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REVIEW LECTURE

Mammalian mating systems

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Male mammals show a diverse array of mating bonds, including obligate monogamy, unimale and group polygyny and promiscuity. These are associated with a wide variety of different forms of mate guarding, including the defence of feeding and mating territories, the defence of female groups and the defence of individual receptive females. Female mating bonds include long-term monogamy, serial monogamy, polyandry and promiscuity. Both male and female mating behaviour varies widely within species.

Variation in male mating behaviour is related to the effect of male assistance in rearing young and to the defensibility of females by males. The latter is, in turn, related to female ranging behaviour and to the size and stability of female groups. Much of the variation in mammalian mating bonds and systems of mate guarding can be attributed to differences in these three variables.

INTRODUCTION

Over the last decade, the predictive framework provided by evolutionary theory combined with field studies of increasing duration and sophistication has led to a rapid improvement in our understanding of the functional significance of social and reproductive behaviour (Wilson 1975; Emlen & Oring 1977; Bradbury & Vehrencamp 1977*b*; Clutton-Brock & Harvey 1978; Rubenstein & Wrangham 1986; Dunbar 1988; Clutton-Brock 1988). Three important generalizations about animal mating systems have emerged, which provide the basis for much current thinking.

First, the mating systems of animals are now seen as the outcome of the reproductive strategies of individuals rather than as evolved characteristics of species (Bradbury & Vehrencamp 1977*b*; Clutton-Brock & Harvey 1978; Rubenstein & Wrangham 1986; Dunbar 1988). Variation in mating behaviour is consequently to be expected both within and between populations as a consequence of the adaptive adjustment of male and female behaviour to differences in the social and ecological environment and to variation in individual capabilities (Rubenstein 1980; Dunbar 1981). The extent to which mating systems vary appears to differ between species, but we do not currently understand the factors constraining this flexibility.

Second, it is now appreciated that almost all social relationships lead to conflicts of interest between individuals, which result in diverse forms of competition. Conflicts of interest are common between mating partners (Davies 1985) as well as between parents and their offspring (Trivers 1974). In particular, competition for breeding opportunities or resources often occurs within social groups, even in species that breed cooperatively, and the reproductive success of individuals is usually constrained by the activities of other group members (see, for example, Silk 1983; Vehrencamp *et al.* 1988). Social behaviour, mating behaviour and parental care are commonly adjusted to minimize these constraints (see Hrdy 1977; Packer & Pusey 1983).

Third, it is now realized that many mating systems represent different forms of mate guarding adapted to the spatial and temporal distribution of receptive females which, in turn, depends on variation in resource distribution, predation pressure, the costs of social living and the activities of other males (Bradbury & Vehrencamp 1977*a*, *b*; Emlen & Oring 1977; Clutton-Brock & Harvey 1978; Lott 1984; Kruuk & Macdonald 1985; Rubenstein & Wrangham 1986; Wrangham 1987).

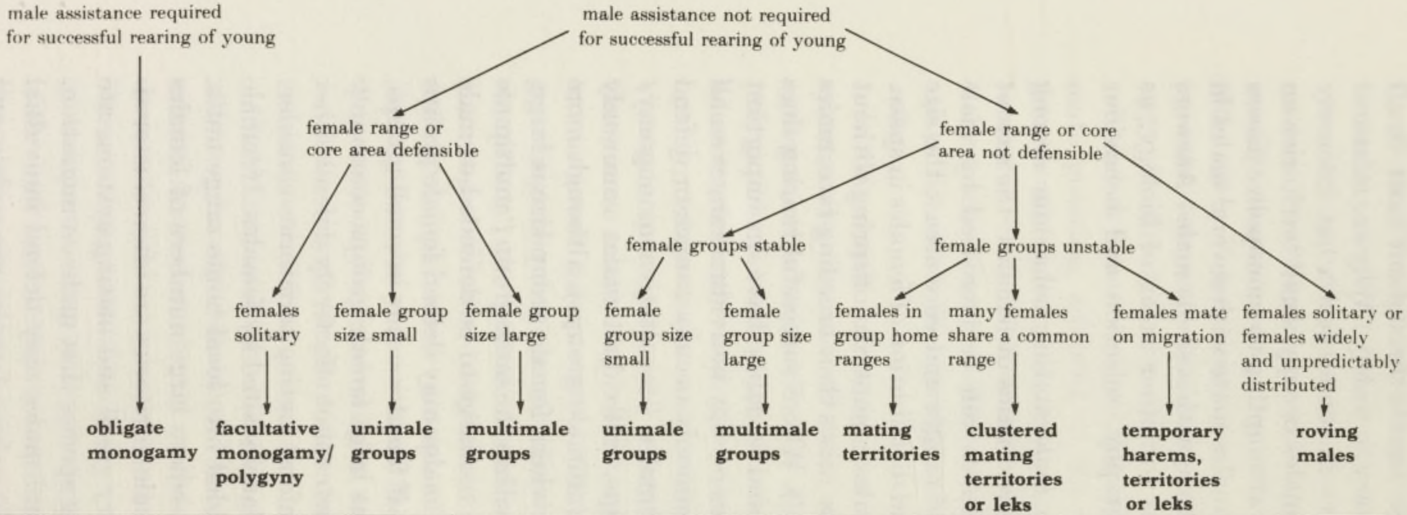
In this review I describe and interpret the distribution of mammalian mating systems. In contrast to birds, where over 90% of species are typically monogamous, the males of more than 90% of mammalian species are habitually polygynous (Kleiman 1977; Rutberg 1983). Mammalian mating bonds include cases where males mate with the same female in several reproductive attempts (monogamy), where males mate with the same group of females in successive mating attempts (polygyny) and where males will mate with any receptive female and there is no continuing bond between individual males and females after mating has occurred (promiscuity). These are associated with four main forms of mate guarding: the defence of individual females during part or all of their period of receptivity; the defence (usually intrasexual) of feeding territories that overlap the ranges of individual females or groups of females partly or completely; the defence of particular groups of females, either during the mating season or throughout the year without the defence of any fixed area; and the defence of dispersed or clustered mating territories within a portion of the female range. In most species single males defend females, but in a few cases several males cooperate to defend access to female groups or their ranges.

Classification of female mating behaviour is hampered by the scarcity of studies able to identify individual females or to determine paternity. However, female mating systems evidently include cases where females usually maintain exclusive or semi-exclusive mating bonds with a single male throughout most of their lifespan (long-term monogamy); where females usually mate with a single male in successive breeding attempts but mate with several different partners in the course of their lifetime (serial monogamy); where females mate with a restricted group of the same males in successive breeding attempts (polyandry); and where females usually mate with different males in successive breeding attempts (promiscuity). In some of the latter species, females usually mate with several different males during each period of receptivity, whereas in others they typically mate with a single male.

The diversity of mating systems among mammals poses a wide array of important questions for the evolutionary ecologist. Why, in some species, do males forego breeding polygynously to pair with a single female throughout most, or all of their lives? Why does the degree of polygyny vary so widely? Why are relations between breeding males tolerant and cooperative in some species but intensely aggressive in others? Why, in a few species, do males occupy small territories on traditional mating grounds or 'leks' rather than attempting to monopolize access to female groups? And why, in some cases, do females mate with several males in each breeding attempt, whereas in others they mate with a single male? Answers to these questions have important implications for other areas of biology, as mating systems affect many aspects of demography, selection and behaviour (Clutton-Brock 1988, 1989*a*).

I argue below that much of the variation in male mating behaviour among mammals is attributable to four important characteristics of females: the extent to which the effective reproductive rate of females can be increased by male assistance in rearing offspring; the size of female ranges and core areas; the size and stability of female groups; and the density and distribution of females in space. This framework is outlined in figure 1. Where females cannot rear offspring without the assistance of their mating partner or assistance raises their breeding rate, males mate with a single female ('obligate monogamy'). Where successful rearing does not require male assistance, female range size and sociality have an important influence on the potential for polygyny. If females occupy individual ranges small enough to be defensible by males, the latter commonly occupy ranges or defend territories overlapping those of one or more females ('facultative monogomy/polygyny'). Where females live in social groups, individual males commonly monopolize breeding access to group members (unimale groups), although more than one mature male may be present whereas, where female group size is large, several resident males are reproductively active within the same group ('multimale groups'). Where the ranges of female groups are too large to be defended or male territoriality is precluded for some other reason, males may defend female groups if their membership is sufficiently stable. Again, if females occur in small groups, unimale harem groups are usually found, whereas large female groups commonly include more than one breeding male. Where males cannot effectively defend either female groups or their ranges, they commonly defend mating territories considerably smaller than the female range in areas regularly visited by females. If female density is low or female populations are subdivided into local home range units, male territories are often widely dispersed, but where large numbers of females share a common range and local density is high, male territories are often clustered. In some of these species, male territories are very small and mating systems are analagous to the leks of some bird species. Among species that mate on migration, mating behaviour appears to be very flexible and males may defend individual females, harems or temporary territories. Finally, where females are widely and unpredictably distributed, males rove widely in search of oestrous females, defending individual females for part or all of their cycle.

