Evolutionary Ecology Research, 2000, **2**: 29–40

The selection of social actions in families: III. Reproductively disabled individuals and organs

David G. Lloyd

Department of Plant and Microbial Sciences, University of Canterbury, Christchurch, New Zealand

ABSTRACT

A wide variety of animals and plants produce a proportion of offspring that are partly or wholly sterile, or are fertile but sacrificed to sibs or mutualist partners, or are diverted to non-reproductive tasks. All these individuals with reduced or zero fitness can be described collectively as being 'reproductively disabled'. Reproductively disabled individuals and organs have received little attention; nonetheless, they provide a challenge to selection theory that is parallel to that recognized by Darwin for sterile castes. In this paper, I examine a variety of disabilities, mostly in plants, and enquire as to whose fitness they benefit, and how. The results indicate, for the case of reproductively disabled individuals, that there is not much conflict between family participants. For the case of individuals disabled by their position on a parent, parental manipulation controls the event. The results also suggest that the level of self-incompatibility in plants is controlled by the pollen, and that in the development of endosperm there is little conflict between parents and offspring. The diversity of outcomes appears to stem in part from the degree to which parents must consider information transmitted by their offspring.

Keywords: disabled seeds, endosperm, feeding anthers, parent–offspring conflict, self-incompatibility, sterile castes, sterile pollen.

INTRODUCTION

> . . . with all my faith in this principle, I should never have anticipated that natural selection could have been efficient in so high a degree, had not the case of these neuter insects convinced me of the fact . . . this is by far the most serious difficulty, which my theory has encountered. (Darwin, 1859, p. 242).

The occurrence of sterile individuals is indeed a challenge to the theory of natural selection. How can selection, which operates by favouring those individuals (and their genes) who leave the most descendants, lead to the production of sterile individuals, who leave none? Darwin explained the existence of sterile castes in social species by postulating that selection operated not on them directly but on their parents. Specialized sterile progeny within a colony may perform certain tasks more proficiently. A division of labour between fertile and sterile colony members then improves the productivity of the colony (the parents' family) and thus the fitness of the parents. The introduction of a quantitative theory of kin selection by Hamilton (1964) provided an alternative hypothesis: sterility of colony members is

selected by their own genes when their inclusive fitness is increased by being sterile. Kin selection offered an exciting new explanation of sterile castes, and particularly of why they have evolved most frequently in haplodiploid species.

Besides sterile castes, a wide variety of animals and plants produce a proportion of offspring that are partly or wholly sterile, or are fertile but sacrificed to sibs or mutualist partners, or are diverted to non-reproductive tasks, or are inviable but actively maintained. All these individuals with reduced or zero fitness can be described collectively as being 'reproductively disabled'. In plants, the disablement often occurs so early that a proportion of a parent's reproductive organs is disabled before the offspring are even produced. Disabled individuals and organs other than sterile castes have received little attention, although they provide a challenge to selection theory that is parallel to that recognized by Darwin for sterile castes. In this paper, I look at a variety of disabilities, mostly in plants, and enquire as to whose fitness they benefit and how.

DISABLED ANIMAL EGGS AND SPERM

Sterile sperm or inviable eggs are produced by a number of animal species (Trivers, 1985). 'Helper' sperm, which in some species easily outnumber fertile sperm, are postulated as helping their sibs to reach eggs, or providing nutrients to the female or her eggs, or interfering with the success of competing sperm. Helper eggs are rare. In certain insects, modified inviable eggs (rapagula) are laid alongside the viable ones and provide chemical protection. In at least some species, the helper sperm or eggs are produced in specialized lobes of the testes or ovaries. The production of the disabled progeny is therefore controlled by the parents and has presumably been selected because of net benefits to them. It is not appropriate to describe the disabled sperm or eggs as altruistic.

DISABLED PLANT STRUCTURES

Seed plants exhibit a much greater frequency and variety of disabled individuals and organs for two reasons:

1. Being sessile, plants enlist the aid of external agents, frequently mutualist animal partners, for pollination and dispersal. As well as producing gametes and progeny, flowers and fruits perform many ancillary functions concerned with attracting, rewarding and manipulating these partners. Some structures may be reproductively disabled but still perform ancillary functions that contribute indirectly to the reproductive success of pollen or seeds produced in other structures.
2. The individuals of most plant species are co-sexual and obtain fitness equally, on average, as maternal and paternal parents. This permits one sexual function to be disabled in some or all flowers if the other function benefits sufficiently to compensate for the disability.

