involved in the control of those separate system but could also be due to the pleiotropic effects of certain genes affecting both measures. A comparison of the genetic architecture for amount and speed of locomotor activity should extend our understanding of the organisation of locomotor activity and reactivity in *D. melanogaster*. Cook (1979) detected strain differences in the ability of courting males to track and maintain contact with moving females. The result proves the observation of Burnet *et al*. (1988). Genes controlling the amount of movement in the open field as well as those controlling the speed of locomotion may also influence the amount of locomotion in courtship.

Van Dijken and Scharloo (1979a) found divergent directional selection on locomotor activity in *D. melanogaster*. Selection for high and low locomotor activity has been applied in two base populations of *D. melanogaster* Divergent directional selection was successful with realised heritabilities of similar value. Tests for reproductive isolation between lines selected for locomotor activity were performed by Van Dijken and Scharloo (1979b). Robertson (1966), Spickett and Thoday (1966) and Thoday and Thompson (1976) suggested that much of the genetic variation of a quantitative character could be the outcome of few genes with large effects. The large effects of the X chromosomes in all three sets of selection lines may be due to one or few loci. Previous experiments suggest that there are differences in NADH dehydrogenase activity between high and low lines. It is now well established that the *Notch* locus of *Drosophila*, which is located on the X chromosome is involved in the synthesis of this enzyme. This enzyme is responsible for energy metabolism and could be crucial for activity of *D. melanogaster*.

Several mutations have been isolated on the basis of aberrant locomotor activity. The *inactive* mutation was described by Kaplan (1977). Seven non-allelic hypoactive mutations, described by Honyk and Sheppard (1977) and Honyk *et al*. (1980) were isolated using a screen for mutants of reduced flight abilities. O'Dell and Burrnet (1986) reported that the mutant genes hypoacitng-B and inactives are alleles. O'Dell and Burnet (1988) reported that the locomotor activity is reduced in adult flies by the mutant genes *inacitve*, *inactive*^{2}, *hypoactive-C* and *hypoacitve E*. The frequency of jumping is greatly reduced by all four mutations and the threshold for the jumping response appears to be related to speed of locomotor activity. Differences in the expression of reactivity in lines selected for changes in locomotor activity have indicated that spontaneous activity and reactivity are at least partially under the control of different genes (Connolly 1967; Van Dijken 1982).

Neurological mutations could potentially affect one or more of the different aspects of expression of locomotor activity in *Drosophila* and detailed description of their effect is a first step toward recognising groups of genes involved in control of specific functional systems. Burnet *et al*. (1988) reported that amount and speed of locomotion are largely under independent genetic control. Homer proteins have been proposed to play a role in synaptogenesis, synapse function, receptor trafficking and axon path finding. Diagana *et al*. (2002) created a mutation of *homer* and showed that flies homozygous for this mutation are viable and show coordinated locomotion, suggesting that Homer is not essential for basic neurotransmission. However, they also found that homer mutant displays defects in behavioural plasticity and the control of locomotor activity. Mutations which have been found to cause abnormalities of the jumping response are *bendless* (Thomas 1980; Thomas and Wyman 1982), *jumpless* (Hall 1982) and *non-jumper* (Thomas 1980), which are associated with abnormalities affecting the giant nerve fiber. Vaj and Jayakar (1976) investigated the importance of autosomal genes in the determination of locomotor activity in *D. melanogaster* and found that chromosome 4 is the most influential in controlling the locomotor activity. Costa *et al*. (1989) attempted to identify genes controlling spontaneous adult locomotor activity in *D. melanogaster*. A wild type stock and 13 morphological marker stocks (6 markers for chromosome X and seven for chromosome 3) were used. Backcrosses were set-up to study linkage relationships between loci affecting the quantitative characters and marker loci. The results clearly show that the expression pattern of spontaneous locomotor activity is under control of several genes. Nakashima-Tanaka and Ogaki (1970) reported the 'pyokori' behav-

iour found in a mutant, *bw; st ss* of *D. melanogaster*. These flies jumped up suddenly when a rapid passage of shadow ran over a vial containing the flies, or when the light was turned off. The pyokori behaviour was genetically controlled by the major genes(s) on the second chromosome and by minor genes on the manifestation of the pyokori behaviour (Nakashima-Tanaka and Matsukara 1980). Asada (1988) studied pyokori-like jumping behaviour in *D. nasuta* sub-group. The results suggest that a large genetic variation in pyokori like jumping behaviour was found among the wild flies of the *D. nasuta* subgroup belonging to the *D. immigrans* species group. The parallel relationship between phylogentic divergence and the degree of pyokori like jumping behaviour was demonstrated; that is the ancestral species *D. pallidifrons* responded more actively than the derived species e.g. *D. kepulauana*. Hence, this behaviour might be used as a marker response for the study of the evolutionary process of *Drosophila*.

Differences at the biochemical level have been hypothesised to account for different levels of locomotor activity in strains of *D. melanogaster* selected for different values of this character. Tuncliff *et al*. (1969) found a significant influence on location of dopamine and noradrenaline levels, implying that a control can be exerted by the balance existing between the two; on the contrary, he did not detect significant differences in serotonin level and cholinesterase activity. Meehan and Wilson (1987) studying the dopamine deficient *tyr1* mutant and giving separate measures for different components of locomotor activity, demonstrated that *Tyr-1* flies have "normal" levels of spontaneous activity on reactivity but higher level of stimulated activity. Localising pathways and certain behavioural properties have been a major effort. Substantial progress has been made in localising the circadian pacemaker for locomotor activity. Several studies using immuno-cytochemistry and transgenic flies have revealed that a small set of neurons in the lateral brain expressing the genes *per* and *tim* control the circadian modulation of locomotor activity (Helfrich-Forster 1996). Ceriani *et al*. (2002) reported genes regulating various physiological processes to be under circadian transcriptional regulation, ranging from protein stability and degradation, signal transduction, heme metabolism, ditoxification and immunity.

