

ARE DISPERSAL AND INBREEDING AVOIDANCE RELATED?

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Abstract. Sex differences in dispersal and inter-group transfer by birds and mammals are often considered to be evolved responses to the phenomenon of inbreeding depression. This belief is derived from 'natural selection logic', which holds that (1) because inbreeding depression is demonstrably costly, selection must have acted to minimize its occurrence, and (2) as sex differences in dispersal often appear to be the only thing preventing inbreeding, these sex differences must be the expected adaptations for avoiding inbreeding depression. However, although the sex differences in median dispersal distance observed among many small mammals and birds may reduce average levels of inbreeding within a population, they nevertheless leave the majority of individuals 'at risk' for inbreeding; such differences can be responses to inbreeding depression only in a group selection model. Furthermore, natal dispersal by both sexes occurs in many group-living species. In these species, emigration by individuals of one sex cannot easily be attributed to avoiding inbreeding because opposite-sex relatives also emigrate. Though most authors acknowledge that sexual dispersal patterns may be epiphenomenal consequences of other factors (e.g. intrasexual aggression), this point is rarely considered further. In this paper we critically review several frequently cited examples of differential dispersal, and conclude that 'other factors', such as intrasexual competition and territory choice, explain these observations more completely and consistently than does the inbreeding avoidance hypothesis. Observed dispersal patterns simply reflect sex differences in the balance between the advantages of philopatry and the costs of intrasexual competition.

Introduction

Most discussions of emigration and inter-group transfer among primates and other vertebrates cite outbreeding as a major consequence of dispersal (e.g. Packer 1975; Wilson 1975, page 79; Kurland 1977, page 128; Gauthreaux 1978; Eisenberg 1981, page 409; Hoogland 1982). Less often, it is explicitly argued that dispersal is an adaptation for the avoidance of inbreeding depression, i.e. that many individuals disperse for the purpose of avoiding inbreeding and would do so even if there were no other benefits to leaving (primates, e.g. Itani 1972; Demarest 1977; Harcourt 1978; Packer 1979; Pusey 1980). Several authors have pointed out that if dispersal is due to something else — for example, avoidance of intraspecific competition, or habitat choice — then inbreeding avoidance may be epiphenomenal (Bertram 1978; Packer 1979) and not an adaptation (*sensu* Williams 1966).

This realization has led to frequent qualifiers, but such caution is often lost in the reading. For example, Packer (1979) states that in wild dogs 'the advantages to an individual male of cooperation with other males apparently exceed the usual advantages of male migration [presumably outbreeding] . . . Females *would be expected* to change groups in order to avoid in-

breeding when the advantages to males of cooperation with other males exceeded the costs to females of transferring' (page 29; emphasis added). Greenwood (1980), referring to Packer, states that female transfer in wild dogs 'has also been interpreted as an inbreeding avoidance *mechanism*' (page 1151; emphasis added) — a somewhat stronger statement than Packer's original. Phrases such as 'one function of dispersal' (Greenwood et al. 1979), '[dispersal] functions, in part' (Greenwood 1980), and 'most credible functional explanation' (for mate preferences that lead to dispersal) (Harcourt 1978) certainly imply adaptational arguments, and Packer (1979) prefaces his discussion of alternative benefits of dispersal (mate availability, avoidance of aggression, etc.) with the phrase 'Even where inter-group transfer *resulted from* the avoidance of inbreeding, there may be other benefits . . .' (page 29; emphasis added).

Whatever the original intent of these authors, this language has led to a general view epitomized by the title of a recent *Natural History* article: 'Gorilla society: avoiding inbreeding is of paramount importance in determining who can belong to the group' (Veit 1982; this may well be an editor's phrase rather than the author's). Though inbreeding depression and

incest avoidance are both very real and important phenomena, we believe that emigration and dispersal generally do not 'function' to minimize inbreeding. In this paper we consider the significance of dispersal patterns among female and male primates and other mammals for the inbreeding-avoidance hypothesis of dispersal in animals. A similar problem exists concerning the evolution of dioecy and outcrossing mechanisms in plants (Jain 1976), and we refer the reader to articles by Givnish (1980, 1982) and Bawa (1980), whose arguments are conceptually analogous to ours. It should also be noted that there is an extensive literature on incest, inbreeding and dispersal in *Homo sapiens* (see van den Berghe 1983 for a recent summary of various sociological, psychological and biological viewpoints on the human case).

We begin by briefly examining the potential costs and benefits of inbreeding, concluding that while inbreeding is not inherently maladaptive, dispersal — usually necessary for outbreeding — probably is. Thus philopatry, and consequently inbreeding, should in general be favoured. We then discuss behavioural mechanisms whereby close inbreeding may be avoided without affecting dispersal patterns. Finally, we review observations which are commonly cited to support the inbreeding-avoidance hypothesis and suggest alternative and more parsimonious explanations for these observations. We agree entirely with May (1979) who argued that mathematical analyses of the costs and benefits of inbreeding and dispersal have enabled us to 'build an enchanting castle that rises free, constrained to earth with too few anchorlines of fact'. We need to look more closely at what animals actually do.

In this paper we will use the following definitions:

Emigration: departure from one's breeding unit. Emigrants may in theory avoid dispersal by remaining in their former group's home range, but both emigrants and dispersers have severed their former social ties. For the purposes of mate selection and inbreeding avoidance, emigration and dispersal are equivalent.

Transfer: emigration followed by immigration into another existing breeding unit.

Natal transfer/emigration: transfer/emigration out of the breeding unit in which one was born (cf. Packer 1979; Greenwood 1980).

Extra-group animals: individuals living as solitary or as members of non-breeding units, primarily all-male bands.

Incest: mating between individuals with coefficient of kinship ≥ 0.25 .

Close inbreeding: mating between individuals with coefficient of kinship ≥ 0.125 (Jacquard 1974, cited in Greenwood et al. 1978).

Behavioural avoidance of inbreeding: avoidance of incest or close inbreeding by refusal to mate with (presumably known) close kin; a 'Westermarck effect' or incest taboo. We prefer the term BAI to 'incest taboo' because it avoids connotations of cultural prohibition.

Inbreeding Depression

Inbreeding Costs and Benefits

Central to the inbreeding hypothesis is the observation of inbreeding depression in matings between close relatives, due primarily to increased homozygosity and the consequent exposure of deleterious recessive alleles (Wilson 1975, pp. 78–79; Ralls & Ballou 1982). Inbreeding can reduce the reproductive success of the inbreeding pair in many ways, most often by increased foetal or offspring mortality (Ralls et al. 1979; Senner 1980), and it is clear that in principle such reductions in reproductive success should be powerful selective forces against inbreeding. However, the increased homozygosity that results from inbreeding also means that inbred siblings are more closely related than are outbred ones, and hence more able to benefit from kin selection: inbreeding can be seen as a potentially beneficial phenomenon that promotes increased altruism and sociality (Brown 1974; Seger 1976; Wade 1979; Hughes 1980; Michod 1980; Breden & Wade 1981). Such altruism may resemble what is usually called inbreeding depression: Seger (1976, 1980) has pointed out that in a viscous population high levels of individual homozygosity will be correlated with a high probability of being surrounded by relatives; under such circumstances competitive restraint (manifested as competitive incompetence) would be favoured by kin selection. This logic probably does not apply to extreme incompetence (e.g. foetal mortality) but may be a factor in less severe inbreeding 'depression'. Shields (1982a, b) has reviewed explanations for the evolution of sexuality and concludes that the costs of sex (see Williams 1975; Maynard Smith 1978) may be largely overcome by inbreeding, whereby the mutation-editing advantages of sexuality are retained while both the cost of meiosis and the rate of break-up of coadapted parental genomes are reduced. Thus, inbreeding may have intrinsic benefits as well as costs.