Non-reproducing organs are usually reduced to inexpensive vestiges. I am concerned here with those unisexual or neuter structures in which the disabled offspring or organs are actively maintained as major expenditures for their indirect benefits. A more detailed account of disabled plant structures is given in Lloyd (1992).

The most frequently evolved disability of plant progeny occurs in the sterile pollen grains of species with 'feeding' anthers, which supposedly attract and reward pollinators while the fertile pollen grains of morphologically distinct 'fertilizing' anthers in the same flowers achieve the fertilizations. Specialized feeding anthers have evolved in at least 15 distantly related angiosperm groups, possibly several times in some groups. A pollen grain and the pollen tube that issues from it constitute a male gametophyte, a haploid individual that produces male gametes. The pollen of feeding anthers is fully capable of fertilizing ovules in some species, but in others it is invariably ungerminable. The little information available suggests that pollen may be arrested at various stages, or in extreme cases even replaced by a milky liquid. The boundary between disabled offspring (pollen) and parental organs (anthers) is not clear-cut. There may well be cases in which pollen is disabled in part by processes of parental development before meiosis and in part by the disruption of offspring capabilities after meiosis.

What matters to the pollen's fitness is not its intrinsic fertility or viability as much as its actual success in achieving fertilization. If a pollen grain is fertile but has a reduced or zero chance of fertilizing an egg, it is disabled as effectively as if it were inherently inviable or sterile. There is probably a continuum in the relative fertilizing success of feeding pollen compared with that of the fertilizing pollen.

In most heteranthic species, the fertilizing anthers occupy a position in the flower that is more similar to that of the stigmas, than is that of the feeding anthers, so the pollen of fertilizing anthers is more likely to be transferred to stigmas. Conversely, the pollen of feeding anthers is characteristically more conspicuous and more accessible to pollen-seeking visitors, so it is more likely to be collected as a reward and thereby be unavailable for fertilization. These factors presumably cause the pollen of feeding anthers to have less success in fertilization and to function better as an attractant and reward than the pollen of fertilizing anthers. Heteranthic species offer excellent opportunities to compare the direct and indirect fitness contributions of able and disabled progeny, but the opportunities have not yet been taken up. Unfortunately, only one experimental comparison of the relative abilities of feeding and fertilizing pollen has been made, and that provided only limited information. Bowers (1975) found that samples of fluorescent dye dusted on the fertilizing anthers of *Solanum rostratum* were redeposited on a higher proportion of the stigmas of the flowers visited subsequently than samples dusted on feeding anthers.

Sterile pollen also occurs in another context, as a reward for pollen-collecting bees visiting the female flowers of nectarless dioecious species such as the kiwifruit (Charlesworth, 1984). The pollen of females is totally sterile (even low fertility would cause considerable self-pollination and consequent inbreeding depression), but functions to increase the maternal fitness of the plants carrying it.

Disabled seeds and fruits also occur. The best-known example is the parasitized embryos of short-styled female flowers of monoecious species of *Ficus* (figs), which provide food for the larvae of the mutualist pollinators, aganoid wasps. When the adult male wasps emerge, they carry pollen to the next generation of receptive female flowers. Other species of plants have specialized ovules, seeds or fruit that serve as attractants or rewards for dispersers. Wild parsnip plants, for example, have pathenocarpic fruit that divert herbivores away from the fruits that contain embryos (Zangerl *et al.*, 1991). As with sterile male structures, the disabled seeds and fruits are sometimes offspring (the fig embryos, although even these have parental envelopes, the seed and fruit walls), but in most species they are maternal structures diverted at various stages of development to ancillary functions of pollination or dispersal.

Neuter flowers also carry out various ancillary functions. The marginal florets of compact inflorescences of species of *Viburnum*, *Hydrangea* and scattered genera of Asteraceae attract pollinators to the fertile flowers they surround. The dark, central, aborted flowers of carrot umbels that Darwin (1877) commented on have been shown to increase the number of visitors to umbels (Eisikowitch, 1980). Other neuter flowers provide nectar, manipulate the movements of pollinators, or aid the self-dispersal of fertile fruit. Some species of *Parkia* produce two kinds of neuter flowers besides the fertile flowers; one kind produces nectar, the other odour (Grunmeier, 1990).