Mutations that abolish expression of an X-linked gene *FMR 1* result in the pathogenesis of fragile x-syndrome, the most common form of inherited mental retardation. Inoue *et al*. (2002) studied the role for the *Drosophila* fragile x-related gene in circadian output. They reported that under constant darkness (DD), a lack of *dfmr 1* expression causes arrhythemic locomotor acitvity, but in light:dark cycles their behavioural rhythms appear normal. These results suggest that DFMR 1 plays a critical role in the circadian output pathway regulating locomotor activity in *Drosophila*. Sarov-Blat *et al*. (2000) reported the characterisation of a novel *Drosophila* clock-regulated output gene, take out (*to*). A *to* mutant has aberrant locomotor activity and dies rapidly in response to starvation, indicating a link between locomotor acitivity, survival and food status. In *D. melanogaster*, earlier studies based on structural brain mutants have suggested that the central complex is a higher control centre of locomotor behaviour. Continuing this investigation Martin *et al*. (1999) studied the effect of the central complex on the temporal structure of spontaneous locomotor activity in the time domain of a few hours. They suggest that the bridge and some of its neural connections to the other neuropil regions of the central complex are required for the maintenance but not for the initiation of walking.

In order to elucidate the behavioural significance of the control complex (CC) Strauss and Heisenberg (1993) examined 15 *Drosophila* mutant strains belonging to eight independent X-linked genes that affect the structure of the CC compared to four different wild-type strain, all are impaired either in a general or in a paradigm dependent manner. Behavioural deficits concern walking activity, walking speed or "straightness of walking" as measured in an object fixation task, in fast phototaxis and in negative geotaxis. Pigment dispersing factor (PDF) neuropeptide is an important petrochemical that carries circadian timing information originating from the central oscillator in *Drosophila*. Although PDF is likely to be a principal clock-output factor, our recent evidence predicts the presence of other neuropeptides with rhythm relevant functions. Furthermore, recent microarrays screens have identified numerous potential clock-controlled genes, suggesting that diverse physiological processes might be affected by the biological clock system (Park 2002).

Geotaxis

Geotaxis is defined broadly as orientation and movement of individuals with gravity. Geotaxis is also defined as a directed movement mediated by gravity. Since an organism performs in an environment replete with other sensory inputs the directive effects of gravity alone is difficult to dissect. The proximal cue for orientation with respect to gravity may in some cases be a function of apparatus used to measure the response. Carpenter (1905) first reported that *D. melanogaster* was negatively geotactic and that this response was accentuated by mechanical stimulation. Geotaxis, defined broadly as orientation and movement of individuals with respect to gravity has been defined operationally for *D. melanogaster* as movement up and down in a multiple unit classification maze (Hirsh 1959; Hirsh and Tryon 1956).

Hirsh (1959) demonstrated that populations of *D. melanogaster* isogenic for different chromosomes showed consistent differences when tested for geotaxis in a verti-

cal maze. Genetic control of geotaxis was found to be polygenic with the X and the second chromosome factors leading to positive geotaxis and the third chromosome factors to negative geotaxis (Hirsh and Erlenmeyer-Kimling 1961). Selection of the base population for negative geotaxis reduced the effect of the X and second chromosomes and enhanced the effect of the third chromosome (Hirsh and Erlenmeyer-Kimling 1962). Hybridisation analysis after 65 generations of selection confirmed the interaction of X and autosomal factors suggested partial dominance of positive geotactic factors, and revealed considerable genetic variation remaining in the population (Erlenmeyer-Kimling *et al*. 1962). Analysis after 133 generations of isolation of the lines using a technique in which morphological mutants identifying the various chromosome did not appear in the flies tested revealed that dosage compensation was present for the X chromosome factors and that males and females differed in the amount of genetic variation for geotaxis present in the X and second chromosomes (Hirsh and Ksander 1969). Selection for negative geotoaxis in *D. melanogaster* showed continued response after generation 65 but the positive selection line showed no further response. Selection of the positive line for negative geotaxis and vice versa, demonstrated that these reverse selection lines achieved nearly the same scores as the lines originally selected for a response in one or other directions.

Rricker and Hirsh (1988a) provide evidence for only one major gene correlate of geotaxis by isolating individual chromosomes from the selected lines. The remaining chromosomes may have two or more loci. Thus, there appears to be at least four correlates, with some of the specific loci differing between sexes. Ricker and Hirsh (1988b) showed that evolution of the genetic systems in the high and low lines involves several types of changes: (a) the appearance of and increases in inter and intrachromosomal interactions, (b) sexual dimorphism in the manifestation of this genetic change and (c) increases in directional dominance over generations followed by decreases.

