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1. Models of sexual selection

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Models of male-male competition and of female choice will be briefly reviewed. Male-male competition can lead to a "runaway" process—i.e. the extreme exaggeration of male traits—without any female choice. In models of female choice, particular attention will be paid to the following question: are the traits preferred by females necessarily such as to increase fitness in contexts other than mating, or can traits that lower viability also evolve because of female choice?

2. What is unique in the mechanism of sexual selection?

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The extravagant characters which are attributed to the consequences of sexual selection function as signals, to attract mates and to deter rivals. Unfortunately the definition of sexual selection includes characters which are not signals. These other characters pose no problem to evolutionary theory. I suggest that the evolution of signals in general is different from that of characters which are not signals. The difference is especially exaggerated in the case of signals which evolved to solve conflicts about reproduction. Signals evolve to be reliable and hence to incur a cost on the signaller while other characters evolve to be useful with the least cost.

I shall point to the properties of the mechanism of signal selection as a unique evolutionary mechanism in which the cost rather than the efficiency of the character selects for the character and suggest a test to the theory. I shall point to several evolutionary problems, such as those of altruism and the evolution of feathers, horns and species-specific characters, which may be resolved with the help of the model I propose for the evolution of signals in general.

3. Sexual selection and the evolution of bird songs

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Male songbirds produce extremely elaborate songs, which are the acoustic equivalent of such visual extravagances as the peacock's tail. Darwin suggested that they were the result of sexual selection by female choice, a view which has received some support from contemporary models of sexual selection. Until recently there has been a lack of experimental evidence to support this view, but bird songs provide an almost ideal system with which to test predictions from sexual selection theory under controlled laboratory conditions. In a modern acoustics laboratory, complex songs can be broken down into constituent elements in a way analagous to sequencing proteins in molecular biology. Captive female songbirds are treated with oestradiol to simulate breeding condition, and then exposed to recordings of natural or synthetic songs and their responses quantified. Song structure can be modified while confounding variables from male or territory quality are controlled or completely eliminated. When linked to parallel studies on song structure and reproductive success in the field, the results suggest that Darwin was right.

4. Bower building and sexual selection theory

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The unique behaviours of bowerbirds have long been of interest to naturalists and recently they have attracted the attention of evolutionary biologists interested in sexual selection theory.

Comparative studies of these species offer the opportunity to test models of sexual selection that have proven difficult to test. Here I describe a comparison of two closely related species: the spotted bowerbird (*Chlamydera maculata*) and the great bowerbird (*C. nuchalis*). We found that the bower and how it is used in display has diverged radically between these two species. Outgroup comparisons shows a high degree of similarity in display traits with the great bowerbird suggesting that (1) most of these display characters have had a relatively conservative pattern of evolution and (2) since the divergence of the species most changes have been associated with the lineage leading to spotteds. It is hypothesised that the changes associated with the evolution of the spotted bower are related to selection on males to build a bower that provides protection to visiting females. The adequacy of the protection model in explaining changes in bower structure and the match between design and function suggest that the observed changes are adaptive. This implies that the runaway model is not sufficient to explain the evolution of elaborated display traits in bowerbirds.

Sexual selection models as evolutionary theories

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Darwin postulated two mechanisms of sexual selection: male competition and female choice. Males would fight for possession of the females; females would mate preferentially with the most attractive and highly ornamented males. Female choice would thus explain the evolution of characters for male display. Fisher later argued that the female mating preference evolved by the sexual selection it produced: male offspring would inherit the preferred character from their fathers and the preference from their mothers; selection of the one would thus select the other. Since 1962, many different genetical models of Fisher's theory have been formulated and analysed mathematically or by computer simulation. Models have been formulated in terms of haploids or diploids and with either single gene or polygenic variation in preferences and preferred characters.

To provide a general explanation of the evolution of a character, a model must obviously be realistic in its genetical assumptions and give rise to the phenomenon to be explained. Equally important, it must give rise to that phenomenon at a realistic rate and from realistic and general assumptions about the starting point. The realism and generality of sexual selection models are examined from these points of view.