A striking feature of disabled plant structures is that they all assist fertile pollen or seeds while they are retained on the parent. In this respect, they contrast with the sterile castes and helper sperm and eggs of animals, which carry out their supportive functions after leaving the parent body. I know no example of sterile seeds, fruit or pollen that assist the dispersal, germination or growth of siblings after pollen or seeds have left the parent that produced them. Furthermore, the disabilities of plant structures seem to be invariably controlled by the maternal parent. In heteranthic species, the fates of feeding and fertilizing pollen are determined by the positions of the anthers they are borne on. Similarly, all neuter flowers and fruits are associated with particular positions in inflorescences. The sex of a plant controls the pollen of male-mimicking females, and the prospects for fig embryos are controlled by the length of the associated style, a maternal tissue. The development of disabled display seeds and parsnip fruits appears to be induced by a lack of fertilization. There is no evidence for the involvement of offspring strategies in any of the disabled plant structures; indeed, in many species the parental decision is made before gametes are produced. The strategies can be explained entirely as differentiation strategies of parents maximizing their fitness by manipulating the number and behaviour of their progeny.

SELECTION OF DISABLED INDIVIDUALS

Although the sterility of various pollen, seeds and fruits cannot be attributed to offspring strategies and conflicts between parents and offspring do not arise as they do for parental care or sterile castes, the question of how parents benefit by producing disabled offspring remains just as important as it is for those more publicized topics. How can the ubiquity of parental manipulation of these disabled animals and plants be understood in terms of the adaptive strategies of parents and their offspring? For this purpose, I compare conditions for the selection of disability genes expressed in the two generations. The model examines the collective fitnesses of autonomous parental and offspring genes.

Consider first a *parental* gene, D, that causes a disability in one or more individuals among N offspring. Disabled offspring suffer a fitness reduction, a cost c, while the remaining able offspring share a fitness benefit b for each disabled individual. Let the frequency of disabled offspring be f. If benefits and costs increase additively (each disabled individual has the same effects), each able offspring gains $bf/(1-f)$ in fitness from each disabled sib. Summing the total fitness effects on the able and disabled offspring (Table 1) gives a net collective fitness effect, $\sum e_i g_i = \frac{1}{2} fN(b-c)$. A disability is selected when the net effect is positive. This is so when

$$b > c \tag{1}$$

A disabled offspring benefits a parent when the benefit arising from each disability exceeds the cost of the disability.

Table 1. Selection of a parent-expressed autonomous gene causing disabilities in some offspring

Parents:	D- × --	
Offspring:		
Numbers	fN disabled	$(1-f)N$ able
Segregation	$\frac{1}{2}$ D-: $\frac{1}{2}$--	$\frac{1}{2}$ D-: $\frac{1}{2}$--
Fitness effects	each costs $-c$	each benefits $bf/(1-f)$
	Total $= -\frac{1}{2}fNc$	Total $= \frac{1}{2}(1-f)Nbf/(1-f) = \frac{1}{2}fNb$
Collective fitness	$\sum e_i g_i = \frac{1}{2}fN(b-c)$	
D is selected if	$\sum e_i g_i > 0$	
	i.e. $b > c$	

Now consider an *offspring-expressed* disability gene. The evidence discussed above indicates that the able and disabled offspring are usually physically separated in different testis lobes, anthers, flowers, etc. Hence, we assume that the able and disabled offspring represent distinct samples of a parent's genes, as in the case of the offspring competing unequally for parental investment that were considered in Lloyd (2000b). Suppose a gene L disables its carriers in one developmental environment (e.g. one type of testis lobe) where a fraction of offspring, f, occur. The disability benefits the remaining sibs in a second environment (e.g. a testis lobe producing fertile sperm). The total benefits and costs to able and disabled carriers of the gene are shown in Table 2. The net effect is advantageous when

$$b > 2c \tag{2}$$

A disability controlled by an offspring gene is selected only if it provides a benefit twice as great as that required for a parental disability gene.

The parent–offspring conflict operating here is parallel to, but in the reverse direction from, that for parental investment. Whereas offspring selfishness towards a full ability is selected under more lenient conditions than parental favouritism, offspring altruism is selected *only under more stringent conditions* than those required for a parentally controlled disability. Nevertheless, the two parent–offspring conflicts have the same underlying cause, the positions of the actors with respect to genes segregating at meiosis. In both cases, a parental gene shares the costs and benefits of its action equally with the other allele in the

Table 2. Selection of an offspring-expressed autonomous gene causing disabilities in some developmental environments