Geotaxis was apparently one of the first behaviours to be analysed genetically in *D. melanogaster* (Hirsh and Tryon 1956). Several researchers have attempted genetic analysis of the differences between lines of flies selected for positive and negative geotaxis by hybrid analysis (Erlenmeyer-Kimling *et al*. 1962) or chromosome analysis (Pyle 1978). These analyses were often incomplete but all researchers claimed that geotaxis was polygenic and that there were genes on all three major chromosomes. Markow and Merriam (1977) tested 10 strains that had been isolated in Benzer's (1967) countercurrent distribution device for geotaxis and phototaxis. Eight of ten mutants showed mean geotaxis scores that differed from the parental Canton special strain. No correlation was found between phototaxis and geotaxis scores. This suggested that single gene mutations might have strong effects on a polygenic trait such as geotaxis. McMillan and McGuire (1992) reported that the homeotic gene spineless aristapedia affects geotaxis in *D. melanogaster*. The homeotic mutation spineless-aristapedia (SS^a) transforms the arista into second tarsi. Flies with a SS^a phenotype also show extremely positive geotaxis as measured in a Hirsh-type geotaxis maze. Other antennal mutants and flies with their aristae amputated do not show such extreme geotaxis. A biometrical analysis has detected additional genes on the X-chromosome that also affect geotaxis. Chromosome analysis has been widely used as a first step in elucidating the genetic architecture of several behaviours of *D. melanogaster*. McGuire (1992) reanalysed two data sets on geotaxis from Pyle (1978) by using a biometrical genetic design. Results from the biometrical genetic reanalysis suggest that individual difference in geotaxis might be due to genes on all three major chromosomes, which show extensive epistatic interactions. Watanabe and Anderson (1976) carried out selection for geotaxis from a natural population of *D. melanogaster*. The frequencies of polymorphic inversions declined in every population during selection, but the population under natural selection seemed to maintain a higher chromosomal polymorphism than those under positive or negative selection.

Several classes of models have been suggested to explain how natural selection can favour non-zero recombination. Directional and fluctuating selection, abiotic and biotic, and selection against harmful mutations seem to be the most plausible factors, but little has been done to test the problem experimentally. Korol and Iliadi (1994) carried out long-term selection experiment for positive or negative geotaxis in *D. melanogaster* which result in a dramatic increase in recombination rates in different genomic regions. Thus in general, selection for geotaxis resulted in increased recombination frequencies regardless of the direction of selection. The behaviour genetic analysis of *D. melanogaster* with geotactic performance as the phenotype is an ideal model system with which to investigate the complex relations between heredity and behaviour.

Previously, all of the major *D.melanogaster* chromosomes (I, II and III) have been shown to be associated with geotaxis, but the Y chromosome has not. Using two methods (back-crossing and chromosome substitution), Stoltenberg and Hirsh (1997) studied the Y-chromosome effect on *Drosophila* geotaxis. The results suggest that the Y chromosome has a small effect on geotaxis whose detection depends on genetic and/or cytoplasmic background. Ricker and Hirsh (1985) described long term divergent selection for geotaxis in lines of *D. melanogaster* after 26 years of intermittent selection, the mean geotactic scores now remain stable upon relaxed selection, a result suggesting that evolutionary changes have

occurred in these lines because the stability is not due to genetic fixation associated with geotaxis or the development of new coadapted gene complexes utilising genes associated with extreme geotaxis expression.

To identify the genes involved in polygenic traits has been difficult. In the 1950 s and 1960s, laboratory selection experiments for extreme geotaxis behaviour in fruit flies established for the first time that a complex behavioural trait has a genetic basis. But the specific genes responsible for the behaviour have never been identified using the classical model. To identify the individual genes involved in geotaxic response, Toma *et al*. (2002) used cDNA microarrays to identify candidate genes and assessed fly lines mutant in these genes for behavioural confirmation and determined the identities of several genes that contribute to the complex, polygenic behaviour of geotaxis.

Analysis of positive and negative geotactic lines of *D. pseudoobscura* revealed that a major proportion of the genes responsible for positive geotaxis are in a discrete region of the X chromosomes (Woolf 1972). A diallel analysis (Walton 1968) confirmed both the polygenic control of the trait and the dominance of positive geotaxis. No morphometric changes were associated with geotactic selection in *D. melanogaster*. In *D. pseudoobscura*, however, selection lines of positively geotactic flies tended to be larger and have more branches on the arista. Selection of *D. pseudoobscura* for positive and negative geotaxis demonstrated that although this species is neutral (Spassky and Dobzhansky 1967) for the trait in the three karyotypes tested rapid divergence of behaviour can occur (Dobzhansky and Spassky 1962). Woolf *et al*. (1978) carried out a selection experiment for positive and negative geotactic behaviour in three different stains of *D. pseudoobscura*. The geotactic scores of the parents and F1 flies indicate that both negative and positive geotactic behaviour in these strains are strongly influenced by genes on the X chromosome. Levene and Dobzhansky (1976) studied homeostatic drive counteracting selection for positive and negative phototaxis and geotaxis in *D. pseudoobscura*. Experiments are described with artificial selection for positivity and for negativity was deliberately made so weak that it only counterbalanced the natural selection or "homeostatic drive" and the effects of cross-migration. Under these conditions, the behaviour of the population artificially selected for positivity diverges only slightly from that of the population for negativity, but at least in females both populations move close to neutrality.

The initial experimental population of *D. persimilis* was photopositive and slightly geonegative. In this respect, the initial population of *D. persimilis* differed for the experimental population of *D. pseudoobscura* described by others, which was close to photo and geotactic neutrality. In *D. persimilis* as in *D. pseudoobscura*, photo- and geotactic selection was efficient in both positive and negative directions, In *D. persimilis* unlike in *D. pseudoobscura* the response to geotactic and photo tactic selection were clearly asymmetrical. Bidirectional selection for geotaxis in *D. persimilis* was effective in both directions and was more efficient than in *D. pseudoobscura* (Palivanov 1975). These findings suggest that *D. persimilis* differs considerably from *D. pseudoobscura* in the composition of the genes determining photo- and geotactic behaviour, most probably reflecting adaptations of these sibling species to different ecological niches. However, both species are capable of reacting quickly to external stresses by reorganising their gene pools and by correspondingly changing their behaviour.

