

Ecology and evolution of mating systems Ökologie und Evolution von Paarungssystemen

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Abstract

This article reviews some aspects of seemingly diverse animal mating systems in terms of two underlying determinants: the mating opportunities and the reproductive effort needed for siring (= mating effort) and raising offspring (= parental effort). Opportunities and efforts are affected by three major factors: (1) *Historical constraints* set the boundaries for whole taxonomic groups and for the two sexes. (2) Within these boundaries *ecological conditions* determine the particular chances and efforts for individuals in different populations. (3) *Individual differences* in size, age or dominance lead to different options among members of the same population. High maternal and low paternal effort combined with low female and high male mating opportunities promotes polygyny; the opposite conditions favour polyandry. Where effort and opportunities for the sexes are about equal, monogamy will result when potential mates are regularly dispersed in space and synchronized in time and when young need extensive parental care; conversely, promiscuity or polygynandry is to be expected under conditions of spatial clumping, asynchronous mating activity and little need for parental care. Wherever mating opportunities and the relative proportions of mating and parental effort differ between the sexes, a conflict between males and females about the best mating system and the amount of parental care will result. Conflict may not always be obvious from behavioural observations, but modern molecular techniques reveal a high degree of extra-pair copulations, even in seemingly cooperative mating systems like monogamy with joint parental care. Although great progress has been made in understanding the ecological causes and evolutionary consequences of differences in mating systems, several questions remain unanswered. Some promising areas of future research are briefly mentioned.

Introduction

The social organisation of animals is characterized by a bewildering diversity of mating systems and forms of parental care. Mating systems range from no lasting social bond between males and females (promiscuity) through associations of one male and one female (monogamy) to various combinations of males and females (polygyny, polyandry, polygynandry). Even within any one category there can be different types such as seasonal and lifelong monogamy or simultaneous and sequential polygyny and polyandry. A further complication is added when we look at different levels of classification. Modern molecular techniques increasingly reveal that many organisms which are monogamous in terms of their social behaviour often engage in extra-pair copulations (EPCs) and thus are polygynous or polyandrous in terms of the genetic contribution. Forms of parental care are equally variable, ranging from no care through care of one parent (female or male) to care of both parents or even of additional helpers as in cooperative breeding systems.

The development of behavioural ecology as a discipline has allowed us to replace this bewildering array of behavioural possibilities with a coherent pattern. The basic principal is to consider the activities of organisms in terms of Darwinian fitness, i.e. in terms of the number of

alleles contributed to the gene pool by individuals pursuing one strategy, relative to the contribution of individuals pursuing different strategies. If we ignore indirect fitness which results from spreading gene copies through relatives (see B. König, this volume), fitness depends on two components (Fig. 1): (a) survival which determines the number of reproductive periods per lifetime and (b) seasonal reproductive success within any one reproductive period. Seasonal reproductive success, in turn, is a function of the number of young produced by mating with a single partner and of the mating success, i.e. the number of attracted mates. Survival and both components of reproductive success vary with the chosen behavioural strategy. The choice of a strategy is constrained by three factors (Fig. 1): (I) *historical constraints* which determine what strategies are genetically available, (II) *ecological conditions* which modify the fitness costs and benefits within the genetic boundaries, and (III) *individual qualities* which determine the best strategy for a given individual with its specific genetic and developmental background.

The purpose of this article is to explain the major mating systems and forms of parental care through some basic connections between these three factors and reproductive success. Within this network mating opportunities and reproductive effort are important intervening variables. More extensive reviews of the topic can be found in Wittenberger (1979), Oring (1982), Vehrencamp and Bradbury (1984), Davies (1991) and in recent textbooks by Alcock (1993) and Krebs and Davies (1993); the relationships with parental care are reviewed by Clutton-Brock (1991).

Historical constraints

Differences between sexes and taxonomic groups

By definition, females are the sex producing large immobile gametes (the eggs), males are the sex producing small mobile ones (the sperm). For males the contribution to offspring production often ends after copulation, while for females it continues to rise. In egg-laying species like reptiles and birds the zygote is surrounded with nutritious and protecting layers; in viviparous species like mammals the embryo is nourished during pregnancy and suckled after

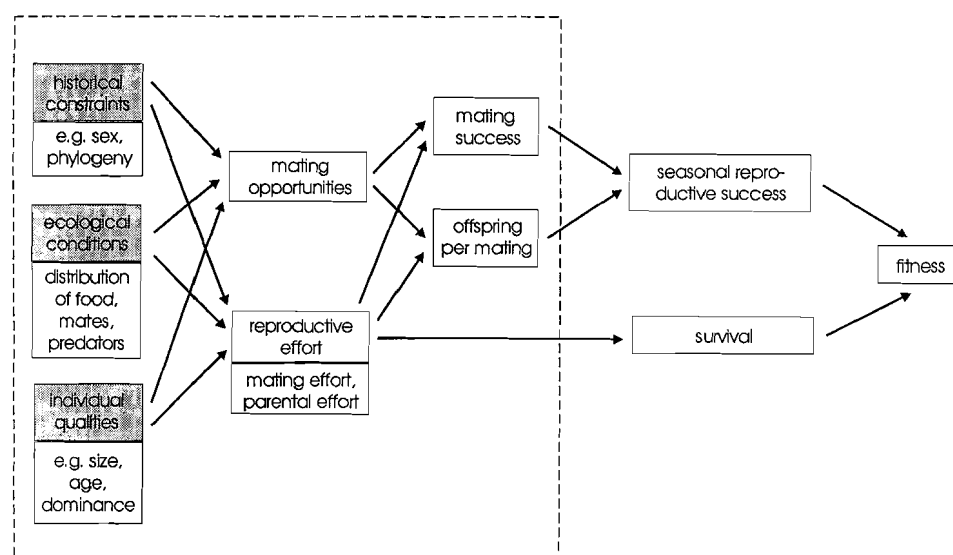


Fig. 1: Some pathways showing how historical constraints, ecological conditions and individual qualities translate into fitness. The network within the dashed lines is reviewed in this paper.

birth. The resulting sex differences in the time and energy expenditure for provisioning and rearing offspring (*parental effort*) can be tremendous. In terms of time, a male mammal may need only a few minutes for siring offspring, but the female loses several weeks, months or even years in pregnancy and lactation. The clutch of several bird species amounts to well over 50% of the female's body weight and in blue tits (*Parus caeruleus*) up to 130% (Perrins and Birkhead 1983, Table 4.1); but the sperm produced for fertilizing the eggs usually will not exceed 1–2% of a male's body mass, even when we consider frequent copulations of males (estimated from data in Moeller 1988 and Birkhead and Moeller 1992).

