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Title: Social evolution in mammals

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Abstract: Long-term, individual-based field studies, the application of genetic techniques and phylogenetic reconstructions have led to substantial advances in our understanding of the diversity and evolution of mammalian breeding systems and their consequences. They show how contrasts in ecology, life histories and phylogeny affect the distributions of breeding females and breeding males; how the distributions of both sexes affect the evolution of breeding systems and the composition and kinship structure of social groups; how contrasts in breeding systems and the social environment that individuals encounter affect the selection pressures operating on both sexes and the evolution of their behavior, physiology and morphology; and how these differences affect the demography and dynamics of populations and their responses to variation in density, climate and human impact.

One Sentence Summary: Long-term studies of mammals shed new light on the causes and consequences of variation in mammalian breeding systems.

Main Text:

Summary

Social evolution in mammals

Background

Early studies of animal evolution focused principally on the evolution of adaptations to the physical environment that increased the survival of individuals while research since the 1960's has explored selection operating through variation in reproductive success as well as through survival, showing how contrasts in breeding systems affect selection on females and males and the evolution of their behavior, physiology morphology and ecology. Field studies of mammals have played a particularly important role since they have been able to explore the causes of individual differences in reproductive success in species with contrasting breeding systems (Fig. 1). Over the last thirty years, the development of genetic analyses of paternity have made it possible to measure the reproductive success of individuals of both sexes and to assess kinship between group members. In addition, gene-based phylogenies have made it feasible to reconstruct evolutionary sequences and to investigate the social and ecological conditions associated with particular transitions. The results of these studies now provide the basis for an integrated understanding of the diversity of mammalian breeding systems and their consequences for the evolution and ecology of both sexes.

Advances

The first mammals were probably nocturnal and breeding females probably lived in separate ranges while males may either have lived in overlapping ranges or shared those of individual females. Where mixed sex pairs share a common range, they often breed together in successive seasons and males commonly contribute to the care of young. Some singular breeders live in

cohesive family groups that include non-breeding adult offspring of the breeding pair (and occasionally, immigrants, too) who assist in rearing the young of the breeding pair. Help from non-breeders can mitigate the effects of fluctuating environments and cooperative systems have often evolved in species that occupy challenging, unpredictable habitats.

In around a third of all contemporary mammals, multiple breeding females aggregate in stable or unstable groups. 'Plural' breeding systems of this kind usually appear to be derived from species where breeding females lived in separate ranges or in mixed sex pairs and are most commonly found where the risk of predation is high, direct competition for resources is reduced or group-living facilitates foraging or range defense. Groups differ widely in stability and size and commonly consist of related females that have remained in their birth groups. However, where there is substantial risk of close inbreeding to females that remain in their birth groups, they often disperse, so that groups consist of unrelated females. While all adult females are fertile in most plural breeders, their breeding success can vary widely, sometimes depending on their social status, which often depends on the number of relatives and allies that will support them in competitive encounters with other group members. Where breeding competition between females is intense, females may kill each other's offspring and can be larger and more aggressive than males.

The aggregation of breeding females in plural breeders strengthens selection on males to guard potential breeding partners and has often led to the evolution of polygynous or polygynandrous mating systems where competition between males is intense. Where female group size is small, a single breeding male usually defends access to each group while larger groups often include several breeding males. The breeding success of males is often correlated with their weight and,

especially in species where single males guard access to female groups, they are commonly larger than females. Males in these species often have more highly developed weaponry and successful breeding is frequently restricted to a relatively short number of years. Intense breeding competition between males also affects their treatment of females: males often adopt coercive mating tactics that can have substantial costs to females and individuals that have recently immigrated into breeding groups may kill the dependent offspring of co-resident females, advancing the timing of their next conception. Intense reproductive competition between males and the adaptations associated with it commonly increase their susceptibility to starvation or predation when resources are scarce and, in some species, can lead to adult sex ratios that are strongly biased towards females.

Outlook

Many important questions about the causes and consequences of mammalian breeding systems remain unresolved. A broader range of field studies is needed that includes more solitary, nocturnal and marine species. Future studies also need to explore the demographic consequences of contrasting breeding systems and their implications for the conservation and management of populations as well as for evolutionary processes.

Review:

Social evolution in mammals

Main text

Mammal societies and breeding systems

Background

Early studies of animal evolution focused principally on adaptations to the physical environment that were likely to increase the survival of individuals (*1-3*). In contrast, research since the 1960's has explored the selection pressures operating through individual differences in reproductive success as well as survival in both sexes and has shown how contrasts in breeding systems and social environments affect the selection pressures operating on females and males and the evolution of their behavior, physiology, morphology and ecology (*4-6*). While studies of a wide range of animals have made important contributions to these developments, research on mammals has played a particularly important role since field studies of species with contrasting breeding systems have been able to explore the extent and causes of variation in the breeding success in large samples of recognizable individuals of both sexes (*7-9*).

Compared to other major groups of vertebrates, mammals are unusual because the evolution of gestation and lactation commits all females to heavy energetic investment in their offspring (*7, 10*). This intensifies intrasexual competition between females for the resources necessary to raise offspring and often reduces the potential benefits of parental investment to males, increasing competition between them to guard access to multiple breeding partners, contributing to the evolution of polygynous mating systems (*7, 11*). As a result, the principal factor limiting breeding success in male mammals is commonly their access to breeding females while the principal factor limiting reproductive success in females is often their access to resources (*7, 12, 13*). Where

breeding females aggregate in groups, this further intensifies breeding competition in both sexes and reduces levels of kinship between group members (*14*), with far-reaching consequences for the evolution of their reproductive strategies and social behavior (*7, 15*).