Phototaxis

Phototaxis is a complex response to light. It has been studied in *Drosophila* since 1905 and it is a complex behavioural response involving several components of perception and neurological processing. Light must first be absorbed by the receptor cells and ellicit neural excitation. These signals must be transmitted across synaptic junctions to points where the information can be integrated and processed in the central nervous system. When at last motor signals are generated, the end point of the behavioural response can be scored as a motor response (Benzer 1967). Few reports are available on the development of orientation behaviour in larvae of *Drosophila* and information about the genetic contribution to such behaviour is very limited. Godoy-Herrera (1994) studied the developmental and biometrical aspects of larval photo response of *D. melanogaster*. The results suggest that the larval genetic structure involved in the expression of larval photoresponse of *D. melanogaster* depends on larval age. Godoy-Herrera *et. al*. (1992) studied the development of photoresponse in *D. melanogaster* larvae. The results show that response of *D. melanogaster* larvae to light varies with genetic background and developmental stage. The phenotypic variance of larval photoresponse associated with genetic differences is age-related. The response to selection for larval photobehaviour is also age-related. The results indicate that *D. melanogaster* larvae of different ages may use their photoresponse to influence the direction of their movements. Differences in photoresponse between larvae of various ages are related to epigenetic changes in the genetic architecture of photobehaviour.

Hirsh and Tryon (1956) suggested photo and geotaxis as heritable traits and proposed use of a multiple unit maze. Hadler (1964a,b) and many other workers have demonstrated the polygenic nature of genetic control on phototaxis in *D. melanogaster*. It has been suggested that selection might be more effective using older flies. Markow (1975) selected for maze photoreponse in

population having one or more chromosomes heterozygous for inversions, which restricted recombination. Restricting recombination in the first and third chromosomes reduced effectiveness of selection for positive phototaxis and the presence of inversions on all these chromosomes restricted selection response for negative phototaxis. Markow and Clarke (1984) found correlated response to phototactic selection. Artificial selection for positive and negative photolaxis was conducted in populations of *D. melanogaster* that was polymorphic at the sepia locus. These sex differences in phototactic behaviour may be due to sex-specific expression of autosomal gene or sex linkage of genes controlling phototactic behaviour. Major sex-linked genes affecting phototaxis have been identified in *D. melanogaster* (Markow 1975; Kohler 1977). The correlation between eye pigmentation and photobehaviour may be relevant in a broader evolutionary context. Among *Drosophila* species there is extensive variation in both eye pigmentation and photoresponse. Results of tests of phototactic behaviour suggest that optomotor response is relevant to phototactic selection experiments. Markow and Scavanda (1977), Kohler (1977) and Kohler *et. al*. (1980) observed that flies with less visual pigment tend to be less photopositive, this may be due either to their poor visual acuity or to an avoidance of high light intensity.

The genetic basis for the phototactic behaviour of *Drosophila* in the maze appears to be polygenic and populations of flies respond rapidly to selection for positive and negative phototactic behaviour (Hadler 1964a,b; Dobzhansky and Spassky 1967). Polygenes influencing phototactic behaviour in *D. melanogaster* probably reside in all chromosomes. The presence of inversion heterozygosity in any one chromosome seems to make little difference in effectiveness of selection. Recombination in the structurally homozygous chromosomes and segregation for the one balanced chromosome appear to have provided variation for selection to be effective. Markow (1975) reported that artificial selection has produced populations of *D. melanogaster*, which show either positive or negative phototactic behaviour. Reciprocal hybridisations between photo-positive and photo-negative populations of flies have revealed the X chromosome of *D. melanogaster* to be important in phototactic behaviour regardless of conditions which restricted genetic recombination during selection. The involvement of the X chromosome in the phototactic behaviour in *D. melanogaster* was first suggested by Hadler (1964a). Of the many genes that are expressed in the visual system of *D. melanogaster* adults, some affect larval vision. However, with the exception of one X-linked mutation, no genes that have larval-specific effects on visual system structure or function have previously been reported. Gordesky-Gold *et al*. (1995) described the isolation and characterisation of two mutant alleles that define the larval photokinesis A (lph A) gene, one allele of which is associated with a P-element insertion at cytogenetic locus 8E1-10. The observations suggest that the *lph A* gene affects a larval-specific aspect of visual system function. In the case of *D. pseudoobscura*, hybridisation of photonegative and photopositive strains failed to reveal any influence of the X chromosome on phototactic behaviour (Woolf 1972). *D. pseudoobscura* has a metacentric X chromosome, of which one arm is homologous to the left arm of the *D. melanogaster* third chromosome and the other arm is homologous to the acrocentric X chromosome of *D. melanogaster*. The repeated finding of sex-linkage for negative phototaxis in *D. melanogaster* and not in *D. pseudoobscura* suggests that the genetic systems controlling phototactic behaviour in these two species may not be completely homologous, Walton (1970) reported that negative phototaxis in *D. melanogaster* was dominant as well as sex-linked.

In *D. melanogaster*, during the mid third instar of larvae cease foraging and commence a period of increased locomotor activity referred to as wandering behaviour. Sawin-McCormack *et al*. (1995) quantified the wild type larval response to light during the foraging (first, second and early third instars) and wandering (last third instar) stages of development. Foraging larvae in the first, second and early third instars exhibited negative phototaxis. From the mid larval third instar, larvae showed a decrease in photonegative behaviour, until just before pupation when the response of wandering larvae to light became random. Larvae carrying three different mutations in the rhodopsin *RH1* gene continued to express negative phototaxis throughout both the foraging and wandering stages. These results suggest that the transition from negative phototaxis toward photoneural behaviour characteristic of the wandering third instar larva requires vision. It was found that phototaxis selection results in changes of fertility whereas it doesn't affect other indices of fitness to environmental conditions as well as the expression. The main polygenic systems of photolaxis inheritance are located in chromosome 2 and chromosome 3. Gibbs *et al.* (2001) reported that soluble guanylate cyclase is required during development for visual system function in *Drosophila*.