This framework differs from models designed to explain the evolution of polygyny in birds, which mostly assume that females are free to choose mating partners on the basis of phenotype or territory quality, preferring polygynous



male mating system	**mating bond**	monogamy	monogamy or polygyny	unimale polygyny	multimale polygyny	unimale polygyny	multimale polygyny	promiscuity	promiscuity	promiscuity	promiscuity
	defence system	defence of territory usual	defence of territory usual	defence of range of female group	defence of range of female group	defence of female group	individual defence of receptive females	individual defence of spaced mating territories	individual defence of clustered mating territories	variable, including defence of individual females, groups, individual or clustered mating territories	individual defence of receptive females
female mating system	**mating bond**	long-term monogamy or polyandry	long-term monogamy, serial monogamy or promiscuity	serial monogamy or promiscuity	polyandry or promiscuity	serial monogamy or promiscuity	serial monogamy, polyandry or promiscuity	promiscuity	promiscuity	promiscuity	promiscuity
	defence system	defence of territory	defence of individual territories in some species	defence of territory in some spp., no defence in others	defence of territory in some spp., no defence in others	no long-term defence of resources by females though female groups may compete for temporary access					

FIGURE 1. A classification of male and female mating bonds and defence systems in mammals. The upper part of the figure shows different combinations of ecological and social conditions arranged hierarchically: the lower cells show the mating bonds and defence systems with which particular conditions are *usually* associated. Different categories intergrade; exceptions are not uncommon and the same species may show several different mating systems. Terms are defined in the text.

matings to monogamous ones when their fitness is increased by doing so (Verner 1964; Orians 1969, 1972; Altmann *et al.* 1977). Models of this kind are of limited relevance to the majority of social mammals where females seldom disperse far from their natal area, female groups commonly persist over several generations and males typically impose themselves on pre-existing female distributions (see Armitage 1986). The mammalian breeding systems that most closely fit the assumptions of these models may be those where *females* disperse from their natal group and consequently have the opportunity to choose among a number of different breeding partners or groups (see Greenwood 1980; Wrangham 1980*a*, 1987). Unfortunately, relatively little is yet known about the factors affecting female movements in these species.

In the following sections, I use the framework outlined in figure 1 to interpret the adaptive significance of variation in male mating behaviour in mammals, devoting most space to mating systems, such as monogamy and lek breeding, that pose important evolutionary questions. Though this framework agrees with current knowledge of mammalian mating systems, exceptions are not uncommon, categories clearly intergrade and the same species may show several different mating systems. Moreover, several important arguments are based on assumptions or extrapolation rather than on firm empirical research (see below). Detailed studies of the costs and benefits of particular mating strategies and quantitative interspecific comparisons are needed to establish the generality of associations between particular forms of mating behaviour and social or ecological conditions.

Mating systems

(*a*) *Obligate monogamy*

In around 5% of mammalian species, males are socially bonded to a single breeding female and, in most of these species, facultative polygyny is rarely or never found (Kleiman 1977; Rutberg 1983). Obligate monogamy is the commonest breeding system among canids (Bekoff *et al.* 1984; Moehlmann 1986) and occurs in some 15% of primates (Rutberg 1983). It also occurs in rodents, mustelids, viverrids, and insectivores and artiodactyls (Kleiman 1977; Rood 1986). In contrast to birds, where many monogamous species are seasonal breeders and change partners each year (Lack 1968), most obligately monogamous mammals appear to pair for life. For example, studies of gibbons show that mated pairs commonly remain together for at least a decade (Chivers & Raemakers 1980; Bennett *et al.* 1983).

In obligately monogamous mammals, mating appears to be largely or totally confined to bonded pairs and adults usually remain in close proximity to their partners and dependent offspring for much of the day (Kleiman 1977). Almost all obligately monogamous species show intrasexual territoriality (Mitani 1984; Dunbar 1988) although in maras *Dolichotis patagonum* the ranges of neighbouring pairs overlap around communal dens where pairs meet in an uneasy alliance in the care of pups (Dubost & Genest 1974; D. W. Macdonald, personal communication). In addition, in a few species where males are monogamous, females are polyandrous, mating with several resident males. For example, in African wild dogs, *Lycaon pictus*, breeding groups commonly consist of a single breeding female and more than one adult male and, in some groups, females have been seen to copulate with more than one male (Malcolm 1979; Malcolm & Marten 1982). A similar mating system is found in some tamarins, *Saguinus* (Garber *et al.* 1984; Sussman & Garber 1987; Terborgh & Goldizen 1985; Goldizen & Terborgh 1987), but it is not yet clear whether polyandrous groups represent a permanent arrangement, or whether polyandry only occurs where a pair lack immature helpers and it is consequently in the interests of the male as well as the female to accept another male if he assists in caring for the young (Goldizen & Terborgh 1987).

In most monogamous mammals, males contribute to care of the young and paternal care may include building dens, burrows or lodges (see, for example, Wilsson 1971), defending feeding territories used by the female and young (Ellefson 1974), provisioning nesting burrows (Wolff 1985) feeding the lactating female (Kleiman & Eisenberg 1973; Yamamoto 1987) or defending or transporting young (Epple 1970; Chivers 1974). For example, in the monogamous prairie vole *Microtus ochrogaster*, males and females contribute to all aspects of care apart from lactation and paternal activities include nest and runway construction, food cacheing, and grooming, brooding and retrieving the young (Getz & Carter 1980; Getz *et al.* 1981). Where the female produces a litter of above average size, males commonly construct a second nest and the litter is subdivided, with males caring for one of the two nests (Thomas & Birney 1979). It is interesting to note that in this species female reproductive activity is activated by olfactory cues from male urine (Carter *et al.* 1980).

Monogamy is one of the most puzzling of mammalian mating systems, for it is not clear why males should confine themselves to breeding with a single female. Four non-exclusive hypotheses concerning the evolution of monogamy in mammals have been suggested (Wittenberger & Tilson 1980):

(1) that where resource distribution favours solitary living, females enforce monogamy by territorial defence (Wittenberger 1979; Wittenberger & Tilson 1980; Slobodchikoff 1984). A similar argument is that monogamy occurs where feeding competition is intense and sociality has little advantage in relation to predation (van Schaik & van Hooff 1983);

(2) that monogamy evolves where differences in (male) territory quality are small and the costs of mating are large, with the effect that, in the population as a whole, polygynously mated females show lower reproductive success than monogamously mated ones (see Verner 1984; Verner & Willson 1966; Orians 1969);

(3) that where female ranges are so large that a male cannot defend an area big enough to contain the range of more than one female, selection favours males that mate monogamously and enhance the reproductive success of their partners by paternal investment (Goss-Custard *et al.* 1972; Emlen & Oring 1977; van Schaik & van Hooff 1983; Rutberg 1983);

(4) that monogamy occurs in species where, for physiological or ecological reasons, male assistance is required for successful rearing of offspring (Kleiman 1977; Clutton-Brock & Harvey 1977) or where males can achieve higher breeding success by monopolizing the reproductive output of a single female than by attempting to breed with several females (Wittenberger & Tilson 1980).

Different circumstances may favour monogamy in different groups but some are probably more important than others. The first of the four explanations is unsatisfactory as it fails to explain why males do not defend the territories of more than one female. The second explanation, too, is unconvincing for it is unlikely that the absence of adequate variation in territory quality commonly limits the development of polygyny. Attempts to test the hypothesis that large female ranges enforce obligate monogamy on males in primates and rodents suggest that this, too, is unsatisfactory (Mitani & Rodman 1979; Dunbar 1988; Cockburn 1988) though it may conceivably explain the evolution of monogamy in the larger Old World primates such as *Indri* and the gibbons (van Schaik & van Hooff 1983). In rodents, there is no evidence that females of monogamous species have consistently larger home ranges than those of polygynous ones and among primates overall, monogamous species do not appear to have unusually large ranges when the effects of body size on range size are controlled (Cockburn 1988; Dunbar 1988). Moreover, attempts to estimate the maximum area that males could defend, based on the length of their day range, suggest that males of several monogamous primates could defend the ranges of more than one female (Dunbar 1988).

