Sex allocation in dynamic mating environments

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Article

Keywords:

Posted Date: January 26th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1281174/v1>

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Abstract

Mating can be a risky stage of the life cycle in many kinds of sexual organisms, particularly those that release propagules—gametes, spores, or alates, depending on the organism—into a mating arena at low density where they may die before finding a mating partner. The abundance of the two sexes and thus the dynamics of a mating arena are affected directly by the sex allocation strategy of the parental organisms that produce propagules. A long-established theory of sex allocation is based on models with static representations of resource investment and mating. In contrast, we present a simple dynamic model based on rate-dependent production, mortality, and mating of male and female propagules. We show that anisogamy or similar sexual size dimorphism shifts optimal investment toward female propagules, while post-investment mortality of either sex favours greater male investment, in direct contrast to predictions from traditional static models. Our model predictions are broadly consonant with some macroevolutionary patterns, such as the typical female-biased reproductive investment by angiosperms, and raise new questions for empirical investigation in many taxa.

Introduction

Mating propagules often lead precarious lives. Short sperm viability and rapid dilution by currents^{1–3} can leave a large fraction of eggs unfertilized among broadcast-spawning aquatic invertebrates^{4–6}. Pollen grains from flowering plants typically remain viable for only hours or days^{7,8} and ovules for days or weeks^{9–14}. Even when removed from flowers, most pollen grains never reach a receptive stigma^{15,16} and may fail to germinate if they do^{17,18}, leaving many ovules unfertilized and reducing seed output^{19,20}. Among social insects, reproductive individuals mate either during flight, as in most ants²¹ and bees²², or thereafter, as in termite queens and kings, which mate once inside a newly created nest²³. Alates are often lost during these synchronized nuptial or dispersal flights from exhaustion or to the many predators they attract^{24–29}.

Mortality or loss may strike the sexes at different rates, usually higher for male than for female mating propagules^{12,14,30}, although the reverse can occur (for example, the larger and calorically valuable female alates of aerial mating ant species seem to suffer higher predation rates than the smaller males^{24,26,29}). Conventional theoretical models have suggested that a sex difference in mortality should have no selective effect on sex allocation in a well mixed mating arena, as such losses occur after the cessation of parental resource investment^{31–34}. In these models, greater pre-mating mortality of one sex reduces the probability that a given individual of that sex will mate, but raises the probability of mating for the survivors because competition is reduced, such that the two effects exactly cancel each other³⁴.

Although the simplicity of this result is satisfying, it is derived from models that implicitly assume time-independence of resource allocation and fitness acquisition, so that mating propagules are produced, dispersed, and mate (or fail) in a single instant. In reality, of course, these processes unfold over time. A dynamic perspective on mating has already offered novel insights into the evolution of anisogamy³⁵ and breeding systems³⁶. Here we develop a dynamic model of sexual allocation when mating propagules search for partners in a mating arena where partners may be scarce and dangers abound. Male and female propagules are produced by hermaphroditic parents, the norm in plants³⁰ and, while rarer in animals, nonetheless phylogenetically widespread³⁷. Propagules of each sex enter a mating arena at rates regulated by the parental resource income and the cost of the propagules. This introduction rate is the first flux in the model. Propagules leave through death or transportation out of the arena, the second flux. They also leave (in pairs) through successful mating, the third flux and the measure of fitness of a sex allocation strategy. We model mating as a mass-action function of male and female propagule numbers in which the two sexes make equal linear contributions per propagule to the mating rate (see the Supplementary Methods for an alternative mating function with nonlinear effects). We incorporate as few biological details as necessary in order to gain general insights on sex allocation that could apply to a broad range of taxa. The optimal sex allocation is found by the phenotypic optimization method of Evolutionary Stable Strategy (ESS)³⁸.