The consequences of these sex differences in parental effort are illustrated in Fig. 2 where the total resources of time and energy which males and females can devote to reproduction (*reproductive effort*) during their lifetime are represented by a full circle. The higher the parental effort (PE) the fewer resources are left for acquiring additional mates (*mating effort*, ME). Because of the physiological reasons mentioned above, in most species females have higher parental than mating effort, whereas in males the reverse is true (Fig. 2a). About 20 years ago, Robert Trivers (1972) pointed out that the relative proportions of parental effort and mating effort in males and females provide the key for understanding the evolution and ecology of mating systems and parental care. When a mating is unsuccessful – e. g. because the eggs are preyed upon or the young starve to death – the sex whose initial investment per offspring is higher (typically the female) will lose a higher proportion of its parental effort and impair its remaining reproductive potential (*residual reproductive value*) more than the sex investing less (typically the male). Therefore, a «typical» female should tend to continue her parental investment in offspring even when the male deserts after copulation. A «typical» male, however, which can devote a large proportion of his total reproductive effort to mating, can be expected to risk the loss of already produced offspring, since he can gain more by inseminating additional females.

Under such circumstances, reproductive success of females primarily depends on their access to resources which are essential for raising young (e.g. food, safe breeding places), while the success of males mainly depends on their access to a large number of females. This

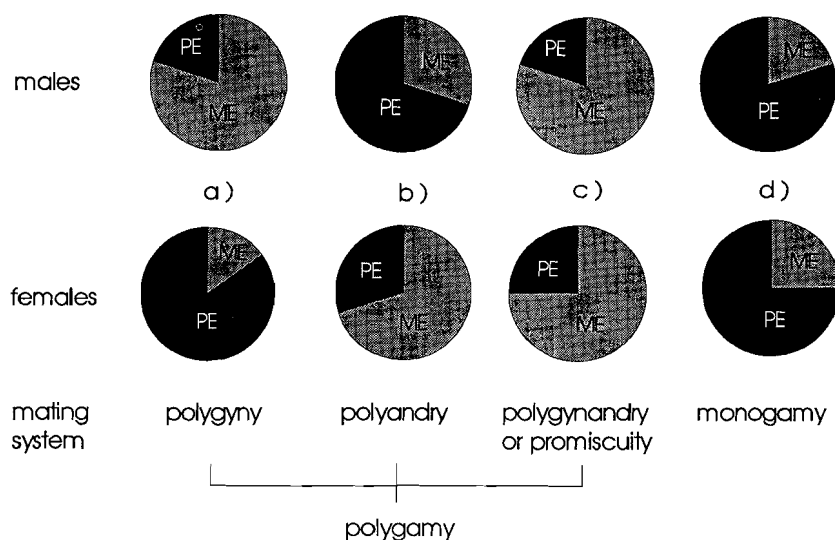


Fig. 2: Typical patterns of reproductive effort in males and females. Total reproductive effort available over lifetime (full circle) is divided into mating effort (ME, grey) and parental effort (PE, black). The sex with the lower parental effort can devote more effort to mating and attract more mates (polygyny, polyandry). When differences between males and females are small, promiscuity or polygynandry will result when little parental effort is required, monogamy will prevail under conditions of high parental effort. Modified from Krebs and Davies (1993).

results in male-male competition for females and will lead to *polygyny*, i.e. a mating system where males mate with several females whereas each female mates with only one male and usually provides the parental care. Conversely, where parental effort is higher in males than in females (Fig. 2b), males will lose more by giving up parental care and females will gain more by searching for additional mates. The result will be *polyandry* where females mate with several males while each male associates with only one female and often cares for the young. Where parental effort is similar for both sexes the resulting mating system will depend on the amount of parental investment required: With low parental and high mating effort (Fig. 2c) both sexes can mate with several mates and either leave them immediately after copulation (*promiscuity*) or associate with them for some time as in *polygynandry*, a mixture of polygyny and polyandry which can be accompanied by either female or male parental care. All cases in which an individual of either sex has more than one mate are often summarized as *polygamy*. With high parental – and consequently small mating – effort (Fig. 2d) both sexes have little opportunity for additional matings. This will result in *monogamy* where a male and a female form a pair bond and often jointly care for the young.

A first test for these theoretical predictions can be provided by comparing the mating systems of birds and mammals. In both groups initial female investment in zygotes exceeds initial male investment in sperm. Thereafter, however, in birds both sexes can incubate the eggs and brood, feed and protect the young, whereas in mammals pregnancy and lactation are restricted to females. Consequently, male and female birds differ less in the relative amounts of their parental and mating effort (Fig. 2d) than mammals do (Fig. 2a). As expected, ca. 90% of all bird species are behaviourally monogamous while more than 90% of all mammals are polygynous (Lack 1968, Wittenberger 1979). Further support for the close link between reproductive effort and mating systems comes from the exceptions in the two groups. Monogamy in mammals occurs mainly among the social carnivores such as foxes and wolves. In these species the young receive not only milk, but also meat. Since meat can be delivered by males and females alike, the provisioning pattern in carnivores has similarities with that of birds, and so has the mating system. Conversely, polygyny in birds is most frequent in species with precocial young. Since these young leave the nest and feed themselves right after hatching, parental care is less important for their survival than in species with altricial young. What parents save in parental effort can be invested in additional mating effort.