The most convincing explanations of monogamy are based on arguments that males can achieve higher breeding success by guarding a single female and helping her rear their joint young than by attempting to breed polygynously. Two potential advantages of monogamy for males are that it increases the reproductive rate of their partners (and hence their own breeding success) as a consequence of the male's involvement in parental care, and that it increases the certainty of paternity because males can accompany individual females. Evidence for both benefits is, at best, circumstantial. No studies of monogamous mammals have yet removed males to investigate the effects on females and young, though several studies of species where non-breeding adults or subadults assist in rearing the young show that the survival of juveniles increases in relation to the number of adults that help to rear them (Moehlmann 1979; Sussman & Garber 1987) (see figure 2).

In addition, there is some evidence that females of monogamous species tend to show higher rates of reproduction or larger offspring than related species of similar size. For example, litter size in canids, (which are mostly monogamous) ranges from 1.8 to 8.8 with an average of 4.4 (Gittleman 1986) and *increases* with maternal body size (Moehlmann 1986), in contrast to virtually all other groups of similar sized mammals, where average litter sizes range from 1 to 3, declining with adult size (see Eisenberg 1981). Similarly, all marmosets and tamarins (Callitrichidae), are either monogamous or polyandrous and, in contrast to all other anthropoid primates, females typically produce twins. Twinning may have evolved in these species because at female body weights of below around 600 g the scaling dimensions of the female's pelvis begin to constrain the size of the infant at birth while a female's capacity for parental investment exceeds the demands of a single offspring (Leutenegger 1973, 1980). Under these circumstances, monogamy and paternal care combined with multiparity may represent the most successful strategy for males as well as females (Dunbar 1988). If we suppose that without male assistance a female can only produce one young per litter and breed once a year, a non-assisting bigamous male would only be half as successful as an assisting

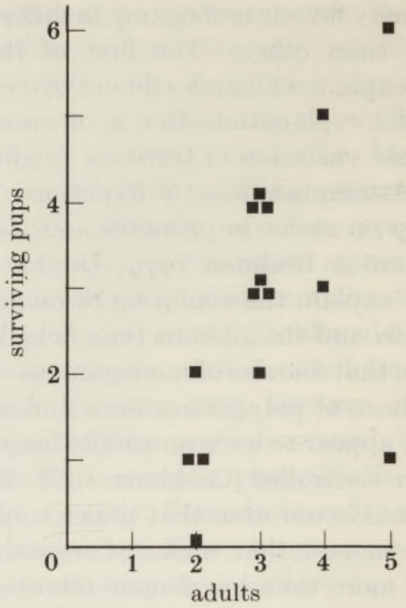


FIGURE 2. Number of surviving pups reared by different family groups of silver-backed jackals, *Canis mesomelas*, in relation to family size (from Moehlmann 1979).

monogamist whose mate produced twins twice a year (see table 1). Even if these assumptions are relaxed to allow a non-assisting bigamous male to produce two single offspring per year, the increased efficiency of mate guarding associated with monogamy may make this the most successful male strategy.

TABLE 1. THEORETICAL PAYOFF MATRIX FOR MALE AND FEMALE MARMOSETS FOR THE ALTERNATIVE STRATEGIES OF MONOGAMY OR BIGAMY FOR THE MALE AND SINGLE OR TWIN BIRTHS FOR THE FEMALE

(In each cell, the payoff to the male is given below, that to the female above (from Dunbar 1988).)

	female strategy	
male strategy	uniparity	twinning
monogamy	2 2	4 4
bigamy	1 2	0 0

However, in many other monogamous mammals the benefits of monogamy to males are not obvious. For example, among the New World primates, sakis *Pithecia*, titis *Callicebus* and night monkeys *Aotus* are monogamous but uniparous. Males commonly carry the young more than females do in these species (Kleiman 1977; Mendoza & Mason 1986; Robinson *et al.* 1987), but it is not clear how they gain by foregoing polygyny (see Wright 1986). One common explanation of monogamy is that the male's role in defending a feeding territory for his mate and their joint young is crucial to the breeding success of the pair. However, there is no direct evidence that this is the case, and this argument does not explain why the male is permanently associated with the female (Dunbar 1988). Another possibility is that the presence of the male improves the detection of predators and thus contributes to the reproductive success of the pair (Dunbar 1988). There is some evidence that this could be the case in monogamous antelopes; for example, in klipspringer *Oreotragus oreotragus*, predation rates are high, males and females alternate in watching for predators while their mate feeds and males contribute to the early detection of intruders (Dunbar & Dunbar 1980; Dunbar 1985). However, it is a less likely explanation for the evolution of monogamy in arboreal primates, especially in nocturnal species such as *Aotus*. The evolution of monogamy in these species remains an enigma.

(*b*) *Facultative monogamy/polygyny*

Where females are solitary when active and occupy independent home ranges small enough to be defensible, males commonly defend territories or occupy ranges overlapping those of one or more females, seldom associating with females that are not receptive. Most explanations of mating systems of this kind rely on largely untested assumptions that it would be uneconomical for males to defend a larger area. Virtually nothing is known of the factors affecting the area that males can defend, though it is reasonable to suppose that this increases with interspecific differences in body size.

Facultative monogamy/polygyny occurs in a wide variety of monotremes (Grant 1983), small marsupials (Charles Dominique 1983; Lee & Cockburn 1985), rodents (Michener 1983; Ostfeld 1985; Kawata 1985), carnivores (Macdonald 1983; Rood 1986), nocturnal prosimians (Charles Dominique 1977; Bearder 1987) and small ungulates (Jarman 1974; Barrette 1987). Male ranges or territories are commonly larger than those of females but the extent of the difference varies widely both within and between species (see, for example, Wolff 1985). Where male ranges cover the range of a single female, males may breed with a single partner (facultative monogamy), whereas where male ranges overlap those of several females they may breed with several females (facultative polygyny). Because female range size varies widely within species, the degree of polygyny probably differs widely between populations. Males of species that are polygynous at high density, such as *Microtus richardsoni* and *M. californicus*, may breed monogamously or rove widely in search of females when density is low (Ludwig 1984; Cockburn 1988; see also Kawata 1985).

Many of these species are nocturnal and difficult to observe; existing knowledge of their mating systems is based largely on trap data or on spot sightings with torches, and is necessarily sparse. However, recent studies show that species which commonly breed in this way in fact show a diverse array of mating systems (Michener 1983; Wolff 1985; Boonstra *et al.* 1987; Cockburn 1988). In some cases, males and females occupy separate ranges or territories whereas in others the ranges of males overlap those of females. Either, neither or both sexes may be territorial and the degree of range overlap varies widely (Wolff 1985; Cockburn 1988). Among microtines, females of species that depend primarily on patchily distributed food supplies, such as fruit or forbs, are usually territorial and widely dispersed and males occupy non-defended ranges overlapping the territories of one or more females (Ostfeld 1985). In contrast, in species that feed primarily on grasses, several females are more likely to be clumped, and males commonly defend territories covering the ranges of several females. Male territoriality may also be favoured where females breed synchronously whereas where breeding is asynchronous roving strategies may be advantageous (Ims 1987).

In many small mammals where females were previously thought to be solitary on the grounds that they generally move around their ranges alone, more detailed research has shown that daughters commonly remain in or near the mother's home range, and that populations are subdivided into kin groups (see Clark 1985; Cockburn 1988). Advanced cooperative behaviour, including cooperative food storing, communal defence of young and communal suckling has been found in a number of species (Michener 1983; Wolff 1985; Cockburn 1988). Little is known about female mating behaviour in these species, but they may include examples of long-term monogamy, polyandry and serial monogamy as well as promiscuity (Cockburn 1988).

(*c*) *Unimale groups with spatial defence by males*

Where females live in social groups or coteries in ranges small enough to be economically defensible, or where their ranges have well-defined core areas, males commonly defend the ranges or core areas of female groups as well as the groups themselves against invasions by other males. As the area occupied by female groups increases, the cost-effectiveness of territoriality presumably declines and males are more likely to defend groups of females or to wander in search of receptive females. In some cases where males defend resources they only do so during the breeding season whereas in others, both seasonal and aseasonal breeders, they do so throughout the year (see Michener 1983; Armitage 1986; Franklin 1983; Cords 1987). So far, relatively few attempts have been made to explain the distribution of seasonal versus aseasonal defence.

