

APPLICATIONS OF 'ALLOCATION AND KINSHIP MODELS TO THE  
INTERPRETATION OF VASCULAR PLANT LIFE CYCLES

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# CERTIFICATE

The work described in this thesis is original and has not been submitted, in any form, for a higher degree at any other university or institution. Information and ideas derived from the published or unpublished work of others has been acknowledged in the text.

David Haig.

David Haig  
December 1989

In these 'Elements' naturally no mention has been made of certain terms and names which recent cryptogamically-minded botanists, with lack of proportion and just perspective, are endeavoring to introduce into phanerogamous botany, and which are not needed nor appropriate, even in more advanced works, for the adequate recognition of the ascertained analogies and homologies.

Asa Gray 1887 (commenting on gametophytes and sporophytes).

Thus for one seed to expand selfishly at the expense of its neighbours may or may not be advantageous to the inclusive fitness of its genotype but is almost certainly not in the interest of that of the parent plant.

W. D. Hamilton 1964.

If you are going to walk on thin ice you may as well dance.

Anonymous.

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Some parts of this thesis develop formal theoretical models; other parts gather together the literature and organize it within

a modern evolutionary framework. All empirical facts within the thesis are drawn from the work of others, and these contributions are acknowledged in the text. Charnov (1979), Westoby & Rice (1982), Queller (1983), and Willson & Burley (1983) were among the first to apply a sociobiological perspective to evolutionary questions in plants. Their work deserves special mention as the immediate inspiration for my work. This thesis is dedicated to Mark Westoby and Dick Frankham who introduced me to evolutionary biology.

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### Summary

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Among vascular plants, different life cycles are associated with characteristic ranges of propagule size. In the modern flora, isospores of homosporous pteridophytes are almost all smaller than 150  $\mu\text{m}$  diameter, megaspores of heterosporous pteridophytes fall in the range 100-1000  $\mu\text{m}$  diameter, gymnosperm seeds are possibly all larger than the largest megaspores, but the smallest angiosperm seeds are of comparable size to large isospores.

Propagule size is one of the most important features of a sporophyte's reproductive strategy. Roughly speaking, larger propagules have larger food reserves, and a greater probability of successful establishment, than smaller propagules, but a sporophyte can produce more smaller propagules from the same quantity of resources. Different species have adopted very different size-versus-number compromises. The characteristic ranges of propagule size, in each of the major groups of vascular plants, suggest that some life cycles are incompatible with particular size-versus-number compromises.

Sex expression in homosporous plants is a property of gametophytes (homosporous sporophytes are essentially asexual). Gametophytes should produce either eggs or sperm depending on which course of action gives the greatest chance of reproductive success. A maternal gametophyte must contribute much greater resources to a young sporophyte than the paternal gametophyte. Therefore, smaller gametophytes should tend to reproduce as males, and gametophytes with abundant resources should tend to reproduce as females. Consistent with these predictions, large female gametophytes release substances (antheridiogens) which induce smaller neighbouring gametophytes to produce sperm.

The mechanism of sex determination in heterosporous species appears to be fundamentally different. Large megaspores develop into female gametophytes, and small microspores develop into male gametophytes. Sex expression appears to be determined by the sporophyte generation. This is misleading. As argued above, the optimal sex expression of a homosporous gametophyte is influenced

by its access to resources. This is determined by (1) the quantity of food reserves in its spore and (2) the quantity of resources accumulated by the gametophyte's own activities. If a sporophyte produced spores of two sizes, gametophytes developing from the larger spores would be more likely to reproduce as females than gametophytes developing from the smaller spores, because the pre-existing mechanisms of sex determination would favor production of archegonia by larger gametophytes. Thus, the predicted mechanisms of sex determination in homosporous species could also explain the differences in sex expression of gametophytes developing from large and small spores in heterosporous species.

Megaspores of living heterosporous pteridophytes contain sufficient resources for female reproduction without photosynthesis by the gametophyte (*Platyzoma* excepted), whereas microspores only contain sufficient resources for male reproduction. Furthermore, many more microspores are produced than megaspores. A gametophyte's optimal sex expression is overwhelmingly determined by the amount of resources supplied in its spore by the sporophyte, and is little influenced by the particular environmental conditions where the spore lands. Gametophytes determine sex expression in heterosporous species, as well as homosporous species. A satisfactory model for the evolution of heterospory needs to explain under what circumstances sporophytes will benefit from producing spores of two distinct sizes.