In spite of this fit between predicted and observed mating patterns, sex differences in parental effort cannot be the only factor determining the mating system. Parental effort alone neither suffices to explain monogamy in species without parental care, such as the marine clown shrimp *Hymenocera picta* (Wickler and Seibt 1981) nor does it explain why males in monogamous species do not reduce their parental effort more often. Assume that the proportion of the sired or surviving young is 1 when a male is monogamous and participates in raising the offspring, but only $1/x$ if he leaves the care to the female alone. If this male succeeds to also produce $1/x$ young with each of x additional females, then $(x+1)/x > 1$, and selection will favour the polygynous strategy with no paternal care over the monogamous strategy with paternal care. According to this argument the tendency to desert and mate polygamously should increase as the value of the present brood decreases and the opportunities for additional matings increase. Fig. 3 shows results from two experiments which support this prediction. Conversely, the tendency to stay should be favoured when chances of encountering receptive females are low. This is the case in the clown shrimp. Females are receptive for only a few hours every ca. 3 weeks, shortly after they have molted. With this narrow time window for copulations a male has a higher chance of mating successfully when he stays with one female and waits for her to become receptive than when moving around and searching for females which are widely dispersed and guarded by other males (Wickler and Seibt 1981). Thus, monogamy results from low options for polygyny.

To summarize this section: In order to understand differences in mating systems we have to consider differences in mating and parental effort as well as differences in mating opportunities. Both, effort and opportunity, can have a historical background like the specific fertilization mode in the clown shrimp, the sex-specific differences in the provisioning of young be-

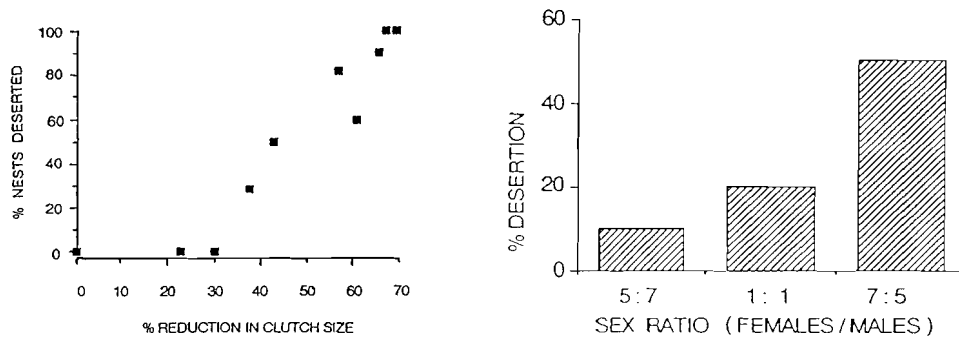


Fig. 3: Probability of brood desertion in female blue-winged teals (*Anas discors*) following experimental reduction of clutch size by 0–70% (left side) and in male cichlid fishes (*Herotilapia multispinosa*) in relation to experimental changes in the availability of females (right side). Both Figs. from Clutton-Brock (1991), left side after Armstrong and Robertson (1988), right side after Keenleyside (1983).

tween birds and mammals or the species-specific differences within birds (e.g. altricial vs. precocial species). But, as already indicated by Fig. 3, reproductive effort and mating opportunity can also depend on ecological conditions, such as predation pressure, quality and quantity of food or number of available mates. These ecological conditions are the subject of the next section.

Ecological conditions

Mating opportunities and mating systems

During the sixties and seventies a number of pioneering comparative studies were published which interpreted mating systems as an evolutionary response to particular ecological conditions. Among them were the papers by Crook (1964) on weaverbirds (Ploceinae), Crook and Gartlan (1966) on primates and Jarman (1974) on African ungulates. In all these animal groups two very similar patterns emerged: (1) In species with evenly distributed food, like insects or specific plants, individuals usually live in evenly distributed monogamous pairs; in species with patchily distributed food, like seeds, they live in clumped polygynous groups. (2) Forest living species are characterized by even distribution of individuals and monogamy, species living in open habitats, like savannahs and grass land, show clumped distribution of individuals and polygyny. This last relationship makes sense in the light of predation: in dense forest protection from predators is best achieved by hiding individually, in open habitat by assembling in groups which can detect and – possibly – deter predators more easily.

Additionally, the benefits and costs of social living can be affected by other factors including advantages and disadvantages of cooperation in mate acquisition (Packer et al. 1988), territorial defense (Koenig 1981), prey hunting (Bertram 1978), brood care (Emlen 1991) or thermoregulation (Arnold 1990). Since the distribution of food and other resources, predation pressure and the benefits and costs of group living can change with time, animal dispersion must be characterized not only by its spatial, but also by its temporal pattern.

Temporal and spatial dispersion patterns represent an important link between ecological conditions and mating strategies. Assuming equal numbers of potential mates, the probability that several will live in the same territory is higher with clumped than with regular dispersion of these mates (Fig. 4a, b). Chances for acquiring multiple mates also increase with increasing time span between their appearance. When all partners arrive at the same time the operational sex ratio of fertilisable females to sexually active males (OSR; Emlen and Oring 1977) is about 1:1 (Fig. 4c). When one sex appears asynchronously the OSR is skewed to an excess of the

other sex. In Fig. 4d the OSR is 1:3, because there are three (competing) males every time a receptive female shows up. Consequently, clumped spatial dispersion and asynchronous sexual activity of one sex increase the other sex' chances for acquiring multiple mates, thus creating a high potential for polygamy. Regular spatial dispersion and synchronous sexual activity results in a low potential for polygamy.

The close connection between temporal distribution and number of potential mates can be illustrated with an example from anurans. In «explosive breeders» like common toads (*Bufo bufo*), with a spawning period of a few days, individual males usually mate with only 1–2 females per season. In «prolonged breeders» like bullfrogs (*Rana catesbeiana*) which spawn over several weeks individual males achieve up to 6 matings (Wells 1977, Howard 1988). The connection between spatial distribution and number of potential mates is obvious in studies on voles (*Microtus californicus*, Ostfeld 1986; *Clethrionomys rufocanus*, Ims 1987, 1988). When food was added to specific sites in their natural environment, males and females concentrated their home ranges around these sites. This can be interpreted in two ways: (1) Both sexes respond similarly to the distribution of the food resource or (2) one sex responds to the food distribution, the other to the altered distribution of this sex. The second explanation applies, as shown by the following experiments. When caged females were distributed either spaced-out or clumped, free-ranging males changed their distribution accordingly; but free-ranging females did not respond to experimentally changed distributions of caged males.

