

Skewed paternity and sex allocation in hermaphroditic plants and animals

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Models predict a reduced allocation to sperm when females preferentially use one of two males' sperm and the males do not know who is favoured. An analogous discounting occurs in plants when their paternity success is skewed by random, non-heritable factors such as location in the population and pollinator behaviour. We present a model that shows that skewed paternity can affect the sex allocation of hermaphrodites, that is it leads to a female-biased investment. The model highlights the close links between local mate competition and sperm competition. We use paternity data from *Ficus* in order to illustrate that skews in paternity success can lead to a high degree of sibling gamete competition in an apparently open breeding system. Since skews in paternity are ubiquitous in hermaphroditic plants and animals these findings should apply broadly.

Keywords: sex allocation; *Ficus*; paternity; sperm competition; local mate competition

1. INTRODUCTION

Hamilton (1967) showed that female-biased sex ratios are favoured when mothers lay clutches in a patchy environment so that brothers compete with each other to mate with their sisters. The reason for the female-biased skew is that mothers can thereby create more mating opportunities for and reduce futile conflict among their sons (Taylor 1981). Due to brothers competing in a local area for mating, this process was coined local mate competition (Hamilton 1967). In a similar way, local mate competition can bias the sex allocation of hermaphrodites, but here the competition is between the male gametes of a hermaphroditic parent (Charnov 1982). It also leads to increased investment in female gametes to the detriment of male gametes (Lloyd 1984; Sakai 2000). Specific focus has been given to selfing (Charlesworth & Charlesworth 1981), where competition between sibling pollen grains is analogous to competition between brothers. The models developed for local mate competition in hermaphrodites do not consider situations where the paternal contributions of different individuals are skewed by random factors, and here we show that this exacerbates the effective degree of local mate competition.

Several studies have looked at the effects of sperm competition on hermaphroditic sex allocation in animals (Charnov 1996; Greeff & Michiels 1999; Pen & Weissing 1999). Parker (1990) showed that when one male's sperm is discounted relative to another male's sperm and the discounting is at random so that the males do not know whose sperm is discounted, then the evolutionarily stable strategy (ESS) (Maynard Smith 1982) is to invest less in sperm and more in acquiring females. Here we develop sex allocation models in order to consider an analogous situation that should be common in hermaphroditic plants as well as animals.

Recently, similarities between sperm competition in animals and similar pollen competition phenomena in plants have been highlighted (Delph & Havens 1998). Multiple paternity is common in many hermaphroditic plants (Delph & Havens 1998), and individuals will have very different proportions of their zygotes sired by different fathers (Devlin & Ellstrand 1990; Godt & Hamrick 1993; Nason *et al.* 1996; Kameyama *et al.* 2000). When such variation in male reproductive success is the result of non-heritable factors such as position in the population (Devlin & Ellstrand 1990; Smouse *et al.* 1999), wind direction or directional pollinator movement (Handel 1982), we have a situation analogous to Parker's (1990) loaded-rafts-with-roles-unknown sperm competition models. We show that, in hermaphrodites, such random variation in paternity success leads to a reduced ESS allocation to male gametes in favour of female gametes. We derive a model describing the problem and illustrate its effect in *Ficus*, where pollinators are known to carry pollen over large distances (Nason *et al.* 1998) and where local mate competition would normally not be considered as being an important factor.

2. THE MODEL

We shall present the model in terms of a hermaphroditic plant, but it applies equally well to hermaphroditic animals. Unless stated differently, 'individual' refers to a hermaphrodite. We shall talk of an offspring's 'mother' or 'father' when indicating the hermaphroditic parent that contributes the male or female gamete, respectively. As will be seen from our *Ficus* example, the competition between sibling gametes need not arise from spatially limited local mating and, in order to avoid confusion, we shall use the term sibling-gamete competition. In order to incorporate sibling-gamete competition into a sex allocation model we assume that a common pool of resources has to be divided between the male and female functions of a simultaneously hermaphroditic organism.

The fertilizations obtained per number of pollen shed will differ between individuals due to random factors. We shall call

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this the plant's pollination efficiency and it is independent of an individual's investment in male gametes (r). The pollination efficiency of a given father may vary from mother to mother as will the number of fathers and their pollination efficiencies with each individual being pollinated. In order to avoid complexity let us assume that the population is divided into mating groups consisting of $d+1$ individuals. If we further assume that no selfing occurs, then d fathers will typically compete to fertilize any one mother and each father can pollinate d mothers. Furthermore, let there be d sets of d e -values e_{ij} . These values are the expected relative pollination efficiencies of the d fathers, which are indicated by the j subscripts, that are competing to pollinate the d mothers, which are indicated by the i subscripts and are scaled so that $\sum_{j=1}^d e_{ij} = 1$. We assume that, for each of the $d+1$ mothers that are pollinated, there will be d fathers each playing one of the e_j roles.