In Chapter 4, I present a model for the origin of heterospory that predicts the existence of a "heterospory threshold". For propagule sizes below the threshold, homosporous reproduction is evolutionarily stable because gametophytes must rely on their own activities to accumulate sufficient resources for successful female reproduction. Whether a gametophyte can accumulate sufficient resources before its competitors is strongly influenced by environmental conditions. Gametophytes benefit from being able to adjust their sex expression in response to these conditions. For propagule sizes above the threshold, homosporous reproduction is evolutionarily unstable, because the propagule's food reserves are more than sufficient

for a "male" gametophyte to fertilize all eggs within its neighbourhood. A population of homosporous sporophytes can be invaded by sporophytes that produce a greater number of smaller spores which could land in additional locations and fertilize additional eggs. Such spores would be male-specialists on account of their size. Therefore, both spore types would be maintained in the population because of frequency-dependent selection.

The earliest vascular plants were homosporous. Several homosporous groups gave rise to heterosporous lineages, at least one of which was the progeniture of the seed plants. The first heterosporous species appear in the Devonian. During the Devonian, there was a gradual increase in maximum spore size, possibly associated with the evolution of trees and the appearance of the first forests. As the heterospory threshold was approached, the optimal spore size for female reproduction diverged from the optimal spore size for male reproduction. Below the threshold, a compromise spore size gave the highest fitness returns to sporophytes, but above the threshold, sporophytes could attain higher fitness by producing two types of spores.

The evolution of heterospory had profound consequences. Once a sporophyte produced two types of spores, microspores and megaspores could become specialized for male and female function respectively. The most successful heterosporous lineage (or lineages) is that of the seed plants. The feature that distinguishes seed plants from other heterosporous lineages is pollination, the capture of microspores before, rather than after, propagule dispersal. Traditionally, pollination has been considered to be a major adaptive advance because it frees sexual reproduction from dependence on external fertilization by free-swimming sperm, but pollination has a more important advantage. In heterosporous pteridophytes, a megaspore is provisioned whether or not it will be fertilized whereas seeds are only provisioned if they are pollinated.

The total cost per seed cannot be assessed solely from the seed's energy and nutrient content. Rather, each seed also has an associated *supplementary cost* of adaptations for pollen capture and of resources committed to ovules that remain unpollinated. The supplementary cost per seed has important

consequences for understanding reproductive strategies. First, supplementary costs are expected to be proportionally greater for smaller seeds. Thus, the benefits of decreasing seed size (in order to produce more seeds) are reduced for species with small seeds. This effect may explain minimum seed sizes. Second, supplementary costs are greater for populations at lower density. Thus, there is a minimum density below which a species cannot maintain its numbers.

By far the most successful group of seed plants in the modern flora are the angiosperms. Two types of evidence suggest that early angiosperms had a lower supplementary cost per seed than contemporary gymnosperms. First, the minimum size of angiosperm seeds was much smaller than the minimum size of gymnosperm seeds. This suggests that angiosperms could produce small seeds more cheaply than could gymnosperms. Second, angiosperm-dominated floras were more speciose than the gymnosperm-dominated floras they replaced. This suggests that the supplementary cost per seed of angiosperms does not increase as rapidly as that of gymnosperms, as population density decreases. In consequence, angiosperms were able to displace gymnosperms from many habitats, because the angiosperms had a lower cost of rarity.

Angiosperm embryology has a number of distinctive features that may be related to the group's success. In gymnosperms, the nutrient storage tissue of the seed is the female gametophyte. In most angiosperms, this role is taken by the endosperm. Endosperm is initiated by the fertilization of two female gametophyte nuclei by a second sperm that is genetically identical to the sperm which fertilizes the egg. Endosperm has identical genes to its associated embryo, except that there are two copies of maternal genes for every copy of a paternal gene.

Chapter 9 presents a hypothesis to explain the unusual genetic constitution of endosperm. Paternal genes benefit from their endosperm receiving more resources than the amount which maximizes the fitness of maternal genes, and this conflict is expressed as parent-specific gene expression in endosperm. The effect of the second maternal genome is to increase maternal control of nutrient acquisition.

Female gametophytes of angiosperms are traditionally classified as monosporic, bisporic or tetrasporic. Bisporic and tetrasporic embryo sacs contain the derivatives of more than one megaspore nucleus. Therefore, there is potential for conflict between the different nuclear types within an embryo sac, but this possibility has not been recognized by plant embryologists. In Chapter 10, I show that many previously inexplicable observations can be understood in terms of genetic conflicts within the embryo sac.