Over the last forty years, our understanding of the diversity and evolution of mammalian societies and breeding systems has improved rapidly as a result of three principal developments. First, an increasing number of long-term field studies of social mammals have monitored the movements and life histories of large numbers of recognizable individuals from birth to death in successive generations (*8, 16*). Second, the application of genetic analysis has provided quantitative measures of individual breeding success and kinship in both sexes in an increasing number of species (*17*), making it possible to move on from categorical descriptions of mating systems to direct estimates of the relative breeding success of individuals and the degree of reproductive skew (*16*). In some cases, it has also been possible to construct multi-generational pedigrees that can be used to assess the heritability of particular traits and the extent of inbreeding (*18*). And third, the development of gene-based phylogenies has made it possible to reconstruct evolutionary sequences and to identify major transitions in behavior and life history parameters and explore their social and ecological correlates (*19-21*).

Here, I review developments in our understanding of the evolution of mammalian breeding systems and their downstream consequences for the morphology, behavior and ecology of females and males. Since the factors limiting breeding success often differ between females and males, it is useful to start by considering the evolution of reproductive strategies in each of the sexes before exploring how their strategies interact (*7*). I group mammals initially into 'singular

breeders', where breeding females live in separate ranges and are usually intolerant of each other during the breeding season even if they aggregate outside it, and 'plural breeders' where several breeding females share a common range and frequently collect in groups (*7, 22*)(see Table 1). Within 'singular' and 'plural' breeders, I then describe how contrasts in the size, stability and kinship composition of female groups affects the evolution of reproductive strategies and phenotypes of both sexes, as well as their population dynamics and demography.

Singular breeders

<u>Solitary breeders</u>

Phylogenetic reconstructions suggest that some form of singular breeding probably represents the ancestral condition in several Orders where social breeding also occurs, including primates and carnivores (*23-25*). It may also have been the ancestral form of social organization in the earliest mammals (*26*), for all three contemporary monotremes are solitary breeders (*27*). A combination of the high energetic costs of gestation and lactation, the limited mobility of non-volant mammals and the need for crypsis to minimize predation on neonates and adults probably explains why breeding females are solitary in the majority of mammals (*7, 10*). As might be expected, systems where breeding females live in separate ranges and avoid or are intolerant of each other during the breeding season ('solitary breeders') are particularly common in insectivores and carnivores as well as in many small mammals, nocturnal species and forest-dwelling terrestrial herbivores (*7, 10*).

Few of these species have yet been studied in detail and the ecological factors maintaining solitary life styles are not well understood (*7, 28*). Aspects of their feeding ecology, anti-predation tactics

and reproduction may all constrain the aggregation of breeding females in these species (*7, 29*). In some of them, females produce litters of relatively altricial young that need to be concealed or protected from predators or conspecifics in nests or burrows (*30*). Others, like many of the smaller cats and nocturnal mongooses, feed on mobile prey that would be disturbed if several individuals

5 foraged together (*31*), though many terrestrial frugivores and herbivores living in closed habitats are also singular breeders, suggesting that feeding competition or the need for crypsis to avoid predation may also limit the evolution of female sociality (*23, 28, 32*).

Social relationships between males and females vary widely between species. In some, like North

10 American red squirrels, males and females occupy separate territories and only come together to mate (*33, 34*) but, in many of them, males occupy ranges or territories that are larger than those of females and overlap the ranges of several females, as in many rodents, cats, bears and nocturnal primates (*7*). The number of breeding partners that males can access consequently depends on the density of females and the relative size of the ranges of the two sexes and often varies with

15 population density (*7, 35, 36*) and the intensity of intrasexual competition between males probably varies with the relative size of male and female ranges (*7*) as well as with the adult sex ratio (*37*) but comparative data are scarce. Males can be substantially heavier than females, similar in size or slightly smaller and rarely contribute to the care of young (*38-41*).

20 In most solitary breeders, offspring typically disperse from their mother's range when they reach breeding age, though the timing of dispersal and the distance moved varies with social and ecological conditions and often differs between the sexes (*7, 42*). Breeding females are often more tolerant of their own daughters than of immigrants and female recruits may settle in areas adjoining

their mother's range, so that populations often have a well-defined genetic structure (*43, 44*). In North American red squirrels, females even prepare food caches for their adolescent offspring and change their ranging patterns to allow them to take over part of their original territory, together with caches of food that will support them through their first winter (*45*).

Pair-breeders

In some singular breeders, individual males occupy ranges or territories whose boundaries coincide closely with those of a single breeding female so that adults form mixed-sex pairs where partners share a common range and offspring of both sexes typically disperse from their parents' ranges (*7, 46*). Pairs commonly persist until one partner dies or is displaced and 'divorce' is often uncommon (*7*). Pair-breeding is frequently associated with the defense of shared ranges by partners of both sexes and is widely distributed, though it is relatively common in rodents, primates and carnivores (*7*). Pair-breeding often appears to have evolved from solitary breeding (*24, 26*), though reversions from plural breeding also occur (*24, 47*). In diurnal species where single males and females share ranges, like titi monkeys and owl monkeys (*48*) or klipspringers and dik diks (*49*), partners commonly forage and sleep together, forming small family groups with their adolescent offspring. In other species, including some nocturnal lemurs, pairs share feeding territories and may sleep together but often forage alone and, in some cases, only associate with each other during the mating season (*50, 51*). Pair-breeders are often described as 'monogamous' (see Table 1) but genetic analyses have shown that, although partners often breed with each other, both sexes may breed with other individuals, too (*46, 52*), and that differences in the frequency of extra-pair breeding are associated with variation in breeding seasonality, population density and group composition (*53, 54*).