Another major consideration is the cost of outbreeding, which may outweigh the benefits (Bengtsson 1978). Outbreeding costs fall into two major groupings, which may be divided into 'genetic' and 'somatic' categories for convenience. The genetic costs (e.g. the breaking of coadapted genomes) are to some extent the inverse of inbreeding benefits (e.g. the establishment or maintenance of locality-specific coadapted genomes). The genetic benefits of inbreeding are discussed above and have been reviewed in further detail by Bateson (1978, 1980, 1983), Shields (1982a, b) and others. We wish to emphasize the somatic costs of outbreeding (i.e. benefits of philopatry): primarily, the risks associated with migration, which is usually necessary for outbreeding (see Shields 1982b and Waser & Jones 1983 for reviews of the somatic advantages of philopatry). A migrant faces increased risks of exposure, predation and disease; lack of familiarity with an area may reduce foraging efficiency; and resident conspecifics may attack strangers more severely than familiar individuals. Among small mammals, at least, it is likely that these risks are too much for most dispersers, and mortality rates among emigrants are usually high (reviewed by Gauthreaux 1978; Gaines & McClenaghan 1980). The demonstration of potential costs and benefits to both inbreeding and outbreeding has led to the concept of optimal outbreeding (or optimal inbreeding), reviewed by Bateson (1983) and Shields (1982b); the latter has even suggested that philopatry may have evolved to promote optimal inbreeding.

Dispersal History

The situation is further confused by the importance of breeding history. When a previously outbred population begins to inbreed (for whatever reason), increased homozygosity will expose deleterious recessive alleles accumulated during outbreeding and inbreeding depression will be relatively severe. In time, however, these alleles will be eliminated from the population, a new equilibrium will be reached, and inbreeding depression will be reduced or absent (Bengtsson 1978; Smith 1979; Ali 1981; Shields 1982b) — or, of course, the population may go extinct: many do. Clearly, if a species has never been outbred then deleterious recessives will not have had the opportunity to accumulate and so inbreeding depression will never be observed. Past dispersal patterns influence acceptable (i.e. non-deleterious) levels of inbreeding; it has not been

shown that acceptable levels of inbreeding can determine future dispersal patterns. The discovery of inbreeding depression in zoo animals (Ralls et al. 1979, 1980; Ralls & Ballou 1982) is of profound importance for zoo management and conservation policy (Senner 1980; Soulé 1980), but it tells us about a species' natural breeding system relative to a restricted environment, not how that system evolved. The evolutionary importance of inbreeding depression must be assessed with regard to the natural history of the species and the costs of outbreeding. There are no uniform, 'inherent' costs to a particular level of inbreeding: female gorillas (*Gorilla gorilla*) are said to emigrate in order to avoid mating with full siblings or parents but 'readily' breed with half-siblings, where $r = 0.25$ (Veit 1982); whereas Packer (1979) argues that young male olive baboons (*Papio anubis*) emigrate to avoid mating with females related on average by $r = 0.1$. Such varying intensities of putatively detrimental inbreeding seem to have been applied in an ad hoc fashion.

Field Evidence

Evidence for inbreeding depression in wild populations of animals comes primarily from two studies: that of Packer (1979) on olive baboons and of Greenwood et al. (1978, 1979) on the great tit (*Parus major*). Although these studies are often cited to support the hypothesis that dispersal patterns are an adaptive response to inbreeding depression (e.g. Maynard Smith 1978), it is not at all clear that they do.

Olive baboons. During 1973–74, Packer observed unusually high infant mortality rates in the A troop of olive baboons at Gombe Stream Research Centre, Tanzania. This troop split off from Beach troop in 1970 and occupied an adjacent home range (Nash 1976). In December 1972 a young adult male (BRM) transferred from his natal Beach troop into A troop; he was thus in the unusual position of being a post-transfer male but still within a section of his natal troop. The females of A troop with whom he began consorting therefore were likely to have been relatives of his (Packer 1979). Using estimates of paternity based on consort records, Packer showed that the survivorship of BRM's offspring was significantly lower than the norm for the troops studied at Gombe, and calculated that if this was due to inbreeding, there was a 40% loss in viability for consanguineous matings among these baboons.

We believe that the figure of 40% is too high, and that some factor other than inbreeding depression was responsible for some unknown proportion of the observed mortality. The infant mortality rate in A troop before BRM began consorting was greater than for other troops at Gombe. Comparing pregnancy records for A, Beach and Camp troops during the period January 1970 to June 1 1973 shows that there was greater foetal and infant mortality in A troop (Table I; $P = 0.089$, Fisher test, one-tailed; $P < 0.05$ using Tocher's modification, Siegel 1956, page 102). BRM began consorting in A troop early in 1973 (Packer, personal communication) and could not have fathered infants born prior to June of that year (one miscarriage, in March, is not included in Table I because the pregnancy may have begun in January after BRM's transfer).

The cause of this higher mortality is unknown. Six of the 10 adult females in A troop had their first pregnancies after January 1970. If firstborn survivorship is lower than for subsequent births (olive baboons: Nicolson 1982; rhesus macaques (*Macaca mulatta*): Drickamer 1974), then A troop's pre-BRM mortality might be due to this firstborn effect. Of the six first pregnancies, three preceded BRM and three followed his entry into the troop; survivorship to one month was the same in both of these groups. In addition, the

Table I. Outcomes of Pregnancies of Olive Baboons at the Gombe Stream Research Centre, 1 January 1970–1 June 1973:* Infant Survivorship

	Numbers of infants surviving	
	< 1 month	> 1 month
A troop†	3	6
Beach and Camp troops‡	3	32

*Pregnancy and birth data were collected systematically beginning in May 1972 (see Packer 1979 for details). Beach and Camp troops were observed more regularly than A troop prior to this, and some A troop pregnancies may have been missed. Because nearly all infants surviving past one month were recorded in all troops, there is a relative bias against detecting miscarriages or perinatal deaths in A troop. These estimates of A troop's pre-BRM failure rate are therefore conservative.

We thank J. Goodall for permission to use the Gombe demographic records.

†Excludes female HW's March 1973 miscarriage (potentially fathered by BRM) and one infant of female SB's who died at an unknown age (born October 1970).

‡Excludes one infant of female Hestia (Camp troop) who died at an unknown age (under 6 months; born May 1972).

pooled pregnancy data for Beach, Camp and A troops for the period January 1970 to June 1974 show no sign of higher mortality among the infants of primipares during the first 6 months (Table II). Because of potential observational biases (see Table I notes), these data do not conclusively demonstrate the absence of a firstborn effect at Gombe. They do, however, show that A troop's observed high pre-BRM mortality was not due entirely to the youth of the A troop females.