Parents:	L- × --	
	Environment 1	Environment 2
Offspring:		
Numbers	fN disabled	$(1-f)N$ able
Segregation	$\frac{1}{2}$ L-: $\frac{1}{2}$--	$\frac{1}{2}$ L-: $\frac{1}{2}$--
Fitness effects	each costs $-c$	each benefits $b \cdot \frac{1}{2}f/(1-f)$
	Total $= -\frac{1}{2}fNC$	Total $= \frac{1}{2}(1-f)N \cdot \frac{1}{2}bf/(1-f) = \frac{1}{4}fNb$
Collective fitness	$\sum e_i g_i = \frac{1}{2}fN(\frac{1}{2}b-c)$	
L selected if	$\sum e_i g_i > 0$	
	i.e. $b > 2c$	

parent body. In contrast, a gene expressed in offspring receives all the effects of its selfish or altruistic act, but shares the recipient effect with sibs carrying the other parental allele. A degree of disability of offspring will therefore be first advantageous to the parent, when $b > c$, and will continue to be selected by the parent but not the offspring while $2c > b > c$.

The explanation is equivalent to the usual kin selection formulation that parents are equally related to all offspring, whereas an offspring is more closely related to itself than to its sibs. The kin selection formulation is more familiar but requires the use of the concept of relatedness, which is a complex parameter in some circumstances.

Why are the disabilities described above all controlled by the parent, whereas we have seen that both parent and offspring have their say over the amount of parental investment? The capacity of offspring to influence events, and the advantage to parents in their doing so, differ dramatically in the two situations. During decisions over parental investment, offspring have an indispensable signalling role and can use this to direct the strategies towards their own interests. Parents cannot ignore the signals because they use them to maximize their own fitness. The offspring have no such source of influence over disabilities. They would oppose disabilities if they could, but they do not participate in the parental strategy and have no effective counter to it. Consequently, parental manipulation rules.

The one-sidedness of these disability strategies actually makes them ideal subjects to examine the relative costs and benefits involved. At the ESS, the marginal advantages of increasing the number of disabled progeny (c) should equal the marginal advantage to the remaining able progeny (b). The direct and indirect effects of a disability can be compared without confusion as to whether the parent or offspring strategy or some intermediate compromise is operating. The latter ambiguity causes a two-fold uncertainty in assessments of the benefits and costs of social actions such as parental investment ($b > c$ versus $b > \frac{1}{2}c$: Lloyd, 2000a) or sterile castes. An experimental evaluation of helper sperm or pollen, for example, might explain why they are present in some moths and bugs and some angiosperms, but not in others. Similarly, a comparison of the costs and benefits of sterility in marginal flowers with exaggerated corollas might explain why such flowers are sometimes disabled in both sexual functions (e.g. *Viburnum* species), sometimes disabled only in the male function (many Asteraceae) and sometimes retain both functions (some species of Apiaceae).

SELF-INCOMPATIBILITY

The self-fertilization of a plant usually results in the progeny suffering reduced fitness from inbreeding depression. In angiosperms, one of the most common mechanisms that discourages self-fertilization is self-incompatibility. In most self-incompatible species, the incompatibility is controlled by a single super-gene, S, with many alleles. In its most common form, gametophytic self-incompatibility, which I consider here, the pollen specificity depends on its own genotype rather than that of its parent. When a pollen tube grows down a style containing the same S allele, its growth is inhibited and fertilization is prevented. Hence self-fertilization is prevented, but as there are many S alleles in a population, cross-fertilization is rarely affected. The pollen deaths constitute a conditional disability, one that occurs only when pollen is deposited on stigmas of the plant that produced it.

Self-incompatibility has customarily been explained as a strategy that benefits parents by increasing the frequency of their outcrossed seeds. On the other hand, the ovules that are spared from self-fertilization are 'sibs' of the inhibited pollen. Self-incompatibility

might therefore be explained as the result of an altruistic act of pollen, as Hamilton (1987) postulated. Neither explanation is adequate by itself, however, because the mechanism requires the matching of S allele specificities in a parental tissue, the style, and an offspring, the haploid male gametophyte. In contrast to the other disabilities just considered, both the parent and the male gametophyte have indispensable roles. Self-incompatibility may benefit the parent, but it eliminates the lineal fitness of an inhibited pollen tube. In essence, the parent and its haploid progeny cooperate in causing the premature death of the progeny; they are partners in a suicide–infanticide pact.

The strategies of parents and their pollen offspring are examined here in collective fitness models of autonomous genes that are expressed either in the style or in pollen and thereby alter the strength of the self-incompatibility reaction. The problem is reduced to its simplest form by examining conditions for an increase in the strength of self-incompatibility that causes one less ovule on a plant to be self-fertilized. The results agree with those from a more formal genetic model that allows changes of any degree in the strength of self-incompatibility (Lloyd, 1992). The models incorporate inbreeding depression, the two-fold cost of outcrossing, and reproductive assurance by autonomous self-fertilization in the absence of pollinators.