In many (but not all) pair-breeding species, males contribute to the care of juveniles, assisting in births, guarding young at the burrow or nest and feeding dependent young (*7*). The death or removal of males is often associated with reductions in the survival of their dependent young: for example, in pair-breeding California mice, the experimental removal of fathers reduces offspring survival by 60% (*55*). Although females are more usually the principal care-givers, in some pair-breeders, like titi monkeys, males contribute more to care and juveniles respond more strongly to the absence of their fathers than that of their mothers (*56*). Male care may also help to reduce the costs of breeding to females and interspecific comparisons suggest that it is often associated with increases in litter size and in the breeding frequency of females (*57, 58*).

Since pair-breeding constrains access to multiple partners for both sexes, it raises important questions about its potential benefits (*52, 59, 60*). Three main groups of explanations of the evolution of pair-breeding have been suggested, though none of them yet provides a satisfactory explanation of its distribution (*52, 60, 61*). First, pair-breeding may evolve in species where bi-parental care is necessary for the protection and successful rearing of young or for their protection against predators or infanticidal attacks by other males and that this generates benefits to pair-breeding in either or both sexes (*52, 62, 63*). However, in some pair-breeders, males are not involved in provisioning or protecting young (*61, 64*) and two independent phylogenetic reconstructions suggest that the evolution of pair-breeding is likely to have preceded or evolved at the same time as the evolution of paternal care (*26, 62*). In addition, there is no obvious reason why males cannot provide adequate defense against infanticide for the offspring of more than one female (*65*). A second group of arguments suggest that males are seldom able to defend breeding

access to more than one female and her range at a time or that they cannot do so effectively and may maximize their breeding success by guarding breeding access to a single partner (*52*). There is anecdotal evidence that males that attempt to guard more than one female soon lose one of their partners (*64*) and comparative evidence that pair breeding species may show low population densities, though there is no consistent tendency for females to have unusually large ranges (*26, 66*). A third group of explanations suggest that pair-breeding enhances coordinated defense of feeding territories (*67*), though this is unlikely where pair members spend most of their time apart. At the moment, there is currently no single satisfactory s explanation of the distribution of pair-breeding and it seems likely that different social and ecological contexts favor its evolution in different taxa (*60, 61, 68*).

Pair-breeding has important evolutionary consequences. In many pair-breeders, females and males both compete with members of the same sex for territories and breeding partners (*7, 60*) and sex differences in reproductive skew, selection for competitive ability and the development of weaponry and ornamentation are typically smaller than in plural breeders where females live in groups and males can monopolize access to multiple breeding partners (*7*). Sex differences in adult size, foraging behavior and mortality are usually small, too, and, in some species, females are larger than males (*7, 41, 69, 70*). The incidence of sperm competition is also reduced and males typically have relatively small testes and lack the reproductive adaptations found in species where sperm competition is common (*71*). The consequences of pair-breeding for population dynamics in mammals have not yet been systematically explored though early studies of the population dynamics of territorial birds suggested that pair-breeding may be associated with increasing

stability in population size (*72*) and adult sex ratios in pair-breeding mammals are usually close to parity, suggesting that sex differences in survival are typically small (*7*).

Singular cooperative breeders

In a small number of mammals, several adult females and one or more adult males typically share a common range and aggregate in breeding groups but a single dominant female in each group prevents other females from breeding regularly and is the mother of a large proportion (usually >75%) of young born in the group (*7, 22, 73*). Breeding systems of this kind have been most intensively studied in rodents, canids, social mole-rats, social mongooses and the marmosets and tamarins (*74, 75*). Subordinate females frequently show lower levels of estrogen, LH and progesterone than dominants and can be temporarily infertile, though they are usually able to activate their reproductive systems within a few days or weeks (*76-78*). Since subordinate females are often 'natal' individuals that have not left the group where they were born, they often lack regular access to unrelated males within their group and this, too, may contribute to reproductive suppression (*7, 76, 79*). All group members usually help to protect and provision young born to the breeding female and, in some species, females are unable to breed successfully without assistance from non-breeding helpers (Fig. 2) (*7, 22*). Subordinates also contribute to communal activities that benefit all group members (*80*) which can include defense of the group's range against intruders (most species), maintaining foraging tunnels (mole-rats), communal hunting (several canids) and alternating as sentinels while the group is feeding (meerkats) (*80*).

Phylogenetic reconstructions suggest that singular cooperative breeders have usually evolved from pair-breeding ancestors (*81*) though this may not be the case in marmosets and tamarins (*75*).

Groups are usually stable, but vary widely in size both within and between species, ranging from less than five individuals to over a hundred in some colonies of naked mole-rats (*82*). In meerkats and mole-rats, female immigration is rare while, in some canids and tamarins, both sexes may immigrate into established breeding groups (*7, 75, 83*). Cooperative breeders share some of the

5   characteristics of eusocial insects but subordinate helpers are potentially fertile in all cooperative vertebrates and there is no clear evidence of discrete castes that have divergent patterns of development in any cooperative vertebrates (*80, 84*), so it is debatable whether any mammals should be regarded as eusocial (*85*). Moreover, qualitative differences in the form and context of cooperation often make it difficult to compare the extent to which breeders rely on helpers or to

10   distinguish clearly between direct and indirect fitness benefits (*80*).

The evolution of singular breeding systems and cooperative care of young raises important evolutionary questions. First, why do dominant females suppress subordinates, kill their young and evict them from their group – especially if they are often their own offspring and are likely to

15   act as helpers? Studies of meerkats have shown that subordinate breeding can have substantial costs to dominants: pregnant subordinates often kill any pups born to dominants (*86, 87*) and the presence of pups from other litters reduces the growth of the dominant female's offspring (*88*). In addition, suppressing their reproduction may often increase the contributions of subordinates to rearing the dominant's offspring (*7*).