The evolution of female mating preferences

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Fisher's runaway process cannot account for the evolution of extravagant male ornamental traits, like the peacock's tail, when mate choice by females carries a cost (e.g. the "sexy son"). Neither will exaggeration occur when genes for the male trait also have "good genes" effects in either sex. However, when there is biased mutation acting on the male trait costly choice can evolve (e.g. the "sexy phoenix"). In addition, bistability and cycling behaviour are observed. These results confirm and extend previous studies of the "handicap principle" that also showed the evolution of costly choice for exaggerated male traits.

7. Measuring the cost of sexually selected characters

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Most genetic models of sexual selection imply that evolutionary elaboration of sexually selected characters is brought to a halt by countervailing costs of the characters. Furthermore, such costs may be important constraints on which characters are subject to elaboration by sexual selection.

Although several sexually selected characters have now been conclusively identified, studies of their costs are still a rarity. This talk will consider the relative merits of phenotypic and genetic approaches to measuring costs.

8. Patroclinous inheritance of egg characters: genomic imprinting?

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Cumulus cells are normally dissociated from each other, and from the egg they surround, by hyaluronidase. The cumulus cells from C57BL/6By mice are more susceptible to hyaluronidase in vitro than those surrounding BALB/cBy eggs (Bander, Watson and Shire, 1988, *J. Reprod. Fertil.*, *84*, 709-714). Eggs from reciprocal F1 females differed significantly in their susceptibility, closely resembling those from females of the *paternal* strain. Such differences, and their direction, rule out autosomal and sex-linked nuclear factors and maternal cytoplasmic and mitochondrial differences. Positive paternal and negative maternal effects both fit the F1 data. Measurements on all four reciprocal F2 hybrids showed that F2 crosses with the same paternal contribution had the same mean, whilst those with the same maternal contribution differed significantly, eliminating negative maternal effects. All F2 crosses had low variances. The only model that fits implies that somatic cells surrounding eggs contain information that is determined by the paternal origin of those cells. This is transmitted to both sexes of offspring, but only by males that inherit the information. Evidence from cross fostering and from crosses between CXB recombinants support the model, as do measurements on the susceptibility of the zona pellucida to proteases.

9. Transposable genetic elements in the genome of the mosquito, *Aedes aegypti*

Ann Warren and Julian Crampton

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Ae. aegypti, the major urban vector of yellow fever, dengue and dengue haemorrhagic fever, is the object of control measures on an immense scale. Many of the existing control methodologies are fraught with problems and it is envisaged that manipulation of the *Ae. aegypti* genome may eventually provide a novel means for controlling this vector population or its ability to transmit pathogens. Transposable genetic elements (TGEs) have been successful in genetic manipulation of a number of organisms. In the same way, indigenous TGEs from *Ae. aegypti* may prove useful tools for the manipulation and characterisation of this mosquito genome.

Using a number of parallel approaches, we have isolated several *Ae. aegypti* sequences sharing biochemical and structural properties with previously characterised eukaryotic retrotransposons. Evidence will be presented for the presence of retroposon-like elements within the *Ae. aegypti* genome. Their potential as tools for characterisation and manipulation of the *Ae. aegypti* genome, with a view to enhancing existing control methods will further be discussed.

10. DNA transfection of an *Aedes aegypti* mosquito cell line

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The genetic manipulation of an organism requires an understanding of processes such as gene recombination, expression and regulation. To study these phenomena in *Aedes aegypti* various techniques for introducing cloned DNA sequences into cultured cells have been attempted. Details and comparisons of these methods, including calcium phosphate, polybrene, lipofectin, and electroporation mediated gene transfer will be described.

The DNA used for transfection was a *Drosophila* P transposable element vector (Stellar and Pirotta, 1985 *EMBO J.*, *4*, 167), with positive selection of transformants by G418 antibiotic resistance. Problems associated with these factors will be discussed, together with an outline of current analyses of transformed cell DNA and possible developments in DNA vector constructs.

11. Transformation of the mosquito *Aedes aegypti* using the "P" element, isolated from *Drosophila melanogaster*

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The "P" element, a transposable genetic element isolated from *Drosophila melanogaster*, is being used as a DNA transformation vector in the manipulation of the genome of the mosquito *Aedes aegypti*.