Consider first a *parental* gene that increases the strength of the stylar reaction to self-pollen. If it causes one less self-pollination, the parent loses the male and female contributions to the selfed seed. The parental gene that is responsible has a 50% chance of being present in either of the two lost gamete contributions. The gene therefore bears a cost, $-\frac{1}{2}[2(1-\delta])]$, where the inbreeding depression, δ, is the proportional reduction in the fitness of a selfed seed compared with that of an outcrossed one. An ovule that is not selfed has a probability p of being outcrossed, and an allele from the parent has a 50% chance of being represented in the outcrossed seed. Hence the allele for increased self-incompatibility gains an outcrossing benefit, $\frac{1}{2}p$. The net effect on the collective fitness of the allele causing one less selfed seed is, therefore, $\sum e_i g_i = \frac{1}{2}[-2(1-\delta)+p]$. The allele is selected when the net effect is positive, that is

$$p > 2(1-\delta) \tag{3}$$

If seed set is not pollinator-limited, $p = 1$ and equation (3) reduces to

$$\delta > \tfrac{1}{2} \tag{4}$$

The cost of meiosis is offset when the inbreeding depression is greater than $\frac{1}{2}$ (Kimura, 1959).

Now consider the selection of a gene that increases the self-incompatibility action of a *pollen grain*. When one less seed is self-fertilized as a result, the allele responsible loses its own pollen contribution. Half the time it also loses the ovule contribution because the pollen allele has a 50% probability of being present in an ovule. Hence the lost selfed seed costs $(1-\delta)+\frac{1}{2}(1-\delta) = 1.5(1-\delta)$. The gain to the pollen allele from outcrossing the ovule is $\frac{1}{2}p$. The total fitness effect is $\sum e_i g_i = -1.5(1-\delta)+\frac{1}{2}p$. The pollen allele is selected when this is positive, that is

$$p > 3(1-\delta) \tag{5}$$

If $p = 1$, equation (5) reduces to

$$\delta > 2/3 \tag{6}$$

The conditions for strengthening the pollen action are slightly more stringent than those for strengthening the style action because a pollen gene bears the full cost of the lost pollen contribution to the seed that is not selfed, whereas a stylar gene shares the cost with the other S allele in the parent. The discrepancy between the parental and offspring strategies is less than in the case of the sterile pollen considered previously because there is an extra cost of self-incompatibility, the lost ovule contribution. This is the same, $\frac{1}{2}(1-\delta)$ for stylar and pollen genes. Consequently, the conflict is confined to a narrow zone of inbreeding depression values. If $p = 1$, the disparity occurs when $2/3 > \delta > 1/2$; an increase in self-incompatibility is then favoured by the parent but not the offspring. At higher and lower values of inbreeding depression, the two participants are in agreement.

Although there is a minor element of conflict in the operation of gametophytic self-incompatibility, the system is based on the mutual cooperation of genes expressed in the diploid female parental tissues and in the haploid male progeny. The cooperation will be forthcoming only if it is selected in both partners. Since the conditions for cooperation are slightly more stringent for pollen, genes in pollen are expected to withhold their participation when pollinators first become scarce and selfing is more favourable. When there is conflict, this will be resolved in favour of the offspring, not the parent. Thus pollen genes should principally determine whether a self-incompatibility mechanism operates. In contrast to the sterile pollen considered previously, offspring manipulation rules here.

In sporophytic self-incompatibility systems, best known in the Asteraceae and Brassicaceae, the incompatibility reaction of the pollen is determined not by its own genotype but by that of its parent. Offspring-expressed genes are not involved in deciding when an incompatible reaction takes place. Sporophytic self-incompatibility is therefore expected under the more lenient parental condition ($\delta > 1/2$) than that for gametophytic systems ($\delta > 2/3$). The two types of incompability system characteristically differ in a number of respects in addition to the determination of the pollen specificity, including the site of inhibition in the pistil. It is not known whether sporophytic control has been selected as a parental strategy to overcome the inter-generational conflict or by some other advantage.