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Summary of published work arising from this thesis

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Five chapters are extensively based on papers that are published or in press. These are:

Chapter 3

Haig, D. & M. Westoby. 1988. Sex expression in homosporous ferns: an evolutionary perspective. *Evolutionary Trends in Plants* 2: 111-119.

Chapter 4

Haig, D. & M. Westoby. 1988. A model for the origin of heterospory. *Journal of Theoretical Biology* 134: 257-272.

Chapter 5

Haig, D. & M. Westoby. 1989. Evolutionary forces in the emergence of the seed habit. *Biological Journal of the Linnean Society* in press.

Chapter 9

Haig, D. & M. Westoby. 1989. Parent specific gene expression and the triploid endosperm. *American Naturalist* 134: 147-155.

Chapter 10

Haig, D. 1990. New perspectives on the angiosperm female gametophyte. *Botanical Review* in press.

The Appendix to Chapter 2 will appear as

Haig, D. 1990. Brood reduction and optimal parental investment when offspring differ in quality. *American Naturalist* in press.

Chapter 6 is based on an invited chapter in a forthcoming book on *The ecology and evolution of cannibalism* (M. Elgar & B. Crespi, eds).

Material from four other published papers is incorporated into

the text. These are:

Haig, D. 1986. Conflicts among megaspores. *Journal of Theoretical Biology* 123: 471-480.

Haig, D. 1987. Kin conflict in seed plants. *Trends in Ecology and Evolution* 2: 337-340.

Haig, D. & M. Westoby. 1988. Inclusive fitness, seed resources and maternal care. Pages 60-79, in J. Lovett Doust & L. Lovett Doust (eds.) *Plant Reproductive Ecology*. New York: Oxford University Press.

Haig, D. & M. Westoby. 1988. On limits to seed production. *American Naturalist* 131: 757-759.

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## Preface

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This thesis applies concepts from sociobiology to understand the evolution of vascular plant life cycles. E. O. Wilson (1975) defined sociobiology as "the systematic study of the biological basis of all social behavior". The central premise of sociobiology is that behaviors are subject to natural selection and can be considered as adaptations in the same sense as physical structures. This assumes that an organism's behavior can affect its chances of survival and reproduction, and that this behavior is in some degree heritable. Sociobiology views a behavioral adaptation as being of advantage to the genes determining the behavior. In most cases, the adaptation can be understood as conferring advantages on the individual expressing the behavior, or on related individuals that share genes in common with this individual. However, the individual expressing a behavior need not carry the genes determining the behavior, or different genes within an individual may have conflicting interests (Dawkins 1982).

Sociobiology is frequently accused of naive reductionism; of attempting to explain the properties of an integrated whole (the organism) solely by the properties of its parts (genes). This is unfair on two counts. Firstly, genes and organisms belong to different hierarchies: neither is decomposable in terms of the other. A gene is a non-material piece of information rather than a specific set of atoms. Thus, the same gene can be present in different individuals. The abstract, intangible "gene" should be distinguished from its physical manifestations. Information replicates but matter does not. The "gene" is the "unit of selection", provided that "gene" is understood in the collective sense of all copies of a piece of information. For example in kin selection, the copies of a gene in one individual promote the replication of the gene in another individual. Secondly, sociobiology is not concerned with *how* a particular gene influences phenotype, but with *why* that gene is present and not others. This is the familiar distinction between proximal and

ultimate explanations. The "how" question is answered by conventional "bottom-up" (reductionist) explanations. The "why" question has a "top-down" answer. For example, why a particular gene is present in a species is determined by the interactions of alternative phenotypes in a complex environment. Both proximal and ultimate explanations are described as causal, but radically different concepts of causation are being employed. Because natural selection explains phenomena present at lower levels (genes, enzymes) by phenomena at higher levels (phenotype, ecology) adaptive explanations are fundamentally non-reductionist.

Natural selection is the differential replication of alternative entities. From the viewpoint of genic selection, individual organisms are not units of selection because their genotypes lack persistence. In Dawkins' (1976) terminology, genes are "replicators" and organisms are "vehicles". A vehicle carries many replicators but, in each generation, the replicators form different combinations in different vehicles. Natural selection is not expressed as the differential replication of vehicles because the distinctive combination (genotype) of a vehicle is ephemeral. From the perspective of an individual replicator, its fellow travellers (other replicators in the same vehicle) are part of the environment.