Given the small samples involved, it would be unwise to accept or reject any hypothesis solely on the basis of these data. Our point is not to deny that there might have been inbreeding depression: A troop's reproductive failure rate approximately doubled when BRM entered (records of the Gombe Stream Research Centre). It is simply that infant mortality in A troop was unusually high even before BRM began consorting there, and that this seems no more due to the youth of the A troop females than was the mortality following BRM's entry. Consequently, the 40% difference in viability found in A troop probably was not due entirely to inbreeding

Table II. Outcomes of Pregnancies of Olive Baboons at the Gombe Stream Research Centre, 1 January 1970–1 June 1974:* Success of Primiparous versus Multiparous Mothers†

Mothers	Infant survivorship (months)				Total
	< 1	1–6	6–12	> 12	
Primipares	2	1	1	6	10
Multipares	11	7	1	37	56

Mothers	Cumulative infant mortality by months:		
	< 1	< 6	< 12
Primipares	20%	30%	40%
Multipares	20%	32%	34%

*See first footnote to Table I; note that Table II contains an additional year of data.

†Excludes a February 1973 miscarriage of LO (Beach troop), a partially infertile female of uncertain parity, and female SB's October 1970 infant, who died at an unknown age (A troop). Three infants born to Camp troop females (Minerva, Arwen and Gay) during this period may have been firstborns but are included with the multipares here. These infants survived for more than 12 months, so regarding their mothers as multipares will potentially exaggerate the failure rate of primipares relative to multipares.

depression; Packer's estimate of the cost of inbreeding is too high, by an unknown amount. An analogous problem exists with regard to Seemenova's (1971) widely cited study of higher morbidity and mortality among incestuous human matings (Bittles 1979). These quantitative uncertainties should be kept in mind when numerically evaluating the costs of inbreeding avoidance.

Great tits. Greenwood et al. (1978, 1979) have analysed a great deal of information on the mating of great tits. Examining cases of mother-son ($N = 5$), brother-sister ($N = 7$) and aunt-nephew ($N = 1$) incest, they found significantly higher nestling mortality among inbreeders (27.7%, versus 16.2% for outbreeders) and a non-significant trend toward fewer inbred offspring returning to breed in the study area (mortality and emigration cannot be separated here). However, nestling mortality itself may not be a good measure to use for assessing the effects of inbreeding. Studying a different population of great tits, van Noordwijk & Scharloo (1981) found that although nestling survival was lower for inbred clutches, eventual recruitment into the breeding population was significantly greater for clutches with one inbred parent. It is not clear if this beneficial inbreeding effect occurs in other populations or if it fully compensates for higher nestling mortality, but it does seem that Greenwood et al. may have overestimated the severity of inbreeding depression in tits.

Significantly, though inbreeding depression was detected, neither Greenwood et al. nor van Noordwijk & Scharloo found any evidence of behavioural inbreeding avoidance: incest among great tits occurs at almost precisely the rate expected given their patterns of dispersal. Greenwood et al. (1978) state that their data provide 'support for the hypothesis that one function of dispersal... is to reduce an individual's chance of inbreeding'. We believe these data equally support the idea that although tits are certainly dispersing, they are not avoiding inbreeding at all.

Kin Recognition

Both of the above studies conclude that since close inbreeding is demonstrably bad, selection must have acted to minimize it. Among both baboons and great tits, individuals do not seem to avoid mating with relatives: they disperse and then mate with whoever they encounter. If inbreeding avoidance has been selected for in these cases, the adaptation must therefore be

dispersal rather than behavioural inbreeding avoidance based on recognition of individual kin.

Kin-recognition systems in vertebrates appear to be highly sophisticated. Studies of macaques and rodents have found differential responses to paternal half-siblings versus unrelated individuals (Wu et al. 1980; Small & Smith 1981; Grau 1982; Kareem & Barnard 1982), and Belding's ground squirrels (*Spermophilus beldingi*) seem to distinguish among full siblings, non-littermate half-siblings and unrelated individuals (Sherman 1981), and between full and half-sibling littermates (Holmes & Sherman 1982). Presumably the mechanism for these discriminations involves some form of phenotype matching (Holmes & Sherman 1982; Lacy & Sherman 1983). A second recognition system is one based on early learning and familiarity with peers and (in mammals at least) common association with one's mother. Here 'kinship' is assessed probabilistically on the basis of f , the coefficient of familiarity, rather than directly on the basis of the coefficient of kinship r , which may be undetectable (Bekoff 1981). There is overwhelming evidence that in general vertebrates do, one way or another, recognize, remember and respond differentially to individuals (see Breed & Bekoff 1981; Holmes & Sherman 1982; Waldman 1982; Cheney & Seyfarth 1982; Bateson 1983).

If individuals recognize kin, and there is a cost to inbreeding that outweighs the costs of outbreeding, then a priori one would expect behavioural incest avoidance mechanisms to be favoured by natural selection. Indeed, such behaviour has been documented for a number of species, including olive baboons (Packer 1979; see also Sade 1968; Itani 1972; Koenig & Pitelka 1979; Pusey 1980; Hoogland 1982; but see Missakian 1973 for preferential son-mother incest among rhesus monkeys). Incest can be avoided without emigration or systematic dispersal, but if more distant relatives (e.g. cousins) are harder to recognize, then behavioural mechanisms to prevent breeding with them may be difficult to evolve. However, in principle not only can cousins be recognized as such, but they may actually be preferred mates (humans: van den Berghe 1980; Hughes 1980; Japanese quail *Coturnix coturnix japonica*: Bateson 1978, 1980, 1982). Great tits, white-crowned sparrows (*Zonotrichia leucophrys*) and vervet monkeys (*Cercopithecus aethiops*) discriminate between members of their local community and foreigners and all prefer local mates even though this leads

to increased levels of inbreeding (Baker 1982; Cheney & Seyfarth 1982; McGregor & Krebs 1982). One must be cautious in generalizing until comparable information is available for more species, but these findings demonstrate clearly that moderately close inbreeding is not always avoided (see Shields 1982b for a more extensive review).

If behavioural mechanisms can evolve to promote such matings, then in principle selection could act to prevent them. The presence or absence of behavioural inbreeding avoidance can thus be viewed as a test of optimality reasoning analogous to that presented by Rothstein (1982), or, if we assume optimality, as evidence for or against the inbreeding-avoidance hypothesis of dispersal. Dispersal is costly (see Gauthreaux 1978; Harcourt 1978; Gaines & McClenaghan 1980), whereas kin recognition and behavioural incest avoidance presumably are not. If inbreeding is costly and behaviour is optimized by natural selection, we would therefore expect to find behavioural avoidance rather than demographic dispersal as a mechanism for avoiding inbreeding.