Consider a hermaphrodite with a limited amount of resources available for reproduction and let the ESS investment in female gametes be a proportion $1-r^*$ of their total resources. Let the fitness returns on investment in female gametes be a linear function. The ESS investment in male gametes is the remaining fraction r^* of the resources. We will consider the fitness of a rare mutant that invests r in male gametes and $1-r$ in female gametes. If all other plants have the same amount of resources to invest in gametes, then the proportion of a specific mother's gametes that the mutant father with a pollination efficiency of e_m will pollinate is the amount of pollen the father produces weighted by his pollination efficiency divided by the sum of these products for all the fathers, which is given by $e_m r / [e_m r + (1 - e_m) r^*]$.

If each father has a random chance of $1/d$ of playing the e_j th role during pollination of each of the d mothers then we can calculate the mutant's average relative pollination success as

$$\sum_{i=1}^d \sum_{j=1}^d \left(\frac{1}{d} \times \frac{r e_{ij}}{r e_{ij} + r^* (1 - e_{ij})} \right). \quad (2.1)$$

The fitness of a mutant investing r in a hermaphroditic population investing r^* is directly proportional to

$$w = (1 - r) + (1 - r^*) \frac{1}{d} \sum_{i=1}^d \sum_{j=1}^d \frac{r e_{ij}}{r e_{ij} + r^* (1 - e_{ij})}. \quad (2.2)$$

The first and second terms give the mutant's fitness through female and male functions, respectively. The term in square brackets gives the proportion of the $1-r^*$ available seeds that the mutant will fertilize. The ESS sex ratio can now be found by solving for r^* in

$$\left. \frac{\partial w}{\partial r} \right|_{r=r^*} = 0, \quad (2.3)$$

(Maynard Smith 1982) and is

$$r^* = \frac{\sum_{i=1}^d \sum_{j=1}^d e_{ij} - \sum_{i=1}^d \sum_{j=1}^d e_{ij}^2}{d + \sum_{i=1}^d \sum_{j=1}^d e_{ij} - \sum_{i=1}^d \sum_{j=1}^d e_{ij}^2} = \frac{1 - E}{2 - E}, \quad (2.4)$$

with

$$E = \frac{1}{d} \sum_{i=1}^d \sum_{j=1}^d e_{ij}^2, \quad (2.5)$$

which is the average value of $\sum_{j=1}^d e_{ij}^2$ over all the mothers.

It can be seen from equation (2.4) that less energy is invested in male function as E increases. E can have a maximum value

of unity and this is achieved when only one tree pollinates the receptive tree. E decreases as more individuals donate male gametes, for instance when d trees are equally competitive in pollen contribution, i.e. when $e_{11} = e_{12} \dots = e_{dd} = 1/d$, $E = 1/d$. A skew in the fertilization abilities of individuals leads to an increase in E . For example, if one tree contributes almost all the pollen and a second tree only contributes a few pollen grains ($e_{11} \gg e_{12}$) then E will be larger than $1/d$, which is 0.5 in this case. Hence, if fewer individuals donate male gametes and if the contribution is more skewed, then sibling-gamete competition is increased and less will be invested in male gametes.

The differences in pollination efficiency have the effect of increasing sibling-gamete competition above that of equal competitors and lead to a more female-biased optimal investment. This effect of paternity skew has been overlooked in current models that consider sibling-gamete competition phenomena in hermaphrodites. Frank (1985) discussed an analogous situation in local mate competition sex ratio models for fig wasps with males and females.

In order to appreciate how the skew in paternity contributes to the extent of sibling-gamete competition we can calculate $\hat{d} = 1/E$, where E has been estimated from the data. \hat{d} is the number of equally competing fathers that would result in the same amount of sibling-gamete competition as is observed in the data with d pollen donors. When we simplify our model so that all d competitors have equal pollination efficiencies $E = 1/d$, equation (2.4) simplifies to $r = (d-1)/(2d-1)$, which was obtained in models that did not allow for differences in pollination efficiencies (eqn (5.2) in Charnov 1982; Lloyd 1984). Sibling-gamete competition due to small mating groups will thus favour female-biased investment and, if the individuals donating male gametes are unequal in their pollination efficiency, it results in a further reduction in male investment.