A micro-injection system has been developed for the introduction of DNA into the developing embryo. Genomic DNA analysis of individuals and their progeny, arising from injected embryos, has revealed putative P mediated transposition events. Further characterisation of similar transformants should determine the precise nature of these integration events.

The expression of the *Drosophila* transposase gene is also being studied. This gene, found on intact P elements, is co-injected with the vector plasmid and its protein product is essential in the mechanism of transposition. Evidence of transposase expression on introduction of the gene into the mosquito embryo, would further support the theory that the *Drosophila* P element may be used in the germline transformation of the mosquito.

12. The segment polarity gene *patched* is involved in pattern formation imaginal discs of *Drosophila melanogaster*

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Many of the genes involved in pattern formation in the *Drosophila* embryo have been identified and characterised. It is now becoming apparent that some of these genes are also required for correct imaginal development.

Patched is a member of the segment polarity class of segmentation genes. We have identified adult viable alleles of *patched*. Hetero-allelic combinations of embryonic-lethal and viable alleles produce a range of imaginal phenotypic abnormalities which include mirror-image duplications and triplications within the anterior compartment of the wing and pattern disruptions and increase in bristle number in the thorax, leg, eye and antenna. Similar disruptions are found when discs are metamorphosed after culture of embryos homozygous for embryonic lethal alleles (see poster abstract by Amanda Simcox, Ian Roberts and J. Robert S. Whittle).

In situ hybridisation of RNA probes from *patched* show that it is expressed in a stripe along the antero-posterior compartment border of most imaginal discs during the third instar, overlapping the expression pattern of *wingless* in the ventral half of the leg disc.

Mitotic recombination clones homozygous for *patched* embryonic lethal alleles show "domineering" non-autonomy even though the *patched* gene encodes a putative transmembrane protein (see abstract by A. Hidalgo, I. Guerrero, Y. Nakano, A. Taylor, A. Forbes, R. Phillips and P. Ingham). These results support the idea that *patched* is involved in the transduction of positional information between cells.

13. A population genetic model of sexual selection without linkage disequilibrium

Alan Grafen

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A population genetic model is presented which demonstrates (1) that Zahavi's handicap principle works, and (2) that sexual ornaments and female preferences can evolve and be maintained without linkage disequilibrium. It is further argued that sexual selection is likely in nature to be largely independent of linkage disequilibrium. The model has two autosomal loci in a haploid population with discrete generations. Males vary for environmental reasons in a continuous trait (called "quality") which females would be selected to use in mate choice if they could observe it. The adver-

tising locus determines the degree of expression of a sexual ornament in males as a function of quality. The preference locus determines a female's preferences over sexual ornaments. The advertising and preference rules specified by an uninvasible pair of alleles are found. Under suitable conditions, they specify that males advertising should increase with quality, and that females should pay costs to use this honest signal in mate choice.

14. Fisher's 'runaway process' in a cline: a model of reinforcement

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A two locus model of Fisher's "runaway process" is combined with selection against heterozygotes at a third locus to find whether pre-mating isolation will evolve to reinforce post-mating differences. In a single population, the increase in frequency of both preference and trait caused by "runaway process" is enhanced by reinforcement. However, because one race quickly becomes extinct, this increase is slight and the outcome is dominated by the "runaway". In a hybrid zone where the two races co-exist, reinforcement can occur through the "runaway process", but only under the very stringent conditions of strong preference and low hybrid viability. Reinforcement leads to increased pre-mating isolation and an increase in the width of the hybrid zone. When preferences are asymmetric and there is reinforcement, clines in preference, trait and the locus under heterozygote disadvantage all advance toward the more weakly preferred race.

15. Further evidence for mate choice in the seaweed fly *Coelopa frigida*

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The likelihood that pairs of adults will mate appears to be associated with their size. Evidence will be presented that the mating success of females is also dependent upon their *Adh* genotype. Furthermore, females possessing certain genotypes appear to show higher mating success when paired with particular male genotypes.