Results

Sexual size dimorphism. We gain an immediate insight from the model. Anisogamy, heterospory, or other difference in size or cost involving more expensive female than male propagules favours female-biased sexual allocation, a bias augmented if larger female size is accompanied by improved survival (Fig. 1a). This female-biased optimum is not the result of inbreeding or spatially structured mating opportunities (such as local mating competition among related males), factors known to favour female investment in theory and empirical results^{32,34,39}, but which are absent from the well mixed mating arena that we model. Nor is it a consequence of a larger ‘target size’ of female propagules⁴⁰. The prediction of female-bias is intriguing because static models have suggested that size dimorphism alone should not displace the sex allocation optimum from equal investment (although equal allocation would yield a numerical imbalance with more individuals of the cheaper sex)^{32,34}. Let us briefly dissect these competing predictions heuristically.

Earlier theoretical developments, including seminal work on the sex ratio⁴¹ used as a foundation for later models³², did not explicitly require that each mating involve one propagule of each sex, the so-called Fisher condition^{42,43}. No model intentionally violates such a fundamental fact, but without explicit inclusion it is easily overlooked. Our model meets the Fisher condition by having the same rate of exit through mating for both sexes (Methods), and the predicted female bias due to size dimorphism is a direct result.

The most immediate consequence of greater female size or cost, all else equal, is to reduce the production of females and the rate at which they enter the mating arena. Because of the Fisher condition, reduced female entry limits the potential fitness payoff from male investment. This would have no selective consequence under time-independent fitness acquisition in a static model. Equal fitness from unequal resource allocation gives one sex greater marginal gains per unit of investment, and selection should then favour increased investment in that sex until allocations are equalized^{32,34}. A dynamic conception of the problem, as our model offers, recognizes that both mortality and mating dispose of reproductive investment, although the mortality component may differ between the two sexes. Due to rapid turnover, the proportional success of short-lived male propagules plummets as females become rarer with increasing size

(Fig. 1b). Long-lived female propagules, in contrast, simply wait for mates and continue to mate in high proportions. Their success is little affected by size; female mortality rate has a far stronger influence (Fig. 1c).

An inherent selective consequence of sexual size dimorphism arises. As rising cost reduces the abundance of female propagules and they become harder to find, the marginal fitness value of ephemeral male investment declines, while the more durable female investment retains high marginal value. Selection then favours a shift to female-biased allocation, increasing female entry and decreasing male entry to the mating arena until the scarcity of males restricts female success to the point that both sexes obtain equal marginal fitness per unit investment. This is the point of selective equilibrium, the ESS optimum, and it has a female bias if females are large or costly (Fig. 1a).

Post-investment mortality. A second notable insight is that mortality of mating propagules following the end of parental investment alters the parent's optimal sex allocation, an effect already noted in Fig. 1 but which has additional and interesting consequences. In particular, the optimal sex allocation shifts toward greater male investment as the mortality rate increases among propagules of either sex (Fig. 2). It may seem intuitive that a more rapid loss of male propagules favours an increase in their production rate, but it is less obvious why a decline in female viability should also favour increased male investment. The seeming paradox is resolved when we recognise that mating and mortality are competing processes that vie for the flux of propagules entering a mating arena. Rising female mortality is countered if they can first be 'rescued' through mating, and the mating rate is elevated by increasing abundance of their mating partners brought about by a shift in sex allocation toward greater male investment. Note, however, the sexual asymmetry at work: rising male mortality cannot so easily be countered through increased female abundance because female propagules are expensive, and shifting a unit of resources to female investment has less influence on propagule abundance and the mating rate than an equivalent shift toward male investment. Thus, selection favours investment in the cheaper sex to counter rising mortality in either sex.

Mating rate. Three other factors in the model affect sex allocation through their influence on the mating rate. A larger parental population or greater budget for reproductive investment on the part of each parent raises propagule density in the mating arena, and thus the mating rate. Mating itself (reflected in the model by the mating rate parameter, γ ; Methods) may occur more readily due to factors like propagule motility or chemotaxis⁴⁴, or transport of propagules by goal-directed pollinators. With a mating rate that is already high, the 'rescue' from mortality afforded by an abundance of male propagules is diminished, and the marginal effect of additional male investment is diminished. Selection then favours a more female-biased allocation (Fig. 3). The effect of the mating rate on sex allocation is opposite to that of mortality, as might be expected for these competing processes.