Hirsh-Hadler photomazes (Hadler 1964a,b) have been used in genetic investigations of phototactic behaviour in several species of *Drosophila*. Results of selection experiments and reciprocal hybridisation largely support a polygenic, additive mode of inheritance for photomaze behaviour in many species (Hadler 1964; Walton 1970; Markow 1975; Dobzhansky and Spassky 1967; Woolf 1972; Palivanov 1975; Markow and Smith 1977). Markow and Smith (1979) studied genetics of phototactic behaviour in *D. ananassae*. During this experiment, selection for photopositive and photonegative behaviour was carried out for 21 generations in *D. ananassae* by using Hirsh-

Hadler phototaxis mazes. The chromosomes that are important in influencing photo maze behaviour in *D. ananassae* are different from what has been observed by other workers of the *melanogaster* sp. group and the difference can not be entirely attributed to the chromosome rearrangements which have occurred during the evolution of these related species. The populations of *D. pseudoobscura* from the two locations were significantly different in both designs. These behavioural differences must be attributable to different genetic determinants. Seiger and Seiger (1979) compared the photoresponse in sibling sympatric species *D. pseudoobscura, D. persimilis* and *D. miranda*. The results suggest that photobehaviour appears to be the result of natural selection acting to optimize that trait relative to adaptation and fitness in a species population. *D. robusta* has been characterised as showing a low level of spontaneous phototaxis (Carson 1958). *D. hydei* showed a considerably higher level of photoresponse. Studies with *D. virilis* (Oshima *et al*. 1972) and *D. robusta* (Carson 1958) suggested that negative phototaxis measured in a maze was partially dominant. Analysis of lines of *D. pseudoobscura* differing in maze phototaxis demonstrates that genes responsible for phototaxis are on the autosomes (Woolf 1972). Dobzhansky *et al*. (1975) reported that the third chromosomes exert the strongest effect on phototaxis with the second, X and fourth chromosomes following in order of effectiveness. In *D. melanogaster* and *D. virilis* negative photoresponse is dominant, with X-linkage for the trait in *D. melanogaster*. The polygenes influencing *D. pseudoobscura* photoresponse are mainly on the autosomes. Thus, the genetic architecture of photoresponse differs among species. There can be correlated morphological changes to selection for photoresponse. There is evidence that species do differ in the genetic architecture of photoresponse and this may be related to their natural environment. Markow and Smith (1977) analysed the phototactic behaviour in *D. simulans*. The results suggest that phototactic behaviour in *D. simulans*, as in other *Drosophila* species is a polygenic trait. Hybridisation using divergent strains revealed that the genes controlling negative phototactic behaviour in *D. simulans* are autosomal, as opposed to *D. melanogaster* in which negative phototactic behaviour is very strongly sex-linked.

Diapause

Most insects living in the temperate and boreal zones spend a considerable period of the year in hibernal diapause and the survival during diapause plays an important role in determining the population sizes in the following seasons. Therefore, information on their activity during diapause is essential in order to understand their adaptations to seasonal environments and the dynamics of their populations. In *Drosophila* however, little information has been reported on behaviour during diapause. Adaptation to seasonal changes, such as diapause allow organism to persist throughout the stress of adverse conditions. These adaptations allow the organism to escape in time (Dingle 1978) by delaying their growth or reproduction and thus increasing their chances of survival. Many organisms rely on cues such as changes in photoperiod to measure time and initiate this escape response. Variation in these responses may be affected by both genetic and environmental factors (Dingle 1978; Danks 1987). Diapause has been investigated for many *Drosophila* species e.g. *D. robusta* (Carson and Stalker 1948; Levintan 1951) *D. littoralis* (Lumme *et al*. 1974; Lumme and Oikarinen, 1977; Lumme 1978), *D. deflex* Duda (Basden 1952, 1954a) D. *subobscura* (Basden 1954b), *D. auraria* complex (Kimura 1984) and *D. melanogaster* (Saunders *et al*. 1989; Izquierdo 1991; for references see Lumme and Lakovaara 1983).

Williams and Sokolowski (1993) studied the diapause in *D. melanogaster* females. Results suggest that diapause in *D. melanogaster* is inherited as a simple autosomal recessive trait with one isofemale line completely dominant to the other one. Maternal and cytoplasmic factors did not affect difference in diapause in these lines. The results of this genetic analysis of diapause in *D. melanogaster* open many avenues for the genetic dissection of this ecologically relevant trait. The genetic dissection of the ovarian diapause phenomenon in *D. melanogaster* can also be accomplished through various kinds of mutagenesis e.g. EMS, gamma radiation and transposable elements followed by screening for diapause mutants (Grigliatti 1986). Genetic and molecular characterisation of genes important to diapause in *D. melanogaster* should also shed light on the genetic control of time measurement in insects. Genetic studies using mutants have contributed to the recent advance in the analyses of physiological mechanisms of development or behaviour. In the study of diapause mechanism, hybridisation or backcross tests between strains that exhibit differences in diapause characteristics or artificial selection for specific characteristics of diapause have been extensively carried out (for review see Tauber *et al*. 1986). Saunders (1990) studied the circadian basis of ovarian diapause regulation in *D. melanogaster*. Females of a wild type strain of *D. melanogaster* and of several clock mutants (period), were able to discriminate between diapause inducing short days and diapause-averting long days with a well-defined critical day-length. The characteristics unique to the alternative developmental state of diapause (morphological stasis, increased thermotolerance, unique hormonal titles, metabolic cycles and cellular changes) are an indication that the continuous developmental programme is switched off and an alternative (diapause) genetic program is initiated.