We suggest that when dispersal patterns carry with them a large risk of incest, behavioural inbreeding avoidance may evolve (e.g. scrub jays, *Aphelocoma coerulescens*, Woolfenden & Fitzpatrick 1978; acorn woodpeckers, *Melanerpes formicivorus*, Koenig & Pitelka 1979; prairie dogs, *Cynomys ludovicianus*, Hoogland 1982; deermice, *Peromyscus leucopus*, Grau 1982). When dispersal patterns happen to reduce such risks, occasional close inbreeding may not impose high enough costs to favour behavioural incest avoidance (e.g. great tits, Greenwood et al. 1978, 1979) and is probably never sufficient to cause changes in dispersal patterns. Finally, when the risks of migration or the benefits of keeping limited resources (e.g. territory, political power) within the kin group are especially high, the costs of inbreeding may be outweighed by the benefits of philopatry (Brown 1974; Bengtsson 1978; May 1979; Smith 1979; Hughes 1980; Emlen 1982; see Kloss's gibbon, *Hylobates klossi*, example below; for a possible exception see Koenig & Pitelka 1979; Koenig 1981).

Inter-group Transfer Patterns

The inbreeding-avoidance hypothesis hangs primarily on the observation that males and females usually disperse differentially: one sex goes farther than the other. Though often per-

ceived as an absolute, categorical difference (e.g. 'the sex that moves': Bateson 1983), among most birds and small mammals this difference is statistical — e.g. Greenwood et al. (1979) report the median natal dispersal distance for female great tits as 879 m, versus 558 m for males; the juvenile male ground squirrels (*Spermophilus elegans*) studied by Pfeifer (1982) moved an average of 90 m, versus 77 m for females. It is important to note that in many of these species, the range of dispersal distances is nearly equal for the two sexes (see Fig. 1). The majority of the individuals represented in this idealized figure have as much chance of suffering the costs of inbreeding depression as they would without differential dispersal, but because the remainder are less likely to inbreed the population as a whole will be less inbred than if there was no sex difference in dispersal. For species with the type of dispersal shown in Fig. 1, we seem to be left with two modified versions of the inbreeding avoidance hypothesis: (1) individual selection has produced a remarkably inefficient, pessimal mechanism; or (2) differential dispersal as a mechanism of reducing inbreeding evolved by interdemic selection. Either is possible, but both emphasize the need to consider alternative explanations; we agree with Greenwood & Harvey's (1982) recent statement that 'Such movements should not... be interpreted as evidence that inbreeding avoidance is a function of dispersal nor that inbreeding is harmful' (page 15).

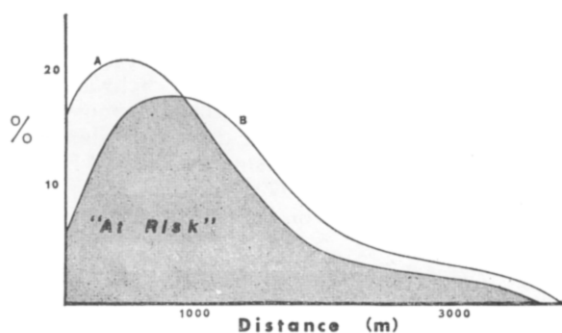


Fig. 1. Differential dispersal by sex for a hypothetical small mammal or bird (based loosely on Fig. 1 of Greenwood et al. 1979). Among most small mammals, males (line B) disperse on average farther than do females (line A): among most birds, males are more philopatric than females (A = male, B = female). Statistical differences in the average distance dispersed by each sex do not affect most individuals' chances of inbreeding (shaded area).

Among many group-living animals, especially primates, sex differences in dispersal are more clear-cut: one either transfers or does not. Early research on baboons and macaques showed that essentially all females remain in their natal group, while males normally transfer at about the age of puberty (Packer 1979; Sade 1980). Exceptions to this pattern provide the strongest available support for the inbreeding avoidance hypothesis: in the few species in which males usually stay in their natal troop, females transfer (e.g. wild dogs, *Lycaon pictus*, Frame & Frame 1976; chimpanzees, *Pan troglodytes*, Pusey 1980). It seems as if one sex has to transfer, presumably to escape inbreeding depression. In the following section we discuss primate transfer patterns and several specific examples of inter-group transfer. We hope to show that the overall one-sex-only-transfers pattern is less widespread than is often thought, and that patterns of transfer in several species that have been cited to support the inbreeding-avoidance hypothesis can also be explained in other ways. Although we feel these alternative explanations are both more consistent with available observations and more robust, we emphasize that they do not disprove the inbreeding-avoidance hypothesis.

Among the colobines and hominoids, inter-group transfer by females occurs regularly, though usually less frequently than male transfer, which is routine; female transfer is apparently less common among other primate taxa (reviewed by Moore, in press a). Melnick (1981) has shown that small, apparently closed primate social groups are not necessarily inbred, owing to the mixing that results from even low rates of transfer of breeding males (see also McCracken & Bradbury 1977; Schwartz & Armitage 1980). Therefore female emigration from such groups cannot be due to avoidance of cumulative inbreeding arising from small breeding group size (Wade 1979; Brereton 1981). Can these females be avoiding incest, presumably father-daughter?

At first glance this seems plausible: female emigration has been recorded from a number of species with small group size and only one breeding male (e.g. *Presbytis*, *Pygathrix*, *Gorilla*). However, behavioural observations of purple-faced langurs (*Presbytis senex*) (Rudran 1973) and douc langurs (*Pygathrix nemaus*) (Lippold 1977) have yielded a remarkable result: young females are aggressively expelled by the breeding male, often just after his entry into the group, when he cannot be the father of the ejected

females (Rudran 1973). Hrdy (1977, page 278) suggested that if average male tenure is very short, young females may not become mature before a new male is himself replaced; such females are therefore not potential mates but do compete with other group members for food. Consequently, according to Hrdy, it is to the new male's advantage to expel them. Another possibility is that extra-group males closely monitor the reproductive status of neighbouring females and time their incursions into troops according to the availability of fertile females (Moore, in preparation). A large troop, or one containing a high percentage of nubile females, would then be at greater risk of invasion and a male might do better to expel some potential mates, if by doing so he reduced his immediate risk of being replaced altogether. Whatever the explanation for this behaviour, it cannot be avoidance of father-daughter incest. If the new male is returning to his natal troop, he could be forcibly avoiding brother-sister incest, but at present there is no evidence that the new male discriminates against any adult females, one of whom (in the case of a returning natal male) would be his mother. Finally, because polygynous males typically invest less than females in each offspring (Trivers 1972), they have less to lose from inbreeding depression than do females (Clutton-Brock & Harvey 1976; Smith 1979). It is therefore unlikely that aggressive male enforcement of inbreeding avoidance against the 'wishes' of a female would evolve.

If most female emigration and transfer evolved independently of inbreeding avoidance in these species, as seems likely, then why do their males transfer? For *Presbytis* at least, the answer seems clear: they do not 'transfer' but typically are forcibly expelled from their natal troop by invading males, and spend much of their lives trying to get back into any bisexual troop they can (Sugiyama 1967; Mohnot 1971; Hrdy 1977; Wolf & Fleagle 1977; Moore, personal observations). It is not clear whether fathers expel their own sons, and this may vary from habitat to habitat. With reported average tenure lengths of 36 and 27 months (*P. senex*, Rudran 1973 and *P. entellus*, Hrdy 1977, respectively), the question of paternal tolerance is usually moot. Even in supposedly 'male-bonded' species, adult males have killed maturing natal males, and inter-male conflict is clearly responsible for at least some emigration (bonnet macaques, *Macaca radiata*, Simonds 1965; red colobus, *Colobus badius tephrosceles*, Struhsaker & Leland 1979) or long

temporary absences (chimpanzees: Riss & Goodall 1977; Goodall et al. 1979, page 42). Given these observations, it seems Panglossian to search for a benefit to the expelled young male (e.g. that he is better off avoiding inbred matings).