These and several other results allow the following general conclusion (Fig. 5): The dispersion of females is mainly determined by resource dispersion, predation and benefits and costs of social living. The dispersion of males is mainly determined by the dispersion of females. This is to be expected when we recall that reproductive success of females mainly depends on access to suitable resources, while the reproductive success of males mainly depends on access to mates.

spatial distribution	a) regular 	b) clumped
temporal distribution	c) synchronous 	d) asynchronous
potential for polygamy	low	high

Fig. 4: Relationships between spatial and temporal distribution of resources or mates and the potential for polygamy. In (a) and (b) (modified from Krebs and Davies 1993) dots are resources, circles defended areas. In (c) and (d) white bars represent females, grey to black bars are males.

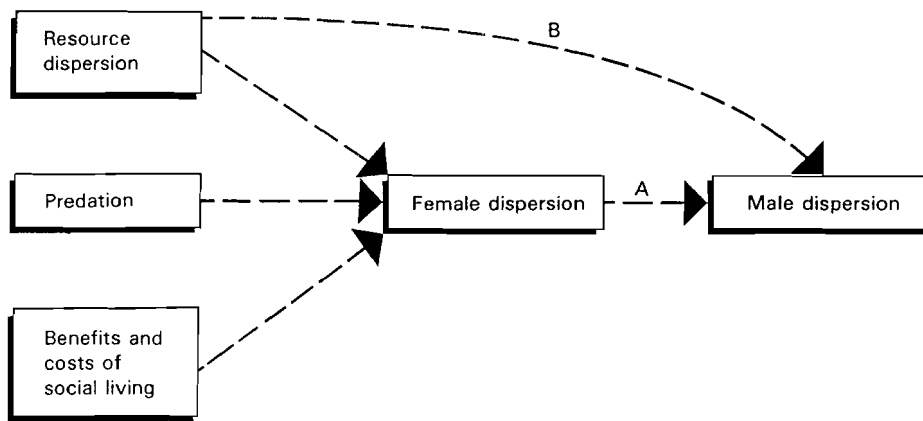


Fig. 5: Diagram illustrating the link between dispersion and mating system in species without paternal care. Female dispersion and reproductive success is mainly affected by resources, predation and benefits and costs of social living, while male dispersion and reproductive success primarily depends on female dispersion. Males can either compete over female groups directly (*female defense polygyny*; arrow A) or defend resources which are likely to attract females (*resource defense polygyny*; arrow B). From Krebs and Davies (1993).

Where males respond directly to the dispersion of females and fight over access to them, we speak of «*female defense polygyny*». This is the typical mating system for mammals with wandering female groups like lions, gorillas or red deer (Davies 1991). Alternatively, males can defend the resources which attract the females («*resource defense polygyny*»). Although in many cases such resource defense should be viewed as mating effort, because it primarily improves a male's chances of attracting females, it blends with parental effort when it also improves the survival of the young. This e.g. is true for dragonflies and birds whose males defend territories which offer the females suitable conditions for egg-laying or sufficient food for raising the young. In such instances, as well as in cases where males provide their mates with nuptial gifts or feed and defend the young directly, the males' contribution to reproduction goes beyond providing cheap sperm. Consequently, males become a resource themselves and can be expected to affect the dispersion of females. Under which conditions does this apply and what are the consequences for the mating system? These questions lead to the second important topic which has to be considered when searching for ecological explanations of mating systems: the amount of parental care needed for successfully raising young.

Parental effort and mating systems

The close link between the required amount of parental care and mating systems becomes obvious when one mate dies or is removed experimentally. In some species (e.g. most seabirds and raptors) reproductive success of the remaining partner then decreases to zero. Thus, joint care of males and females seems to be absolutely necessary and, indeed, these species show obligate monogamy (Oring 1982). In other species (e.g. several passerines) a female losing its mate can raise some young alone, indicating that male care is less important. In several of these species males do leave their females at least occasionally and become polygynous (Moeller 1986). Interestingly, this occurs more often in species which feed on easily exploitable food like seeds and fruits than in species feeding on insects which are more difficult to find (Crook 1964, Lack 1968).

The connection between required effort and cooperation in brood care has also been shown experimentally. In the cichlid fish *Lamprologus brichardi* Taborsky (1985) could change the amount of cooperation in brood care by manipulating competition and, thus, the need for help. In cooperatively breeding pied kingfisher (*Ceryle rudis*) the number of helpers which

assist a breeding pair in feeding young is a direct consequence of the time and energy which adults need to catch fish (Reyer and Westerterp 1985, Reyer 1988, 1990). At Lake Victoria, with its rough, turbid water and relatively small fish (*Engraulicypris argenteus*) close to the surface, adults expend about three times as much energy per gram fish provided for the young than at L. Naivasha with its calm, clear water and bigger fish (*Tilapia sp.*). As predicted from energy calculations, breeding groups were smaller at L. Naivasha than at L. Victoria (Fig. 6). That this is a direct consequence of the foraging effort could be shown experimentally: When at L. Victoria the feeding effort was lowered through reducing the number of nestlings to one or two, the percentage of pairs with helpers decreased from the usual 65% to 13%. Conversely, when at L. Naivasha feeding effort was raised through increasing the number of nestlings, the percentage of pairs with helpers increased from normally 17% to 80% (Reyer and Westerterp 1985).

The polygyny threshold model

In the above examples reproductive success of one organism is clearly affected by the resources provided by others. This has important consequences for the mating system. If all potential mates or territories are equally good, settling on an already occupied territory will mean sharing the resources and reducing the reproductive success. If resources differ in quality then a female may be better off sharing a good territory and mating polygynously than being monogamous in a bad one. This is the basic idea of the *polygyny threshold model*, originally proposed by Verner and Willson (1966) and Orians (1969). The model is illustrated and further explained in Fig. 7.

