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Primate Dispersal:
Proximate and Ultimate Causes and Consequences (Part 1)

Cover Photo: Adult male (left) and female (right) Japanese macaques (*Macaca fuscata*) near an urban area. Habitat disturbance has increased the incidence of female dispersal in this species. (Photo by Fumio Fukuda).

Editor: Dr. Dr. Michael Schwibbe and Dr. Clara B. Jones
Assistance: Heike Klensang
German Primate Center (DPZ)

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PREFACE: THE PROXIMATE AND ULTIMATE COSTS AND BENEFITS OF DISPERSAL IN PRIMATES. JONES, C.B.

Primate units (e.g., genes, individuals, groups, populations, species) may be viewed as patches in temporally and spatially heterogeneous regimes. The study of primate dispersal entails an investigation of the motivations, causes, and consequences of movement between social groups (CLOBERT et al., 2001 a) for these units. The present special issue addresses this domain of inquiry from a variety of theoretical and empirical perspectives.

The "patch" view of physical and biotic (including social) environments, initiated by MAC ARTHUR and WILSON (1967) and LEVINS (1968; also see LEWONTIN, 1957; LEVIN, 1976) has received increased attention in recent years due to researchers' attempts to document the effects of habitat fragmentation and other anthropogenic perturbations upon plant and animal species (HANSKI et al., 1997; CLOBERT et al., 2001 b). Despite this renewed emphasis upon spatial dynamics in ecology and population biology, there has been relatively little work in primatology on the effects of spatial factors within and between populations. A search of the database, PrimateLit (http://primatelit.library.wisc.edu), yields 1,327 abstracts, articles, or books on the topic, "space" (Table 1). However, most of these publications concern the spatiotemporal distribution of mates or space as studied by experimental psychologists and neuroscientists, the latter literature reflecting the traditional social scientific origins of the discipline of primatology as well as an emphasis upon proximate mechanisms. Table 1 also documents the relative poverty of primate literature on a variety of topics related to spatial dynamics (e.g., habitat selection: see OSTRO et al., 2000; refuges: see KINZEY, 1982; JONES, 1987), although the search yielded 463 publications on the topic, "dispersal", 189 on the topic "community" (see FLEAGLE et al., 1999; JONES, 1995), and 117 on the topic "fragmentation" (see JONES, 1999).

Table 1: Results of search on PrimateLit on topics related to spatial dynamics (1940-present).

Topic	**Number of Citations**
Space	1,327
Dispersal	463
Community	189
Fragmentation	117
Biogeography	103
Metapopulation	7
Refuges	1
Spatial foraging	0
Models and theory	0
Patch dynamics	0

Topic	**Number of Citations**
Population regulation	0
Competition and space	0
Spatial ecology	0
Island biogeography	0
Habitat selection	0

From an evolutionary perspective, dispersal is of fundamental importance since it may counteract the effects of genetic drift by maintaining the connection between subpopulations and populations, preventing isolation. The papers in this special issue address dispersal at several levels of analysis, from gene to species, reflecting a concern for the benefits and costs of dispersal to the inclusive fitness of individuals, the ultimate selection pressures leading to gene flow (CLOBERT et al., 2001 a). Table 2 presents a list of proximate and ultimate factors that may lead to primate dispersal, including those factors proposed by PUSEY and PACKER (1987) in their classic review. Table 2 is not intended to be exhaustive; nonetheless, it does reflect a contemporary view that primate dispersal may have physiological and developmental, in addition to abiotic, behavioral, and social causes and consequences. In addition, Table 2 includes factors pertaining to sexual conflict (e.g., mating rates) which occurs when traits facilitating the reproductive success of one sex reduce the fitness of the other sex (see CHAPMAN et al., 2003; NUNN, 2003). Hypotheses for theoretical and empirical tests of primate dispersal can be generated from Table 2 such as that sexual conflict might drive female dispersal in some species.

Table 2: Possible proximate and ultimate causes of primate dispersal.