Case Studies of Competition and Dispersal

The importance of competition versus inbreeding avoidance in determining dispersal is well illustrated in three non-colobine primates — howler monkeys, bonnet macaques, and Kloss's gibbons — as well as in zebras and wild dogs.

Howler Monkeys

Among howler monkeys, natal emigration is routine for both sexes (*Alouatta seniculus*: Rudran 1979; *A. palliata*: Glander 1975, 1980; Jones 1980a; but see Scott et al. 1978). Jones (1980a, b) has described the demographic and behavioural antecedents of emigration in *A. palliata*, with special reference to dominance rank and age. Her findings can be summarized as a rule of 'up or out'. Maturing individuals of either sex challenge the older members of the group. Young animals who fail to rise in rank tend to emigrate; older animals eventually either give way and fall in rank within the group, or emigrate. However, all the immigrants seen were young. Evidently the only option available to an old emigrant is to colonize a new area and establish a new troop. Several observed emigrations were preceded by attacks on the disperser by intrasexual coalitions, and it is clear that aggressive competition for group membership can be intense. Coalitions and deaths during immigration have also both been reported for *A. seniculus* (Sekulic 1981 and Rudran 1979, respectively). Jones hypothesizes that for females this competition for group membership is ultimately over access to food, whereas males compete with each other for high social rank, which is strongly correlated with access to fertile females (Glander 1980; Jones 1981).

Bonnet Macaques

Social structure in the southern race of the bonnet macaque, *Macaca radiata diluta*, shows many interesting patterns which differ considerably from those of the northern race. These include (1) male care of non-offspring infants; (2) ties between adult and juvenile males that become stronger as juveniles grow older; (3) low rates of aggression within the group; (4) a pattern of choice of coalition partners that appears

random and does not follow any known kinship pattern; and (5) high feeding tolerance among animals of all age-sex classes. Furthermore, the probability of two animals forming a coalition is independent of the probability that they will form coalitions against one another (Ali 1981). When the (single) male in a small group was removed for 6 days, no outside male attempted to move in, although one female was in oestrus and at least six inter-group encounters involving this group occurred during this time. In the main study troop, both adult males disappeared after a cyclone, and a subadult male became 'alpha' overnight. Following this, the troop's ranging patterns destabilized and became erratic. About 18 months later two out of three females left the group and one female transferred into it. One subadult male and two large juvenile males also emigrated as a subgroup and joined a neighbouring troop. The remainder of the troop subsequently merged with a neighbouring group (Ali 1981).

Electrophoretic studies have found that genetic differences between troops of bonnet macaques are of the same order of magnitude as interspecific differences among other macaques (DeVor, unpublished MS), and at least one known mother-son mating produced viable offspring during this study (Ali 1981). After detailed laboratory observations, Wade (1979) inferred that populations of bonnet macaques may be inbred. Taken together with the above demographic and behavioural data, these observations suggest that the normal social system of these monkeys involves considerable inbreeding, but that dispersal bouts can be initiated by major ecological or demographic catastrophes. Such catastrophes must be regular features for any 'K-selected' species (see Southwood 1977; Wiens 1977; Moore, 1983).

Kloss's Gibbons

Gibbons are monogamous and territorial. Offspring are generally expelled by the same-sex parent at sexual maturity, when they begin to compete for the available habitat (see Carpenter 1940; Tenaza 1975; Gittins & Raemakers 1980). This competition is often intense, and Tilson (1981) has estimated that among Kloss's gibbons (*Hylobates klossi*) an individual of either sex has no better than a one in three chance of joining or establishing a territory (and hence breeding). Tilson discussed several tactics employed by these gibbons when faced with such odds. He observed parents cooperating with offspring to

defend an area until a potential mate for the youngster was attracted and the territory consolidated; the parents then withdrew to their original neighbouring range. In one case the original owners of the new territory had disappeared and the family defended it against transient males; in another, parents and son together carved out a portion of a neighbour's range (this attempt was ultimately unsuccessful and the son presumably became a transient). Both sons and daughters were assisted.

This parental aid is accompanied by intra-sexual aggression. The relative importance of incest avoidance versus aggression for natal dispersal in this species can be gauged from the following observations of Tilson's (1981) group 16. Aggression by the adult female toward her subadult daughter increased from ca 1.1 bouts/day to ca 3.5 bouts/day between October 1973 and May 1974. The subadult responded by becoming more peripheral, moving from an average distance of 4.4 m from her mother to 10.8 m. 'By July the subadult female began to associate more frequently with the adult male. They initially engaged in mutual grooming, but within 3 weeks the male began to touch, smell and lick her genitalia. These sexual contacts occurred daily. Meanwhile the adult female sat apart in another tree and was visited only by the juvenile. Two weeks later the adult female's aggressive behaviour increased dramatically, from an average of 3.5 bouts per day to 26.6. . . . This caused the subadult female to lag 20–30 m behind the group, avoid entering food trees occupied by the adult female, and stop associating with the adult male.' During this period group 16 expanded its range and allowed a neighbouring transient male to associate with the group. The daughter and the transient male finally bonded in October 1974 and the parents promptly withdrew into their original range (Tilson 1981, pp. 266–268).

Of particular interest are Tilson's observations of sons replacing their absent fathers and mating with their mothers. He observed the formation of four family units from beginning to end (first reproduction): of these, one was a mother–son pair. He also saw two apparently stable units form, but could not confirm reproduction by these pairs: both were mother–son. Thus between 25% and 50% of the family formations observed were incestuous. This is doubly significant because in two cases (the confirmed incest and one of the possibles) the female aggressively rejected transient and presumably unrelated males. These

two females apparently preferred incest. Whether this preference was 'for' having more closely-related offspring (Maynard Smith 1978) or was a form of kin-directed altruism (Smith 1979) is unknown. These observations are reminiscent of Bertram's (1978) on incest among lions (*Panthera leo*): in both species, breeding situations are hard to obtain, and cooperation has evolved as a strategy for gaining access to mates (see Bygott et al. 1979; Packer & Pusey 1982). In these species, the benefits of philopatry (retention of a breeding site) apparently outweigh the costs of inbreeding. If the rate of incest in *H. klossi* is typically as high as Tilson's data indicate, presumably most deleterious recessives have been lost from the species and the genetic 'costs of inbreeding' may be insignificant. For this gibbon, and possibly for other species, the only costs of incest may be the somatic ones associated with competing with an older and stronger individual. When dispersal is not enforced intrasexually, inbreeding or incest occurs.