Resource-based polygyny is common among rodents that are diurnal and social. For example, in Columbian ground squirrels, *Spermophilus columbianus* (Festa-Bianchet & Boag 1982), yellow-bellied marmots, *Marmota flaviventris* (Armitage & Downhower 1974; Armitage 1986), and black-tailed prairie dogs, *Cynomys ludovicianus* (Hoogland 1981), males defend exclusive territories overlapping the ranges of female groups. In contrast, in Belding's ground squirrel, *S. beldingi*, female ranges often overlap the territories of several males and females may have several mating partners in each breeding season, producing multiply sired litters (Hanken & Sherman 1981; Sherman & Morton 1984). However, reproductive success still varies widely among males: for example, in Belding's ground squirrel around a quarter of the males are responsible for two thirds of copulations.

Polygyny associated with male defence of ranges or territories extending over a large part or all of the range of several females is also common in the cercopithecine and colobine monkeys (Struhsaker 1969; Struhsaker & Leland 1979; Hrdy 1977; Clutton-Brock & Harvey 1978; Cords 1987) and in some of the more sedentary ungulates, including camellids (Franklin 1983), cervids (Wemmer 1987) and some antelopes (Leuthold 1978; Gosling 1986). For example, in the vicuna, *Vicugna vicugna*, adult males defend feeding territories of around 18 ha† and separate sleeping territories of 2–3 ha at higher altitude used by groups of 2–10 females throughout the year (Franklin 1983). Adolescents *of both sexes* are ejected from female groups by the adult male who defends the group's territory against wandering males and other breeding groups, apparently limiting the number of resident females (Franklin 1983). In other species, territorial males only defend burrows, caves or roosts occupied by females. For example, in rock wallabies, *Petrogale*, males defend caves occupied by groups of related females (Jarman & Southwell 1986). Similarly, in some bats, males defend territories within roosting sites that are regularly used by the same groups of females (Bradbury 1977; Bradbury & Vehrencamp 1977*b*).

Where males defend part or all of the range of stable female groups, harem groups may include more than one adult male though a single male is usually responsible for most or all matings, as in grey langurs, *Presbytis entellus* (Hrdy 1977), or waterbuck, *Kobus ellipsiprymnus* (Wirtz 1982). Satellite males may benefit by attaching themselves to harems because by establishing social bonds with resident females they increase the chance that they will be able to take over the harem group, while the dominant male may benefit from their presence because they contribute to defending the group or territory against intruders (see Wirtz 1982; Dunbar 1984).

Though it is widely assumed that resident males are responsible for most of the mating during their period of tenure, this may not be the case in all species. In several primates that live in unimale troops throughout most of the year, additional males join the group during peak breeding periods and females mate promiscuously with intruders as well as with the resident male (Cords 1987). In some cases, the resident male is still able to monopolize most of the mating, but in others he apparently has no advantage and much of the mating involves intruders (Chism *et al.* 1984; Tsinglia & Rowell 1984; Cords 1984). However, in none of these studies has it yet been possible to assess paternity. Verification that intruders do obtain considerable numbers of fertilizations and long-term records of the relative breeding success of intruders and residents are badly needed.

In populations where males defend resource-based harems, the tenure of males is often relatively short. For example, in grey langurs, *Presbytis entellus*, tenure is usually less than three years (Hrdy 1977; Hausfater & Vogel 1982) and male tenure may be even shorter in some guenons (Cords 1987). In many of these species, usurping males kill dependent infants fathered by the previous occupant

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† 1 ha = 10^4 m^2.

(Sugiyama 1965; Hrdy 1977; Struhsaker 1985). In other species, male tenure appears to be substantially longer (see Robinson 1988).

(*d*) *Multimale groups with spatial defence by males*

In some species, breeding units consist of several adult females and several reproductively active males who cooperatively chase and attack intruders within their home range. Whether or not this should be regarded as territorial behaviour depends on how territoriality is defined. Range overlap is frequently extensive and the defence of particular resources is unusual (see Wrangham 1986*a*, *b*; Packer 1986) but, as the hostility of resident males is not confined to intruders that attempt to joint the group, male aggression often leads to group displacements (see Wrangham 1986; Packer 1986). Consequently, these systems may be best classified as a form of spatial defence. Examples include African lions, *Panthera leo* (Schaller, 1971), banded mongooses, *mungos mungo* (Rood 1975, 1986), ringtail lemurs, *Lemur catta*, and sifakas, *Propithecus verrauxi* (Jolly 1966; Richard 1987), chimpanzees, *Pan troglodytes*, and bonobos, *P. paniscus* (Wrangham 1986; Nishida & Hiraiwa-Hasegawa 1987), and possibly spider and woolly monkeys, *Ateles* and *Lagothrix* (van Roosmalen 1980; Robinson & Janson 1987). At least some populations of red colobus, *Colobus badius*, should probably be allocated to this group, too, (Clutton-Brock 1972) though, at high density, groups avoid each other and male defence is confined to the immediate area of the troop (Struhsaker 1975; Struhsaker & Leland 1987).

Multimale groups usually include more than five breeding females (figure 3), though, in some cases, females spend part of their active time alone or in subgroups that range separately. Where females aggregate in large groups, as in red colobus, a single male may be unable to monopolize breeding access to the whole group, and cooperative defence may have substantial advantages. For example, in lions,

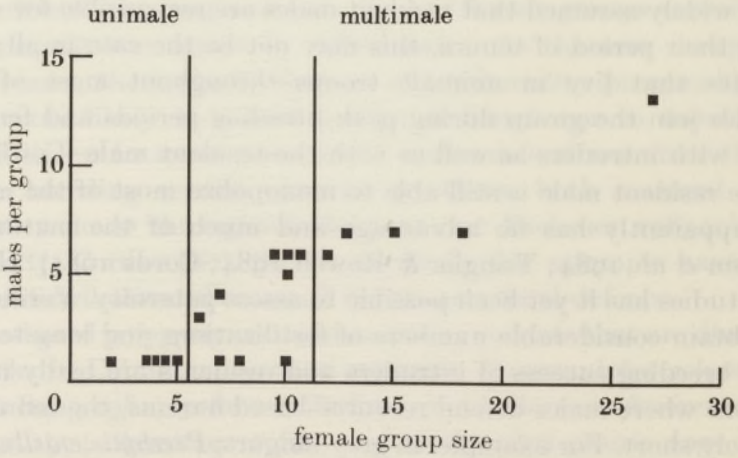


FIGURE 3. Numbers of resident males and females in troops of cercopithecine primates (from Andelman 1986). Where females live in groups of less than six, single-male harems are usual. Where female group size lies between six and ten, some groups contain more than one adult male, although in many of these species a single male is responsible for a larger proportion of the matings than other individuals. Where females live in groups of more than ten, several reproductively active males are usually associated with the group.

Panthera leo, the probability of acquiring a pride, the duration of tenure and the average reproductive success of resident males increases with the size of the defending coalition (figure 4). Similar benefits may be important in chimpanzees where males from neighbouring communities compete intensively and male groups sometimes exterminate their rivals, incorporating additional females into their own community (see Wrangham 1979; Goodall 1983, 1986; Dunbar 1988).

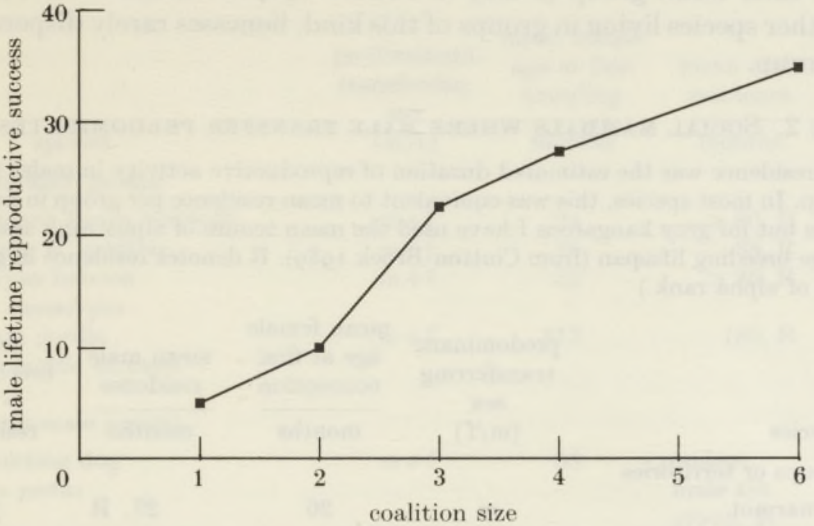


FIGURE 4. Reproductive success per head of male lions in relation to the size of the male coalition to which they belong (from Packer *et al.* 1988).