Kimura (1988) studied male mating activity and genetic aspects in imaginal diapause in *D. triauraria*. The results suggest that the critical daylength and the dia-

pause duration inherited in a quantitative manner. Since no apparent difference was observed in the photoperiodic response or diapause duration of F_1 hybrids of reciprocal crosses or of progenies of backcrosses, genes controlling these traits are assumed to be linked to autosome(s). Analyses by hybridisation and artificial selection methods are not sufficient to fully understand the genetic control of such complex systems. Oleverio (1979) reported a new method to the analysis of complex genetic system using recombinant inbred lines. Kimura and Yoshida (1995) analysed the genetic basis of reproductive diapause in *D. triauraria*. The genetic study suggests that the difference in the photoperiodic response between the parental diapausing and non-diapausing strains of *D. triauraria* is due to genes three or four unlinked or loosely linked loci. It also appears that at least one of these loci is located on the X chromosome. Since this species has only three sets of chromosomes, two sets of autosomes and one set of sex chromosome. In addition, the effect of these diapause-promoting genes is assumed to be additive, because the photoperiodic response curves of recombinant inbred lines scatter around the response curves of F_1 hybrids which are heterozygous for these alleles. Diapause-associated gene expression was studied in *D. triauraria* using subtractive hybridisation. Two genes that were shown to be upregulated in diapausing flies by Northern hybridisation have similarity to genes encoding antifungal peptides of *D. melanogaster*, members of the drosomycin family (drosomysin CG10812, CG10813, CG10815 and CG11520). In addition a signal peptides and *Knot 1* domain are shared with them. The genes cloned from *D. triauraria* are tentatively named drosomysin like. However, the similarities between drosomycin like *D. triauraria* and the members of the drosomycin family in *D. melanogaster* are lesser than those between other homologous genes in these species. The drosomycin-like gene is expected to have a few copies, because at least two sequences having unique 3′-ends were obtained in Rapid Amplification of cDNA Ends (RACE), and multiple bands were observed in southern hybridization. Carson and Stalker (1948) reported reproductive diapause in *D. robusta*. The results suggest that *D. robusta* overwinters as an adult and that this hibernation period is preceded by a physiological change-over from egg production to the deposition of body fat. The factors, whether genetic or environmental or both, which may be responsible for the initiation of the diapause are unknown and will be the object of further investigation. A somewhat similar diapause has been described for *D. nitens* (Buzzati-Traverso 1944).

Kimura *et al*. (1993) reported the influence of gene flow on latitudinal clines of photoperiodic adult diapause in the *D. auraria* species complex. Earlier genetic studies of diapause are usually based on hybridisation and backcross tests between strains that exhibit different diapause characteristics and artificial selection for specific diapause traits. These studies have shown that quantitative traits such as critical daylength or diapause duration are usually controlled by polygenes (Tauber *et al*. 1986; Danks 1987). The expression of diapause involves a complex system whereby environmental signals are received integrated and converted to endocrine or cellular information required for the development or reproduction (Kimura and Yoshida 1995).

Lumme (1981) described a gene for critical day length character, which they localised to the fourth chromosome of *D. littoralis*. Many workers studied the genetics of diapause in other insects and found a polygenic basis of inheritance (see reviews in Beck 1980; Danks 1987; Denlinger *et al*. 1995). Lankinen (1986) studied genetic correlation between circadian eclosion rhythm and photoperiodic diapause in *D. littoralis*. The results suggest that the same pacemaker that is seen in the eclosion rhythm could also participate in day length, measurement after diapause. However, there are also non-correlated variable parts in the measuring systems of both traits, which may mask the correlated variation. Lakovaara *et al*. (1972, 1973) showed that adult reproductive diapause was under polygeneic control in *D. ovivorarum* and *D. littoralis*. It is quite difficult to analyse genetic features of diapause of drosophilid flies because of the lack of localised gene markers and of the threshold nature of photoperiodic diapause. The most extensive study on the genetics of diapause has been made in *D. littoralis* Meigen 1930 a member of the *virilis* species group by a Finnish research group (Lakovaara *et al*. 1972; Lumme 1978; Lumme *et al*. 1974, 1975; Lumme and Oikarinen 1977). Lumme and Keranen (1978) have demonstrated in cross-experiments with some mutants of its closely related species *D. virilis* sturtevant 1916 that the photoperiodic diapause of *D. lummei* is controlled by an X chromosome factor. Watabe (1995) studied genetic analysis of the photo-periodic diapause of *D. lummei* and the result suggest that another genetic unit may take part in the critical day length of *D. lummei* and it may not be located on sex chromosomes but on autosomes, although a furtheranalysis using mutant markers in needed to clarify this.

Diapause is a state of arrested development accompanied by physiology for somatic persistence. Among insects, diapause may occur in embryos, larvae, pupae or adults. At the adult stage reproductive diapause arrests development of oogenesis, vitellogenesis, accessory gland activity and mating behaviour. Reproductive diapause in *Drosophila* is proximally controlled by down regulation of the juvenile hormone, a phenotype that is also produced by mutants of the insulin like receptor InR, homologous to *C. elegans* daf-2.