Proximate Factors	**Ultimate Factors**
Interaction rates (including mating rates)	Seek unexploited resources for conversion to offspring
Coercion	Avoid mate competition, especially with kin
Force	Avoid resource competition, especially with kin
Persuasion	Avoid inbreeding and/or areas of lower genetic heterogeneity
Attraction to extragroup individuals	Avoid other factors deleterious to survival and/or reproductive success (e.g., sexual conflict, sperm competition, increasing population size [see Gavrilets, 2000], predation, disease, infanticide, parasites, including social parasites)
Nutrition	Locate higher quality mates
Physiological factors (e.g., hormones)	Locate genetically compatible mates
Response to environmental perturbation (e.g., habitat disturbance)	Locate phenotypically compatible mates
	Locate more mates

The organization and editing of this special issue was made possible by the good-natured involvement of professionals, including the contributors, Dr. Dr. Michael Schwibbe, Editor of Primate Report, and Heike Klensang, Schwibbe's Editorial Assistant. I am very grateful for the cooperation of these individuals at all stages of the present project. I also wish to thank Dr. Rob Horwich for giving me the opportunity to study black howler monkeys (*Alouatta pigra*) at the Community Baboon Sanctuary in Belize in association with his organization, Community Conservation, Inc. (U.S.A.). I hope that this special issue will promote the study of spatial dynamics in primates, both theoretically and empirically, in order to achieve a better understanding of the spatial patterning of primate populations and the communities of which they are components.

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Correspondence to:
Dr. Clara B. Jones, Livingstone College, School of Liberal Arts, 701 W. Monroe Street, Salisbury, NC 28144, U.S.A.; E-mail: **cjones@livingstone.edu**; **howler425@cs.com**.

DISPERSAL AND THE INBREEDING AVOIDANCE HYPOTHESIS. FIELD, M. AND GUATELLI-STEINBERG, D.

Key words: dispersal, primates, inbreeding avoidance, mate competition, resource competition, mate selection

Abstract

There has been much debate over the role of inbreeding avoidance versus the roles of competition for mates and resources as primary causes of primate dispersal. The first half of this paper evaluates the primate literature in relation to the underlying assumptions of the inbreeding avoidance hypothesis and reviews the variety of behaviors, including dispersal, that limit inbreeding in primates. The underlying assumptions of the inbreeding avoidance hypothesis hold for most primates: (1) inbreeding is evolutionarily costly; (2) the costs of inbreeding outweigh its benefits; and, (3) there exist a variety of behaviors that limit inbreeding: behavioral avoidance of inbreeding, extragroup copulation, reproductive suppression, and dispersal. Thus, inbreeding avoidance cannot be relegated to a minor cause of primate dispersal on theoretical grounds. However, the costs of dispersal are highly variable, taking on condition-specific values for individual organisms. The high variability of dispersal costs among individuals may explain why several mechanisms of inbreeding avoidance can be present within a single primate species.

The second half of the paper is an empirical assessment of the concordance between dispersal data gleaned from the primatological literature and the predictions of each hypothesis for dispersal: inbreeding avoidance, competition for mates/mate selection, and competition for resources. We find that while most cases of dispersal are consistent with the predictions of the competition hypothesis (for mates and resources), there are several species for which the dispersal data are better explained by the inbreeding avoidance hypothesis. Thus, the variability of dispersal patterns evident within and among primate species results from a complex mix of these three major causes, the existence of non-dispersal mechanisms for inbreeding avoidance, and the variability of dispersal costs.

Introduction

Discussion of the primary causes of primate dispersal has principally focused on the roles of three factors: intragroup competition for resources, intrasexual competition for mates/mate selection, and inbreeding avoidance (e.g. MOORE and ALI, 1984; PUSEY and PACKER, 1987). This paper evaluates the role of inbreeding avoidance as an ultimate cause of primate dispersal. The first half of the paper examines the theoretical basis of the hypothesis that primates avoid inbreeding, evaluates the primate literature in relation to the underlying assumptions of the inbreeding avoidance hypothesis, and reviews the variety of behaviors, including dispersal, that limits inbreeding in primates. The second half of this paper is an empirical assessment of the concordance between dispersal data gleaned from the primatological literature and the predictions of each hypothesis for dispersal: inbreeding avoidance, competition for mates/mate selection, and competition for resources. The empirical portion of this paper has several advantages over previous reviews (MOORE and ALI, 1984; PUSEY and PACKER, 1987; PUSEY, 1992), namely that (1) more data are now available to assess the applicability of these hypotheses; (2) each genus is represented by a single species to minimize sampling bias resulting from phylogenetic inertia; and, (3) predictions of each hypothesis are examined for each of the representative species.