16. Male mate choice in seaweed flies?

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Mating success has been determined in pairs of seaweed flies (*Coelopa frigida*) derived from a stock homozygous for the *AdhC* allele. Animals of this stock are known not to exhibit female choice. The mating success of pairs was not associated with the size of the male, but a strong positive correlation was found with female size. With respect to the difference in size between male and female, only when the males were very much larger than the females was mating success low. Preliminary results from trials in which a male was allowed a choice of one small and one large female will be described. The mechanisms and consequences of male mate choice will be discussed.

17. Interspecific courtship in *Cepaea*

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The courtship of *Cepaea nemoralis* and *Cepaea hortensis* are compared, and shown to be very similar. Courtship between the two species is common when they have a choice between members of their own or of the other species. Paradoxically, when snails of each species were paired up without a choice of conspecifics, interspecific courtship was rare. Interspecific copulation is very rare. There is no evidence of reproductive character displacement when the courtship behaviour of snails from mixed- and single-species sites is compared, although the test for this is not very powerful. The problem of looking for assortative mating in simultaneous hermaphrodites is discussed.

18. Alcohol dehydrogenase and adaptive behavioural responses of larvae in sibling species of the *Drosophila melanogaster* species subgroup

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Drosophila larvae show toxic and kinetic responses in relation to food and metabolic byproducts in the environment. A kinesis is expressed as a change in the rate of performance of a behaviour, such as locomotion (orthokinesis), or feeding (phagokinesis). These responses are likely to be of adaptive significance when environmental resources are patchy in distribution. Ethanol is attractive to *D. melanogaster* larvae at low concentrations, but aversive and toxic at high concentrations. Variant alleles coding for the enzyme alcohol dehydrogenase (Adh^{F}, Adh^{S}, Adh^{UF}, and Adh^{null}) differ in their effects on the kinetic responses of larvae to ethanol and acetaldehyde. Two variant alleles for alcohol dehydrogenase in the endemic island species *D. mauritiana* and their effects on larval behaviour and alcohol tolerance are described. The kinetic responses of *D. mauritiana* and the cosmopolitan sibling species *D. simulans* are those expected of alcohol sensitive species.

19. Identification of DNA damage inducible proteins in higher plant cell suspension cultures

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Higher plants show a range of stress responses to stimuli including heat shock, anaerobiosis and saline stress. We have examined the possibility that plants may respond to the effects of DNA damaging agents by mounting a stress response analogous to the SOS system of *E. coli* or the induction of *DIN* genes in yeast. Cell suspension cultures were generated from callus of parsley, carrot and oat. The cultures showed coupled growth kinetics, indicating unstressed growth conditions. In order to test whether cell suspension cultures can respond to stress in a similar way to the whole plant, the patterns of protein induction following heat shock were analysed by 1- and 2-dimensional gel electrophoresis.

Ultraviolet light at 254 nm and the mutagens 4-nitroquinoline-1-oxide and mitomycin C were used as DNA damaging agents. They caused little change in *in vivo* protein synthesis analysed by 1-D SDS-PAGE, but 2-D separation revealed changes in the protein profile of carrot due to NAO and MMC. Induced and enhanced proteins were observed, as well as "downshifted" proteins. This evidence suggests that higher plant cells can respond to DNA damage by changes in gene expression. The significance of these results will be discussed in the light of current knowledge of DNA repair systems.

20. The *vasa* gene of *Drosophila melanogaster*

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Vasa is a maternally-active gene involved in the specification of correct anterior-posterior positional information in the embryo. The function of *vasa* is also required at a very early stage in oogenesis, since in females homozygous for a deletion of *vasa*, germ-line development usually becomes aberrant at the time of differentiation of the oocyte. Females homozygous for weaker alleles of *vasa* develop eggs, but these are abnormal; the resulting embryos lack their pole cells and show abnormal posterior development. Males homozygous for a *vasa* deficiency (or for the weaker alleles) are indistinguishable from wild-type in their viability or fertility, indicating that the requirement for *vasa* is specific to the female germ line.