Zebbras

Both Burchell's (*Equus burchelli*) and Hartmann's (*Equus zebra hartmannae*) zebras live in stable uni-male harems of about two to four adult females each; in both species, bachelor stallions form all-male groups (Joubert 1972; Klingel 1972; Grubb 1981; we have used the original authors' nomenclature). Fillies experience their first oestrus at about 12 to 13 months and apparently do not usually conceive for at least one more year (Joubert 1974). During this lengthy period of adolescent infertility, oestrus fillies adopt a conspicuous head-lowered, tail-raised posture that attracts bachelor males who aggressively abduct the fillies from their natal groups; adult mares do not visually signal their oestrus and are not pursued by extra-group males (Joubert 1972; Klingel 1972). These authors note that a consequence of this natal abduction is that father–daughter incest is avoided, and this behaviour has been cited as an example of incest avoidance (Bischof 1975, page 48; Packer 1979, page 29; Greenwood 1980, page 1151).

Several additional observations cast some doubt on the incest-avoidance explanation, however.

(1) A filly continues her conspicuous posturing from her first oestrus until 'the age of two to two and a half years when she becomes a permanent member of a group' (Klingel 1972) — presumably some 10–15 oestrous periods later, as cycles

last about 1 month and there is little or no seasonality (Grubb 1981). A young female may change stallions repeatedly during any single oestrous period, as well as from one oestrus to the next (Joubert 1972; Klingel 1972), and each change is accompanied by inter-male fighting.

(2) Resident females of both species may attack displaying fillies and sometimes succeed in expelling one from her natal group despite the stallion's attempts to defend her (Joubert 1972). It should be noted that harems are small and Joubert (1972) points out that resident females also actively resist the stallion's attempt to introduce new mares to the group.

(3) Packer (1979, page 29) states (of Burchell's zebras) that 'harem leaders tolerate the kidnapping of their daughters by outside males'. This is true in the case of unusually large harems (Joubert 1972), but normally 'The family stallion defends by attacking individual stallions, but eventually the young mare will be separated from her group because of the large number of suitors' (Klingel 1972). Klingel observed only one case out of 44 in which a father succeeded in retaining his daughter (cited in Kingdon 1979), but this need not imply 'tolerance' on the family stallion's part.

Zebra stallions actively defend members of their groups, and may even kill attacking lions (Kingdon 1979). Joubert (1972) cites observations of stallions attempting infanticide and of Hartmann's zebra mares aggressively resisting takeover attempts by strange males; though this evidence for male infanticide in zebras is weak, it should not be dismissed (see Berger 1983). Whether males are protecting them from predators or from conspecifics, clearly male fitness is of great potential importance to mares and one should expect them to choose mates carefully. Furthermore, females apparently prefer small harems and are observed to resist aggressively the addition of new reproductive females by recruitment or maturation. We believe that the lengthy adolescence and conspicuous oestrous postures of zebra mares are more parsimoniously explained as a mechanism for mate choice via inciting male-male competition (Cox & LeBoeuf 1977) than as a means of ensuring outbreeding. Stallions do not tolerate the kidnapping of their daughters: faced with numerous bachelors and intra-group fighting among females, they simply cannot prevent it without risking injury and the subsequent loss of their mares.

Wild Dogs

Reproductive groups of African wild dogs (*Lycan pictus*) typically contain several related males and one or two females, usually sisters, who are unrelated to the males. More than 45% of males remain in their natal group and inherit the pack's territory, whereas nearly all females emigrate (Frame & Frame 1976; Frame et al. 1979). As discussed above, both Packer (1979) and Greenwood (1980) cite this female-biased dispersal to support the inbreeding-avoidance hypothesis.

Frame et al. (1979) mention the absence of close inbreeding as a consequence of dispersal, but their discussion of the evolution of dispersal patterns in wild dogs centres on the role of intra-sexual competition. Litters are large and only one can be supported by the pack at any given time. Furthermore, because packs must move to follow game, they can ill afford several females breeding asynchronously. As a consequence, usually only one female in a pack breeds; when subordinate females pup they may be severely harassed and their pups killed. With no opportunity of breeding in sight, all subordinate females eventually emigrate. Male-male competition within the group is ameliorated by paternity uncertainty, lability of the male hierarchy, and to some extent kinship. In contrast, male competition between groups is intense, with violent takeovers and probable killings observed. Solitary males or pairs appear to be at a disadvantage, so larger cooperative male coalitions are favoured, much as Bygott et al. (1979) and Packer & Pusey (1982) have argued for lions.

Without direct evidence for dispersal to avoid incest (e.g. natal emigration of a female in the absence of older, dominant resident females), we feel that it is more parsimonious to consider these dispersal patterns the outcome of intra-sexual competition rather than as representing adaptations for avoiding inbreeding. This conclusion is supported by Reich's (1978) account of a young wild dog who replaced her mother as the breeding female of a pack. On becoming dominant, this young female bred successfully with her father (Reich 1978) and, following her father's death, with one of her brothers (Reich, personal communication).

Chimpanzees

A final example that must be considered is that of female transfer in chimpanzees (Pusey 1979, 1980). Because of their phylogenetic closeness to

humans, patterns of transfer and incest avoidance in chimps have been of special interest to anthropologists trying to reconstruct human behavioural evolution (e.g. Symons 1979, pp. 132–138). Male chimpanzees rarely transfer (Nishida 1979; but see Sugiyama & Koman 1979) and chimps clearly show behavioural incest avoidance (Goodall 1968; Pusey 1980); the observation that '[female] transfer generally occurs during oestrous periods and that females may return to their natal community between oestrous periods or when they are pregnant, strongly implicates inbreeding avoidance as the function of such movements' (Pusey 1980, page 550). Because of the sexual asymmetry in the cost of inbreeding depression in mammals discussed above, females rather than males should transfer if transfer functions to prevent inbreeding (there is no a priori reason to believe that the costs of transfer are greater for females, especially given the observation that many of the female primates that do disperse are pregnant or carrying infants (Haddow 1952; Moore, in press a)). Thus chimpanzees fit the inbreeding-avoidance model precisely — the sex with most at stake actively avoids incest while in the natal group and is the sex that transfers; it does so when sexually receptive and actively seeks out mates in non-natal communities.

Though Pusey's argument is strong and her explanation probably correct, it is important to note (as she does) that of nine females who matured in habituated communities, one probably died, one possibly died, and four of the remaining seven permanently returned to their natal community after temporary absences during oestrus (Gilka, Fifi, Miiff and Gigi). Three of these females subsequently conceived infants with distantly-related males of their natal communities (Pusey 1980, pp. 547–548); the fourth female (Gigi) is apparently sterile (Riss & Goodall 1977). Thus about half the females studied did breed at least once within their natal group. Pusey suggests that this may have been a consequence of the artificial provisioning at Gombe, which by concentrating the Kasekela chimp community at the centre of their range prevented them from making contact with adjacent communities; 'such contact may be essential before permanent transfer can take place' (Pusey 1980, page 550).