Discussion

A race between mortality and mating frames the issue of sex allocation in an unfamiliar way but captures the essential dynamics of reproduction in many kinds of organisms with dispersed mating propagules. Female-biased sex allocation should be common in these organisms because sexual size dimorphism in a dynamic mating environment has different effects on the potential marginal gains from male and female investment. This is the most fundamental and unexpected³² prediction of the model, and we briefly survey the known extent of female bias in nature.

Female-biased allocation seems to be frequent among simultaneously hermaphroditic animals³⁷, but much of the available quantitative information concerns hermaphrodites that mate by copulation or pseudocopulation of potentially long-lived and iteroparous parents, a circumstance very different to mating by broadcast of ephemeral propagules. For example, increased mating group size among copulating organisms favours greater emphasis on sperm production^{37,45}, an effect opposite to the predicted effect of higher density of parents producing dispersed mating propagules (Fig. 3). Among hermaphroditic animals that broadcast sperm or both sperm and eggs, a female bias in gonadal tissue is found in the freshwater mussel *Anodonta imbecilis*⁴⁶ and the starfish *Asterina phylactica*⁴⁷, and a female bias in zooid ratio (at least at large size when most reproductive zooids are produced) occurs in the bryozoan *Celleporella hyalina*⁴⁸ and the scleratinian corals *Acropora hyacinthus*, *A. gemmifera*, and *A. nana* (although not *A. millepora*, and a male-biased ratio occurs in *Goniastrea retiformis* and *Stylophora pistillata*)⁴⁹.

A far stronger signal of female bias emerges among angiosperms. Investment in endosperm and fruit tissue from the maternal sporophyte typically greatly exceeds earlier floral investment, when male function occurs, and creates strongly female-biased allocation at the fruiting stage, although flowering allocations are often male-biased^{50–52}. These generalizations hold among outcrossing species, and are therefore not due only to the selective effect of self-pollination and local mating competition. But the temporal pattern of investment in the angiosperm life cycle (like that of aquatic invertebrates with brooding of eggs and zygotes⁵³) is not explicitly represented in our model. Is maternal investment in seed and fruit maturation part of a plant's sex allocation strategy, or is it a separate expense layered on top of sex allocation? If the cost of seeds and fruit limits the effective number of female propagules (even if initial overproduction of ovules is later restricted via abortion of incipient seeds and fruits^{54,55}), then the marginal fitness value of male and female investments would be altered in much the same way we predict for large female propagules (Fig. 1): part of the cost of female propagules is merely an 'anticipated' cost. Theoretical work that specifically incorporates the details of the angiosperm life cycle is needed, but we believe the model presented here provides a heuristic guide to how sexual size dimorphism will affect sexual allocation even with delayed female investment.

Sex allocation in eusocial insects is complicated by the occurrence of repeated mating flights^{56,57} and multiple mating by both queens and males^{58,59}, the presence of multiple queens²¹ or mated pairs^{60,61} in a single colony, and queen-worker conflict⁶² due to the relatedness asymmetry created by haplodiploid sex determination in ants and bees⁶³. Because of these complicating factors, both male- and female-biased sex ratios exist among eusocial insects^{64–66}.

Often (universally in seed plants) only male mating propagules are released while females are retained by the parental organism⁵³ or colony⁶⁷. It has been suggested that egg retention in brooding cavities by aquatic invertebrates should favour male allocation due to local mating competition among eggs, as the flow of water into a brooding cavity may not deliver sufficient sperm from a dilute suspension to allow complete fertilization³⁶. Such an effect seems very

plausible, but there is meagre evidence that it produces male-biased allocation among sperm-broadcasting invertebrates³⁶. We suggest that retention of eggs in brooding cavities and ovules within ovaries creates an additional effect of potentially greater selective importance: protection and lower mortality rate for female propagules. As high female mortality favours male allocation through the 'rescue' mechanism described above, low mortality would have the opposite effect. If protection and longevity are the dominant consequences of retention, sperm broadcasters should have more strongly female-biased allocations than related species that broadcast both eggs and sperm, and similarly among plants. A degree of confirmation comes from comparison of the free-sporing lycophyte *Selaginella*, which broadcasts both microspores and megaspores and has strongly male-biased allocation⁶⁸, with angiosperms, which retain and protect megaspores within ovules and typically have strongly female-biased sex allocation. This enigmatic pattern is explicable if broadcasting confers shorter viability or higher rates of loss on *Selaginella* megaspores than typically experienced by angiosperm megaspores in ovules.