In the first portion of the paper, we argue that inbreeding and dispersal benefits and costs are not fixed, but are variable in nature, taking on situation-specific ("conditional" or "condition-dependent") values for individual organisms. We find, however, that for most primate species, the costs of inbreeding are greater than its benefits, while the costs of dispersal are highly dependent on varying social and environmental conditions. Thus, the inbreeding avoidance hypothesis cannot be excluded from the discussion or relegated to a minor cause of dispersal (see, for example, MOORE and ALI, 1984) on theoretical grounds. In addition, we demonstrate that dispersal is among several mechanisms that can be present within a single primate species which limit inbreeding. In the second portion of this paper, we find that, while most cases of dispersal are consistent with the predictions of the competition hypotheses (for resources and mates), as argued by MOORE and ALI (1984), there are several species for which the dispersal data are better explained by the inbreeding avoidance hypothesis. Thus, the variability of dispersal patterns evident within and among primate species results from a complex mix of these three major causes, the existence of non-dispersal mechanisms for inbreeding avoidance, and the variability of dispersal costs.

PART I: INBREEDING: COSTS, BENEFITS, AND MECHANISMS OF AVOIDANCE

Inbreeding avoidance hypothesis

The inbreeding avoidance hypothesis proposes that individuals will avoid inbreeding because of its fitness costs. Three major assumptions underlie the hypothesis: that inbreeding is evolutionarily costly, that the costs of inbreeding outweigh the benefits, and that, thus, inbreeding avoidance mechanisms should evolve to limit inbreeding. The next section addresses these three assumptions of the inbreeding avoidance hypothesis and evaluates their applicability to primates.

Assumption 1: Inbreeding is costly

Inbreeding is commonly understood as the breeding of related individuals. Individuals can be assigned an "inbreeding coefficient" known as "f" (first defined by WRIGHT in1922), expressing the probability of receiving two alleles identical by descent from a common ancestor. Thus, more inbred individuals have a higher proportion of homozygous, and specifically autozygous, genetic loci than less inbred individuals. Deleterious effects of inbreeding resulting from this increase in homozygosity are ascribed to two mechanisms. The first, known as "the dominance model", refers to the expression of deleterious phenotypes resulting from increased homozygosity of deleterious recessive alleles (MITTON, 1993). For example, a single recessive allele has been identified as responsible for seedling deaths in selfing *Pinus radiata* (KUANG et al., 1998). The second mechanism implicated in the negative effect of increased homozygosity due to inbreeding is "the overdominance model" (MITTON, 1993). According to this model, although each pair of deleterious alleles may be only slightly damaging, the combined effect of homozygosity over many loci results in an organism that is less able to cope with its environment. For example, the inbred offspring of greater horseshoe bats (*Rhiolophus ferrumequinum*) exhibit reduced survival to their first and second summers (ROSSITER et al., 2001). These authors attribute this result to loss of heterosis rather than to any single locus.

Reduction in fitness due to increased homozygosity is referred to as "inbreeding depression", the effects of which were first noted by DARWIN in 1876. Empirical evidence for inbreeding depression in both wild and captive populations is well documented (reviewed in KELLER and WALLER, 2002). In their study of captive individuals of 38 mammalian species, including 12 primate species, RALLS et al. (1988) found that mortality was 33 % higher in the offspring of inbred matings than it was in non-inbred matings. A similar study done on wild populations of 35 species of various animals and plants, including 4 primate species and subspecies, showed even higher levels of inbreeding depression: a mortality increase of 215.5 % in inbred individuals as compared with non-inbred individuals (CRNOKRAK and ROFF, 1999).

The most notable effect of inbreeding depression is an increase in prenatal, infant, and juvenile mortality. Several non-human primate examples of inbreeding depression exist. For example, PACKER (1979) found that in olive baboons (*Papio anubis*), all inbred offspring (n= 4) died before one month of age, as compared to the deaths of only 6 of the 32 outbred infants born to the group during the same period. In yellow baboons (*Papio cynocephalus*), all inbred (n= 3), as compared to 27 out of 140 outbred, offspring died before one month of age (ALBERTS and ALTMANN, 1995). In golden lion tamarins (*Leontopithecus rosalia*), close inbreeding resulted in the deaths of all 14 inbred infants, as compared to 1 out of 5 outbred offspring (DIETZ and BAKER, 1993).