We have isolated and characterised the *vasa* gene (Lasko, P. F. and Ashburner, M., *Nature*, *335*, 661–667). The predicted *vasa* protein exhibits 29·1 per cent amino acid identity to murine eukaryotic initiation factor-4A (eIF-4A) over a 376-amino-acid overlap which includes the eIF-4A ATP-binding site. Together with seven other proteins, from *E. coli*, yeast, mice, and man, *vasa* and eIF-4A form a new protein family. The family includes a murine protein, PL10, whose expression is specific to the male germ line, and which shares 47 per cent amino acid identity to *vasa* over the same 376-amino-acid overlap.

21. Structure, function and regulation of the gap genes in *Drosophila*

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The metameric pattern of the *Drosophila* embryo is generated by a dynamic system of spatial cues at the blastoderm stage of embryogenesis. The genes providing the molecular basis for this interaction are defined through their mutant phenotypes, which show characteristic disruptions of the segment pattern (segmentation genes) or transformations of segment identity (homoeotic genes). Segmentation genes are grouped into three broad classes: "gap genes" subdivide the longitudinal axis of the embryo, "pair-rule genes" establish alternating segmental units and the "segment polarity genes" establish the sequence of pattern elements within each segmental unit.

The gap genes are at the top of the zygotic gene hierarchy and are directly regulated by maternally provided factors. Three gap genes, namely *hunchback*, *Krüppel* and *knirps* have so far been analysed more closely. All three contain presumptive DNA-binding finger domains and are therefore most likely transcription factors, which directly regulate the expression of the pair-rule genes and possibly also the homoeotic genes. Previous results suggested that the gap genes regulate also each other, but new experiments show that these interactions are more complex. It appears that each of the gap genes has a very specialized role and that their functions are insufficiently described by the current models of pattern formation in the *Drosophila* embryo.

22. Trans-acting modifiers of homoeotic gene function in *Drosophila*

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In order to identify potential regulators or targets of homoeotic gene activity in *Drosophila*, we have screened for mutations that behave as dominant enhancers or suppressors of the phenotype of a variety of dominant homeotic mutations. The isolation of mutations that behave as dominant suppressors of the heterozygous adult *Polycomb* phenotype (transformation of second and third leg to first leg) has led to the identification of twelve loci not previously known to be involved in the determination of segment identities in *Drosophila*. Genetic characterization of several of the new loci has shown that their activity is required for the proper determination of segment identities. The nature of the homoeotic transformations associated with mutations in several of the new loci are formally consistent with a function as upstream activators (or downstream targets) of the homoeotic loci of the *Antennapedia* and *bithorax* complexes. A combination of genetic and molecular techniques are being used to determine the role of the new loci in *Drosophila* development and to determine the nature and directionality of their interaction with other homoeotic loci in *Drosophila*.

23. The genetic control of intrasegmental pattern in *Drosophila melanogaster*

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Classical studies of pattern regulation in the insect epidermis have led to two contrasting models for the positional specification of cells. One of these postulates that cells read their position in the segmental field in response to the level of gradially distributed diffusible morphogens, whereas the other proposes that positional specification depends only upon local interactions between cells.

The segment polarity mutations of *Drosophila* cause pattern perturbations in every segment of the larva, suggesting them to be intimately involved in the specification or interpretation of positional information. Molecular analyses have revealed that they are a structurally and probably functionally heterogeneous class. Some, such as *engrailed* and *gooseberry* encode DNA binding proteins which are most likely involved in cell

autonomous responses to positional cues generated in the blastoderm. By contrast, the protein product of *wingless* has similarities to a mammalian secreted protein, *int-1*, and consistent with this structure, *wingless* appears to mediate signalling between cells after the embryo has gastrulated. Earlier studies suggested that the response of cells to the *wingless* signal depended upon the expression of a fourth segment polarity gene *patched*. We have cloned the *patched* gene and find that it encodes a putative transmembrane protein. We will describe the pattern of expression of the gene in developing embryos and its interaction with other members of the class. Our results support models of positional specification which invoke local interactions between neighbouring cells rather than responses to long range diffusible signals (morphogen gradients).

24. *Wimp*, a maternal-effect mutation affecting segmentation in *Drosophila*

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Metameric pattern in *Drosophila* requires the action of a specific set of segmentation genes. With the action of each successive class of genes (material → gap → pair-rule → segment polarity), spatial domains within the embryo become increasingly refined. Mutations described to date can be assigned a position within the hierarchy based on their phenotypes and time of action. However, there are genes that have escaped detection because their mutations have subtle cuticular phenotypes or do not make cuticle, have multiple functions, or have maternal contributions which overshadow their zygotic requirement.