THE ENDOSPERM OF ANGIOSPERMS

The endosperm is a genetically distinct sterile tissue that accompanies the formation of an embryo in an angiosperm seed. In most angiosperms, the endosperm is the product of a second fertilization between a haploid sperm that is identical to the one that fertilizes the egg (the two sperm come from the same male gametophyte) and a diploid central cell that contains two genomes that are identical to each other and the egg (all are derived from the same megaspore). The triploid fusion cell divides rapidly and the resulting endosperm surrounds and nourishes the more slowly growing embryo associated with it. The endosperm is eventually consumed, either during the growth of the seed or when the seed germinates. In the evolution of the flowering plants, the triploid post-fertilization endosperm has replaced the haploid post-fertilization gametophyte tissue that nurtures the developing embryo of gymnosperms.

The endosperm has traditionally been regarded as an intermediary *tissue* that transfers nutrients from the maternal parent to the embryo. But it is also a genetically distinct *individual*, albeit a short-lived one that is entirely dependent on the parent that it develops within. Following the advent of kin selection theories, it has been recognized that the evolution of this sterile individual requires special consideration (Charnov, 1979). The

origin of the endosperm concerns the elaboration *de novo* of a sterile individual, and is perhaps even more anomalous than the disabilities of fertile individuals that were considered in the previous examples.

In angiosperms, reproduction by seeds involves the active participation of five genetically distinct types of individual – the male and female gametophytes, maternal parent, embryo and endosperm. Each individual may express genes that influence the outcome of reproduction, and each may have its own selection interests. In the past decade, a number of broadly similar hypotheses have compared the degrees to which each genetical entity should favour parental investment in its 'own' embryo over investment in other embryos developing on the same plant. Inclusive fitness calculations using identity by descent (IBD) measures of relatedness predict that increasing favouritism should be associated with an increasing order of relatedness ratios (relatedness to own embryo : relatedness of other embryos). On this basis, the five individuals are ranked in the following order of increasing egalitarianism and decreasing own-favouritism: male gamete, embryo, endosperm, female gametophyte, maternal parent (Westboy and Rice, 1982; Queller, 1983, 1984, 1989; Law and Cannings, 1984; Bulmer, 1986). There appears to be unparalleled scope here for kin selection and for interacting conflicts among relatives. The evolution of the endosperm has additional interest because it is one of the few syanpomorphies that define the angiosperms as a clade.

Qualitative models of kin conflict during seed development have assumed there is one central object of selection, the optimal investment for each individual in its own embryo. This is biologically unrealistic, however. At no time are all five participants present together. The male and female gametophytes no longer exist when an embryo and its associated endosperm are formed. Only the parent is present throughout the period of investment in an offspring. Seed development is not a single competition for parental resources. Instead, the evolution and selection of the system for nurturing angiosperm embryos involves several distinct matters. A short breakdown of the component events includes the reduction of the female gametophyte, fusion of the secondary nuclei, the genetic nature of the endosperm, the development and activity of the endosperm, termination of parental investment in a seed, and germination. Only two or three of the five individuals are involved in each component of the whole system.

Here, I concentrate on the major issue in recent models, the activity of the endosperm and perceived conflicts between the endosperm, its associated embryo and the maternal parent over the amount of resources that are optimally disbursed to each embryo. The parental and embryo strategies for optimal investment have already been derived (Lloyd, 2000b). Endosperm cells are assumed here to contain one paternal genome and two identical maternal genomes, each also identical to one of the genomes in the associated embryo. This is the most common constitution of the endosperm among flowering plants, but not the only one.

It is again necessary to distinguish between equally and unequally competing seeds and to specify the mode of inheritance of a gene that causes more resources to be directed to embryos associated with it. The ability of a rare dominant allele, H, to invade a population is analysed; this describes its ability to increase at any frequency (Lloyd, 2000a). Assume that the presence of one or more copies of H in an endosperm causes the endosperm to obtain more parental resources at the expense of a random sample of its full sibs (mating is monogamous, offspring compete unequally). The endosperm's own embryo obtains a fitness gain b, while other embryos suffer a total fitness cost c. Either the mother or the father may contribute allele H to a family. In either case, H benefits all its own embryos and shares the costs equally with the other allele from the same parent (Table 3), as does an

Table 3. Conditions under which a rare dominant allele that is expressed in endosperm is selected to increase when rare; the allele causes its 'own' embryos to obtain more parental resources. The costs are borne by the same number of unequally competing embryos in a family of size m

	Father		*Mother*	
Parents:	H- × --		H- × --	
Endosperm:	m/2 H--		m/2 HH-	
Embryo:	own embryo	other embryos	own embryo	other embryos
Genotypes	m/2 H-	m/4 H- : m/4--	m/2 H-	m/4 H- : m/4--
No. copies	$g = m/2$	$g = m/4$	$g = m/2$	$g = m/4$
Effects	b	c	b	c
Collective fitness	$\sum e_i g_i = b(m/2) - c(m/4)$		$\sum e_i g_i = b(m/2) - c(m/4)$	
Selected if	$b > c/2$		$b > c/2$	

embryo gene. Hence the endosperm's strategy is the same as the embryo's, signal for more resources whenever $b > c/2$.

