Animal breeding systems

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In 1977, Emlen and Oring[1] published an article destined to become a citation classic, in which they presented an ecological framework for understanding animal breeding systems. This paper, based on solid foundations built by many people from Charles Darwin to John Crook, Peter Jarman, David Lack and Gordon Orians, defined a breeding system, originally called a 'mating system' (Box 1), as a behavioural strategy for obtaining mates. It encompassed both sexual selection – specifically the number of mates obtained and the manner in which they are acquired – and parental care. The two decades since this paper was published have seen an explosion in empirical and theoretical studies of reproductive behaviour. Breeding systems have proven more complicated, more interesting and more perplexing than originally thought. This review will focus primarily on research during the 1990s, highlighting challenges to previous syntheses, and attempting to accommodate recent findings in an updated theoretical framework.

The study of breeding systems explores relationships between mating behaviour and parental care. Recent findings have shown that in many birds, fishes, anurans, and insects, females play a more active role than previously thought, by engaging in mate choice, mating with more than one male, and selecting genetic partners separately from social partners. Theoretical advances have improved our understanding of the effect of parental care on sex differences in mating behaviour, though less attention has been devoted to feedback in the opposite direction. The original emphasis on the role of ecology in determining breeding systems has been overshadowed by studies of individual interactions, but modern comparative techniques may provide a new fusion between ecology, life histories, and reproductive behaviour.

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The classical view

The consensus has been that the breeding system of a population depends on the ability of one sex (usually males) to acquire mates either by associating with them directly or by defending territories and other resources for breeding[1-3]. In this view, the relative availability of mates is determined by their parental contributions because the sex contributing most to the young (usually females) limits reproduction by the opposite sex. The limiting sex is therefore a commodity to be courted and fought over. Thus, the theory goes, females, as the high-investing sex in most species, will distribute themselves around food or safe breeding sites, and males will compete to monopolize those resources or the females themselves, to enhance their mating success (Fig. 1).

This reasoning has led to ecological classifications of breeding systems based on the distribution of food and breeding sites in space and time[1-4]; typical examples of terms used are 'resource defense polygyny', defined as 'males control access to (multiple) females indirectly, by monopolizing critical resources', and 'monogamy', described as 'neither sex has the opportunity of monopolizing additional members of the opposite sex; fitness often maximised through shared parental care'[1].

Empirical updates

Recent observations have posed serious challenges to our understanding of breeding systems for several reasons, including appreciation of an active role played by females in many taxa[5,6] and of an important distinction for many species between genetic partner and social partner.

Multiple mating

The benefit of multiple mating to the sex whose reproduction is limited by the opposite sex (usually males) has always been easy to understand[7]. But advances since the late 1980s in the use of genetic markers, particularly DNA profiling, have shown that both sexes often mate with more than one partner. This includes taxa where females have control over copulations, such as most birds[6,8], and also applies to many species of mammals[2], insects[9] and fishes[10]. Indeed, some rather famous 'exceptional' avian breeding systems, such as the 'polygynandry' of the rhea (*Rhea americana*), where several females lay eggs into each of the nests of several males, are widespread in other taxa such as fishes, which never fit comfortably into the early classifications, which were largely avian-inspired[1]. In light of this new research, yesterday's 'polygyny' often becomes today's 'high variation among males in fertilization success; frequent multiple-mating by females'. Indeed, this description now applies to many species formerly considered monogamous!

When multiple mating by females has been examined, it has often been from the male perspective of sperm competition. Thus, the battle for females is seen as waged by the sperm of multiple males, rather than occurring solely before mating takes place. This view of multiple mating has greatly increased our understanding of why males mate repeatedly with the same female, as well as male adaptations such as mate guarding, genital structure, testis size, ejaculate volume and sperm design[8,11].

But what about females? Recent studies of birds show that females actively solicit multiple copulations, often from more than one male[8]. Furthermore, females may have various options for controlling paternity, by manipulating the timing of mating, or exercising 'postcopulatory choice'[12].

Box 1. What's in a name?