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Second, why should subordinate females 'allow' themselves to be suppressed and remain in their birth groups rather than dispersing or struggling against suppression, as they do in many plural breeders? Part of the answer appears to be that resident groups are territorial, local habitats are

often saturated, mortality during dispersal is often high - so that a female's best chance of acquiring a breeding position may often be to remain in her breeding group and to maximize the chance that she will inherit the dominant position there (*7, 89, 90*). When vacant habitat is available, adolescents commonly disperse and attempt to breed independently, so social groups may be

5   reduced to breeding pairs (*91, 92*). Since dominants often evict subordinates that attempt to breed, unsuccessful breeding attempts may also reduce the chances that subordinates will inherit the breeding position in their birth group (*7*).

Third, why do subordinates assist with rearing the offspring of dominants rather than conserving

10   their resources? There is little evidence either that cooperative behavior is enforced or that it is directed selectively at an individual's closest relatives in any of these species (*7, 93*). However, genetic analyses suggest that, in most groups, a single female and a single male are usually the parents of a large proportion of the surviving young and that average kinship between group members is unusually high (*94, 95*) (see Fig. 1). As a result, the indirect benefits of helping are

15   often likely to be relatively large, facilitating the evolution of cooperation (*94*). Moreover, the contributions of helpers to cooperative activities are often adjusted to their foraging success and condition, so that the fitness costs of helping may be small (*96, 97*). Finally, dominant breeders are often more likely to rear young successfully than subordinates and may evict them if they attempt to breed. As a result, the combined direct and indirect fitness benefits that subordinates

20   derive from attempting to breed may often be lower than those of forgoing reproduction and helping to rear the dominant's pups.

Singular cooperative breeding systems have a number of unusual evolutionary consequences. Individual differences in female breeding success are large and competition for breeding status between females is intense (*98*). For example, in meerkats, most females that reach sexual maturity fail to breed at any stage in their lives while successful individuals can rear more than eighty surviving young (*90*) and even larger differences in breeding success may occur in the social mole-rats where litter size is larger and their potential breeding lifespans are longer than in meerkats (*80, 99*). In several of these species, breeding females have unusually high testosterone levels (*77, 100*) and tend to be more frequently aggressive than males and dominant to them, even where sex differences in growth and adult size are small (*7*). In some of them (including meerkats and social mole-rats) individuals that acquire breeding positions also show a secondary period of growth in the months following their acquisition of dominant status that increases their size and their capacity to maintain their position against potential competitors or to bear larger litters (*77, 101, 102*). In meerkats, subordinates also increase their growth rates in response to potential breeding opportunities as well as to potential challenges by competitors (*101, 103*).

Cooperative breeding also has demographic consequences. In some cases, it is associated with increases in breeding frequency: for example, among the African mole-rats, species that breed cooperatively also breed more frequently than solitary breeders and often produce relatively large litters (*80*). By sharing the costs of raising young among multiple adults, helpers mitigate the effects of adverse climatic conditions and low food availability on growth, survival and reproduction (*104, 105*), which probably explains why cooperative breeders are often found in challenging, unpredictable environments (*106, 107*). However, as the breeding success of dominant females is positively related to the number of helpers which falls when population

density declines, recruitment rates often fall when population density is low, generating 'inverse' density dependence and delaying the recovery of populations (*7, 108*). Environmental events that reduce population density, like droughts or epidemics, may consequently depress recruitment in cooperative breeders and groups and local populations can be slow to recover, increasing their instability and the risk of local extinctions (*108, 109*).

While cooperative breeding systems involving nonbreeding helpers have often evolved in association with singular breeding, they also occur in some plural breeders. For example, banded mongooses live in large groups of around twenty or more individuals in more mesic environments than meerkats (*110*). In contrast to meerkats and dwarf mongooses, multiple females in each group breed in almost perfect synchrony, mostly giving birth on the same day and pups born out of synchrony are usually killed (*110*). Allo-parental care by females is limited, but non-breeding males escort and feed particular pups, which are not necessarily close relatives. Why dominant females do not suppress breeding in subordinate females in banded mongooses is still unclear, but one possibility is that reductions in relatedness between group members resulting from increases in group size (r=0.11:(*111*) limit the indirect fitness that subordinate females can gain by helping to rear the dominant female's young and so make them more resistant to suppression.

Plural breeders

<u>Female sociality in plural breeders</u>

In plural breeders, multiple breeding females typically share a common range and aggregate in stable or unstable groups (*7, 22, 112*). All adult females are usually fertile and attempt to breed regularly, although individuals differ in their breeding success. 'Plural' breeding systems of this

kind are common in bats, rodents, ungulates, primates and cetaceans and are less common in carnivores and insectivores (*7, 22, 73, 113*). In several Orders, including primates and ungulates, plural breeding appears to have evolved from solitary breeding or pair-breeding ancestors (*23, 24, 26*), often in association with the production of single, relatively precocial young (*73*). In some species, populations oscillate between singular breeding when density is low and plural breeding when it is high while, in others, females continue either to occupy separate ranges or to live in groups at all densities although territory size often declines when density is high (*114, 115*).

Since the movements and distributions of breeding females are commonly adjusted to the distribution of resources while those of breeding males are adjusted to the distribution of receptive females or to the distribution of resources that attract them it is often useful to explore the factors affecting sociality in females and males separately (*7, 12, 22, 112*). Groups of breeding females vary widely in size ranging from small, stable groups that frequently defend feeding territories and usually include no more than two or three breeding females to the unstable herds of migratory deer and antelope that can include several thousand individuals (*7, 23, 116*) and the colonies of some bats that can have more than a million members (*116*). Group size also varies widely both within and between populations and commonly increases with population density (*114, 115, 117*).