A parallel argument for a dominant allele in endosperms that compete equally on behalf of their own embryos shows that the embryo and the endosperm strategies again agree completely (Law and Cannings, 1984). The agreement occurs because allele H is always present in an endosperm if it is present in the associated embryo, and vice versa. The qualitative distribution of alleles from the parent to 'own' and 'other' seeds is identical for the embryo and the endosperm. For a dominant allele, the number of identical maternal genomes present in an endosperm is immaterial. In fact, the number is not invariably two, but varies from one to 14 in various angiosperms (Maheshwari, 1950).

Inclusive fitness arguments using IBD measures of relatedness lead to the conclusion that an endosperm should display more egalitarianism towards another embryo than its own embryo would. The relatedness of an endosperm and another full-sib embryo is 2/3, whereas the relatedness between full-sib embryos is 1/2. Therefore, an endosperm should favour its own embryo when $b > 2c/3$, a condition that is intermediate between parental egalitarianism and offspring selfishness. In this context, IBD measures of relatedness are invalid because they assume that each copy of an action allele in actors and recipients is transmitted independently of other copies. This is not true for the two maternal alleles in an endosperm tissue, as Queller (1989) pointed out. In most angiosperms, the two alleles are derived from cells formed from the same megaspore and are therefore identical. Similarly, in species in which the female gametophytes are derived from two or four spores, the two maternally derived alleles of a locus in endosperm cells are not a random sample of the maternal alleles.

Fully dominant (or recessive) endosperm and embryo genes have the same resource-gathering strategy because an allele has the same effect every time that effect is expressed, regardless of how many copies are present. A gene in either tissue is expressed in the same seeds and bears the same costs. Thus the difference in the number of genomes in an embryo and its endosperm is unimportant. This is not true of some other modes of expression of embryo and endosperm genes, however (Law and Cannings, 1984; Queller, 1984, 1989; Bulmer, 1986), which exhibit conflicts between embryo and endosperm genes because the ratio of allele copies experiencing benefits and costs differs for diploid embryo and triploid endosperm genera.

The different dominance and dosage relationships of genes and types of competition among seeds give varying degrees of discrepancy between kin selection models using IBD measures of relatedness and genetic models (Queller, 1989). The discrepancies have been attributed to inexactness of the kin selection models. When factors other than randomness influence the distribution of genes from an ancestor to its descendants, IBD measures of relatedness are invalid. The correct result can be obtained simply as above by the use of the collective fitness rule, which traces the lineal transmission of alleles from an ancestor to its descendants and weights the effects on the participants from first principles. Alternatively, covariance measures of relatedness can be used to weight effects of endosperm genes on their own and other embryos (Queller, 1989).

Regardless of the modes of action of the genes concerned, another factor often causes endosperm and embryo genes to agree on the amount of parental resources that are optimally gathered. In many angiosperms (and probably primitively; Stebbins, 1974), the endosperm is not consumed prior to seed maturation, but persists during dispersal and subsequently aids seed germination. After dispersal, the endosperm and embryo (and parent; Lloyd, 2000b) act in unison, simultaneously maximizing the fitness of free-living individual seeds and the collective fitness of the parent. The post-dispersal activities of the endosperm, which presumably determine the amount of resources it is selected to gather for its own embryo, are not in conflict with the embryo or the parent.

Kin conflict theories of the nature and activity of endosperm have presented a very incomplete and unbalanced view of seed biology. They have concentrated on genetical matters and have largely ignored ecological, physiological and ultrastructural aspects of seeds. The concept of kin conflict has not yet contributed anything definite towards an explanation of the nature and activity of the endosperm, let alone the huge diversity among species in its expression. The answers to the operation of endosperm are more likely to come from a combination of intensive and comparative studies of seed development and ecology than from consideration of the inclusive fitness of the genetic entities involved in seed reproduction.