Similar effects of inbreeding depression on prenatal and infant mortality have been seen in many human populations (ARCHANA, 1998; BADARUDDOZA, 1998; BULAEVA et al., 1997; GRANT and BITTLES, 1997; HUSSAIN et al., 2001; JORDE, 2001; RAMANA et al., 1999; REDDY et al., 2001; SUDHAKARAN and VIJAYAVALLI, 1997; SUDHAKARAN and VIJAYAVALLI, 1998). However, some human groups demonstrate higher fertility rates among consanguineous (inbreeding) couples, thus compensating for higher infant and juvenile mortality rates (BAVU et al., 1999; OBER et al., 1999; HANCIOGLU and TUNCBILEK, 1998; LUNA et al., 1998).

Although most studies demonstrate a strong effect of inbreeding depression on young individuals, adult inbred offspring can also be adversely affected through both their reproductive abilities (FRANKHAM, 1996; MARGULIS and WALSH, 2002; PACKER and PUSEY, 1993; WALDMAN and MCKINNON, 1993) and increased susceptibility to diseases and parasites (COLTMAN et al., 1999; HEDRICK et al., 2001; VAN DER BEEK et al., 1999).

Genetic load

The degree of inbreeding depression varies both between and within species, depending on the number of lethal recessive alleles present. This is also referred to as the number of "lethal gene equivalents" or "genetic load" (MAKOV and BITTLES, 1986). For example, in contrast to the baboon inbreeding studies of PACKER (1979) and ALBERTS and ALTMANN (1995) noted above, BULGER and HAMILTON (1988) noted no differences in mortality rates of inbred versus outbred offspring of Chacma baboons (*Papio cynocephalus ursinus*). In addition, RALLS et al. (1988) found that among the 38 species studied, the number of lethal equivalents ranged from –1.4 to 30.3 per species.

However, there is strong evidence suggesting that many primate species do carry substantial genetic loads. RALLS and BALLOU (1982) studied the effects of inbreeding in sixteen captive primate colonies representing six families and both suborders. In fifteen of these, infant mortality was higher in inbred than outbred pairs. Thus, for many primates and other mammals, inbreeding depression is substantial and therefore is likely to select for inbreeding avoidance behaviors.

It has been argued that inbreeding is not necessarily genetically costly because genetic load can be reduced under continued inbreeding (BENGSSTON, 1978; MOORE and ALI, 1984). According to this argument, deleterious recessives are removed from the gene pool through the greater mortality rate of homozygous, inbred individuals. Indeed, after a few generations of inbreeding, the frequency of deleterious alleles in a group can diminish dramatically (PERRIN and GOUDET, 2001). For example, genetic load in a typically outcrossing hyacinth (*Eichhornia paniculata*) became reduced through continued inbreeding (BARRETT and CHARLESWORTH, 1991). However, the "purging" of deleterious alleles in this way seems unlikely for the majority of species for several reasons. First, some deleterious alleles can become fixed in populations (due to Muller's ratchet: PUSEY and WOLF, 1996). Second, mildly deleterious alleles are not as effectively purged from populations as lethal alleles and can continue to contribute significantly to inbreeding depression (FRANKHAM, 1996). Third, since mutation is a continuous process, it would seem unlikely that a population could ever free itself of its genetic load despite persistent inbreeding (P. RODMAN, personal communication). Finally, species that exhibit reproductive compensation (such as the human populations noted above) can maintain high frequencies of deleterious alleles regardless of the high mortality rates of homozygotes.

Interestingly, some cases in which genetic load has been thought to be reduced by continued inbreeding may actually not hold true. For example, the Speke's gazelle (*Gazella spekei*) captive breeding program has been presented as an example of inbreeding reducing the genetic load of a population (e.g. TEMPLETON and READ, 1994). However, a recent study indicates that the mortality reduction demonstrated is likely to be due to differences in husbandry practices and not due to genetics at all (KALINOWSKI et al., 2000).