Retention of virgin queens by army ant colonies and dispersal of winged males seem similar to egg and ovule retention, but are accompanied by extremely male- rather than female-biased allocations^{67,69}, apparently contrary to our model's prediction. The explanation seems to lie in reproduction by colony fission, a rare occurrence among eusocial Hymenoptera but one which probably originated early in the army ant radiation because swarm foraging is incompatible with small incipient colonies founded by independent queens⁶⁷. Candidate queens retained within their maternal colony therefore compete for a resource, the colony itself, essential to successful establishment. Such local resource competition among females strongly favours male allocation³⁴, and seems, in this case, to override any selective effect of protection and female longevity. Male-biased allocation characterises other eusocial species that reproduce by colony fission, including honeybees, *Apis mellifera*^{34,67}.

Macroevolutionary patterns like these are important, but tests are needed that directly address the mortality and mating mechanisms underlying the model predictions. There is considerable but unexploited potential for comparative tests, particularly among plants, which exhibit wide variation in mortality rates of pollen^{7,70-72} and ovules^{9-11,13}. We expect species with higher mortality rates among propagules of either or both sexes to have higher male allocations, in the absence of other selective factors that influence sex allocation. Unfortunately, it is rare^{12,14,73} for viability of both pollen and ovules to be measured in the same species, and almost unknown for sex allocation to be quantified along with propagule viability. In the single instance we know, *Cucurbita pepo* (Cucurbitaceae) has a strongly biased ratio of about eight male flowers per female flower; its pollen is particularly short-lived, losing viability more rapidly than so-called orthodox pollen⁷⁴ because it remains hydrated at anthesis, an atypical condition⁷³. This combination of traits is qualitatively consistent with the prediction that severe propagule mortality should favour male investment (Fig. 2). Other species in the same family as *C. pepo* present partially dehydrated pollen likely to be more resistant to desiccation and have longer viability⁷¹, thus offering an opportunity for comparative tests. A similar circumstance occurs in the genus *Callitriche* (Plantaginaceae), which includes species with terrestrial, amphibious, and submerged habits and pollen that is dispersed by either air or water⁷⁵. Among free-sporing plants, *Selaginella* has wind-dispersed spores while its extant sister genus, *Isoetes*, includes terrestrial, amphibious, and submerged species with water-borne spores. As pollen viability is likely to vary with dispersal mode among these related plants, they offer an opportunity to examine sex allocation in relation to propagule mortality.

Loss from a mating arena is equivalent to propagule death, and one well known interspecific pattern concerning pollen loss involves pollen:ovule ratios, which tend to decline among species whose floral visitors provide superior pollination service^{76,77}. These patterns are commonly interpreted in terms of the efficiency of pollen transfer⁷⁶⁻⁷⁹, the proportion of pollen grains eventually deposited on stigmatic surfaces. But there is no theoretical basis for thinking that selection responds to efficiency *per se*³². Self-pollination, for example, provides efficient pollen transfer, but selection then favours reduced male allocation not because efficiency reduces the number of pollen grains needed to fertilize ovules but because selfing creates local mating competition among sibling pollen grains³². Our dynamic model explains the empirical association of pollen:ovule ratios with pollination efficiency, even among outcrossing plants, not as a result of efficiency itself but because a lower loss rate for pollen, the selective factor that truly favours reduced male allocation (Fig. 2), is observed empirically as improved efficiency. Pollen transfer efficiency is an epiphenomenon that must be understood in terms of a dynamic process.