CONCLUSION

I expect kin selection to be admirably suited to explain the disabled individuals and organs discussed in this paper because it integrates the direct contributions to the fitness of an action allele in actors and the indirect (non-lineal) contributions from related recipients. The above analyses confirm that kin selection does indeed increase our understanding of the various disabilities. But the outcomes are more diverse than previous accounts of kin selection operating during parental investment and in the selection of sterile workers might have led us to expect. In the case of the individuals disabled, there is not much active conflict between the family participants involved in reproduction. In the case of the individuals disabled by their position on a parent, parental manipulation controls events. At the other extreme, the level of self-incompatibility is controlled by the progeny (pollen) withholding cooperation in the narrow zone of parent–offspring conflict. And in the development of endosperm, there is little more conflict than between parents and their offspring, which I conclude has been over-emphasized, especially for plants (Lloyd, 2000b). The variety of outcomes appears to depend in large part on the degree to which parents must consider information transmitted to them from the offspring. The value of this information varies from its being entirely unnecessary in the cases of sterile gametes and seeds, to its being

indispensable for the operation of self-incompatibility. Events in seed development are generally intermediate both in the quality of information conveyed from seeds and the ability of the offspring to influence the course of their own development.

ACKNOWLEDGEMENT

The completion of this manuscript was supported through contract C09524 from the New Zealand Foundation for Research, Science and Technology.

REFERENCES

Bowers, K.A. 1975. The pollination ecology of *Solanum rostratum* (Solanaceae). *Am. J. Bot*., **62**: 633–638.

Bulmer, M.G. 1986. Genetic models of endosperm evolution in higher plants. In *Evolutionary Processes and Theory* (S. Karlin and E. Nevo, eds), pp. 743–763. Orlando, FL: Academic Press.

Charlesworth, D. 1984. Androdioecy and the evolution of dioecy. *Biol. J. Linn. Soc*., **23**: 333–348.

Charnov, E.L. 1979. Simultaneous hermaphroditism and sexual selection. *Proc. Nat. Acad. Sci. USA*, **76**: 2480–2484.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. London: Murray.

Darwin, C. 1877. *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*. London: Murray.

Eisikowitch, D. 1980. The role of dark flowers in the pollination of certain Umbelliferae. *J. Nat. Hist*., **14**: 737–742.

Grunmeier, R. 1990. Pollination by bats and non-flying mammals of the African tree, *Parkia bicolor* (Mimosaceae). *Mem. NY Bot. Gard*., **55**: 83–104.

Hamilton, W.D. 1964. The genetical evolution of social behavior I, II. *J. Theor. Biol.*, **7**: 1–51.

Hamilton, W.D. 1987. Discriminating nepotism: Expectable, common, overlooked. In *Kin Recognition in Animals* (D.J.C. Fletcher and C.D. Michener, eds), pp. 417–437. New York: Wiley.

Kimura, M. 1959. Conflict between self-fertilisation and outbreeding in plants. *Ann. Rep. Nat. Inst. Gen. Japan*, **9**: 87–88.

Law, R. and Cannings, C. 1984. Genetic analysis of conflicts arising during development of seeds in the Angiospermophytes. *Proc. Roy. Soc. Lond. B*, **221**: 53–70.

Lloyd, D.G. 1992. Evolutionary stable strategies of reproduction in plants: Who benefits and how? In *Ecology and Evolution of Plant Reproduction: New Approaches* (R. Wyatt, ed.), pp. 137–168. London: Chapman and Hall.

Lloyd, D.G. 2000a. The selection of social actions in families: I. A collective fitness approach. *Evol. Ecol Res.*, **2**: 3–14.

Lloyd, D.G. 2000b. The selection of social actions in families: II. Parental investment. *Evol. Ecol. Res*., **2**: 15–28.

Maheshwari, P. 1950. *An Introduction to the Embryology of Angiosperms*. New York: McGraw-Hill.

Queller, D.C. 1983. Kin selection and conflict in seed maturation. *J. Theor. Biol*., **100**: 153–172.

Queller, D.C. 1984. Models of kin selection on seed provisioning. *Heredity*, **53**: 151–165.

Queller, D.C. 1989. Inclusive fitness in a nutshell. *Oxford Surv. Evol. Biol*., **6**: 73–109.

Stebbins, G.L. 1974. *Flowering Plants: Evolution Above the Species Level*. Cambridge, MA: Belknap Press of Harvard University Press.

Trivers, R. 1985. *Social Evolution*. Menlo Park, CA: Benjamin/Cummings.

Westoby, M. and Rice, B. 1982. Evolution of the seed plants and inclusive fitness of plant tissues. *Evolution*, **36**: 713–724.

Zangerl, A.R., Berenbaum, M.R. and Nitao, J.K. 1991. Pathenocarpic fruits in wild parsnip: Decoy defense against a specialist herbivore. *Evol. Ecol*., **5**: 136–145.