Emigration behaviour

The importance of genotype-environmental interaction

has been demonstrated in the temperature-influenced emigration behaviour of *D. melanogaster* (Mikasa and Narise 1986). Genetic variation of the behaviour in a natural population appeared as qualitatively and quantitatively different response patterns. Mikasa and Narise (1989) found interactive effects of temperature and geography on emigration behaviour and productivity of *D. melanogaster* in Northern and Western Japan. Sakai *et al*. (1958) began the study on emigration response behaviour of *D. melanogaster* in laboratory. Mikasa (1990) studied the genetics of emigration behaviour of *D. melanogaster* in a natural population. The results suggest that most of genetic variance components for emigration activity was the additive genetic variance, although a small portion of dominance variance was detected. Over dominance is not related to the mechanism of the maintenance for genetic variation of emigration activity in a natural population of *D. melanogaster*. When there is a genotype × sex interaction for the same trait, the significant interaction can manifest itself in several ways as follows: (i) The additive genetic correlation between sexes for the same trait is less than unity (ii) There are different heritability, or (iii) Differences in the composition of phenotypic variation between sexes. Mikasa (1992) conducted an experiment to examine sexual difference of emigration activity and to quantify a few genetic parameters for emigration activity in each sex and the genes affecting the emigration activity operate differently between sexes of *D. melanogaster* in natural populations.

Temperature is one of the generally recognised important factors for *Drosophila* in its natural condition. Emigration system is a polygenic character and is also affected by temperature (Mikasa and Narise 1983). In addition, the interaction of genotype with temperature has been demonstrated in emigration response to temperature among laboratory strains (Tantawy *et al*. 1975). Mikasa and Narise (1986) reported the genetic variation of temperature-influenced emigration behaviour of *D. melanogaster*. The results suggest that the genetic variability for temperature-influenced emigration behaviour would provide evolutionary flexibility to a population under changing temperature conditions. Natural populations of *Drosophila* have shown seasonal changes with respect to gene arrangement, morphology, wing length, allozyme, resistance to desiccation and reproductive potential. Mikasa and Narise (1990) studied seasonal change in the temperature-influenced emigration behaviour of *D. melanogaster* in a natural population. Iliadi *et al*. (2002) studied sexual differences for emigration behaviour in two contrasting climatic and geographical populations. A highly significant difference between sexes in emigration activity was found for both localities. Emigration activity of females appeared to be higher than that of males. They also reported that the flies' geographic origin affects emigration behaviour. Mikasa (1988) reported the intraspecific variation in the effects of mating on the emigration response behaviour and fecundity of *D. melanogaster*. Mikasa (1990, 1992) conducted a quantitative genetic analysis on emigration response behaviour using 140-second chromosome lines of *D. melanogaster*. The results suggest that the genes affecting emigration activity would operate differently between sexes of *D. melanogaster* in natural populations. Narise and Narise (1991) isolated two chemical substances from adult flies of *D. melanogaster*, which affect the emigration activity of genetically different strains. These substances were identified as palmitic acid and olic acid respectively.

Circadian rhythm

The spectrum of biological processes controlled by circadian clocks in living organisms ranges from the daily sleep/wake cycle and level of various enzymes/hormones to synthesis and cell division. These circadian rhythms indeed have a genetic basis. Circadian rhythms have four well-defined characteristics: (i) The rhythm can persist in the absence of environmental cues, such as light or temperature, (ii) this endogenous rhythm can be tuned by oscillation of environmental stimuli (entrainment); (iii) the phase of the rhythm can be reset by brief environmental stimuli and (iv) the rhythm is little affected by temperature. These features of circadian rhythms can be found in a variety of organisms, suggesting that circadian rhythm is an ancient and highly conserved process and raising the possibility that different organisms have similar clock mechanisms (Iwasaki and Thomas 1997).

The *per* gene of *Drosophila* is one of the best-studied components of the circadian clock (Myers *et al*. 1995; Sehgal *et al*. 1995). Recently a new *Drosophila* clock gene has been identified, called *timeless* (*tim*). In *tim* mutant circadian rhythm is absent and per mRNA levels do not oscillate. Konopka and Benzer (1971) discovered the X-chromosome-linked period (*per*) mutations that altered the daily rhythms of locomotor activity exhibited by *Drosophila* and its pupal eclosion. Our current understanding of the molecular regulation of circadian rhythmicity in *Drosophila* comes from studies integrating genetics and molecular biology, and *Drosophila* is perhaps one of the best models in the field of circadian rhythm research. Following the initial discovery of the *per* (period) gene some decades ago, several other genes, e.g. *timeless*, *dclock*, *cycle* and *double-time*, that function in the generation of circadian rhythm, have been identified during the past years. Molecular genetic studies have provided exciting insights into the regulation of the body clocks. Heterodimeric complexes of positive elements (*dclock* and *cycle*) and their interactions with feedback loops and negative elements of *per* and *tim* genes and their products have been identified and these are providing cues to the general layout of the molecular looks that generate circadian rhythms. The *lark* gene, which encodes

an RNA-binding protein, might function as a regulatory element in the circadian clock output pathway controlling pupal eclosion rhythms (for review see Subramanian and Lakhotia 1999; Subramanian *et al*. 2003).

The period (*per*) gene of *D. melanogaster* has been studied extensively at the molecular level, and its gene structure and rather complicated pattern of expression have been described (for review, see Hall and Rosbash, 1988). Peterson *et al*. (1988) analysed and compared the circadian locomotor activity rhythms of *D. melanogaster* and *D. pseudoobscura*. The rhythms of *D. pseudoobscura* are stronger and the periods shorter than those of *D. melanogaster*. *D. melanogaster* flies have been transformed with a hybrid gene containing the coding region of the *D. pseudoobscura* period (*per*) gene. Free-running locomotor activity and eclosion rhythms of *D. melanogaster* mutant at the disconnected (*disco*) are substantially different from the wild-type phenotype. Dowse *et al*. (1989) have reanalysed the locomotor activity data using high-resolution signal analysis. The results suggest that the *disco* mutants are much like flies expressing mutant alleles of the period gene, as well as wild-type flies reared throughout life in constant darkness.