As with mortality, we predict that variation in mating rate should be accompanied by variation in sex allocation, with rapid mating favouring the evolution of higher levels of female investment (Fig. 3). Large variation in the final proportion of mated female propagules occurs among aquatic broadcast spawners⁶ and flowering plants¹⁹. Some of this variation in outcome may reflect intrinsic variation in the ease of mating, but in the absence of a theoretical motive to examine this factor there is little existing evidence of a connection between mating rate and sex allocation. Populations of the freshwater mussel *Anodonta imbecilis* had more highly female-biased gonadal tissue ratios when they were at higher density and thus likely to experience higher sperm density and faster mating⁴⁶. The colonial ascidian, *Botryllus schlosseri*, increased egg production more than sperm production when placed at a high productivity site⁸⁰, plasticity that was interpreted in terms of resource availability but which might reflect an adaptive response to high density and mating rate under favourable growth conditions. Pollination ecologists have accumulated a wealth of empirical data on rates of pollinator visitation and pollen deposition among flowering plants⁸¹⁻⁸⁵, but generally without examining a link to sex allocation. Nonetheless, there appears to be sufficient variation in nature to allow testing the existence of such links.

The theory of sex allocation based on traditional static models has been one of the outstanding successes of evolutionary biology³⁴, but our approach points to additional and unappreciated dynamic processes that affect selection on male and female investment. In particular, we identify an inherent female-biasing effect of sexual size dimorphism among propagules, a male-biasing effect of propagule mortality after parental investment has ended, and a female-biasing effect of higher mating rate (which may be due to improved search and encounter mechanisms, such as pollination using animal vectors) (Fig. 4). None of these selective consequences for sex allocation is anticipated in existing theory. Static models have predicted that in the absence of any other selective factor, the Fisher condition alone favours equal sexual allocation, even with sexual size dimorphism. The dynamic perspective does not recognize such a default allocation under size dimorphism (Fig. 1), because mortality and mating rates are inherently present and have selective effects (Fig. 4). These effects are relevant to organisms broadcasting ephemeral mating propagules. Even among mammals, however, sex differences in life history schedules, including mortality, may affect sex ratio strategies⁸⁶, suggesting that a dynamic perspective on sex allocation, appropriately tailored to the biology of particular taxa,

may offer new insights for animals that mate through copulation or pseudocopulation. Available evidence to test our model is limited but often supportive of the model predictions. There are further opportunities to study sex allocation patterns among a wide variety of organisms.

Methods

Ecology of mating. Our model supposes a population of N parental organisms at steady-state, such as an ecological carrying capacity. The parents may be hermaphrodites, or mated queens in hymenopteran colonies able to produce sexual sons and daughters selectively. The parents produce male and female propagules that disperse and mate. Gametes, heterospores, and social insect sexual alates are examples of such sexual propagules in different taxonomic groups. Following mating, the resulting zygotes, immature seeds, foundresses, or other mating products exit the mating arena and begin development into the next generation of parental organisms. Ecological processes regulate the products to restore the steady-state parental population size N . If post-mating death is independent of the sex allocation strategy of an individual's parents, then selection on sex allocation derives solely from the dynamics of the mating arena.

Each parent has a reproductive resource budget at a rate B for production of mating propagules; thus, they are 'income breeders' rather than 'capital breeders'⁸⁷. Parents divide this income stream into a fraction r devoted to male propagules and $1 - r$ devoted to female propagules. We suppose that r can evolve continuously over the domain $[0, 1]$. The rate of production of propagules of each sex then depends on the parental budget B , the sex allocation r , and the resource costs s_m and s_f of male and female propagules: an individual parent produces Br/s_m male propagules and $B(1 - r)/s_f$ female propagules per unit time. We assume that female propagules are larger than male.

Propagules enter a mating arena upon production, and leave through death (or equivalent loss such as being swept out of the arena by water or wind currents) or through successful mating. At any given time there are $M(t)$ male and $F(t)$ female propagules in the arena, although we omit the explicit time-dependence in the notation below and use simply M and F .

We set mortality at sex-specific constant rates μ_m and μ_f for individual male and female propagules, respectively. (Hence, longevity is exponentially distributed with means $1/\mu_m$ and $1/\mu_f$ for males and females, respectively). The mortality loss from the arena at any moment is then $\mu_m M$ and $\mu_f F$. There remains scope to explore models with more complex mortality functions, such as density-dependent mortality of mating propagules, but we defer such elaborations for the sake of simplicity.