We have been characterising one such gene, the *wimp* (*wmp*) locus, a dominant maternal-effect gene that acts as a trans-regulator of a large subset of early pattern forming genes. When derived from a *wmp*/+mother, embryos heterozygous for a number of segmentation genes including *Krüppel* (Kr), *hairy* (*h*), even-skipped, and *fushi tarazu* (*ftz*) do not survive (P. Ingham, pers. comm.). The cuticular phenotype of these lethal embryos resembles that of the mutant gene tested. *wmp*/+ mothers which are heterozygous for several maternal genes such as *bicoid* (i.e. *wmp*/*bcd* mothers) yield dead progeny which mimic the phenotype of the material gene tested. Consistent with this observation, the level of protein expression of many segmentation genes such as *ftz* is reduced in embryos derived from *wmp*/+mothers. This reduction in protein is also seen for a *ftz-βgal* fusion gene, suggesting that the interaction is at the level of transcription rather than translation.

In addition to a reduction in the level of segmentation gene protein expression due to the maternal effect, the pattern of expression is disrupted in *wmp* homozygotes, wild-type for all other segmentation genes. Therefore, *wmp* has a zygotic function. Homozygous *wmp* embryos show a strong segmentation phenotype and cellularisation defects, presumably due indirectly to interactions with gene(s) required for these processes.

Using genetic duplications and deficiencies of the locus, we have shown that the existing *wmp* allele represents a change-of-function for the locus (ncomorph). To help define its role during normal development, we have isolated a *wmp* revertant (loss-of-function allele) and have mapped the locus to an ~80kb region near *red* (88B). Thus, the *wmp* locus represents a novel class of genes required for correct pattern to be established. The scope of both the maternal and zygotic contributions of the *wmp* mutation implies that it is involved in a general function of early development, such as that of a general transcription factor. We are currently characterising the putative revertant, refining the molecular mapping data, and screening for additional *wmp* alleles.

25. How, and how precisely, is the initial pattern of homoeotic gene expression established on *Drosophila* blastoderm?

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The initial patterns of homoeotic gene expression in the blastoderm of *Drosophila* are controlled by the activities of maternal and zygotic gap gene products, and refined by the action of other segmentation genes.

We will discuss experiments which suggest that the role of the posterior maternal determinants is mediated primarily by their effects on the distribution of maternal *hunchback* protein. We shall also discuss observations which suggest that the initial

positional cues available in the early blastoderm establish domains of activation in the Bithorax complex which correspond to double segment units.

26. On the specificity of expression of the *yellow* gene of *D. melanogaster*

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The *yellow* (*y*) gene of *Drosophila* encodes a product necessary for the pigmentation of a variety of larval and adult cuticle structures. Using P-element mediated transformation, we have assessed the DNA sequence requirements for the correct spatial pattern and phenotypic expression of *y* in the late embryo/larvae. The wildtype larval phenotype requires both the regions between -294bp and -92bp and a portion of the single intron of *y*; the sequence element located within the intron can act in a position independent manner to effect the wildtype larval phenotype. The larval expression pattern was examined by tissue *in situ* hybridisation experiments and by staining germline transformants derived from various *y/LacZ* fusion constructs. The expression of *y* in larvae is restricted to the mouthparts, microsetae, and anal plates. While the -294bp to +194bp region alone cannot effect a wildtype pattern, this region in conjunction with the intron is sufficient to drive *Bgal* expression in an essentially wildtype pattern. Our data further suggests that the -294bp to -92bp region contains element(s) which specify the larval pattern and that the element(s) in the intron normally act to enhance the level of expression necessary for the wildtype larval phenotype.