There are a number of observations and experiments, mainly for birds, which support predictions from this model (e.g. Ewald and Rohwer 1982, Ezaki 1990, Bensch and Hasselquist 1992), but there are also species in which females of polygynous males raise fewer offspring

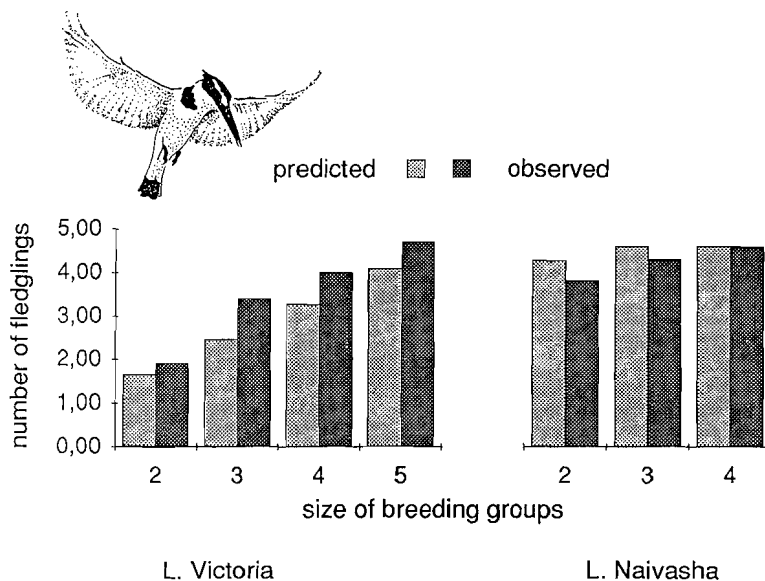


Fig. 6: Predicted and observed reproductive success of pied kingfishers (*Ceryle rudis*) in breeding groups of 2–5 adults (i.e. pairs with 0–3 helpers) at Lake Victoria and L. Naivasha. Predictions are based on three sets of data: (a) energy expenditure of feeding adults, measured with the doubly-labelled water technique, (b) upper threshold for parental energy expenditure, measured through changes in body mass and (c) energy requirements of the young, measured through hand-raising nestlings. The good agreement between predicted and observed values indicates that reproductive success is mainly determined by feeding effort.

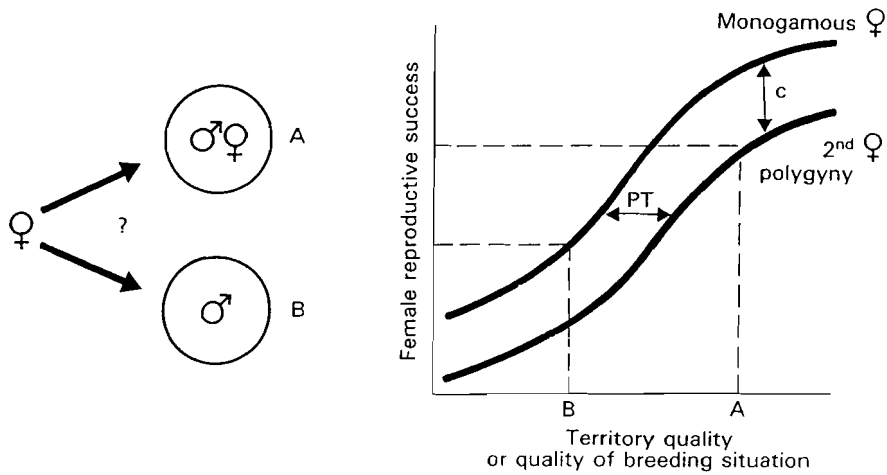


Fig. 7: The Verner-Willson-Orians polygyny threshold model. The model assumes that the reproductive success of a female increases with the quality of a territory, the assistance of the male and other factors improving the breeding situation. Under such circumstances, females arriving first will choose the best territories (e.g. territory A), later arriving ones must make a decision: they can either associate with an unmated male in a poorer territory (B) or become a secondary female of an already mated male in a good territory (A). In the latter case the female will have to share the resources with the primary female. Consequently, the fitness curve of the secondary female will lie below that for a monogamous female. The vertical distance between the two curves (c) represents the female's cost of mating polygynously. If, however, differences in breeding conditions between territories A and B exceed the horizontal distance between the two fitness curves (the so-called polygyny threshold, PT), it pays to share the resources in A, because a second female in territory A will achieve a higher reproductive success than a monogamous female in territory B. From Krebs and Davies (1993).

than those of monogamous ones. Why then do females «choose» to become secondary females?

There are various, not mutually exclusive answers to this question:

(1) The number of young is a poor measure for fitness; what counts is their quality (e.g. «sexy son» hypothesis of Weatherhead and Robertson 1979) and/or positive effects on the female's survival (e.g. Pleszczyńska and Hansell 1980).

(2) Searching for the, perhaps few and widely distributed, unmated males means higher time- and energy expenditure and increased predation risk. Thus, for later arriving females monogamy, too, would incur fitness costs (Stenmark et al 1988). These may be higher than the polygyny costs (c) shown in Fig. 7.

(3) Females have no choice. This situation can occur when a few males monopolize all suitable breeding sites, leaving other males without territories. It also can occur when females have no information about the mating status of the males or even are deceived by them. This «deception» hypothesis was originally proposed to explain polygyny in the pied flycatcher (*Ficedula hypoleuca*) (Alatalo et al. 1981). In this species females of polygynous males produce on average 20% (primary females) to 40% (secondary females) fewer young than females of monogamous males (Alatalo and Lundberg 1984). These differences in reproductive success arise, because polygynously mated females must share the parental care of their common male and this assists his primary female more than his secondary one. Consequently, females should tend to be monogamous, males should strive to be polygynous. According to Alatalo and his co-workers about 10–15% of all males succeed in becoming polygynous, because they deceive the females about their mating status through polyterritoriality. When their first female sits on eggs, they set up a second territory which can be up to 3.5 km away from the first one (average 200 m). Here they resume singing to attract a second female. Recently, Alatalo et al. (1990) have supported their deception hypothesis through experimental manipu-

lation of nest boxes, but alternative explanations like restricted mate sampling resulting from costly search for unmated males have not yet been fully excluded (Slagsvold and Dale 1994).