The connection between sperm competition and sibling-gamete competition (and local mate competition) can be made explicit using our approach. When a proportion q of females are mated twice and a proportion $1-q$ are mated once and sperm competition is fair, we can use equation (2.4) for deriving the optimal allocation to sperm. With probability $1-q$, $e_{i1} = 1$ and with probability q , $e_{i1} = e_{i2} = 0.5$. By substituting these values into equation (2.4) we obtain

$$r^* = \frac{1 - [(1-q)1^2 + q \times 2 \times (0.5)^2]}{2 - [(1-q)1^2 + q \times 2 \times (0.5)^2]} = \frac{q}{2+q} = \frac{p}{4-p}, \quad (2.6)$$

with $p = 2q/(1+q)$ (Parker *et al.* 1997) being the proportion of ejaculates experiencing sperm competition with unrelated ejaculates. The right-hand fraction of equation (2.6) is the basic equation calculated by Parker (1982, 1990), which specifies the proportion of resources that should be invested in sperm. In this way sperm competition can be viewed as a special case of local mate competition between the male gametes of one individual.

3. THE CASE OF *FIGUS*

Fig trees have a specialized inflorescence and fruit, i.e. the fig. The inside of a monoecious fig is lined with many small uniovulate female flowers and fewer male flowers (Wiebes 1979). Each fig tree species is generally serviced by a species-specific pollinator wasp (Agaonidae: Chalcidoidea: Hymenoptera), which is itself totally dependent upon the fig tree (Wiebes 1979; Michaloud *et al.* 1996). Pollinated female flowers can support the development of

Table 1. The number of fig trees sampled per species, the average number of figs sampled per tree, the average observed number of donors identified from allozyme data, E calculated from these data using equation (2.5), the effective number of pollen donors and the optimal allocation to male function in seven hermaphroditic *Ficus* species.

species	number of trees sampled	figs sampled per tree	observed donors per tree	E	effective donors (\hat{d})	r^*
<i>F. obtusifolia</i>	6	26.2	17.2	0.095	10.53	0.475
<i>F. dugandii</i>	1	15.0	11.0	0.102	9.78	0.473
<i>F. pertusa</i>	2	14.0	9.5	0.135	7.38	0.464
<i>F. popenoei</i>	3	14.7	10.7	0.173	5.77	0.453
<i>F. perforata</i>	2	20.5	5.5	0.320	3.12	0.405
<i>F. nymphifolia</i>	2	28.5	9.5	0.334	3.00	0.400
<i>F. citrifolia</i>	2	35.0	13.5	0.354	2.83	0.393

a seed, but when the wasp galls and oviposits into the flower a wasp larvae will develop at the cost of a seed (Nefdt & Compton 1996). The life cycle of fig wasps of monoecious trees can be summarized as follows. After being mated, female pollinating wasps eclose from the galled seeds in which they developed. They proceed to pick up pollen from male flowers either actively or passively and then leave their natal fig through a hole chewed in the fig wall by the male wasps. The females fly away in order to locate young receptive figs that are normally on another tree. They enter these through a bract-lined tunnel called the ostiole, which loosens temporarily when the female flowers become receptive, thereby allowing the wasps to squeeze their way to the inside. A short while after pollination it becomes tight and impenetrable again (Galil & Eisikowitch 1968). Once inside, the wasps pollinate the female flowers, but also gall and oviposit in a number of them. After some weeks the figs ripen, producing seeds and a new generation of pollen-bearing wasps.

Female flowers that are sacrificed in order to rear pollinating wasps are thus part of the fig tree's male function since these wasps disperse the pollen. Female flowers that produce seeds serve the female reproductive function.

A factor that may bias *Ficus* sex allocation stems from their unusual fruiting phenology: crops are normally very synchronized within a tree but not between trees (but see Cook & Power (1996) for an exception). Only a small fraction of trees are producing wasps and pollen at any one time, and mating groups may be very small. This will result in pollen from one tree competing mostly against sibling pollen from that same tree and should favour female-biased allocation. Elevated sibling-gamete competition is often the result of spatial confinement of mating groups (Lloyd 1984), but can also be temporal, as is the case here. However, fig wasps are known for travelling over great distances, suggesting that pollen can be drawn from a large area and many trees may sometimes pollinate a receptive tree (Nason *et al.* 1996, 1998).

We used the data reported in the studies by Nason *et al.* (1996, 1998), which used allozyme electrophoresis in order to identify pollen donors. In order to estimate e_{ij} from these data we assume that all the fathers siring seeds on a specific mother had been identified (below we show that the error introduced by this assumption is minimal) and that their relative contribution to pater-

nity reflects their pollination efficiencies. Hence, if the j th male sired n_{ij} of the N_i scored seeds of the i th mother, then $e_{ij} = n_{ij}/N_i$. We can estimate E as the average value of $\sum_{j=1}^d e_{ij}^2$ over the i mothers (see equation (2.5) and table 1). \hat{d} can be estimated as $1/E$ and r^* by using equation (2.4).