Mating might be structured in complex ways, as would occur, for example, if the two sexes dispersed at different rates through the environment, but we make the assumption that mating occurs in a well-mixed arena under mass-action dynamics governed by a parameter γ , a small number that represents the fraction of all possible encounters between individual male and female propagules that actually occur and result in successful mating per unit time. That is, mating occurs at the rate γMF . While not derived from specific dynamics of propagule motion, encounters, or interactions, this function has the merit of simplicity, is commonly used to represent mating dynamics, and remains biologically realistic under small values of the parameter γ ⁸⁴. Each mating event removes one male and one female propagule from the arena, thus satisfying the 'Fisher condition'⁴³ of equality in total reproductive success of each sex.

Suppose that the parental population receives a single mutant that allocates $\hat{r}$ and $1 - \hat{r}$ of its resource budget to male and female investment, rather than the common values r and $1 - r$, but which is in every other respect identical to the common parental type. For large N and small γ , the mating rate between mutant male and mutant female propagules is trivially small and can be ignored, but the mutant propagules enter into matings with the common types.

Denoting the abundance of mutant male and female propagules by $\hat{M}$ and $\hat{F}$, the fluxes described above lead to the dynamical equations:

$$\frac{dM}{dt} = \frac{NB r}{s_m} - \mu_m M - \gamma M (F + \hat{F})$$

1a

$$\frac{dF}{dt} = \frac{NB(1 - r)}{s_f} - \mu_f F - \gamma (M + \hat{M}) F$$

1b

$$\frac{d\hat{M}}{dt} = \frac{B\hat{r}}{s_m} - \mu_m \hat{M} - \gamma \hat{M} F$$

1c

$$\frac{d\hat{F}}{dt} = \frac{B(1 - \hat{r})}{s_f} - \mu_f \hat{F} - \gamma M \hat{F}$$

1d

At equilibrium, abundances do not change and each of equations (1a–d) equals zero, providing a system of four equations in four unknowns, which can be solved to determine the equilibrium values M_{eq} , F_{eq} , $\hat{M}_{eq}$ and $\hat{F}_{eq}$. Initially we solve (1c) and (1d) yielding:

$$\hat{M}_{eq} = \frac{B\hat{r}}{s_m(\mu_m + \gamma F_{eq})}$$

2a

$$\hat{F}_{eq} = \frac{B(1 - \hat{r})}{s_f(\mu_f + \gamma M_{eq})}$$

2b

We substitute the expression in (2b) for $\hat{F}$ in (1a) and solve for M at equilibrium:

$$M_{eq} = \frac{NBrs_f\gamma - Bs_m\gamma(1 - \hat{r}) - s_ms_f\mu_f(\mu_m + \gamma F_{eq}) + \sqrt{4NBrs_ms_f^2\mu_f\gamma(\mu_m + \gamma F_{eq}) + [NBrs_f\gamma + Bs_m\gamma(\hat{r} - 1) - s_ms_f\mu_f(\mu_m + \gamma F_{eq})]^2}}{2s_ms_f\gamma(\mu_m + \gamma F_{eq})}$$

2c

The expression above and the expression for $\hat{M}_{eq}$ in (2a) can now be substituted into (1b) and the resulting equation solved for F_{eq} . The solution contains several hundred terms and is too lengthy to reproduce here but is available in the form of a Mathematica 11 notebook (Supplementary Software). Once parameter values have been specified, we can numerically calculate F_{eq} . The resulting value can then be used in (2c) to yield M_{eq} , and the values of M_{eq} and F_{eq} in turn used in (2a) and (2b) to calculate values of $\hat{M}_{eq}$ and $\hat{F}_{eq}$.

Standard techniques of analyzing dynamical models³⁸ indicate that the equilibrium $(M_{eq}, F_{eq}, \hat{M}_{eq}, \hat{F}_{eq})$ is stable, meaning that the system would return to equilibrium following small perturbations in the numbers of any propagule type. Specifically, the linearized dynamics at the equilibrium are contained in the Jacobean matrix

$$J = \begin{pmatrix} -\mu_m - \gamma(F + \hat{F}) & -\gamma M & 0 & -\gamma M \\ -\gamma F & -\mu_f - \gamma(M + \hat{M}) & -\gamma F & 0 \\ 0 & -\gamma \hat{M} & -\mu_m - \gamma F & 0 \\ -\gamma \hat{F} & 0 & 0 & -\mu_f - \gamma M \end{pmatrix}$$

We confirmed numerically for all ESS solutions presented in this report that the eigenvalues of J

were negative, thus satisfying the condition for local dynamical stability.