Conflicts between males and females

The specific example of the pied flycatcher introduces a much more wide-spread phenomenon: sexual conflict about the most profitable mating system. A quarter-century ago, David Lack (1968) stated that monogamy predominates in birds, because «. . . each male and female will, on average, leave most descendants if they share in raising a brood.» According to this view both sexes «agree» about the most profitable mating system and the necessary amount of parental care. Nowadays, behavioural ecologists claim that monogamy arises «. . . not because each sex has the greatest success with monogamy, but because of the limited opportunities for polygyny» (Krebs and Davies 1993). According to this view there is a conflict between males and females and each sex could do better and should pursue a different strategy if it were available.

The actual existence of such a conflict can be best illustrated by dunnocks (*Prunella modularis*), a small passerine bird which Nick Davies and his co-workers studied in the botanical garden of Cambridge (summarized in Davies 1992). In this species the three major mating systems (monogamy, polygyny and polyandry) occur side-by-side. This allows us to compare the fitness of males and females in the various mating systems unconfounded by species differences. For females average annual reproductive success decreases from 6.7 young in polyandry, where they have two males to assist them, through 5.0 young in monogamy where only one male helps, to 3.6 young in polygyny, where they must share the paternal care with another female. For males the sequence is reversed: they produce 7.6 young when they mate polygynously with two females, 5.0 when they are monogamous and 3.0 (beta-male) to 3.7 (alpha-male) under polyandry, where only some of their joint female's young are their own. This situation leads to a behavioural conflict with both, males and females, trying to increase the number of their own mates and to limit those of the other sex. Males prevent other males from approaching their females by defending territories and guarding their mates. Females try to escape the guarding and to solicit copulations from another male which then will help to feed her young. Although a rare mating system, this «cooperative polyandry» is neither limited to dunnocks nor to birds (see e.g. Faaborg and Patterson 1981, Terborgh and Goldizen 1985).

The extent of the conflict between males and females depends on the ecological conditions (Fig. 8). For females the order of fitness gain is polyandry > monogamy > polygyny. It remains the same under all ecological conditions, only the fitness differences increase when conditions become harsher. For males, however, the order changes from polygyny > monogamy > polyandry under good conditions to polyandry > monogamy > polygyny under poor conditions. The reason is that e.g. with decreasing food supply more and more adults are needed to guarantee survival of the young. Therefore, under harsh conditions, two males providing enough food for the young of one female may leave more young than one male which insufficiently feeds the young of one or two females. Consequently, shared paternity will pay; explaining cooperative polyandry does not pose a problem for the evolutionary biologist.

Polyandry and sex role reversal

But what about polyandric systems in which females not only produce young with several males, but also leave brood care to the males alone? Often the typical sex roles are reversed even further: females compete among themselves for access to males and perform the courtship, males choose among females. Examples come from insects, crustaceans, fishes, frogs and about 30 species of birds (reviewed by Gwynne 1991). Under the hypothesis that mating systems result from sexual differences in parental and mating effort we would expect that such species differ from the typical conditions (Fig. 2). This is indeed the case. For phylogenetic and/or ecological reasons males of polyandric species usually have a higher parental effort

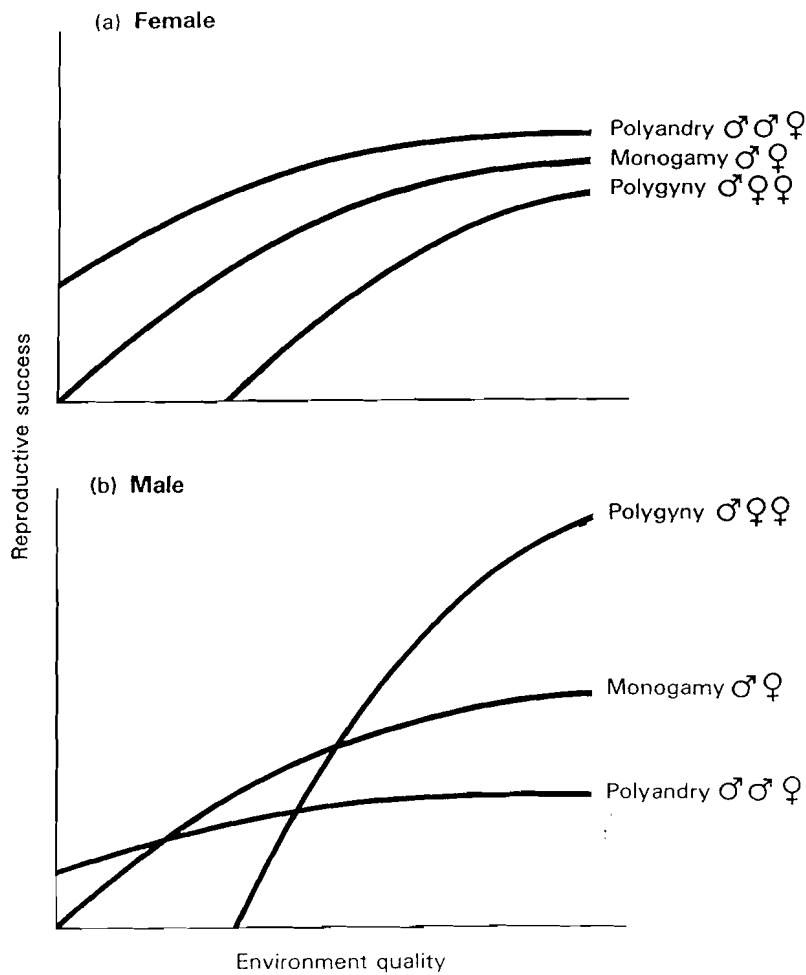


Fig. 8: A graphical illustration of sexual conflict. For each mating system reproductive success increases with environmental quality, but the fitness curves differ between the sexes. In females (a) success follows the order polyandry > monogamy > polygyny over the whole range of ecological conditions. In males (b) the order is the same in environments of low quality, but is reversed in high quality environments. From Davies (1991).