The stability of female groups also varies widely. In plural breeders that live in relatively small ranges or territories, like many primates and carnivores, females commonly live in 'closed' groups where female immigration is rare, group membership is stable over long periods and group members are often hostile to intruders (*7*). Members of closed groups may either forage together, as in meerkats and chacma baboons, or in unstable parties whose size varies with food abundance

and distribution, as in chimpanzees and spotted hyenas (*118, 119*). In species where females range over relatively large areas, including many deer and antelope and some bats, cetaceans and seals, females often form 'open' groups whose membership changes from hour-to-hour as individuals or parties join or leave each other (*7, 120*). In some of these species, like red deer and African

5   elephants, maternally related females associate with each other disproportionately often and larger herds usually consist of females from several different kin groups (*120, 121*) though, in migratory species, like blue wildebeest, there may be no long-lasting social connections between individuals (*122*).

10   Interspecific differences in female sociality usually appear to be a consequence of variation in the relative costs and benefits of group-living to females, though these can be affected by the reproductive strategies of males (*7, 123*). Contrasts in female sociality are often associated with differences in life-history parameters, diet, habitat type and activity timing, or with variation in the risk of predation and anti-predator tactics (*7, 23, 29, 32*). Associations between group size and

15   food distribution are common within species, too (*7, 124*). The costs of living in groups can include reductions in foraging success, breeding success or lifespan as a result of increases in direct or indirect competition for resources (*7, 23, 125*), increased detectability of groups by predators (*126*), increased transmission of parasites (*127*), and increased breeding interference between resident females (*128*). Direct benefits of sociality are sometimes divided into benefits associated

20   with the defense of resources or nests and those associated with foraging (*129*) and can include heat conservation (*130*), the defense of territories against neighboring groups (*131*), increases in the ability of individuals to find, catch or subdue prey (*83*) and reduced risks of predation as a result of dilution effects or improvements in vigilance or defense (*7*). Where resident individuals

are related, sociality may also generate important indirect fitness benefits arising from the benefits of aggregation to the fitness of kin (*7, 132*).

The kinship composition of female groups also varies widely. In many plural breeders that live in stable groups, females are individuals that have either remained in their birth groups or have founded new groups, so that most female group members are maternal relatives. In contrast, in a minority of species (including some bats, several social equids, several Old and New World monkeys and all three African apes) females usually disperse from their natal groups and often immigrate into established breeding groups, so that most co-resident females are unrelated (*7, 133*). There is extensive evidence of inbreeding costs in wild mammals and of female avoidance of mating with familiar males that are likely to be close relatives (*7, 134, 135*). Contrasts in female dispersal often appear to be related to variation in the breeding tenure of resident males and the risks of inbreeding to females that remain in their natal group (*7*): where the breeding tenure of individual males is relatively short, so that breeding males have usually been replaced by the time their daughters reach sexual maturity, females do not need to disperse to obtain access to unrelated breeding partners and often remain and breed in their birth groups (*133*), avoiding mating with familiar males that are likely to be siblings (*7*). In many of these species, males usually disperse from their birth groups after reaching sexual maturity (*7, 133, 136*). In contrast, in species where the tenure of individual breeding males or male kin groups is typically longer than the age at which females mature, females often disperse to breed after reaching sexual maturity and either join other established groups or found new groups (*137, 138*). In some of these species (including several of the larger New World monkeys and chimpanzees) males may remain in their birth groups, mating with females that immigrate from neighboring groups (*137, 139*). One interesting

exception to the tendency for members of one sex to disperse from their birth groups occurs in killer whales, where both sexes may remain in their birth groups throughout their lives and adults of both sexes usually mate with members of other groups (*140*, *141*).

Plural breeding and competition between females

The aggregation of breeding females often intensifies reproductive competition between females though escalated fights are seldom as frequent as they are in males, which probably explains why weaponry is seldom as highly developed in females (*7*, *142*). Increases in group size reduce levels of maternal kinship between group members and average coefficients of relatedness between group members fall rapidly as the number of breeding females increases (*14*, *95*) or where female immigration is common, as in chimpanzees, intensifying conflicts of interest between group members (see Fig. 1). In species that live in relatively large stable groups, where average levels of kinship are low, aggressive interactions between females are often relatively common and related females frequently support each other so that the status, breeding success and longevity of individuals often depends on the number of relatives and allies that will support them (*143*, *144*). Intense competition between females can be associated with reductions in the relative survival of female juveniles. For example, in spotted hyenas, siblicide is more frequent between female litter-mates than between males (*145*) while, in some plural breeders where related females form coalitions with relatives, dominant females focus aggression on the daughters of subordinates (*7*, *146*).

In a substantial number of plural breeders, resident females also interfere directly with each other's breeding attempts and both socially induced abortions and female infanticide are common

in subordinate females (*147, 148*). Where female competition is particularly intense, as in spotted hyenas and some lemurs, females can have relatively high androgen levels and may show a variety of male-like anatomical and physiological traits (*149, 150*). The evolutionary consequences of intense female competition are well illustrated by research on Alpine fighting cows, where selective breeding of females for competitive ability over multiple generations has raised testosterone levels in females and produced a complex of male-like traits, so that females closely resemble males (*151*) (Fig. 3).