In several of these species, including lions, chimpanzees and bonobos, males cooperate with relatives to defend female groups or communities and social relations between resident males are usually tolerant, though individual males may guard particular females during their period of receptivity. For example, male lions belonging to the same pride rarely interrupt each others' matings and reproduction is apparently relatively evenly distributed among males (Packer & Pusey 1982). In chimpanzees, too, interruption of mating is unusual, though maternally related males cooperate with each other to compete for status and high ranking males obtain a large proportion of matings on days of probable ovulation (Tutin 1979; Riss & Goodall 1977; Hasegawa & Hiraiwa-Hasegawa 1983; Nishida 1983). In contrast, in red colobus, relations between troop males appear to be more competitive (Struhsaker 1975; T. H. Clutton-Brock, unpublished observations). In all these species, relations between males of neighbouring troops are usually intensely hostile (Cheney 1987), and in lions and chimpanzees intruders may be chased and killed (Schaller 1971; Goodall 1986).

Where males cooperate with their relatives to defend breeding access to groups of females, takeovers by competing male groups are usually infrequent and reproductive activity in particular female groups is usually dominated by the same group of males for several years. Though the precise length of male tenure is unknown for most species, in most cases it exceeds the average age of females at first breeding (Pusey 1987; Pusey & Packer 1987*a*; Clutton-Brock 1988) and females typically disperse from their natal group at or after adolescence, presumably to avoid inbreeding with close relatives (see tables 2 and 3). African lions are an interesting exception. Here, takeovers by rival coalitions of (usually) related males are relatively frequent and the average tenure of a male group in a pride of females (26 months) is *less* than the average age of females at first breeding (38 months) with the result that females rarely risk inbreeding with close relatives by remaining in their natal group (Pusey & Packer 1987*b*; Packer *et al.* 1988). In contrast to other species living in groups of this kind, lionesses rarely disperse from their natal group.

TABLE 2. SOCIAL MAMMALS WHERE MALE TRANSFER PREDOMINATES

(Average male residence was the estimated duration of reproductive activity in males within a particular group. In most species, this was equivalent to mean residence per group in non-natal breeding groups but for grey kangaroos I have used the mean tenure of alpha rank and for red deer the average breeding lifespan (from Clutton-Brock 1989). R denotes residence in group; α denotes tenure of alpha rank.)

species	predominant transferring sex (m/f)	mean female age at first conception (months)	mean male residence (months)	female breeding age > male residence[a]
unimale groups or territories				
yellowbellied marmot *Marmota flaviventris*	m	36	27, R	yes
blacktailed prairie dog *Cynomys ludovicianus*	m	24	< 24, R	yes
red deer *Cervus elaphus*	m	40	36, R	yes
wedge-capped capuchin *Cebus olivaceus*	m	72	120, R	no
redtail monkey *Cercopithecus ascanius*	m	24	< 24, R	yes
Campbell's guenon *C. campbelli*	m	36	< 34, R	yes
blue monkey *C. mitis*	m	66	< 40, R	yes
gelada baboon *Theropithecus gelada*	m	54	43, R	yes
grey langur *Presbytis entellus*	m	36	28, R	yes
purple leaf monkey *P. senex*	m	48	36, R	yes
multimale groups				
eastern grey kangaroo *Macropus giganteus*	m	24	12, α	yes
African lion *Panthera leo*	m	38	26, R	yes
ringtail lemur *Lemur catta*	m	30	< 24, R	probably
vervet monkey *Cercopithecus aethiops*	m	33	32, R	yes
yellow baboon *Papio cynocephalus*	m	72	< 51, R	yes
rhesus macaque *Macaca mulatta*	m	66	19, R	yes
Japanese macaque *M. fuscata*	m	54	< 30, R	yes
toque macaque *M. sinica*	m	60	50, R	yes

[a] Does female age at first breeding exceed average male residence in a single group?

TABLE 3. SOCIAL MAMMALS WHERE FEMALE TRANSFER PREDOMINATES OR WHERE BOTH SEXES USUALLY TRANSFER

(In four species, groups of related males defend access to groups or communities of females. The average residence of male kin groups are unknown in all cases, but takeovers are rare and the average tenure of male groups is evidently long. In one species (hamadryas baboons) females leave their natal units but remain within a larger social unit, consisting of several harems, often belonging to related males. R denotes residence.)

species	predominant transferring sex (m/f)	mean female age at first breeding months	mean male residence months	female breeding age > male residence[a]
unimale groups				
plains zebra *Equus burchelli*	m+f	24	> 60, R	no
feral horse *E. caballus*	m+f	25	38, R	no
hamadryas baboon *Papio hamadryas*	m+f	52	> 36, R	probably not
mountain gorilla *Gorilla gorilla beringei*	m+f	119	180, R	no
multimale groups				
Cape hunting dog *Lycaon pictus*	m+f	38	resident male kin group, R	no
red howler monkey *Alouatta seniculus*	m+f	49	71, R	no
red colobus monkey *Colobus badius*	f	46	resident male kin group, R	no
chimpanzee *Pan troglodytes*	f	120+	resident male kin group, R	no
bonobo *P. paniscus*	f	120+	resident male kin group, R	probably not

[a] Does female age at first breeding exceed average male residence in a single group?

(*e*) *Unimale groups without spatial defence by males*

Where females aggregate at particular sites during the breeding season or live in stable social groups in ranges too large to be effectively defended, males commonly defend access to groups rather than their ranges. In some of these species, males defend particular sites where females aggregate before breeding groups form but these systems differ from those of type (*c*) in that male territories do not extend over the entire range of females. Harem size varies widely in response to differences in the distribution of females. For example, in seals breeding on pack ice or fast ice, females are widely dispersed and males defend single females or small groups of females, whereas in land-breeding species where breeding females are densely aggregated on particlar beaches, males defend large harems (Stirling 1975; LeBoeuf 1978). Where males defend harem groups, females usually mate with the resident male though, as in mating systems of types (*c*) and (*d*), influxes of extra-group males may cause periods of promiscuous mating (Cords 1987).

If reproduction is strongly seasonal, males may compete intensely to defend temporary harems, as in elephant seals, *Mirounga angustirostris* (LeBoeuf 1974), red deer, *Cervus elaphus* (Clutton-Brock *et al.* 1982) and sperm whales, *Physeter catodon* (Caldwell *et al.* 1966). In contrast, where breeding seasons are longer or reproduction is seasonal, harems are commonly defended throughout the year and overt competition is generally less intense. Harem systems of this kind are found in a variety of primates, including geladas, *Theropithecus gelada*, and hamadryas baboons, *Papio hamadryas* (Dunbar 1984; Kummer 1968), as well as in some ungulates, including Burchell's zebra, *Equus burchelli* (Klingel 1974; Rubenstein 1986), and eland, *Taurotragus oryx* (Hillman 1976). In some of these species, including Burchell's zebra (Klingel 1974), hamadrayas and gelada baboons, and the forest-dwelling drills, *Papio leucophaeus*, and mandrills, *P. sphinx* (Gartlan 1970; Jouventin 1975), harem groups regularly associate with each other to form larger herds.

As in mating systems of type (*c*), harem groups may actually contain more than one adult male although only one male is responsible for most or all of the matings, a breeding system sometimes referred to as an age-graded male group (Eisenberg *et al.* 1972). For example, in gelada baboons, around 50% of all groups contain an alpha male who is responsible for most copulations and a secondary male who rarely or never mates (Dunbar 1984, 1988). Though they seldom breed, secondary males may benefit by joining groups if they eventually take over part of the harem from the dominant male. Gelada males gain harems either by attacking a resident male or by joining an existing harem as a subordinate and gradually developing social bonds with females until they eventually split the group. Individuals that follow the former course gain the entire group of females but have little hope of success until they are nearly eight years old and risk being beaten or wounded in the attack. Those that join existing groups as followers suffer lower risks and start to breed at a younger age, but acquire a smaller number of females. Calculations suggest that both strategies have equal lifetime pay-offs (Dunbar 1984). Where males defend harems, females usually mate with the resident male though, as in type (*c*) and (*d*) mating systems, influxes of extra group males may cause periods of promiscuous mating (Cords 1987).