Environmental variation

The amount of inbreeding depression exhibited is not only dependent on genetic load, but also on the interaction of that load with environmental variables. In recent years, a number of studies of plants, birds, and mammals have indicated that inbred populations exhibit much higher mortality levels in the wild than in laboratory conditions. In *Crepis sancta*, a Mediterranean outcrossing plant, the magnitude of inbreeding depression is dependent on environmental variables such as the presence or absence of interspecific competition (CHEPTOU et al., 2000). In song sparrows (*Melospiza melodia*), inbred individuals exhibited much higher mortality than outbred individuals during severe winter weather (KELLER et al., 1994). JIMENEZ et al.'s (1994) study comparing inbred and outbred groups of white-footed mice (*Peromyscus leucopus moveboracensis*) showed that when the two groups were released in the field and their survival compared, the inbred group exhibited a much higher mortality level than the outbred group. In addition, the difference in mortality between the two groups was much greater in the field than in the laboratory. These studies are important for two reasons. First, they demonstrate that the levels of inbreeding depression previously noted in captive populations are likely to be underestimates. Second, they indicate that the ability of any inbred individual or population to survive can vary according to environmental conditions. Thus, the effect of inbreeding depression (regardless of genetic load) cannot be considered as a constant in natural conditions.

Assumption 2: The costs of inbreeding outweigh its benefits

MOORE and ALI (1984) argued in their controversial paper on the ultimate causes of primate dispersal that "inbreeding is not inherently maladaptive" (p. 95). In this vein, this section discusses the possible benefits associated with inbreeding. Many theoretical benefits have been proposed in the literature, of which four will be discussed here: (1) development of sociality within populations of closely related individuals; (2) reduction of the cost of meiosis; (3) reduction of the recombinational load entailed by sexual reproduction; and, (4) increased genetic variation at the population level.

The first proposed benefit is that sociality can be enhanced through inbreeding. In this context, inbreeding should favor the evolution of sociality because it increases the inclusive fitness of individuals who cooperate with close relatives (WILSON, 1975). Evidence for this has been reported in a wide variety of organisms, including termites (*Reticulitermes flavipes*: REILLY, 1987), naked mole rats (*Heterocephalus glaber*: REEVE et al., 1990), shrimps (*Synalpheus regalis*: DUFFY, 1996) and spiders (*Agelena consociata*: RIECHERT and ROELOFFS, 1993). In addition, this mechanism may be important for cooperatively hunting species, such as social carnivores (e.g. *Panthera leo*: SPONG et al., 2002).

In addition to the within group benefits provided by inbreeding there is also the possibility of between group benefits (SPONG et al., 2002). For example, in dwarf mongoose (*Helogale parvula*: KEANE et al., 1996) and white-nosed coatis (*Nasua narica*: GOMPPER et al., 1998), groups formed through fissioning are often closely related. In these cases, kin selection benefits enhanced by inbreeding may be derived by group members during intergroup encounters, decreasing the likelihood of aggressive interaction.

However, there have been recent suggestions that the importance of kin selection in the development of sociality may be overstated (SPONG et al., 2002). The appearance of a genetic effect on social group cooperative behavior may in fact be merely a consequence of the benefits that accompany natal philopatry (LAMBIN et al., 2001;

CLUTTON-BROCK, 2002). For example, the benefits that one derives from being in one's natal group, such as cooperation with familiars (based on reciprocal altruism), may be misinterpreted as kin selection. Also, intragroup competition among relatives can reduce (or erase) the benefits provided by inbreeding (WEST et al., 2002).

The second proposed benefit of inbreeding is its effect on reducing the "cost of meiosis", the decrement in future genetic representation experienced by sexually reproducing organisms (WILLIAMS, 1975). However, no definitive empirical evidence that organisms act on this benefit has been published. In addition, note that kin selection can also provide this type of benefit (without incurring inbreeding depression) if an individual either assists multiple relatives or assists relatives in addition to producing its own offspring.

The third inbreeding benefit is the reduction of recombinational load. Inbreeding can defray the disruptive genetic cost of sexual reproduction because it preserves successfully integrated parental genomes. This "cost of recombination" corresponds to "the average reduction in progeny fitness resulting from the disruption of favored coadapted genomes during gametogenesis" (SHIELDS, 1982, p. 248). Thus, inbreeding can function to "increase the probability that successful parental genomes are more faithfully transmitted to progeny" (SHIELDS, 1982, p. 248).