Male sociality in plural breeders

Since the size and stability of female groups affects the number of females that individual males can guard, female sociality also increases the intensity of direct competition between males and affects the tactics they adopt, which vary widely both between and within species (*7, 152*). Where females live in small, stable groups and mating is not highly synchronized, single males often defend access to female groups throughout the year while, where stable groups are larger, several breeding males frequently associate with each group of females, forming 'multi-male groups' and both sexes often mate with more than one partner (*7, 153*). In litter-bearing species, like lions and meerkats, males commonly emigrate from their birth groups together and immigrate into established groups together, so that co-resident males are often close relatives that have been familiar with each other since birth. In contrast, in species that produce single young, like many group-living monkeys, males usually emigrate and immigrate independently, so that co-resident males are seldom closely related to each other (*7, 95*). In some species, like plains zebras and gelada baboons, multiple stable breeding units aggregate together in large, unstable herds (*154, 155*) .

Where female groups are unstable and females range widely but regularly visit resource-rich sites, as in many antelope and some deer, breeding males often defend resource-based territories in areas regularly used by females (*156, 157*) or small, clustered territories on traditional mating grounds or 'leks' where they are joined by receptive females, as in some bats and a number of ungulates (*158-160*). Finally, where the density of receptive females is low and receptive females are widely dispersed, as in whales and elephants, males often cruise in search of receptive partners, defending individual females for short periods before moving on to search for other breeding opportunities (*7, 152*).

Plural breeding and male competition

The aggregation of breeding females commonly increases the number of females that individual males can guard, leading to increases in reproductive skew among males and intensifying reproductive competition between them (*7*). Fighting is particularly frequent in plural breeders where mating is seasonal and individual males collect and defend large 'harems' of females, mating with females as they become receptive as in many deer and land-breeding seals (*7, 161, 162*) (see Fig. 4). The aggregation of multiple breeding females often generates strong selection in males for traits that increase their competitive ability and is frequently associated with the evolution of large sex differences in body size and weaponry, especially in species where single males guard access to female groups and breeding is seasonal (*7, 163*). Where females form relatively large, stable groups, several males often associate with each female group, polygynandrous mating systems and sperm competition are common and the reproductive anatomy of males is frequently adapted to maximize their success in fertilizing mating partners. Ejaculate

volumes and testes are often unusually large, penises may be modified to displace sperm from previous mating and the size and swimming speed of sperm is often increased (*164-166*).

Intense breeding competition between males also has important consequences for their treatment of females. In plural breeders with polygynous mating systems, males often adopt coercive mating tactics to induce females to mate with them. These can include persistent attempts to mate, forced copulation and punishment of females that are reluctant to mate or which associate with subordinate males (*167, 168*). Male coercion can cause serious damage to females, who may be wounded during the attempts of males to mate with them or in the course of punishing attacks by dominant males (see Fig. 5). Although this might appear to be counter-productive for males, if coercive tactics increase their chances of mating, collateral damage to females is unlikely to constrain the evolution of coercive tactics, unless costs to females are very large (*169*). Males that have recently acquired breeding positions may also kill dependent young fathered by their predecessors if this advances the next conception of females and so increases their mating opportunities and, in some species, male infanticide is one of the commonest causes of mortality in infants and juveniles (*170, 171*). For example, in lions and bears, male infanticide can be frequent enough to affect rates of recruitment and population size (*172, 173*). Females frequently respond by cooperatively defending their young, by forming close social bonds with mating partners or, in some species, by prematurely aborting young that are likely to be killed (*174, 175*).

Breeding competition between males can have profound consequences for the evolution of male life-histories. Intense competition between males often delays the onset of successful breeding in males until they approach full adult weight while their capacity to guard females successfully often

ends as soon as their strength and condition begin to decline with increasing age (*7*). As a result, the breeding careers of males can be very short (*176*) and are often considerably shorter than those of females (*7, 177*) (see Fig. 4). Several processes contribute to reductions in the duration of male tenure and increased mortality in males, including fighting injuries, loss of appetite and condition during the breeding season, increased susceptibility to predators and reductions in immune response associated with increased parasite loads (*176, 178, 179*).

The shortening of breeding lifespans in males has important consequences for both sexes. In males, it is often associated with the evolution of tactics that help to extend their breeding lives. For example, in Cape buffalo and Uganda kob, breeding males alternate between periods of reproductive activity and 'resting' periods in bachelor groups (*7, 157*). In other species, it has led to the evolution of age- or size-specific breeding tactics in males (*180*) and, in some, to the evolution of alternative reproductive strategies and balanced polymorphisms in anatomy and breeding tactics (*181*) (see Fig. 6). The effects of male competition on the breeding tenure of males may also help to explain why males tolerate the presence of potential rivals in their group, for the tenure of breeding males declines less rapidly with female group size if more than one breeding male is present and similar effects occur within as well as across species (*7, 65, 182*). Reductions in the breeding tenure of males also reduce the likelihood that females will reach sexual maturity when their father still monopolizes reproduction in their birth group and that they will need to disperse to locate unrelated breeding partners (*7*) and so may help to explain the prevalence of female philopatry and male dispersal in mammals.

The evolution of male characteristics associated with breeding competition has ecological and demographic consequences, too. In many dimorphic species, male infants are born heavier and grow faster than females and male infants nurse more frequently, extracting more milk from their mothers and females that have reared sons are less likely to survive the following winter than those that have raised daughters (*183-185*). The greater costs of raising male infants can also enhance the effects of the mother's phenotype on the post-natal survival, development and eventual breeding success of her sons compared to that of their daughters (*186, 187*), which can lead to selection for qualitatively superior mothers to produce male-biased sex ratios and inferior ones to produce female-biased ones (*188*). Biased birth sex ratios have been documented in several ungulates, though it is often difficult to tell whether they are a consequence of biases in the sex ratio at conception or of sex differences in pre-natal mortality (*7, 183, 189*).