Mating systems of this kind can be further divided into those where males attach themselves to pre-existing groups of matrilineally related females and those where most females disperse from their natal group and attach themselves to particular males, as in hamadryas baboons (Kummer 1968), zebra (Klingel 1974) and feral horses (Berger 1986). This difference again appears to be connected with the risk of inbreeding to females; where females usually remain in their natal groups, the average reproductive tenure of individual males in particular groups is generally less than the average age of females at first breeding (table 2), with the result that the risk to females of inbreeding with close relatives is low (Clutton-Brock 1988). Conversely, in species where females typically transfer from their natal group to breed in other social units, average male tenure usually exceeds the age of females at first breeding and females would risk inbreeding with close relatives if they remained in their natal unit (see table 3).

(*f*) *Multimale groups without spatial defence by males*

Where the ranges of female groups are too large to be defensible and group size exceeds five or six breeding females, more than one reproductively active male is commonly found in each group (Jarman 1974; Andelman 1986; see figure 3). Examples of multimale breeding groups of this kind include yellow and olive baboons (Devore 1965; Altmann *et al.* 1988), talapoins, *Miopithecus talapoin* (Gautier Hion 1973); squirrel monkeys, *Saimiri sciureus* (Baldwin & Baldwin 1981) and Cape buffalo, *Syncerus caffer* (Sinclair 1977; Prins 1987). These mating systems differ from those of type (*d*) in that males do not defend territories covering the range of female groups. In addition, resident males rarely cooperate to defend female groups against intruding males, though they commonly defend receptive females against other group members as well as against intruders.

Relations between resident males are usually intolerant; males compete intensely for receptive females and are frequently ranked in a dominance hierarchy that affects their access to females (Melnick & Pearl 1986; Sinclair 1977; Mloszewski 1983; Packer 1979*a*, *b*; Dunbar 1988; but see Bercovitch 1986) though, in some primates, they form reciprocal alliances with other males that they use to gain rank or females (Packer 1977; Strum 1982; Smuts 1985). Relations between the males of neighbouring groups are seldom as hostile as in species where related males cooperate to defend groups, and male immigration is comparatively common (see Melnick & Pearl 1987).

In mating systems of this kind, males usually migrate from their natal troop and resident males are seldom closely related to each other, though in vervet monkeys, *Cercopithecus aethiops*, and some macaques, *Macaca*, males sometimes emigrate in company with their brothers or natal group peers (Cheney & Seyfarth 1983; Pusey & Packer 1986). Males may change groups several times during their lifetime, often at times of peak reproductive activity (Pusey & Packer 1987*a*; Cheney *et al.* 1988; van Noordwijk & van Schaik 1985; Altmann *et al.* 1988). In some species, this is associated with a decline in mating success the longer a male is resident in a group. For example, in yellow baboons the rank and reproductive success of males is high immediately after they enter a group and subsequently declines, partly because females apparently prefer to mate with fresh immigrants (Altmann *et al.* 1988; see figure 5). In Cape buffalo, bulls lose condition while they live in female herds and switch every few weeks between membership of mixed-sex herds and bachelor parties (Prins 1987).

It is not yet clear why, in mating systems of this kind, dominant males tolerate each others' presence in the group nor why they do not cooperate to defend female groups against intruders. In contrast to mating systems of type (*d*), it seems unlikely that dominant males benefit from the presence of other males, though firm evidence is lacking. One possible explanation is that it is difficult to exclude other males effectively because female groups are often widely dispersed in small foraging parties (Jarman 1974; van Schaik & van Hooff 1983; Andelman 1986). Moreover, the benefits of excluding other males may be low where relations between dominance rank and mating success reduce the cost of the presence of other males to dominant animals or where mating is seasonal and more than one female is often in oestrus at the same time (Ridley 1986; Dunbar 1988).

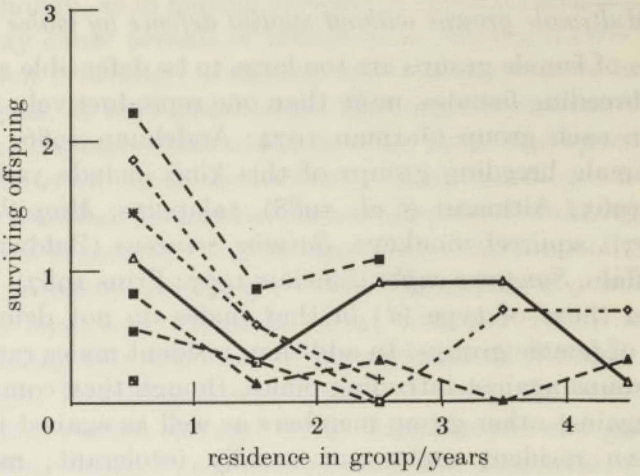


FIGURE 5. The yearly reproductive success of male yellow baboons, *Papio cynocephalus*, as a function of the length of time they have been resident in a group (from Altmann *et al.* 1988).

In many of these species, females mate with several males during the course of a single oestrus period. However, in some cases, females develop long-lasting social bonds with particular males and are more likely to mate with them than with other males (Smuts 1985, 1987).

(*g*) *Mating territories*

Where females range over areas too large to be defensible and female groups are small or change in membership from hour to hour, males commonly defend mating territories smaller than the home range of female groups, sited in areas visited regularly by females in search of resources (Estes 1974; Gosling 1986). These mating systems differ from those of type (*c*) in that the male territory covers a small fraction of the female range and associations between males and particular females are usually temporary and unstable. These systems are common in antelopes (Gosling 1986), though they also occur in some cervids, antilocaprids, equids and rhinoceroses (Chapman & Chapman 1975; Kitchen 1974; Rubenstein 1986; Owen-Smith 1975). They appear to be associated with relatively large female ranges where clumped resources cause females to visit particular sites regularly. For example, in waterbuck, *Kobus defassa*, males defend contiguous territories of from 30 to over 200 ha in areas of grassland regularly used by female groups who range over an area three to four times this size (Spinage 1982). In species where resources favoured by females are more widely dispersed, as in Grevy's zebra, *Equus grevyi*, male territories are often discontinuous (see Owen Smith 1977; Rubenstein 1986; Gosling 1986).

Mating territories may either be defended seasonally or throughout the year (Gosling 1986). In some species, including waterbuck and white rhinoceros, *Ceratotherium simum* (Owen Smith 1972, 1975), satellite males are also found living in male territories and may contribute to their defence (see, for example, Wirtz 1982). Cheetah, *Acinonyx jubatis*, apparently have a mating system that represents a variant on this theme. Mature males form stable coalitions that defend territories much smaller than female ranges in areas of high resource (gazelle) availability (Caro & Collins 1987).

(*h*) *Clustered mating territories and leks*

In some cases, mature males defend small mating territories in clusters. Mating systems of this kind have been recorded in hammer-headed fruit bats, *Hypsignanthus monstrosus* (Bradbury 1977), and walrus (Fay *et al.* 1984) as well as in several ungulates. Some of these mating systems clearly intergrade with type (*g*) systems. For example, male puku, *Kobus vardoni*, defend clustered territories of around 5 ha throughout the year on old river meanders which are regularly visited by females in search of annual grasses and forbs (Rosser 1987). Both in puku and in some populations of topi, *Damaliscus korrigum*, the numbers of females visiting different territories are closely related to their vegetation content (Rosser 1987; S. D. Albon & A. Balmford, unpublished).

In other cases, males defend very small territories that do not contain significant resources but are sited in areas regularly used by large herds of females. For example, in Kafue lechwe, *Kobus leche kafuensis*, clusters of very small territories, often less than 0.01 ha in size, are sited at the intersection of paths regularly used by females in their diurnal migration to feed at the edge of the floodplain (Schuster 1976; T. H. Clutton-Brock, personal observation). Females in oestrus commonly remain on the lek when female herds move on to feed. Similarly, in other populations of topi, males defend small, clustered territories in areas of short grassland close to preferred feeding habitats that are regularly used by females for resting because of improved predator detection (Gosling 1986, 1987). By defending territories in areas regularly visited by large numbers of females, males may maximize their chances of attracting females in oestrus and these mating systems may be intermediate between those where males defend resources attractive to females (see above) and classical leks (see below).