Persistence is an essential property of a unit of selection. The persistence of a replicator is closely related to the concept of linkage. Two entities will be subject to natural selection as parts of a single entity if they show a consistent non-random association. For this reason, Dawkins (1976) defined the gene as a length of DNA sufficiently short to be rarely broken by recombination. Higher units of selection exist because of non-random associations among genes. Examples are chromosomal inversions that prevent recombination with alternative chromosome types, and asexual lineages in which natural selection is expressed as the differential replication of entire genotypes.

Perhaps the greatest source of non-random associations among genes are the barriers to interbreeding among species. The random association of genes within a species is compatible with a strong non-random association of genes between species. Therefore, the

appropriate unit of selection depends on the question being considered. If the question at issue is the spread of a new character (such as heterospory) within a species, the individual is not a replicator for the reasons given above. If the question at issue is competition between a homosporous and heterosporous species, individuals are replicators of their species' character. In a sense, individuals within a species are copies of the same supergene. In this thesis, I will often shift from considering natural selection within species to natural selection among species. As D. S. Wilson & Sober (1989) have argued, "selfish-gene theory" and "levels-of-selection theory" are both logically consistent frameworks for describing the same phenomena.

E. O. Wilson's seminal text *Sociobiology: The New Synthesis* (Wilson 1975) was almost totally devoted to the social behavior of animals, with the exception of a brief discussion of colonial bacteria and slime molds. Other groups of organisms were neglected. In this thesis, I apply a sociobiological perspective to the life cycle of vascular plants. Vascular plants do not possess social behavior in a sense ethologists would recognize, but their life cycles do involve interactions between individuals with different genetic constitutions. The life cycle alternates between haploid and diploid generations. Diploid sporophytes form spores by meiosis. These spores germinate to produce haploid gametophytes which produce gametes by mitosis. The union of gametes forms a zygote which is the first cell of the next sporophyte generation. There are at least three stages at which individuals of different genotype interact: gametophytes receive resources from their parental sporophyte; "male" gametophytes fertilize "female" gametophytes; and young sporophytes are nourished during early development by a previous generation. Sociobiology suggests that the genetic interests of these interacting individuals are not identical.

Though my original aim was to investigate conflicts among relatives, a recurring theme emerged that was not directly related to genetic conflicts. The evolution of heterospory, of the seed habit and of angiospermous reproduction are all associated with changes in either the minimum or maximum size of propagules. Chapters 1-2 are introductory. Chapters 3-8 are

concerned with these major evolutionary transitions between different types of life cycle and their relationship to propagule size. The central theoretical idea is that of a trade-off between the size and number of propagules (Smith & Fretwell 1974). Chapters 9-10 are concerned with developmental processes in angiosperms and related plants. I argue that some aspects of development can only be understood in the context of genetic conflicts. The Glossary contains definitions of some technical terms used in the description of plant life cycles.

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### A guide to the chapters of this thesis

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Chapter 1 introduces the major types of life cycle found in vascular plants; summarizes when each type appears in the fossil record; describes changes in the relative importance of different life cycles over evolutionary time; and, describes the range of propagule sizes associated with each type of life cycle.

Chapter 2 reviews models of parental allocation, with particular emphasis on the Smith-Fretwell model of the trade-off between offspring size and number. In the appendix to this chapter, I develop a model of the optimal pattern of parental investment when offspring differ in quality.

Chapter 3 addresses the reproductive strategies employed by gametophytes of homosporous pteridophytes. I conclude that a gametophyte should determine its sex expression in response to information about the physical environment, its own food reserves, and the reproductive status of nearby gametophytes.

Chapter 4 presents a model for the origin of heterospory. In this model, homosporous reproduction becomes evolutionarily unstable once propagule size exceeds a "heterospory threshold."

Chapter 5 discusses which characters distinguish pteridophytes from seed plants, and suggests what evolutionary forces were responsible for these changes. I conclude that pollination is the critical innovation that was responsible for the great success of seed plants relative to other heterosporous lineages.

Chapter 6 discusses the mechanisms and functions of brood reduction in gymnosperms. Chapter 7 discusses adaptive consequences of pollination. Chapter 8 reviews adaptive explanations for the evolutionary success of angiosperms.

Chapter 9 presents a simple model of genetic conflict between maternal and paternal genes within a single genetic "individual". This model is used to suggest an evolutionary explanation of why there is a ratio of two maternal genomes to one paternal genome in the endosperm of most angiosperms.

Chapter 10 presents a developmental classification of angiosperm female gametophytes based on modifications to an underlying "developmental algorithm". The classification takes account of potential conflicts of interest between different genetic individuals within embryo sacs.