The term 'mating system', as defined by Emlen and Oring[1], included parental care by each sex and sexual selection, with the latter encompassing the number of mates acquired, the manner of mate acquisition, and the presence and characteristics of any pair bonds. The term 'breeding system' is used in this review to reflect better the inclusion of parental care.

'Breeding system' is defined here as a description of mating behaviour and parental care by both sexes. It includes variation among individuals in:
• form and duration of parental care
• form and duration of any pair bonds
• number of mates (both 'genetic' and 'social')
• forms of courtship, coercion and competition
• mating resources defended and offered
• extent of mate choice (including sperm choice after mating)

For example, when females of a species of arctiid moth (*Utetheisa ornatrix*) are mated with two consecutive males, the larger male sires most of the offspring, regardless of the order of mating[13]. Could this be under the female's control? Circumstantial evidence was provided by experiments in which females were anaesthetized, thereby preventing the peristaltic pulses of their reproductive tract. Sperm were rarely able to find their way into the female's spermatheca, implying that 'sperm competition' might be mediated by females, and hence might be better termed 'sperm choice'.

The challenge to explain multiple mating by females has been met with far more hypotheses than data (Table 1). Many of these have been reviewed recently for the case of multiple mating with the same mate[14]. Benefits concerned with paternity can be ruled out for taxa where high frequencies of mating occur prior to the female's fertile period. Even when females are fertile, none of the proposed direct or genetic benefits can explain all cases. For example, group-spawning enhances fertilization in some sessile marine invertebrates, but appears to be unrelated

Table 1. Hypotheses to explain multiple mating by females[a]

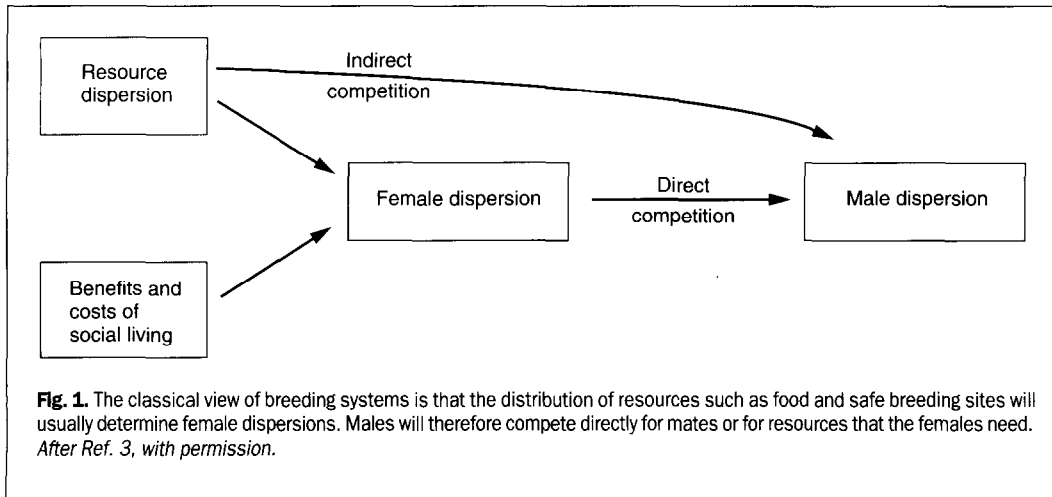| Hypothesis	Applies to same or different mates?	Explanation	Refs
Direct benefits			
Stimulation of reproduction	Same mate Different mate	Copulation or ejaculate stimulates ovulation As above	42
Fertilization assurance	Same mate Different mates	Ensures adequate sperm As above	15
Access to food, nuptial gifts	Same mate Different mate	Food or nutrients for female or ova during mating As above	4
Parental care for current brood	Same mate Different mate	Mate provides care if confident of paternity Additional males provide care	29 28
Extra broods obtained	Different mates	In successive pairings, males provide care	1
Mate retention	Same mate	Multiple copulations reduce chance of mate loss	14
Male harassment	Same mate Different mate	Copulation by female less costly than resisting As above	16
Mate assessment	Same mate Different mates	Male copulation may reflect his quality As above	14
Genetic benefits			
Choice of paternity	Same mate Different mate	Devalues other males' sperm Choice of better male's sperm	8
Sex ratio manipulation	Different mates	In haplodiploid insects ensures adequate sperm, hence females produced	19
Avoidance of genetic defects from stored sperm	Same mate Different mates	Old sperm might be more prone to genetic defects As above	41
Choice of mixed paternity	Different mates	Reduces competition among genetically dissimilar siblings	18
Sperm competition	Same mate Different mates	Allows high-quality sperm to out-compete rivals As above	43
Inbreeding avoidance	Different mates	Mating with multiple males reduces inbreeding	44
Selfish females	Same mate	Prevents other females from obtaining high-quality males	14
Genetic correlation with male multiple mating	Same mate Different mates	Females inherit tendency of males to mate often As above	41