Finally, there are a small number of mammals where males defend very small, clustered territories and where females in or close to oestrus move to the lek alone or in small parties. In several of these cases, territories are seldom visited by female herds and it is reasonable to assume that females do not visit the lek for ecological reasons. Ungulates that breed in this fashion include some populations of fallow deer, *Dama dama dama* (Schaal 1986; Clutton-Brock *et al.* 1988), Uganda kob, *Kobus kob thomasi* (Buechner & Schloeth 1965; Leuthold 1966), and, possibly, white-eared kob, *Kobus kob leucotis* (Fryxell 1987). In all three cases, females usually live in large, unstable, mixed-sex herds, sometimes including several hundred animals, which share a common range. A proportion of males defend single territories off the lek but seldom mate successfully (Leuthold 1966; Clutton-Brock *et al.* 1988).

At present, more is known about the mating system of fallow deer, which are highly seasonal breeders, than about that of kob, which breed throughout the year. In fallow deer, herds of anoestrous females gather at the beginning of the rut in resource-based territories under oak trees where they forage for acorns. However, females rarely mate on these resource territories and over 95% leave their herds shortly before they come into oestrus and move to a traditional lek where around

20 males hold small territories 5–20 m in diameter. When they reach the lek, females are attracted to other groups of females already there and preferentially join bucks with large harems. They usually mate once with a single male, leaving the lek and rejoining feeding herds within two hours of mating. Mating success varies widely between bucks, with the most successful animal mating over 50 females per year and the least successful ones totally failing to mate. In some populations, bucks rarely mate successfully on more than three or four days and turnover on the lek is rapid, whereas in others some males mate successfully throughout the mating season (Clutton-Brock *et al.* 1988; Apollonio *et al.* 1989).

Leks raise three important questions: why do males defend clustered territories when, by doing so, they are forced to share with other males the females attracted to the lek? Why do females mate on leks? And what accounts for the distribution of lek breeding across species? As more detailed information is available for lek-breeding ungulates than for other species, this group holds the best chance of providing answers to all three questions.

In all lek-breeding mammals that have been studied in detail, males holding territories on the lek have much higher mating rates than any of those that hold resource territories off the lek (Buechner & Schloeth 1965; Leuthold 1966; Schaal & Bradbury 1987; Rosser 1987; Clutton-Brock *et al.* 1988; L. M. Gosling, unpublished observations; S. D. Albon & A. Balmford, unpublished observations) and there is little evidence to support any of the other suggestions concerning the benefits to males of breeding on leks, such as reduced vulnerability to predation (see Bradbury 1981; Bradbury & Gibson 1983; Gosling 1986). Bradbury's suggestion that leks originate from the placing of male territories in areas where female home ranges overlap, causing a reduction in the potential mating success of male territories placed elsewhere in the female's range (the 'hotspot' theory: Bradbury & Gibson (1983), Bradbury *et al.* (1986)) may help to explain the siting of leks but does not account for the extent to which male territories are clustered. The related idea that leks form because inferior males parasitize the females attracted to superior animals (the 'hotshot' theory: Beehler & Foster (1988)) may account for the presence of some inferior males on leks but is unsatisfactory as a general explanation because it fails to account for the presence of several 'hotshots' on the same lek.

Five reasons why receptive females mate on classical leks have been suggested:

(1) that the stronger signals produced by clustered males may either attract more females to the lek or may render females more likely to mate there (Lack 1939);

(2) that females benefit from reduced predation by mating on leks because the presence of other animals reduces chances of predation (Wittenberger 1978; de Vos 1979; Gosling 1986);

(3) that the presence of males in the normal range of females has important costs to females, because males compete for food or increase the risk of predation, that are reduced if females mate on leks in areas separate from their normal feeding ranges (Brown 1964; Crook 1965; Wrangham 1980*a*, *b*);

(4) that females benefit from increased opportunities to choose mating partners on leks (Alexander 1975; Emlen & Oring 1977; Parker 1978; Bradbury 1981;

Bradbury & Gibson 1983; Bradbury *et al.* 1986). Mating on leks might enhance the opportunity for mate choice for several reasons, including the increased number of males available to choose from, the opportunity to compare males closely and the ability to monitor the choices of other females (Bradbury & Gibson 1983);

(5) that oestrous females in mixed-sex groups are likely to be subjected to dangerous harassment by several courting males and consequently are attracted to any area where they are effectively defended by a single male (see Wrangham 1980*b*; Foster 1983; Trail 1985). Under these circumstances, clusters of male territories may provide the safest haven, because females driven from one territory can run to another.

It is quite possible that more than one of these factors may be involved, but some are more likely to be important than others. It is unlikely that the increased strength of vocal or olfactory signals from clustered males increases their range sufficiently to account for the large numbers of females that commonly mate on leks (Bradbury 1981; Bradbury & Gibson 1983). Second, there is no reason to think that females mating on the lek are safer from predators than females mating off it: predation on leks is not uncommon and in all the lek-breeding ungulates, females typically live in large herds and are found in smaller groups when on leks than when off them. Similarly, there is no evidence to support the idea that females mate on leks to avoid feeding competition with males: in several lek-breeding ungulates, males and females aggregate in large, mixed-sex herds during the time of year when food is least plentiful.

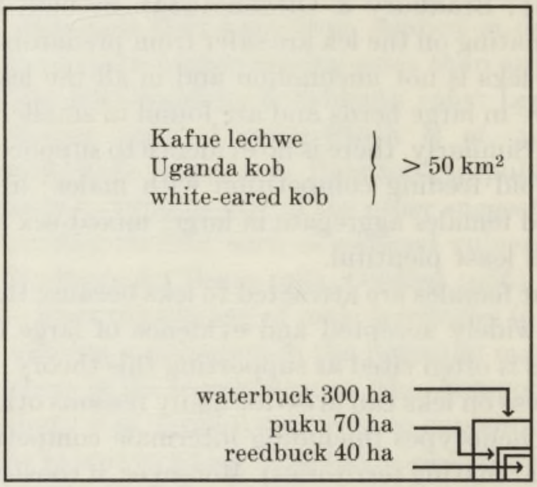
The argument that females are attracted to leks because this facilitates choice of mating partners is widely accepted and evidence of large differences in mating success among males is often cited as supporting this theory. However, differences in male mating success on leks can arise for many reasons other than female choice of particular male phenotypes (including intermale competition and female preferences for particular mating territories). Moreover, if consistent mate choice does occur on leks, this does not necessarily indicate that females move to the lek for this reason. Current theory suggests that mate choice is unlikely to have substantial genetic advantages unless there are large heritable differences in fitness among males (see Kirkpatrick 1985, 1987). Moreover, unless it is supposed that female choice is substantially more important in some species than in others, this explanation fails to account for the distribution of lekking.

The final explanation, that females mate on leks to avoid harassment from young males, provides a credible reason why oestrous females might leave large, mixed-sex herds, for they rapidly attract a large retinue of competing males and mating under these circumstances is probably dangerous (Clutton-Brock *et al.* 1988; T. H. Clutton-Brock & M. Hiraiwa-Hasegawa, unpublished observations). However, it does not explain why they do not mate on single territories where resident males can presumably defend them as effectively as on the lek. One possible explanation, which agrees with research on fallow deer, is based on the observation that mating territories are regularly disrupted by young males. When harems are dispersed by young males, does on single territories are quickly chased away, but on the lek they merely run to a neighbouring territory, often returning to their original male soon afterwards (Clutton-Brock *et al.* 1988; Clutton-Brock

& Hiraiwa-Hasegawa 1989). Oestrous females may prefer leks to single territories because they provide a safer haven from harassment by young males, and by placing their territories next to those of other animals bucks may be able to retain a share in a pool of receptive females.