Adaptive dynamics. While mating is a loss from the arena in the dynamical sense, it is a gain of fitness and the measure of success of a given sex allocation strategy. The fitness, $\hat{W}$, of the rare mutant parent can therefore be expressed as

$$\hat{W} = \frac{1}{2}\gamma\hat{M}F + \frac{1}{2}\gamma M\hat{F}$$

3

The first term on the right-hand side represents the half of the (nuclear) genome contributed to offspring through matings by the mutant's male propagules and the second term is the equivalent for matings involving the mutant's female propagules. If the mutant is more fit than the common type, its sex allocation strategy will tend to spread under natural selection. Because M , F , $\hat{M}$, and $\hat{F}$ are implicitly functions of both r and $\hat{r}$ (as they affect abundances and therefore mating rates and departures from the mating arena), therefore $\hat{W}$ is also a function of both r and $\hat{r}$. It is possible to identify whether there exists a sex allocation that, when common, cannot be displaced through natural selection by a mutant with any other allocation strategy. This allocation, $r = \hat{r} = r^*$, is the evolutionarily stable strategy (ESS)³⁸. Candidates for the ESS occur at values of $\hat{r} = r$ that satisfy the condition

$$\partial \hat{W} / \partial \hat{r} |_{\hat{r}=r} = 0$$

4

To produce the results presented above, we evaluated (4) numerically for various suites of parameter values in order to locate values of $\hat{r} = r$ that satisfy this condition.

We chose parameter values that reflect populations of intermediate size ($N = 500$ to $N = 5,000,000$ in Fig. 3) with rates that are reasonably interpreted on a daily basis (e.g., mortality rates from 0.01 to 1 give mean propagule lifespans of 100 days to 1 day). Sexual size dimorphism is considered by fixing male size at $s_m = 1$ and varying female size from $s_f = 2$ to $s_f = 5000$, a range that would encompass relative size differences in social insect alates and heterospore volumes in plants, although differences in egg and sperm volumes are often even more extreme. A reproductive budget that varies from $B = 200$ to $B = 500,000$ then allows a daily production per individual of a maximum of hundreds to hundreds of thousands of male propagules or correspondingly fewer female propagules, depending on s_f .

Two additional conditions, convergence stability and non-invasibility, must also be met to ensure that $\hat{r} = r = r^*$ is an ESS³⁸. As it emerges, equations (1a–d) produce well behaved adaptive dynamics in which ESS sexual allocations are readily identified (Extended Data Fig. 1).

Convergence stability requires that directional selection favour a decrease in r when it is above r^* , an increase when it is below, and cease to act when $r = r^*$. For this to be true, the sign of the fitness gradient must change from positive when r is too low, pass through zero at $r = r^*$, and become negative when r is too high. This condition is fulfilled for the candidate r^* if

$$\left. \frac{d}{dr} \left(\frac{\partial \hat{W}}{\partial \hat{r}} \right) \right|_{r=r^*} < 0$$

5

that is, if the fitness gradient itself has a negative slope where it takes on the value zero³⁸. We confirmed this condition numerically in each instance of finding r^* . Moreover, it can be confirmed graphically that the fitness gradient has a negative slope over the entire possible domain $[0, 1]$ of r for a wide range of parameter values (Extended Data Fig. 1b, e, h), suggesting that condition (5) will be satisfied in all biologically reasonable cases.

Finally, to be non-invasible, no alternative phenotype near r^* should be able to invade a population in which the resident allocation is r^* . This criterion is satisfied if

$$\partial^2 \hat{W} / \partial \hat{r}^2 |_{r=r^*} < 0$$

6

Again we confirmed this condition by numerical evaluation of (6) for all candidate values of r^* . Numerical evaluation of the second derivative in (6) over the entire potential domain of r and for a wide range of parameter values suggests that this derivative is negative for all biologically reasonable parameter values (Extended Data Fig. 1c, f, i).