[a]Modified and updated from Refs 14 and 41, with an emphasis on recent studies.

to fertilization in tropical fishes, presumably because the latter are able to spawn in close proximity to one another[15]. Parental care benefits can be ruled out for many species in which females obtain only sperm from their mates, but might apply to many insects in which males transfer nutrients at the time of mating[4]. Harassment may be particularly important in some primate species living in multi-male groups, but this could also select for monogamy if dominant males punish infidelity by females[16,17]. Parasitoid Hymenoptera were the subject of an interesting comparative study by Ridley[18], who speculated that mixed paternity may help diversify siblings genetically, thereby reducing competition when females lay more than one egg per host. However, lower relatedness among siblings could also weaken any restraints on competition stemming from kin selection. An alternative explanation of this case is that multiple mating increases the chances of fertilization[19]. This is important because unfertilized eggs would develop into sons, which would be disadvantageous because the optimal sex ratio for many species with sibling mating is female-biased.

The challenge is to test these hypotheses. Experimental tests with both internally and externally fertilizing species should be helpful, and broad correlations with ecology and life histories might be uncovered by comparing variation among taxa in the extent of multiple mating and fertilization. It would also be profitable to pay more attention to differ-

ences among individual females in their extra-pair mating behaviour. For example, Gowaty[6] has argued that different females may pay different costs if their social mates withdraw parental care in response to low confidence of paternity. Thus, differences among females in extra-pair copulations may be explained by variation in female quality as well as the quality of their breeding environments.

Mate choice for genetic benefits

Perhaps the solution to the mystery of multiple mating by females during their fertile period is contained in a related discovery that mate choice may yield genetic benefits to offspring. For example, laboratory experiments with guppies (*Poecilia reticulata*) showed that females prefer large-bodied and long-tailed males[20]. Males with either or both of these traits sired fast-growing offspring of both sexes, which translated into enhanced fecundity for daughters. Furthermore, some females attacked the males which had been assigned to them, and the males that received the most attacks proved to be poor genetic partners, siring daughters with low fecundity[20]. Female peacocks (*Pavo cristatus*) also engage in active mate choice, and attractive males with long trains sire offspring with enhanced growth and survival[21].

The importance of such findings for the theory of breeding systems is that if genetic quality of mates supplements[22] or supplants[23] direct resources when animals shop for mates,

Fig. 1. The classical view of breeding systems is that the distribution of resources such as food and safe breeding sites will usually determine female dispersions. Males will therefore compete directly for mates or for resources that the females need. *After Ref. 3, with permission.*

the link shown in Fig. 1 from resources to females to male control may be considerably weaker than previously thought. For example, female barn swallows (*Hirundo rustica*) prefer to mate with long-tailed males, despite such males providing less food for the young[24]. Could females be choosing genetic quality, indicated by the ability of males to survive despite their long tails, and be paying for it with reduced provisioning by the fathers?

Trade-offs between the quality of genes versus resources, and distinctions between social and genetic partner, cut to the heart of breeding system theory by challenging the 'polygyny threshold model' (reviewed by Refs 3 and 25). This hypothesis, which has been largely inspired by and tested in birds, attempted to explain why females would choose to settle on the territory of a male who had already attracted a female. Females could be selected to join an already-mated male if his territory quality were high enough to compensate the cost of sharing his attention and resources with another female. Rigorous tests with a variety of bird species have favoured alternative hypotheses based on a reconsideration of either the costs or benefits of sharing male territories[3,25]. Perhaps females actually pursue a mixed strategy of balancing direct resources against genetic considerations such as heritable viability benefits to offspring or 'sexy' sons: they could have more choices for settlement, and could nest with a good parent within easy reach of a genetically superior male for extra-pair copulations[26].