E , r and \hat{d} were estimated for seven *Ficus* species (table 1). Notice that the effective number of pollen donors is less than the observed numbers because of the skewed paternity contributions of the fathers. Despite the pollinator's long-distance dispersal, asynchronous fruiting and skewed paternity lead to fairly small effective mating groups (\hat{d}) and high sibling-gamete competition. This is particularly true for *Ficus perforata*, *Ficus nymphifolia* and *Ficus citrifolia*, which have between three and four effective donors. For comparative purposes, the competition between male gametes is equivalent to the local mate competition experienced between sons of species with separate sexes with 3.12, 3.00 and 2.83 foundresses per local patch. However, since no inbreeding occurs, extra female gametes do not result in extra fertilization opportunities for male gametes and the skew in sex allocation is not as much as in standard local mate competition models (Lloyd 1984), for example compare our $r = (d-1)/(2d-1)$ to the standard $r = (d-1)/2d$ (Hamilton 1967). Even so a skew of ca. 40–60% can be expected for these three species. In species where selfing is possible, the sex allocation would be more female biased.

Nason *et al.* (1996) showed that, in their paternity study, a number of fathers were missed due to incomplete sampling of figs from maternal trees. Here we perform a sensitivity analysis in order to show that fathers that contribute a tiny fraction of pollen have a very small and effectively negligible effect on E . Two scenarios, i.e. a and b, are given in table 2 where five fathers were identified but an additional four fathers were overlooked. Cases a1 and b1 give the estimates as we would have made them. Cases a2 and b2 and a3 and b3 give the corrected estimates if the additional fathers sired 4% or 8% of the seeds, respectively. In case a, where there was no skew, the errors introduced by our estimate of r^* were negligible, namely 0.002 and 0.009. In case b, where paternity was skewed, the errors in our estimate would have been 0.027 and 0.051, which are still relatively small. Hence, even though our estimates are slightly biased due to small sample sizes, it will not affect our conclusions qualitatively.

Table 2. The effective pollination efficiencies and estimates of E , \hat{d} and r^* for hypothetical mothers where four of the nine fathers were missed during paternity tests.

(Series a is a population where the five observed fathers contributed equally and series b is a population where there was a skew in paternity. Cases a1 and b1 are the incorrect estimates where four fathers were overlooked, cases a2 and b2 are scenarios where the unidentified fathers contributed 4% to the paternity and cases a3 and b3 are scenarios where they contributed 8% to the paternity.)

	e_1	e_2	e_3	e_4	e_5	e_6	e_7	e_8	e_9	E	\hat{d}	r^*
a1	0.2	0.2	0.2	0.2	0.2	0	0	0	0	0.2	5	0.444
a2	0.192	0.192	0.192	0.192	0.192	0.01	0.01	0.01	0.1	0.195	5.138	0.446
a3	0.184	0.184	0.184	0.184	0.184	0.02	0.02	0.02	0.02	0.171	5.852	0.453
b1	0.8	0.1	0.05	0.025	0.025	0	0	0	0	0.654	1.530	0.257
b2	0.768	0.096	0.048	0.024	0.024	0.01	0.01	0.01	0.01	0.603	1.659	0.284
b3	0.736	0.092	0.046	0.023	0.023	0.02	0.02	0.02	0.02	0.555	1.802	0.308

4. CONCLUSIONS

Our model shows that skews in paternity can significantly increase the degree of sibling-gamete competition. Concomitantly, the model predicts an increasingly female-biased sex allocation in hermaphrodites as sibling-gamete competition increases. Skews in paternity are commonplace in many hermaphroditic plants (Devlin & Ellstrand 1990; Godt & Hamrick 1993; Nason *et al.* 1996; Kameyama *et al.* 2000) and animals, including snails (Baur 1994), nudibranchs (Todd *et al.* 1997), ascidians (Bishop *et al.* 2000) and planarians (Pongratz 2000). Hence, the model should be of general biological significance. One consequence of such female-biased investment is that it can serve to stabilize hermaphroditism and thereby prevent separate sexes from evolving (Lewis 1941; Charlesworth & Charlesworth 1978).

Ficus species are known for their long-range pollination and it is common to identify more than 10 pollen donors, thereby suggesting that sibling-gamete competition should be negligible. Yet, we show that a high paternity skew caused a high degree of sibling-gamete competition in three of the seven species investigated.

Our model demonstrates an explicit link between local mate competition sex ratio models (*sensu* Hamilton 1967) and sperm competition models (*sensu* Parker 1982), i.e. similar to brothers who compete locally in order to mate with females, sperm from one ejaculate compete locally in order to fertilize a limited number of ova. As a result, investment in sperm by hermaphrodites is analogous to investment in sons in species with separate sexes. The model differs from the conventional framework, within which sperm competition is modelled as a function of the risk of competition between unrelated ejaculates. Notwithstanding these differences, the respective approaches predict the same optimal investment in sperm.

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