27. Molecular genetics of the complex *suppressor of forked* locus of *D. melanogaster*

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The *suppressor of forked* (*Su(f)*) locus is the most proximal gene in the euchromatic portion of the X chromosome of *D. melanogaster*. The phenotypes of mutations of *su(f)* indicate that it has a cell autonomous vital function, and also acts in trans to affect the phenotype of some unlinked mutations which have insertions of retroviral-like transposable elements into introns. All mutations fall into one complementation group with respect to this modifying phenotype, but there is some intra-allelic complementation between lethal mutations of *su(f)*. In order to investigate both this and the euchromatic/heterochromatin transition, we cloned the *su(f)* region by P element tagging. There are single copy sequences embedded in repeated sequences. Single copy sequences hybridise to the very proximal polytenized β-heterochromatin of the *X* chromosome in squashes of salivary glands. DNA lesions associated with *su(f)* mutations are clustered and this interval is transcribed to give 3 RNAs. Analysis of cDNAs predict that one protein product of the *su(f)* gene has a molecular weight of 80 kD, and shows no significant homology to other proteins sequences in databases. It has an unusual C terminal region, largely devoid of alpha-helical or beta sheet structures. Data on the nature of the repeated sequences will also be presented.

28. Allocating cells in the *Drosophila* embryo

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The pattern of expression of some segmentation genes in *Drosophila* has been studied using antibody methods for light and electron microscopy.

29. Mitotic cell division during *Drosophila* development

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When *S*-phase is prevented in wild-type *Drosophila* embryos by injecting aphidicolin, centrosome replication continues, together with other aspects of cyclical M-phase activity. If aphidicolin is injected when nuclei are in the interior of the embryo, centrosomes dissociate from the nuclei and migrate

to the cortex. Pole cells without nuclei then form around those centrosomes that reach the posterior pole. Thus, interactions between cytoskeletal components and polar granules are likely to be important for pole cell formation. We have looked at the distribution during embryogenesis of *m*RNAs for Cyclins, proteins thought to play a role in controlling the G2 to M transition. We have shown that whereas the cyclin A maternal RNA is relatively uniformly distributed prior to cellularisation, the cyclin B mRNA becomes localised to the developing pole cells. This remains the predominant site at which cyclin B mRNA is found throughout embryogenesis. In larvae, cyclin A is expressed predominantly in brain and discs, whereas cyclin B transcripts are abundant in testes. It seems therefore that one of the cyclin genes might be needed specifically for mitotic activity in the germ-line.

30. Molecular approaches to mouse developmental genetics

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There are several ways to approach the molecular characterisation of mouse developmental mutations. I will discuss two areas;

1. cloning genes for which mutations are already known, and
2. making novel mutations using embryonal stem (ES) cells.

1. The development of hair colour represents a well characterised genetic system in the mouse.

We have identified a cDNA which is the product of the pigmentation locus *brown*. I will present genetic and molecular characterisation of a number of mutant alleles at the locus. In addition alleles are being examined which are homozygous embryonic lethal, and are deletions removing adjoining, essential genes.

2. ES cells provide a way of manipulating the mouse genome *in vitro* and subsequently introducing those alterations into the germ line.

We have utilised a dominant selectable marker (neo^R), which lacks a promotor, to direct integration of exogenous DNA into active genes. A number of random integrants have been analysed, and shown to be selectively inserted into genes. Replacement of these cells into mouse embryos provides a more efficient means of obtaining mouse mutants than embryo injection or retroviral infection.

We have gone on to use similar vectors to develop methods for homologous recombination into putative murine developmental genes, the *Hox* genes, in order to make null mutations at these loci.

31. Detection of RFLPs in *Lolium perenne* using heterologous probes

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Variation in DNA sequence between homologous chromosomes can be revealed by Southern hybridisation in the form of Restriction Fragment Length Polymorphisms (RFLPs), which act as codominant cryptic genetic markers. The development of genetic maps based on RFLPs promises to be of great importance for agronomically important species such as perennial ryegrass, *Lolium perenne*, for which morphological and isozyme markers have generated only a rudimentary genetic map.

We have begun the analysis of RFLPs in the *Lolium* genus by assessing the use of heterologous probes derived from other members of the Gramineae. A number of uncharacterised cDNAs from maize have been assessed, proving generally unsatisfactory. Characterised cDNAs from maize, and especially from the more closely related wheat tribe, should prove more effective. By analysis of a small family of *L. temulentum* × *L. perenne* diploid hybrids, we have detected heterozygosity in a *L. perenne* line with a number of wheat cDNA probes. Other aspects of our approach to genome analysis in the *Lolium* genus will be discussed.