Feedback from sexual selection to parental care

Sexual selection may dictate parental care, rather than vice-versa, as is often assumed by the classical theory of breeding systems. For example, in the cichlid fish *Herotilapia multispinosa*, males desert their brood earlier when there are more potential mates available[27]. More recently, studies of dunnocks (*Prunella modularis*)[28] and reed buntings (*Emberiza schoeniclus*)[29] have shown that males feed nestlings more when they have higher paternity. The bird studies show (from the males' point of view) that success in this component of sexual selection leads to increased care. Conversely, from the female viewpoint success in multiple mating leads to decreased care from her mate (though this is compensated in dunnocks because both males feed the young[28]). Interestingly, not all the burgeoning number of avian studies have found positive correlations between certainty of paternity and male parental care (reviewed in Ref. 6). Substrate-spawning fishes might be an interesting group for comparisons, particularly those with care provided by the male alone, where one might expect low costs

of care per brood to lead to reduced correlations between certainty of paternity and care.

Classifications revisited

Multiple mating by females, the distinction between genetic and social partner, and the potential for genetic benefits suggest that the two original components of breeding systems – parental care and sexual selection – do not covary as cleanly or as consistently as previously thought. This is a challenge for classifications, which also need to give more emphasis to female behaviours in general, including aggression[25] and mate choice (Box 1). It is also difficult for classifications to accommodate variation among individuals in reproductive behaviours, as well as changes in the intensity and direction of sexual selection caused, for example, by food levels[30] and temperature[31].

Thus, the preoccupation during the 1960s and 1970s with distinctions among breeding systems and their ecological correlates has switched during the past two decades to greater attention to the details of interactions between individuals. One result has been that studies of ecological correlates of breeding systems have not kept pace with studies of sexual selection. In addition, many of the original distinctions between breeding systems have become unavoidably blurred. As far as classifications are concerned, we may therefore have little choice but simply to describe variation among individuals in any or all of the components of breeding systems listed in Box 1. In practice, this is what many researchers do already, to avoid generalizations focusing on only one sex or ignoring variation among individuals, environments, time in the breeding season, and so on[32]. Quantitative comparisons of taxa[33] according to the components in Box 1 may show new patterns of association and discontinuities, which will enable us to build new classifications tailored to particular purposes (e.g. descriptive versus explanatory).