Approximation. ESS evaluation of equations (1a–d) produces lengthy, although otherwise straightforward, expressions requiring numerical solutions. A somewhat more tractable system is obtained through the following approximation. Suppose that the N common types in the population are sufficiently numerous that the mutant has no effect on the equilibrium values of M_{eq} and F_{eq} , and that the mating rates involving mutant propagules, $\gamma \hat{M}F$ and $\gamma \hat{M}\hat{F}$, are trivially small compared to matings between the common types. Then the total mating rate can be approximated by γMF . If the mutant obtains a fraction of total matings proportionate to its contribution of propagules into the mating arena, then mutant fitness will be maximized at the same sex allocation that maximizes $\gamma M_{eq} F_{eq}$ among the common type. Repeating the steps of the ESS analysis above on this simplified system (Appendix) yields an expression for the optimal sex allocation:

$$r_{approx}^* = \frac{NBs_m\gamma(s_m + s_f) + s_m^2s_f\mu_m\mu_f - s_m^2s_f^2\mu_m\mu_f + \sqrt{s_m^2s_f\mu_m\mu_f(s_m - s_f)^2(s_m^2s_f\mu_m\mu_f + NB\gamma[s_m + s_f])}}{NB\gamma(s_m + s_f)^2}$$

7

Equation (7), although an approximation, turns out to be highly accurate for the suites of parameter values that we examined. The value of r_{approx}^* always lay within 0.1% and usually within 0.01% of the value of r^* determined numerically for the full system in equations (1a–d).

In the Supplementary Methods we use a similar approximation to investigate a model that represents the mating rate as a Michaelis-Menten function, under which the rate saturates with increasing numbers of propagules. The optimal sex allocation patterns produced by this nonlinear function (Extended Data Figs. 2–4) are very similar to those shown in Figs. 1–3 and do not alter the conclusions drawn from the model with a mass-action mating function.

Declarations

Acknowledgements

Financial support came from the Australian Research Council Discovery Projects scheme, grant no. DP140103196.

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Figures

Figure 1

Sexual size dimorphism favours female investment: effect of relative female size on (a) optimal sex allocation and (b) male and (c) female mating success. Sex allocation, r , is the proportion of a parent's reproductive budget devoted to production of male propagules, and $1 - r$ to production of female propagules. Curves indicate results for different values of female mortality rate from 0.5 to 0.01, as indicated in panel (a). Other parameter values (see Methods) are: population size, $N = 10000$; reproductive budget rate, $B = 1000$; male propagule size, $s_m = 1$; female propagule size varies accordingly to produce the relative sizes indicated on the horizontal axis; male mortality rate $\mu_m = 1$; mating rate parameter, $\gamma = 10^{-8}$.

Figure 2

Rapid death of either sex favours male investment: predicted optimal sex allocation, r^* , in relation to mortality rates of male (μ_m) and female (μ_f) propagules. Other parameter values (Methods): population size, $N = 10000$; reproductive budget rate, $B = 1000$; male propagule size, $s_m = 1$; female propagule size, $s_f = 1000$; mating rate parameter, $\gamma = 10^{-8}$.

Figure 3

High propagule abundance or encounter rate favours female investment: effects of (a) population size, (b) reproductive resource rate, and (c) ease of mating on optimal sex allocation. Parameter values (Methods): population size, N , as indicated in (a), or $N = 10000$ in (b) and (c); reproductive budget rate, B , as indicated in (b), or $B = 1000$ in (a) and (c); male propagule cost, $s_m = 1$; female propagule cost, $s_f = 1000$; male mortality rate $\mu_m = 1$; female mortality rate, μ_f , varies from 0.01 to 0.5 for all panels as indicated in panel (a); mating rate parameter, γ , as indicated in (c), or $\gamma = 10^{-8}$ in (a) and (b).

Dynamic effects on sex allocation

Figure 4

Summary of the selective forces acting on sex allocation in a dynamic mating arena. Provided that female propagules are larger and more costly than male propagules (a dimorphism that favours greater female allocation), there is no default allocation that should arise in the absence of other forces, because of the necessary existence of a mortality rate (which creates selection for male investment as it rises no matter which sex is most affected) and a mating rate (which favours female investment as it rises).

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