Sex differences in juvenile growth and adult size also increase the relative nutritional requirements of males (*7, 190*) and, in strongly dimorphic species, are often associated with sex differences in feeding behavior, diet and habitat use (*191-193*) as well as with male avoidance of areas of high female density outside the breeding season (*69, 194*). Sex differences in growth are often also associated with higher parasite loads in males than females (*179*) and with increased risks of starvation (*7, 195*) and mortality is often higher in males than females at most stages of development (*187, 195, 196*). Sex differences in survival are often most pronounced when weather conditions are unfavorable or food is scarce (*7, 197*) and, together with increases in male dispersal, can generate strong female biases in local adult populations (*7*). Analyses of temporal changes in age-related breeding success among males show that female biased adult sex ratios reduce the intensity of breeding competition between males and the degree of reproductive skew

(*197, 198*). In some cases, these biases are large enough to have important consequences for the management of populations (*199*) and they may even reduce the resilience of populations for, in some animals, sexually dimorphic species have substantially higher rates of extinction than monomorphic ones (*200*).

5

Recent theoretical studies have argued that female-biased adult sex ratios may encourage males to breed with multiple partners and so may intensify reproductive competition between males (*201*) and have suggested that sex differences in size may be a consequence of sex differences in size and growth (*37, 202*). While this may be the case in some taxa, in group-living mammals variation

10   in the spatial and temporal distribution of breeding females appears to be the principal driver of variation in reproductive competition between males and associated adaptations – and breeding competition and associated adaptations, in turn, generate increases in male mortality and female-biased adult sex ratios (*7, 123, 203*).

15   **Outlook**

Research on mammals over the last forty years has revealed the extensive connections and interactions between ecology, social behavior and evolutionary processes. It has shown how contrasts in ecology, life histories and phylogeny affect the size and composition of social groups and the nature of breeding systems; how contrasts in breeding systems affect the selection

20   pressures operating on both sexes and the evolution of their behavior, physiology and morphology; and how contrasts in behavior, physiology and morphology, in turn, affect the demography and dynamics of populations and their responses to changes in population density, resource availability, climatic factors and human impact.

Technical developments in data collection and analysis have played an important role in these advances. The development of automated recording techniques had extended the range of biological parameters that can be measured in wild mammals and the species that can be studied in detail (*204-206*). Improvements in the storage and analysis of long-term data have made it possible to answer questions about temporal and spatial variation in a matter of minutes that would previously have taken months or years. And new developments in genetical and genomic analysis have transformed our understanding of variation in reproduction and breeding success in both sexes, of the development of social and reproductive behavior within individuals (*18, 207*) and of evolutionary sequences and major transitions in behavior between species (*208-210*).

Despite these advances, many important questions are still unresolved. Much of our knowledge of the causes and consequences of mammalian breeding systems relies on detailed studies of a small number of diurnal, terrestrial plural breeders that live in relatively open habitats and we still know relatively little about the larger number of species where breeding females are solitary (*7, 211*). There are many specific questions that have still to be resolved: for example, we do not yet understand the distribution of pair-breeding (*60, 61*), the factors affecting interspecific differences in male tenure (*7*) and the lack of development of weaponry in females (*142*). In addition, we are only starting to glimpse the consequences of variation in breeding systems for the demography, dynamics and genetic structure of populations and their responses to environmental change (*212, 213*).

In the future, theoretical, empirical and technical developments are all likely to play an important role in extending our understanding of the causes and consequences of breeding systems in mammals as well as in those of other species. The further development of automated recording techniques will help to extend the range of biological parameters that can be measured in wild

5   mammals and the species that can be studied in detail (*204-206*). Continuing improvements in genetical analysis are likely to provide new insights both into the development of behavior in individuals and the causes of individual variation (*214*). And genomic comparisons should provide an improved understanding of evolutionary sequences and the causes of major transitions in behavior (*215, 216*). However, neither automated recording techniques nor genetical analyses can

10   replace the information that can be gained from long-term, individual-based field studies and maintaining existing long-term studies and developing new ones will continue to be a priority.

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Acknowledgements

Table 1

Definitions

_____

5   **Breeding systems**

Singular breeders:

Solitary breeders: species or populations where most breeding females live in separate ranges that overlap to varying extents and avoid or are intolerant of each other during the breeding season, though they may aggregate at other times of year.   Males may occupy

10   separate ranges or ranges overlapping those of several adult females, providing access to more than one potential breeding partner.

Pair breeders: species where a single adult male and a single adult female and her dependant offspring share the same range and usually breed together in successive seasons or breeding attempts.

15   *Singular cooperative breeders*: species living in groups including more than one adult of either or both sexes where a single female in each group virtually monopolizes reproduction and subordinates of either or both sexes help to rear her young.

Plural breeders: group-living species or populations where two or more breeding females share the same range and associate with each other in stable or unstable groups during the breeding

20   season, either foraging together in cohesive groups or foraging in unstable parties. Breeding groups may include one adult breeding male (*Single male groups*) or more than one breeding male (*Multi-male groups*).   Where female groups are unstable, males may defend temporary groups of females, cruise between female groups or defend mating territories in areas regularly used by foraging females or in clusters that are visited by receptive females (*Leks*). In some species, groups

of related females or breeding groups that include both sexes aggregate in larger herds (***Multi-level societies***).

Mating systems

Monogamy: mating systems where the same mixed sex pair usually mate together in successive breeding attempts.

Polygyny: mating systems where single males commonly mate with several different females in the same breeding season and multiple breeding females may mate with the same   male.

Polyandry: mating systems where individual females commonly mate with multiple males in the course of a single season, while males do not mate with more than one female.

Polygynandry: mating systems where both sexes commonly mate with multiple different partners in the same or successive breeding seasons.

Benefits and costs

Direct fitness benefits or costs: increments or reductions to the survival or breeding success of individuals

Indirect fitness benefits or costs: increments or reductions to the survival or breeding success of non-descendent relatives.