Theoretical developments

Although reproductive behaviour defies simple classification, recent theoretical advances have helped clarify links with other aspects of life histories. First, it has been suggested that an important effect of parental care is its influence on the potential rate of reproduction of each sex[34–36]. For example, if males contribute no parental care, they will have a high potential rate of reproduction and their fitness will be limited by access to females. Males should therefore be the most competitive sex. Second, we should incorporate costs and benefits of mate choice explicitly into the theoretical framework, to accommodate the many species where mate choice has been implicated in the form of the breeding system.
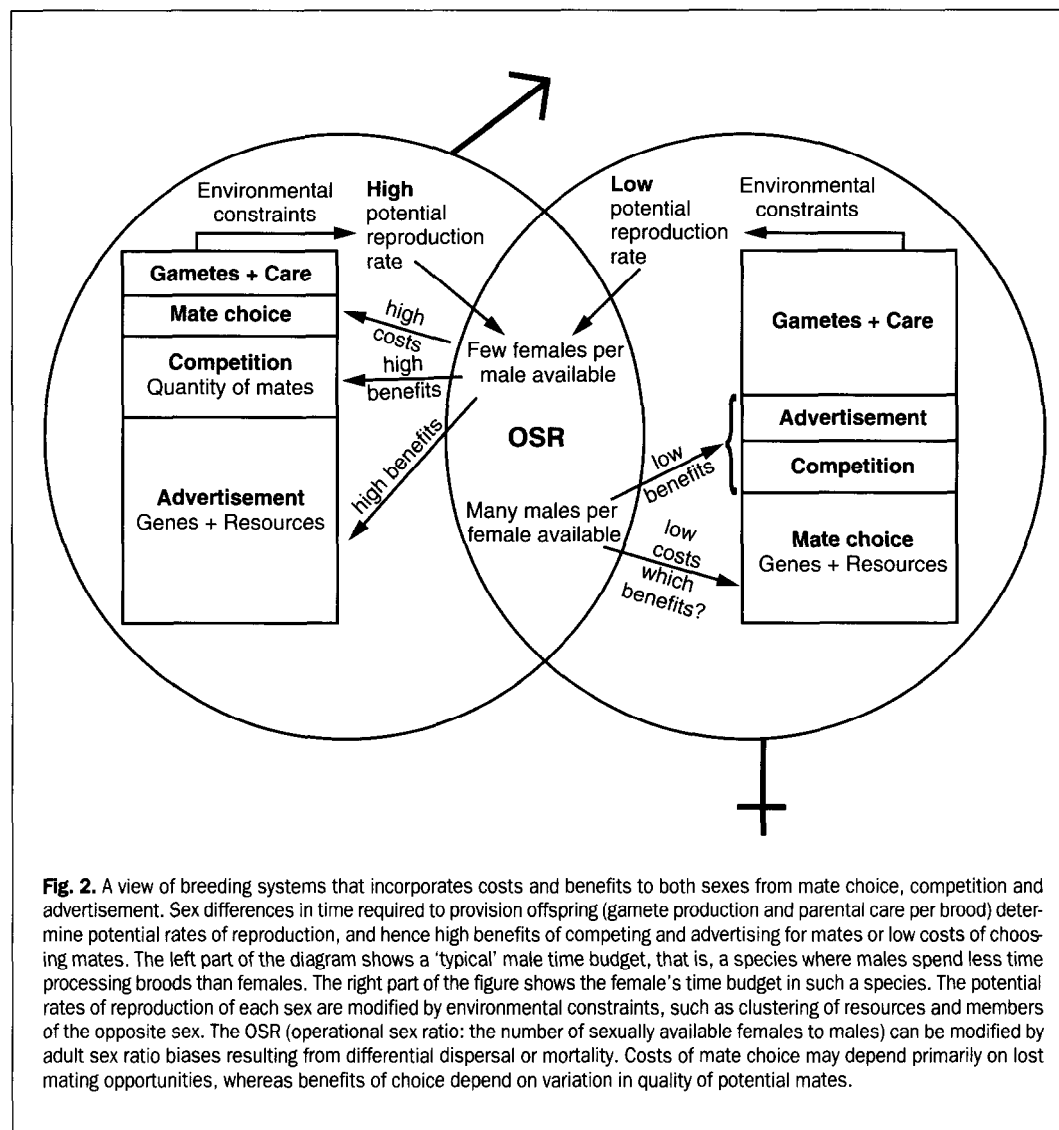
An attempt to update the theoretical framework for breeding systems is shown in Fig. 2. This shows time budgets for each sex separately, and is best understood by first considering one sex at a time. The male's point of view shows why low parental input per brood selects for mate competition. This applies to most species in which males provide less parental care per offspring than females, including the latter's provision of eggs. This part of the diagram is broadly

similar to a scheme proposed by Clutton-Brock and Parker[36]. The sex with the highest potential rate of reproduction (males in this scenario) will be limited by availability of the opposite sex. The availability of each sex will also depend on adult sex ratios, yielding an overall ratio of available females to males – the 'operational sex ratio', OSR, from Emlen and Oring's original formulation[1]. When receptive or high-quality females are rare, males are selected to compete for them, and this may occur at the expense (in both time and energy) of male mate choice and parental input. Thus, the allocations are not fixed; there is feedback between sexual selection and parental care.

An analogous scheme from the point of view of the other sex links parental care to mate choice (Fig. 2). This is not meant to imply that only one sex is choosy, but illustrates a common asymmetry between the sexes. Low potential rates of reproduction by one sex (e.g. females) give them the luxury of low costs to mate choice, because the opposite sex remains available for mating[37–39].