than females. In mormon crickets (*Anabrus simplex*) and some other insects copulating males provide not only cheap sperm, but also large, protein-rich spermatophores. These are eaten by the females and increase their fecundity. Sandpipers, phalaropes and some other polyandric birds inhabit areas of extremely high productivity like e.g. shallow ponds on the tundra (Erkman 1983). Here females find an excellent food supply and can produce eggs at a faster rate than males can incubate them. In some polyandric fishes like seahorses and pipefishes (Syngnathidae) the brood pouch of a single male is not big enough to take up the eggs of one female. In all these examples reproductive output is limited more by male than by female capacities. Consequently, the OSR of receptive females to sexually active males is skewed towards an excess of females. In some species this excess is further enhanced through a surplus of females in the population.

Where these conditions apply, competition among females for access to males and parental care by males is to be expected. We should, however, not turn the argument around and infer

polyandry and higher male than female parental effort whenever we observe male paternal care. In several fish species, for example, females come to the territories of males to spawn there. Once a female has laid her eggs, the male continues defense of the territory to attract further mates. By doing so, he incidentally defends the eggs and the fry as well (Gross and Sargent 1985). In giant water bugs (*Abedus herberti*) females glue their eggs to the back of a male which then guards and aerates them. As long as there is space on his back he is attractive for other females (Smith 1979). In such cases the apparent parental effort of males results, at least in part, from their mating effort. Therefore, the differences between these and the typical polygynous males are not as large as they first appear.

Extra-pair activities

Even when males and females «agree» about the best mating strategy, e.g. because poor ecological conditions demand high joint parental care (Fig. 8) or when parental care increases the chances of attracting additional mates as in fishes and water bugs, even then the sexual conflict does not disappear. Each sex tries to improve its own reproductive success and to decrease its share of parental care at the expense of the other sex. This statement is supported by a rapidly increasing number of studies which apply DNA-fingerprinting and other molecular techniques to identify real paternity (Burke 1989). These studies show that males and females often produce young with more mates than they are behaviourally paired with. In several seemingly monogamous passerines fairly high percentages of the young in a nest originate from extra-pair copulations (EPCs) (Fig. 9). In the splendid fairy wren (*Malurus splendens*) more than 60% of the young seem to be sired by extraterritorial males and in the the red-winged blackbird (*Agelaius phoeniceus*) EPCs account for about 20% of a males's reproductive success (for a summary and further literature see Birkhead and Moeller 1992). Thus, animals which are behaviourally monogamous can be genetically polygynous or polyandric.

For males the benefits from such EPCs are obvious: they produce more offspring. But what do females gain? The following list of possibilities is by no means complete. In species with nuptial feeding, females obtain additional food which may translate into larger eggs or clutches. In species like the dunnock they recruit additional males to feed their young. In still other species a female may get access to the nest of the other male and dump an egg there. This would increase the number of her own offspring without increasing her parental effort. Finally, females may copulate with genetically superior males and leave better descendents.

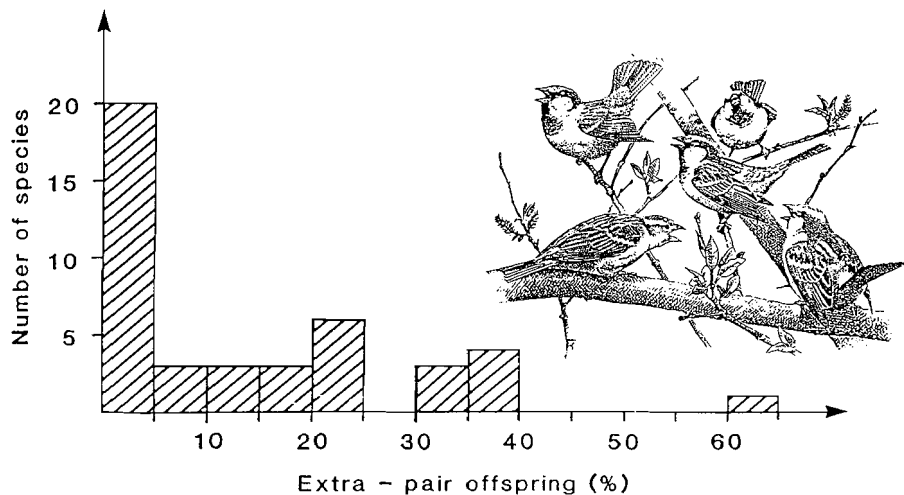


Fig. 9: Frequency distributions of the percentage of offspring fertilized by extra-pair copulations and sketch of communal display of house sparrows. Modified from Birkhead and Moeller (1992).

This hypothesis is supported by studies on birds which show that females apparently do not engage in EPCs randomly, but choose males with longer tarsi, better body condition, certain plumage characteristics and other traits which may indicate male quality (e.g. Kempenaers et al. 1992).

Individual differences and alternative strategies

The last example indicates that mating chances not only depend on the genetic background and the ecological conditions, but are also affected by individual differences between members of a population. The same is true for reproductive effort. Individuals which for genetic or developmental reasons are stronger, more skillfull or in other ways superior can devote more effort to mating or raising young than weak or unexperienced individuals. Therefore, we can expect different mating strategies to occur even within the same species, sex or habitat. An example in case are species which grow throughout their lives, such as fishes, amphibians and reptiles. In the lizard *Anolis garmani* small males with low fighting ability and, consequently, small territories can monopolize one female at best and thus are monogamous. The larger they grow, the more space they can defend. This gives them access to up to four females and allows polygynous mating (Trivers 1976). In species which do not grow continuously like birds and mammals available mating strategies and reproductive success are usually related to age or dominance (Fig. 10). In contrast to such continuous variation in reproductive success males of some fishes and amphibians adopt distinct alternative mating strategies. Large anuran males fight, call and/or are territorial, smaller ones move around in search for females or stay as satellites close to bigger males and try to intercept approaching females (Arak 1983). The first set of strategies is more successful than the second one.