32. Relationship between mitotic cycle time, genome size and amounts of heterochromatin and euchromatin DNA in plants

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Mitotic cycle time in species of higher organisms is strongly influenced by genome size, large amounts of nuclear DNA prolong all phases of cell cycle. Heterochromatin is known to replicate late in S phase although its rate of replication may

be higher than that of euchromatin. In this investigation mitotic cycle times of *Lathyrus* and *Vicia* species which embrace a large variation in nuclear DNA amounts are compared. The effects of variation in the amounts of nuclear DNA and in the amounts of DNA constituents such as heterochromatin and euchromatin on cell cycle time are discussed.

33. Chromosome damage caused by oral tobacco extracts

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A number of experimental studies have been carried out on the effects of cigarette smoke on genes and chromosomes. Other forms of tobacco usage such as snuff and oral tobacco may also present a health hazard. We have examined the ability of aqueous extracts of oral tobacco to cause chromosomal damage to two established cell lines, the murine Friend erythroleukaemia and the Chinese hamster cell line CHO-K1.

In both cases tobacco extract caused an increase in the frequency of aberrations. The level of sister chromatic exchange in CHO-K1 cells showed a small but significant increase. In this cell line we observed that exposure to tobacco extract caused a sharp increase in the number of endoreduplicated metaphases. No increase was detected in the frequency of thioguanine-resistant mutants in Friend erythroleukaemia cells after exposure to the extract.

The presence of clastogenic effects in the apparent absence of gene mutation is unusual but is observed in agents such as ethionine and azacytidine which are carcinogenic but have little ability to induce gene mutation.

34. Detection of meiotic-associated proteins in male grasshoppers (*Stauroderus scalaris*)

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Developing grasshopper testes have been used to obtain comparable samples of material, only one of which has meiotic cells present. At hatching, grasshopper testes are rudimentary. The follicles grow quickly and fill with premeiotic spermatogonia. These enter meiosis when the nymphs are 5 to 6 days old, and by 12 days the first cells complete meiosis. One and two dimensional electrophoresis show differences in proteins between pre-meiotic and meiotic testes. Polyclonal antibodies against pachytene cells show that some antigens are present in meiotic, but not pre-meiotic testes. This is clearly demonstrated in Western blots of 2D gels using both types of testes. It is possible that some of these antigens are due to early synthesis of spermatid proteins, however fluorescent cytology demonstrates that antibodies against synaptonemal complexes are also present, and we are attempting to produce monoclonal antibodies against specifically meiotic antigens.

35. Isolation of P-450 genes from the genome of the mosquito, *Aedes aegypti*

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P-450 genes are one of the main detoxication pathways in eucaryotic organisms. They are involved in rendering toxic substances, such as insecticides, harmless. It has been demonstrated that they are responsible for resistance to permethrin in a Dubai species of *Anopheles stephensi* (Landoni and Townson, pers. comm.).

A cosmid library has been constructed from the *Aedes aegypti* Mos 20A cell line. This library was screened with a degenerate 18-mer oligonucleotide, homologous to the carboxy terminal of P450 genes belonging to rat and rabbit. Twenty clones were isolated and ordered in 5 different restriction groups. The characterisation and organisation of the P-450 genes in these cosmid clones will be described.

36. Organisation of imaginal discs from segmentation mutants in *Drosophila* as revealed by engrailed expression

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Embryos of the segment polarity mutants *naked* and *patched* develop when cultured *in vivo* and

produce larval tissues and imaginal discs (Simcox *et al.*, *Genes and Development*, submitted). *ptc* discs have abnormal morphology and metamorphose into adult cuticular structures with increased numbers of pattern elements. *nkd* discs also appear abnormal but produce apparently normal adult cuticle.

Using expression of a B-gel gene inserted in the *engrailed* locus (Kornberg, unpublished) as an indication of *engrailed* expression and thus posterior disc material we have examined the organisation of cultured *nkd* and *ptc* discs. These results and some concerning pair-rule mutants will be presented.