Adults of *D. melanogaster* had their locomotor activity monitored under conditions of cycling light and dark (12 h each per cycle). The elementary behaviour of wild type flies under these 'LD' conditions fluctuated between level of high and level of low activity. Alt *et al*. (1998) reported that the period gene controls courtship song cycles in *D. melanogaster*. The per gene has been well characterised at the molecular level (for a review see Hall 1995), including efforts to determine which region of the gene is responsible for observed effects on song. Allemand and David (1984) studied genetical aspect of the circadian ovipositon rhythm in *D. melanogaster*. There is evidence of drift in laboratory strains. Chromosome substitutions between isofemale lines demonstrated a polygenic inheritance with a significant effect of the three major chromosomes.

Application of genetic variants and molecular manipulations of rhythm-related genes have been used extensively to investigate features of insect chronobiology that might not have been experimentally accessible otherwise. The *Drosophila* circadian clock consists of two interlocked transcriptional feedback loops. In one loop, dClock/Cycle activates *period* expression and Period protein then inhibits dClock/Cycle activity. dClock is also rhythmically transcribed, but its regulators are unknown. *vrille* (*vri*) and *Pdp1* (encodes Par Domain Protein 1) encode related transcription factors whose expression is directly activated by dClock/Cycle. Vri and Pdp1, together with dClock, comprise a second feedback loop in the *Drosophila* clock that leads to a rhythmic expression of *dClock*, and probably of other genes, to generate accurate circadian rhythms (Cyran *et al*. 2003).

Circadian clocks in a wide range of organisms are thought to consist of two inter dependent transcriptional feedback loops. In *Drosophila*, the first loop has been well characterised and controls rhythmic period expression. Allada (2003) defined a role for a transcriptional activator and a repressor in the second feedback loop. The post translational modification of Clock protein is critical for the function of a circadian oscillator. By genetic analysis of a *D. melanogaster* circadian Clock mutant known as Andante, which has abnormally long circadian periods Akten *et al*. (2003) show that casein kinase 2 (CK2) has a role in determining period length. Most living things have a daily cycle that reflects the rising and setting of the sun. The term used to describe this coincidental cycle is circadian rhythm, which comes from the Latin *circa Diem* literally about a day. In *Drosophila*, a number of key processes such as emergence from the pupal case, locomotor activity, feeding, olfaction and aspects of mating behaviour are under circadian regulation.

Although we have a basic understanding of how the molecular oscillations take place, a clear link between gene regulation and downstream biological processes is still missing. Ceriani *et al*. (2002) reported that genes regulating various physiological processes are under circadian transcriptional regulation, ranging from protein stability and degradation, signal transduction, heme metabolism, detoxification and immunity. By comparing rhythmically expressed genes in the fly head and body, they found that the clock has adapted its output functions to the needs of each particular tissue, implying that tissue-specific regulation is superimposed on clock control of gene expression. The fruit fly, *D. melanogaster* has been an object for circadian rhythm researchers over several decades. Behavioural, genetic and molecular studies helped to reveal the genetic basis of circadian time keeping and rhythmic behaviour. On the contrary, mammalian rhythm research until recently was mainly restricted to descriptive and physiologic approaches. As in many other areas of research, the surprising similarity of basic biologic principles between the little fly and our own species, boosted the progress of unraveling the genetic foundation of mammalian clock mechanisms (Stanewsky 2003).

Conclusion

The aim of this review was to summarise the studies revolving around the genetical aspects of non-sexual behaviour of different species of *Drosophila*. The genetic analysis remains the best means to define mechanisms and to begin the process of assigning the contributions of genes to behaviour. The observation that behavioural mutants isolated in the laboratory are mostly pleiotropic, mild alleles relative to the null phenotype links them mechanistically with the kinds of genetic variation that

exist in nature. This fundamental pleiotropy of the behavioural genes suggests that we need to think in terms of overlapping networks, rather than simple pathways, in order to do justice to the complexity of the system.

Geotaxis has long been important for experimental behaviour genetic analysis. Once the genes that affect geotaxis have been isolated and genetically characterised, it will be possible to carry out chromosomal and hybridisation analysis to construct flies of a known genotype. The fusion of the molecular genetic perspective of genetic dissection with the interaction perspective of quantitative/biometrical genetics should provide a powerful analytical framework to understand the biological bases of behaviour. Applications of genetic variants and molecular manipulations of rhythm related genes have been used extensively to investigate features of insect chronobiology that might not have been experimentally accessible otherwise. In *Drosophila*, a number of key processes such as emergence from the pupal case, locomotor activity, feeding, olfaction and aspects of mating behaviour are under circadian regulation.

The genetic study of neural, hormonal and behavioural control mechanisms has been done by a thoroughly different approach, by analysing of the role of single genes on the one hand and of dissecting physiological processes by manipulating the genotype on the other. If the functional portions of these molecules have been relatively conserved in evolution, molecular genetic methods could be used to introduce the genes into wild populations of pest insects, rendering females conditionally unreceptive.

The genetic dissection of the ovarian diapause phenomenon in *D. melanogaster* can also be accomplished through various kinds of mutagenesis for example EMS, gamma radiation and transposable elements followed by screening for diapause mutants. Genetic and molecular characterisation of genes important to diapause in *D. melanogaster* should also shed light on the genetic control of time measurement in insects.

The natural population of an organism maintains a large amount of genetic variation. The maintenance of the variation is the fundamental premise of evolution and evolution is caused by the change in genetic components of population. Most of the genetic variance components for emigration activity were the additive genetic variance, although a large portion of dominance variance was deleted. Our understanding of molecular organisation of the circadian clock is not yet complete. Understanding the molecular bases of the clock in *Drosophila* will shed light on its working and influence on the behaviour and physiology of higher animals and humans.

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