If Kasekela chimps had little contact with neighbours, their neighbours had little contact with them — yet out of eight nulliparous strangers who joined the habituated communities

only two did not remain. The possible existence of undetected visits by strangers (Pusey 1979) makes the pattern somewhat suspect, but 11 of the 16 known females exposed to both the habituated, provisioned communities and adjacent unprovisioned ones chose to stay with the provisioned groups. An alternative interpretation of these data is that temporary transfer by young females constitutes a period of habitat selection: after visiting several communities the young female then settles in the one of her choice (irrespective of the potential for inbreeding, since behavioural incest avoidance is well developed and sufficient). This is merely an alternative, and we can only agree with Pusey that 'Further observations from unprovisioned communities are necessary in order to establish what are the normal patterns of inter-group transfer in this species'.

Alternatives to Expulsion

The above examples appear to support the hypothesis that most inter-group transfer is simply the outcome of intrasexual competition for resources (food and mates) and not the result of positive selection for dispersal. However, several objections to the forced dispersal model have been advanced in support of the inbreeding hypothesis: much natal dispersal appears to be voluntary and not associated with aggression; dominant males sometimes 'abdicate', transferring after several years' residence; and females often seem to prefer strange males.

Voluntary Natal Dispersal

The relationship between competition and forced dispersal has been discussed extensively in the literature on small mammals. For practical reasons, the social demography of larger mammals has been less well studied; however, the patterns discussed here are probably general (see e.g. Packard & Mech 1980, on forced dispersal and emigrant mortality in wolves, *Canis lupus*). Among rodents, many dispersers are underweight, wounded and/or ill, and it is reasonable to assume that this low physical fitness is at least to some extent responsible for their lowered reproductive fitness. In most cases, this poor physical condition with its resultant mortality can be attributed to social competition leading to expulsion (for reviews see Christian 1970; Lidicker 1975; Gauthreaux 1978; Gaines & McClenaghan 1980; Tamarin 1980; Dobson 1982; but see Dobson 1979). However, there is often no overt aggression associated with natal

dispersal and adolescents may seem to peripheralize themselves; often it is large, healthy apparently dominant individuals who emigrate (Howard 1960). There may even be 'disperser' genotypes in some rodents (Krebs 1978).

These observations do not invalidate the 'competition hypothesis', or necessarily support the inbreeding one. Expulsion of potential challengers before they pose a real threat is a better strategy than allowing them to fully mature first, and consequently an immature faced with an imminent attack by a larger, dominant adult would do well to avoid the contest before it occurs (Gauthreaux 1978; Lomnicki 1978). The absence of a precipitating fight at the time of dispersal does not mean that the disperser is acting without regard to established social relationships. Bekoff (1977) has shown for canids that relationships formed as pups influence dispersal behaviour as yearlings, and argues that interactions at the time of dispersal may be much less important than the developmental history of the individual in question. Similarly, in a long-term study of male transfer by olive baboons, Manzollilo (1982) detected changes in the behaviour of emigrants some 6–8 months prior to their actual departure from the troop. The most reliable indicator of impending emigration was a drop in affiliative greeting behaviour between the emigrant and other males, suggesting that intrasexual relationships played a greater part in the emigrant's decision to leave than did intersexual ones.

The mere experience of being subordinate appears to be stressful: working with talapoin monkeys (*Miopithecus talapoin*), Keverne et al. (1982) have shown that levels of stress hormones (cortisol and prolactin) in subordinate males increase over time even as levels of overt aggression actually decrease. As Marler (1976) has pointed out, 'aggression' need not be violent to produce an effect. 'The prohibitions [on incest in early humans] maintained themselves from generation to generation, perhaps only as the result of a tradition set up by paternal and social authority. But in later generations they have perhaps already become "organized" as a piece of inherited psychic property' (Freud 1918, page 52; see also Darwin 1871, page 675, and Fox 1980).

Packer (1979) has stated that among the Gombe baboons some natal males achieve high dominance status before emigration, but nevertheless rarely copulate. However, it might be more accurate to say they do not consort with

females at peak oestrus: when opportunities to copulate surreptitiously arise, they are — at least sometimes — quickly seized (e.g. while the consort male is involved in a fight: Packer 1979; Moore, personal observations; Missakian 1973 for rhesus). In addition, at Amboseli at least two male baboons have remained and bred within their natal troop, and this difference in dispersal may be due to the relatively higher percentage of males (and hence greater inter-male competition) among the Gombe troops (G. Hausfater, personal communication). This suggestion is supported by recent events at Gombe: during a period when there were few large post-transfer males in Beach troop, a natal male (SG) was able to become the resident alpha male of the troop (Collins et al., in press). Furthermore, at Gilgil a putatively natal male (DV) has attained high rank and consort success in a group with a low male:female ratio compared with Packer's study groups (PHG troop; Manzollilo 1982).

The outcome of male-male competition may tend to be resource-specific (Gartlan 1968; Popp & DeVore 1979; Smuts 1982), and natal males may be avoiding doomed fights over females while asserting themselves over food. To the extent that weight is correlated with rank (Popp 1978; Packer 1979; Smuts 1982), food may be more valuable to a young, still-growing natal male than to an adult. Williams (1966) has suggested that reproductive effort should increase with age, so older males should be willing to invest more in competition for females than should young males. In fact, older males who rank highly in consort success may be low-ranking in relation to other resources (e.g. DeVore 1965; Smuts 1982). As Tilford (1982) has shown, we cannot assume that young natal males could defeat adult post-transfer males in fights over females until we see them try.

For adult males there will be a fine balance between kin selection favouring retention of offspring in the group, and sexual selection favouring expulsion or elimination of potential rivals at the earliest opportunity (Bertram 1978). A good illustration of this general point is found in rhesus and Japanese (*Macaca fuscata*) macaques: subadult males normally become peripheral to their natal troop and eventually transfer, with very little overt aggression directed toward them. Occasionally, though, the sons of dominant mothers remain and with the support of their relatives are able to attain high rank within their natal troop (Koford 1963; Sugiyama 1976; Tilford 1982). As with howler monkeys, it is

'up or out'. If dominant males father more offspring (see Dewsbury 1982; Robinson 1982) and prefer to mate with dominant females (Wolfe 1979; Takahata 1982; Wilson et al. 1982; but see Small & Smith 1982), then on average the sons of dominant females will be paternally related to more troop members than will the sons of lower-ranking females. Furthermore, dominant matriline are often larger than subordinate ones (Sade et al. 1976; Chepko-Sade & Olivier 1979) and so sons of dominant females will have more maternal relatives in the group as well. Compared with sons of subordinate females, the young dominant male will have more relatives, with higher average r , within his natal troop. According to the inbreeding-avoidance hypothesis, these young dominants should be under the greatest pressure to emigrate. Contrary to this expectation, they are the ones most often observed remaining in their natal troops.

Abdication

Dominant adult males occasionally 'abdicate' and voluntarily emigrate, and it has been suggested that this behaviour is an adaptation to avoid father-daughter incest (Japanese macaques: Itani 1972; vervet monkeys: Henzi & Lucas 1980; prairie dogs: Hoogland 1982; see Hrdy 1981, page 111). (Note that Itani (1972) cites an equal number of males who have remained in the alpha position in one troop for periods ranging from 8 to 18 years, though females are sexually mature by 4 years; this suggests that opportunities for incest are in fact frequent.) Assuming the abdicated male is transferring or joining solitary females (Sugiyama & Ohsawa 1982), he may be selecting a group that contains a larger number of sexually receptive females (cf. Drickamer & Vessey 1973; Packer 1979), or the behaviour might represent some form of dispersal 'bet hedging' (see Stearns 1976; Rubenstein 1982).