Finally, what accounts for the distribution of lek breeding? All the ungulates in which males defend very small, clustered territories are predominantly grazers, characterized by high local densities and living in large, unstable herds that range over substantial areas (Rosser 1987; Clutton-Brock *et al.* 1988). Within the Reduncinae (kobs, lechwe, waterbuck and reedbuck), for example, the territory size of males is largest where female populations are divided into local spatial units and female range size is relatively small, and smallest where large herds of females range over big areas (see figure 6*a*, *b*). In addition, within most lek-breeding species,

(*a*) female ranges



(*b*) male territories

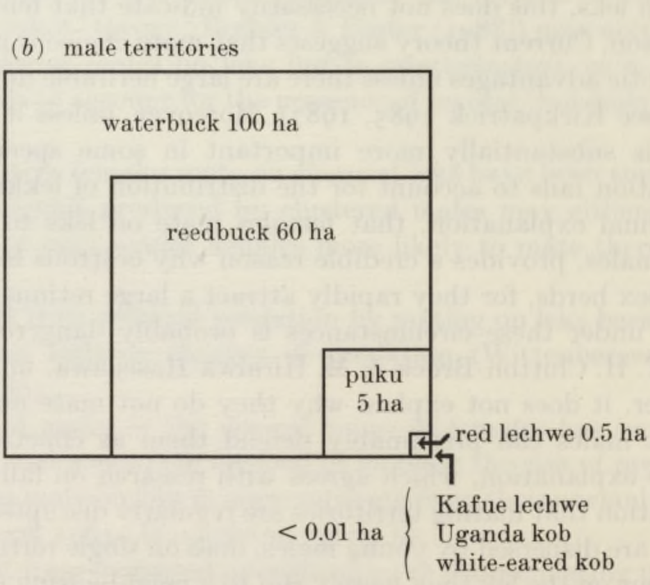


FIGURE 6. Relative sizes of (*a*) female ranges and (*b*) male territories in antelope of the subfamily Reduncinae. Data from Rosser (1987).

there is a positive association between local population density and lek size (Modha & Eltringham 1976; Clutton-Brock *et al.* 1988) and leks are replaced by dispersed male territories or roving strategies in low-density populations (Leuthold 1966; Clutton-Brock *et al.* 1988). Leks may be associated with large, unstable herds because the effective defence of females by males is impossible under these conditions (see Foster 1983) and high local densities and extensively overlapping female ranges permit large numbers of females to collect at particular sites where maximum harem size is limited. This may reduce the costs of clustering to males (Clutton-Brock *et al.* 1988).

In summary, lek breeding poses a variety of important questions to which, as yet, we have no firm answers. Though it is possible that leks may have evolved as a consequence of evolutionary mechanisms associated with female choice (see Queller 1987), alternative explanations based on more immediate benefits to females are also feasible. Two questions that need to be investigated in future are to what extent the size of leks affects their ability to attract and retain females, and whether or not females visiting leks select potential mating partners on the basis of physical or behavioural characteristics.

(*i*) *Temporary harems, territories or leks*

In a number of ungulates, including some populations of wildebeeste, *Connochaetes taurinus*, topi, and reindeer, *Rangifer tarandus*, (Espmark 1964; Lent 1965; Watson 1969; Henshaw 1970; Jewell 1972; Estes 1974; Geist 1974; Gosling 1986; Leader-Williams 1988), females aggregate in large, unstable, migratory herds, mating during the course of migration. No studies have yet been able to monitor the breeding success of individually recognizable males in moving herds. However, incidental observations suggest that their mating behaviour is unusually flexible and that males may defend individual females, small harems or temporary territories, sometimes grouped in clusters, in the path of the herd.

(*j*) *Roving males*

Where females range widely and are solitary or live in small groups that are unpredictably distributed at low population density, males range widely in search of oestrous females, consorting with them and defending them against other males (see Gosling 1986; Dunbar 1988). Moose, *Alces alces* (Peterson 1955), polar bears, *Thalarctos maritimus* (Ramsay & Stirling 1986), some populations of orang utans, *Pongo pygmaeus* (Mackinon 1974), several of the larger macropods (see Croft 1981*a*, *b*; Lee & Cockburn 1985) and some cetaceans (Gaskin 1982) show mating systems of this kind.

Roving males that guard only females in oestrus are also found in a number of mountain ungulates, including many of the ovids and caprids (Schaller 1977; Lovari 1985) as well as in some of the more sedentary macropods (Jarman & Southwell 1986). Why male territoriality does not occur in these groups is not clear, but it may be that in neither case are resources aggregated in clumps large enough to attract sufficient numbers of females. Moreover, in both cases, populations are subdivided into local home-range units and male dominance hierarchies affecting reproductive access are well defined (Geist 1971; Jarman & Southwell 1986). As a result, dominant males may gain more matings by actively searching for females than by guarding a territory. In Eastern grey kangaroos, this mating system is associated with continuous growth in males and a close correlation between body size and dominance (Jarman & Southwell 1986).

CONCLUSIONS

Though categories of mating systems intergrade and a variety of different mating systems can occur within a single species, much of the diversity of mammalian mating systems can be interpreted within a simple framework of ecological relationships governing effects of male assistance of female breeding success and the defensibility of females by males. However, many important questions remain unanswered. In particular, little attempt has been made to investigate the extent to which different male strategies are frequency dependent or to compare species differences in the variability of mating systems. We do not yet understand the evolution of monogamy in uniparous species, especially in those where males do not assist in carrying the young. Though the available evidence suggests that the duration of male reproductive tenure declines with increasing competition for mates, little attempt has so far been made to explain interspecific differences or to investigate their consequences. Similarly, we do not yet understand the distribution of defensive coalitions among related males; although these appear to be associated with spatial defence (see above), it is not clear why this is the case nor why they are not more common. The benefits of dispersal to males and females are in dispute (see Moore & Ali 1984; Pusey & Packer 1987*a*,*b*; Pusey 1987) as are the potential benefits of defending territories on leks.

Some of the most important questions that remain to be answered concern the mating behaviour of females. At present, there are few mammals for which the female mating system has been adequately described and we rarely know the number of partners females typically mate with nor the basis on which mating partners are selected. Moreover, although our understanding of male mating systems is based on the distribution and sociality of females, there is surprisingly little firm evidence of the benefits of sociality to females in any mammal (see Jarman 1974; Clutton-Brock & Harvey 1977, 1978; Wrangham 1980*a*; Wrangham & Rubenstein 1986).

Understanding the diversity and adaptive significance of mating systems is important because their form affects the opportunity for selection and the factors affecting reproductive success and survival in the two sexes (Trivers 1972; Clutton-Brock 1988). For example, in monogamous species, variance in lifetime reproductive success and the factors affecting breeding success are usually similar in males and females, whereas in polygynous species they differ between the sexes (Clutton-Brock 1988). As a result of the contrasting selection pressures on males and females, sexual dimorphism in body size, growth, weaponry and aggressive behaviour is typically most pronounced in highly polygynous species and least in monogamous ones (Brown 1975; Clutton-Brock *et al.* 1977; Alexander *et al.* 1979). This has important energetic consequences and juvenile and adult males commonly require more food than females of the same age and may consequently differ from females in habitat use and food selection (Clutton-Brock & Harvey 1983; Illius & Gordon 1987). Size dimorphism may also be responsible for the widespread tendency for food shortage to affect the growth and survival of males more than that of females (Widdowson 1976; Clutton-Brock 1977; Clutton-Brock *et al*. 1983, 1986). In many sexually dimorphic ungulates (and probably also in other groups of mammals) high population density is associated with a strong female bias in the adult sex ratio, caused by the relative reduction in survival among males (Clutton-Brock *et al*. 1982). This in turn has important consequences both on population dynamics and on the genetic structure of populations (Clutton-Brock 1989*b*).

Female mating systems may also have an important influence on male characteristics. For example, in rodent species where males are territorial and females are unlikely to mate with several partners, males exhibit fewer intromissions before ejaculation and lower ejaculatory frequencies than where females mate promiscuously (Cockburn 1988). Similarly, among primates, the frequency with which individual males copulate with particular females is higher in species such as yellow and olive baboons where females frequently mate with several males than in those that live in unimale groups (Dunbar 1988). Males also have relatively larger testes in primates that live in multimale groups compared with monogamous or harem-living species (Harcourt *et al*. 1981), presumably because sperm competition is common and selection favours large ejaculate size, frequent ejaculation and, consequently, large testes.

This review of mammalian mating systems emphasizes two logistic points. First, there is an urgent need for reliable estimates of paternity to check the findings of observational studies. In the future, the technique of DNA fingerprinting (Jeffreys *et al*. 1985) holds great promise and may lead to important changes in our understanding of male and female mating systems. Second, it is clear that, especially in species living in complex social groups, a reliable description of mating systems can seldom be achieved unless the breeding careers of recognizable individuals are followed over a substantial proportion of their lifespan. As our understanding of mammalian mating behaviour has developed, it has come to rely increasingly on the results of a small number of long-term studies. As the costs and benefits of different forms of mating behaviour are likely to vary widely within and between species, extrapolations based on these studies may well be less secure than is often assumed. Further long term studies, both of novel mating systems and of those that have been previously investigated, are badly needed.

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