Fig. 2. A view of breeding systems that incorporates costs and benefits to both sexes from mate choice, competition and advertisement. Sex differences in time required to provision offspring (gamete production and parental care per brood) determine potential rates of reproduction, and hence high benefits of competing and advertising for mates or low costs of choosing mates. The left part of the diagram shows a 'typical' male time budget, that is, a species where males spend less time processing broods than females. The right part of the figure shows the female's time budget in such a species. The potential rates of reproduction of each sex are modified by environmental constraints, such as clustering of resources and members of the opposite sex. The OSR (operational sex ratio: the number of sexually available females to males) can be modified by adult sex ratio biases resulting from differential dispersal or mortality. Costs of mate choice may depend primarily on lost mating opportunities, whereas benefits of choice depend on variation in quality of potential mates.

For example, imagine a species of mammal such as the Uganda kob (*Kobus kob thomasi*) in which males display on aggregated mating arenas (leks) and provide nothing to females other than copulations, which they can perform several times in one day (J.C. Deutsch, pers. commun.). In contrast to males, females have much lower potential rates of reproduction, reproducing at 11-month intervals because of the demands of long gestation and parental care. If a male were to reject a receptive female, this would be a direct loss to his fitness, whereas if a female were to reject a male, there would be little cost to her since the high male 'recycling time' ensures that there will always be other receptive males available[38,39].

How well does this scheme accommodate the three recent empirical challenges to classical breeding system theory outlined above? Multiple mating and choice of genetic benefits by females will be facilitated by high potential rates of reproduction by males, because males will be available continuously. Thus, there are lower costs of lost mating opportunities for females from mate choice (Fig. 2). Such costs, in conjunction with other costs such as risk of predation and harassment, should be balanced against benefits due to variation in quality among members of the opposite sex[40]. In the figure, two-way feedback within the sexes between parental care and sexual selection is represented by the partitioning of their time budgets among these activities, and by the arrows pointing out the costs and benefits according to the OSR.

The framework also accommodates variation among individuals in courtship and competition. Such variation is expected from differences in attractiveness to mates and ability to dominate rivals. Thus, young or small males might be selected to engage in sneak copulations rather than to defend territories. This would be represented as low benefits from competition and advertisement in the male budget (Fig. 2). Similarly, environmental constraints such as temperature (especially in ectotherms) and food can change seasonally or may differ among habitats. This alters the relative rates of reproduction of each sex by changing the time or energy required to provide gametes and parental care. The resultant change in the OSR alters the benefits of competing and advertising for mates, or the costs of choosing mates.

An important goal of research on breeding systems has been to relate diversity among species to the environment. The 'environmental constraints' linking the time budgets of each sex to their potential rates of reproduction (Fig. 2) include resource dispersion in time and space, and benefits and costs of social living such as risk of predation and parasitism[1–3]. Such aspects of the environment, in conjunction with pressures from the opposite sex, will determine the economics of providing care, of defending territories versus mates, of forming pair bonds or associating only for mating, and of breeding alone or in groups. For example, if breeding sites are readily defendable, males may use territoriality to coerce one or more females to mate with them. In contrast, token mating arenas (leks) may evolve in habitats where

resources are sufficiently homogeneous in space and time that benefits to males of defending breeding sites or providing care are outweighed by a combination of selection to invest solely in mate competition, together with female willingness to forgo help from the male.

Questions for the future

Animal breeding systems are the outcome of a battle among competing interests, with opportunities and constraints set by the environment. Sexual conflicts are inevitable since males and females in most species differ in the costs and benefits of mating with one another[28]. It would be interesting to know whether one or the other sex tends to dominate the direction of evolution of particular breeding systems in particular taxa. This might occur if one sex is more constrained in trade-offs among allocations to parental care, mate choice, competition and advertisement. Phylogenetic studies would be a useful way of testing for historical constraints and opportunities set by the life histories of each sex in predisposing taxa towards particular breeding systems in particular environments. Ironically, this would bring us full circle to the original inferences used in formulating breeding system theory, but with the added rigour of modern comparative techniques incorporating recent discoveries of a rich array of behavioural interactions between the sexes.

Acknowledgements

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