In species living in unstable environments with high inter-group variance in mortality, such as vervet monkeys (Wrangham 1981), males who have offspring in several troops would spread personal extinction risks (see also van Valen 1971 and Hamilton & May 1977 on selection for dispersal, and Rowell & Richards 1979 for vervets and r -selection). Similarly, Sade et al. (1976) report dramatic differences in growth rates among troops of rhesus macaques, apparently due to social/demographic rather than physical or biotic factors. These differences could not be explained by gross variation in

troop size or inter-group rank; if they are as unpredictable to monkeys as to primatologists, males who left offspring in more than one troop would safely hedge their bets. The bet-hedging hypothesis is testable: the rate of abdication should be correlated with variance in group survival rates between species and perhaps between populations. For example, among the marginal-habitat vervets studied by Whitten (1982), dominant males usually abdicated after only one breeding season, whereas the abdications cited by Itani for *M. fuscata* occurred after at least 3 or 4 years' residence. Though this comparison fits the bet-hedging hypothesis (and incest avoidance cannot explain abdication after only one breeding season), a true test of this prediction awaits more long-term demographic studies.

The phenomenon of abdication at first appears to strongly support the inbreeding-avoidance hypothesis. However, observed tenure lengths are apparently not closely correlated with the age of females' first conceptions, and several alternatives to the inbreeding-avoidance hypothesis exist. These alternative explanations imply nothing about mate relatedness and, in contrast to the inbreeding-avoidance hypothesis, they are testable.

Female Preference for Strange Males

Packer (1979, pp. 26-27) argues that female baboons, by refusing to mate with a natal male, are avoiding inbreeding and thereby forcing males to transfer (outbreed). However, the females of A troop presumably recognized male BRM; to them he was genetically a natal male but demographically a transferred male. Richard (1974) and Kurland (1977) have suggested that female preference for transferred males could arise through sexual selection for traits that display male quality, in this case the ability to successfully transfer against the opposition of resident males (cf. Zahavi 1975).

This hypothesis (female incitation of male-male competition; Cox & LeBoeuf 1977) would explain a very puzzling observation: a female baboon would often present to a new male 'so persistently that he would finally slap or charge her; apparently to make her stop' (Packer 1979, page 27). It is hard to see why an immigrant would object to such overtures unless they were calling the unwanted attention of resident males to his potential as a competitor. Female langurs (*Presbytis entellus*) appear deliberately to provoke fights in male bands by repeatedly pre-

senting to subordinate males, who typically try to avoid the female's attention as long as dominant males are in sight (Moore, personal observations); and Packer (1979) notes that female baboons approached other troops more often when in consort than otherwise (pp. 14–15). As discussed above, the behaviour of young zebra mares is also best explained by Cox & LeBoeuf's hypothesis. Packer's observations are consistent with the incitation hypothesis.

A second possibility, also consistent with the observed attraction of females to recent immigrants (as distinct from rejection of natal males), is that females are maximizing the number of males with whom they breed, thus increasing the genetic diversity of their offspring (see Gladstone 1979). Females employing such a strategy would not necessarily be expected to avoid inbreeding, as inbred offspring might be better adapted to local conditions (Shields 1982a, b). However, in the first field study explicitly focused on individual mate choice by baboons, Smuts (1982) found that females solicit new males but tend to breed with familiar associates. This suggests that the females are seeking long-term relationships with tested males rather than sperm from an unselected variety of mates.

A third explanation for female solicitation of new males is that males are transferring for their own reasons (e.g. expulsion, inbreeding avoidance) and females are concealing the paternity of their offspring in an attempt to (a) forestall infanticide (Hrdy 1977) or (b) elicit paternal investment from more than one male (Taub 1980; Stacey 1982). This explanation may be correct, but at present sheds no light on the causes of natal dispersal.

Conclusion

We believe, then, that the major cause of natal dispersal and transfer among mammals is competition, usually between males fighting for access to females (see also Dobson 1982). By extension, this conclusion should apply to other vertebrates as well, and the 'inbreeding hypothesis' is both inadequate and unnecessary to explain general dispersal patterns. Females may also disperse, usually for reasons connected with habitat quality and socially mediated access to food but also for defence against aggressive male strategies such as infanticide (Baker 1978, pp. 92–94; Harcourt 1978; Marsh 1979a, b; Wrangham 1979, 1980); again, there is no evidence or logical necessity for invoking

inbreeding avoidance. Similarly, human exogamy is more accurately viewed as a socio-political phenomenon independent of incest avoidance (van den Berghe 1980). Range extension, outbreeding and population density regulation 'are unselected consequences of selection for individuals that aggressively procure breeding sites but move away from dominant individuals' (Murray 1967).

In his extensive review of dispersal patterns in birds and mammals, Greenwood (1980) suggested that inbreeding avoidance is the driving selective force behind sex differences in distance dispersed, but that which sex disperses farther is determined by the mating system. For most birds, males defend a territory; this is easier to do near one's birthplace because (1) familiarity may make defence, predator avoidance and foraging easier, and (2) some borders are likely to be shared with kin, who are potentially 'nicer' neighbours (see also Waser & Jones 1983). Therefore males tend to be philopatric, and females, to avoid inbreeding, must disperse farther (see also Greenwood et al. 1978). Male mammals, Greenwood argues, are more likely to defend access to mates, rather than a territory. For them the key is where the females are; females tend to be philopatric for essentially the same reasons as male birds, and male mammals disperse to avoid inbreeding.

Greenwood's overall explanation of mammalian and avian dispersal patterns is just as valid if all mention of inbreeding is eliminated. Among birds, male philopatry is strongly favoured and females are more likely to shop around for a high-quality territory, resulting in the observed dispersal patterns. For mammals, female philopatry is the norm and intense competition between males tends to space them out.

A more general conclusion from this discussion is that *ceteris paribus* sociobiological models of behaviour based on complex mathematical relationships among genes may be less widely applicable than commonly argued. The fault is not in the logic, but in the ease with which one falls into various 'traps' associated with it (Dunbar 1982). We have argued here that sex differences in dispersal are unselected consequences of sex differences in competition and the distribution of key resources, rather than of some more complicated inclusive fitness factor such as inbreeding avoidance. Similarly, the existence of social groups and cooperation in animals does not necessarily imply the operation

of kin selection (e.g. McCracken & Bradbury 1977; Packer & Pusey 1982; Rood 1983; Moore, in press a): mutualism or simple individual competition is adequate for explaining the origin and function of many apparently altruistic, cooperative or nepotistic behaviours (Busse 1978; Wrangham 1982; Moore, in press b). Clearly, extended nepotism can operate (e.g. Sherman 1981) and dispersal in some species probably does function to avoid inbreeding (e.g. Pusey 1980), but simpler processes of competition, parental investment, and sexual selection are probably sufficient to explain most observed behaviour, and should be considered first (see Richard & Schulman 1982).

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