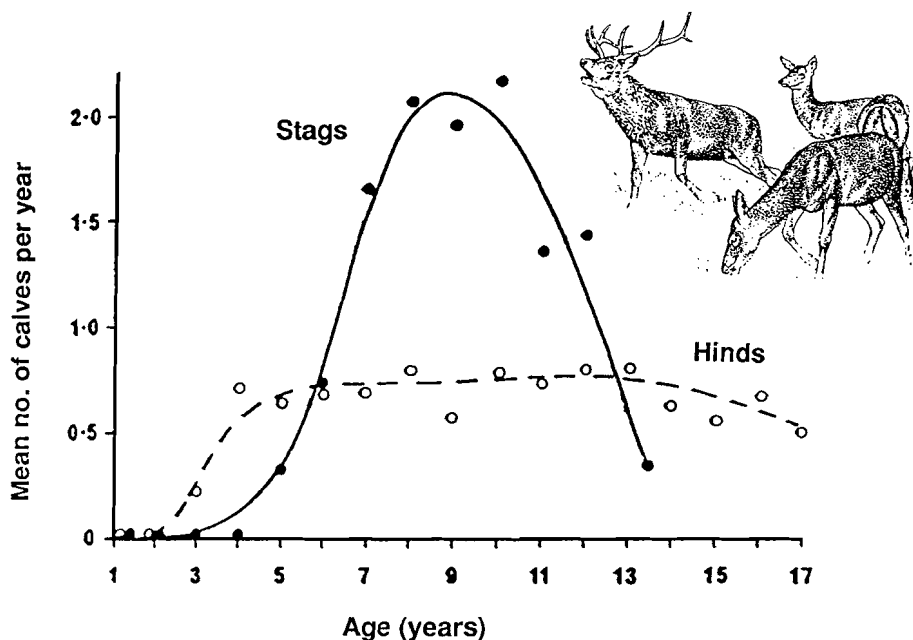


Fig. 10: Age-specific reproductive success in red deer hinds and stags. The age-effect is more pronounced in males whose reproductive success primarily depends on access to females than in females whose success is mainly determined by the quality of the resources. Combined and modified from Clutton-Brock et al. (1982, 1988).

In all three examples the small and young individuals do not choose the strategies with the lower reproductive success «voluntarily»; they simply «make the best of a bad job», because bigger and older individuals prevent them from adopting a more profitable mating strategy. This can be demonstrated in experiments like the one which Anthony Arak (1988) performed with natterjack toads (*Bufo calamita*). When he removed large, calling males from a chorus, small and previously silent satellite males began to call. Conversely, when he broadcasted calls from a loudspeaker, small males became silent satellites next to it.

In some cases, however, individuals adopting different strategies do not differ in their average reproductive success. This is typically the case under frequency-dependent selection. When the proportion of individuals adopting a strategy A (e.g. calling in male anurans) is high, those adopting the rarer strategy B (e.g. satellite males) will enjoy a reproductive advantage and vice versa. Therefore, the rarer strategy will always be favoured by selection, and strategies A and B will coexist in the population at a proportion where their reproductive success is equal.

Since – for methodical reasons – it is difficult to prove that different strategies yield the same fitness (discussed in Krebs and Davies 1993), the most convincing examples for alternative mating strategies with equal pay-offs come from cases in which such equality can be taken for granted. This is true for the sex ratio. Since every individual has one mother and one father, average reproductive success of females (strategy A) and males (strategy B) must be the same. This does not only explain why sex ratios in most species are 1:1 (Fischer 1930), it also helps to understand the patterns of sex change which we find in some species of fishes (Warner 1975). In all these species, female reproductive success increases with body size, because large females lay more eggs. Male reproductive success also increases with body size, but only in species with intense male–male competition. Here, only the largest individuals can mate successfully; for small individuals being a female is a better strategy. As expected, these species show *protogynous hermaphroditism* where individuals start life as females and change to males as they grow bigger. In species with little or no competition small males can sire offspring as effectively as larger ones. In these species changing from a small, but successful male to a large female with high fecundity is the better strategy (*protandrous hermaphroditism*). In both cases the sex change is socially controlled. Like in natterjack toads a strategy change can be triggered by removing individuals pursuing the other strategy.

Outlook

As this brief review shows, behavioural ecologists over the last 25 years or so have made great progress in unravelling the network between the differences in mating systems which we observe, and the historical constraints, the ecological conditions and the individual qualities causing them (Fig. 1). Although the basic picture is there, many of its details still remain obscure. Among the future theoretical and empirical studies which are needed to complete the picture are the following four topics:

1. We should increasingly replace plausible adaptive stories through rigorous experimental tests. This is particularly necessary in cases where the same phenomenon (e.g. lower reproductive success of secondary females) has been explained by alternative hypotheses (e.g. deception vs. restricted sampling).
2. We need to better understand the relative proportions of mating effort and parental effort in species where the same behaviour (e.g. male territorial defense) improves both the chances of attracting additional mates and the survival of the young. Presently, this mixture renders theoretical predictions about the expected mating systems difficult and hampers empirical tests.
3. We must clearly distinguish between the description and analysis of mating systems in terms of social behaviour and in terms of genetic contribution. Application of DNA-fingerprinting and other molecular techniques has shown that many animals which are behaviourally monogamous are genetically polygynous or polyandric, because they engage in

extra-pair copulations. The ecological determinants of such EPCs are largely unknown (Reyer 1994).

4. We need more studies to test how well the proximate quantities which we usually measure (e.g. time/energy-budgets and risk) reflect the ultimate fitness consequences – usually measured through reproductive success – which we interpret. Although fitness is the only currency that matters for selection and the evolution of behavioural strategies, individuals need proximate correlates of fitness for making the ultimately right decisions.

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