Figure legends

Summary figure

Twenty-two mammals that are the subject of continuing long-term, individual-based field studies covering multiple generations. Dates show the approximate date of the beginning of each study (*7*). Gene-based estimates of variation in the breeding success of individuals of both sexes are now available for the majority of these species.

Continuing long-term individual-based field studies of wild mammals.

    a) Rhesus macaques, Cayo Santiago, Puerto Rico © Alex Georgiev

    b) Chimpanzees, Gombe, Tanzania © Ian C. Gilby

    c) Yellow-bellied marmots, Colorado, USA © Dan Blumstein

    d) Spotted hyenas, Tanzania & Kenya © Tim H. Clutton-Brock

    e) African lions, Serengeti, Tanzania © Craig Packer

    f) Northern elephant seals, Año Nuevo, USA © Burney Le Boeuf

    g) Mountain gorillas, Rwanda © Alexander Harcourt/Kelly Stewart/Anthrophoto

    h) Red deer, Rum, Scotland © Tim H. Clutton-Brock

    i) Yellow baboons, Amboseli, Kenya © Elizabeth Archie

    j) Bighorn sheep, Alberta, Canada © Fanie Pelletier

    k) African elephant, Amboseli, Tanzania © Harvey Croze

    l) Black-tailed prairie dogs, South Dakota, USA © Elaine Miller Bond

    m) Cheetah, Serengeti, Tanzania © Dom Cram

    n) White-faced capuchin monkeys, Santa Rosa, Costa Rica © Tom Houslay

o) Northern muriquis, Cataringa, Minas Gerais, Brazil © Thiago Cavalcante / Projeto Muriqui de Caratinga

p) Sifakas, Beza Mahafaly, Madagascar © Claudia Fichtel

q) Soay sheep, St. Kilda, Scotland © Arpat Ozgul

r) Red squirrels, Yukon, Canada © Ryan W. Taylor

s) Kalahari meerkats, Southern Kalahari, South Africa © Tim H. Clutton-Brock

t) Banded mongooses, Queen Elizabeth National Park, Uganda © Harry Marshall

u) Red-fronted lemurs, Kirindy Forest, Madagascar © Claudia Fichtel

v) Owl monkeys, Province of Formosa, Argentina © E. White / Owl Monkey Project.

Fig. 1.

Average kinship between group members in four plural breeders and four singular breeders. The figure shows average coefficients of relatedness between resident females (upper values) and all group members (lower values) for four plural breeders (Upper row: (**A**) Chimpanzees; (**B**) yellow baboons; (**C**) spotted hyenas; (**D**) African lions) and four singular breeders (Lower row: (**E**) African wild dogs; (**F**) moustached tamarins; (**G**) Kalahari meerkats; (**H**) Damaraland mole-rats).

Sources: (*94*) and (*95*) and (**A**) (*139, 217*); (**B**) Tung, J., pers. comm.; (**C**) (*218*); (**D**) (*219*); (**E**) (*220*); (**F**) (*221*); (**G**) (*222*); (*223*); (**H**) (*224*).

Photo sources: (**A**) © Ian C. Gilby; (**B**) © E. Archie; (**C**) © T. Clutton-Brock; (**D**) © Craig Packer; (**E**) © Lorna Harvey; (**F**) © Hector Bottai under Creative Commons Attribution - ShareAlike 4.0 International License; (**G**) © Tim Clutton-Brock; (**H**) © Kyle Finn.

Fig. 2.

Cooperative activities in Kalahari meerkats

In meerkats (*Suricata suricatta*), non-breeding subordinates of both sexes assist dominant breeders by caring for their young, guarding and feeding pups and acting as sentinels when their group is foraging (*90*).

Photo source: © Kalahari Research Trust.

Fig. 3

Consequences of selection for competitive ability in females in fighting cows

In spring in the Italian Western Alps, fights are staged between cows which have been selectively bred for their aggressiveness and fighting ability and now share many of the characteristics of bulls, including relatively high testosterone levels.

Photo source: © Cristina Sartori

Fig. 4.

Age-related changes in reproductive success in male red deer and elephant seals

In many polygynous mammals, like red deer and elephant seals, there is intense competition between breeding males, with the result that only 'prime' males breed successfully and males have substantially shorter breeding lifespans than females (*225, 226*).

Photo sources: © Tim Clutton-Brock; Burney Le Bouef.

Fig. 5.

Costs of male competition to females in chacma baboons

Coercive mating tactics are common in males in terrestrial mammals. In chacma baboons, adult males frequently threaten or attack cycling females (**A**), sometimes generating serious injuries (**B**). The frequency with which cycling females show injuries increases with the rate of male-female aggression (**C**). The probability that males will be able to monopolize access to females during

the period when they are likely to conceive (POP) increases with the rate at which individual males have directed aggression at them (**D**) (*168*).

Photo sources: © Alecia Carter; Alice Baniel.

Fig. 6.

The evolution of horn types in Soay sheep

In Soay sheep on the island of St. Kilda, high survival costs of breeding competition between males maintain a balanced polymorphism in horn size which is associated with differences in behavior. Fully horned males (**A**, **B**) are either homozygous or heterozygous for an allele (Ho+) at the horns locus (RXPF2), while males that either have very small horns or no horns at all (**C**) are homozygous for an alternative allele (Hop). Males that are homozygous or heterozygous for Ho+ have higher annual breeding success than individuals that are homozygous for Hop (**D**) while individuals that are heterozygous for Ho+ and those that are homozygous for Hop show higher survival that those homozygous for Ho+ (**E**). As a result, heterozygotes for Ho+ have the highest fitness (**F**) and both alleles are maintained in the population.

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