The breaking apart of coadapted genes is also referred to as "outbreeding depression". This phenomenon was first noted by DOBZHANSKY (1970), who found that in *Drosophila,* inversion heterozygotes from the same population had higher fitness than inversion homozygotes. According to DOBZHANSKY, chromosomal heterozygotes from the same geographic region must be "coadapted" to each other since interpopulation heterozygotes had reduced fitness. Evidence for outbreeding depression has been reported for a number of other species, including earthworms (*Eisenia fetida* Sav.: NAKAGAWA et al., 2002), Pacific oysters (*Crassostrea gigas*: GARNIER-GERE et al., 2002), pink salmon (*Oncorhynchus gorbuscha*: GHARRETT et al., 2002), ornate dragon lizards (*Ctenophorus ornatus*: LEBAS, 2002) and various plants (*Eucalyptus camaldulensis*: BUTCHER and WILLIAMS, 2002; *Anchusa crispa*: QUILICHINI et al., 2002; *Lotus scoparius*: MONTALVO and ELLSTRAND, 2001; *Chamaecrista fasciculata*: FENSTER and GALLOWAY, 2000; *Agrostemma githago*, *Papaver rhoeas*, *Silene alba*: KELLER et al., 2000).

In light of the cost of outbreeding depression, the concept of "optimal" outbreeding has been developed. In this context, individuals choose mates of a certain level of relatedness in order to strike an evolutionary balance between the costs of inbreeding and the costs of outbreeding. BATESON's (1981,1982, 1983) landmark studies on Japanese quail (*Coturnix coturnix japonica*) showed that individuals prefer unfamiliar members of the opposite sex who are similar to them in appearance (in particular, first cousins). Optimal outbreeding has also been demonstrated for other species, including common voles (*Microtus arvalis*: BOLHUIS et al., 1988), prairie dogs (*Cynomys ludovicianus*: HOOGLAND, 1992), and white-footed mice (*Peromyscus leucopus*: KEANE, 1990).

The fourth proposed benefit of inbreeding is that, in cases where there is limited gene flow between inbred populations, there is a reduction of within-breeding population genetic variation but higher within-species variation (FUTUYMA, 1998). The argument behind this is that high levels of outbreeding among populations can eventually lead to homogenization of the gene pool. Thus inbreeding, by maintaining high levels of within species variation, lowers the possibility of species extinction. Evidence for the effect of inbreeding on population variation in this manner has been found in several species, including conifers (*Abies* spp.: AGUIRRE-PLANTER et al., 2000), radishes (*Raphanus sativus*: ELLSTRAND and MARSHALL, 1985), and prairie dogs (*Cynomys ludovicianus*: CHESSER, 1983).

This discussion has demonstrated that inbreeding can have benefits as well as costs in a variety of plants and animals. What is important to note, however, is that there are specific conditions under which these benefits accrue. Consideration of these benefits for primates, in particular, reveals that these conditions are rare. There is little evidence in primates for benefit number one, that individuals can enhance the rewards of sociality through inbreeding. This benefit could conceivably apply to cooperatively breeding species, such as callitrichids (e.g. *Callithrix kuhli*: SCHAFFNER and FRENCH, 1997; *Callithrix jacchus*: ABBOTT et al., 1997; *Saguinus fuscicollis*: GOLDIZEN et al., 1996), but the effect of inbreeding on kin selection benefits in these species has not (yet) been demonstrated empirically. In addition, there are primate cases in which group members are socially bonded, but not genetically related, such as in bonobo (*Pan paniscus*) females (e.g. HOHMANN et al., 1999), indicating that the benefits of sociality can develop among individuals without their being related.

There has been much discussion of the theoretical advantage of benefit number two, that inbreeding reduces the cost of meiosis, particularly in the context of the evolution of sex (e.g. WILLIAMS, 1975; MAYNARD SMITH, 1978; SHIELDS, 1982). However, there is currently no empirical evidence that this benefit operates to promote inbreeding.

Considering benefit number three, that inbreeding can reduce recombinational load, evidence of outbreeding depression has been noted in captive primates, such as Goeldi's monkeys (*Callimico goeldi*: LACY et al., 1993), and has been recognized as a potential problem in captive chimpanzees (*Pan troglodytes*: MORIN et al., 1992). However, outbreeding depression is unlikely to occur in wild primate populations. This is because most cases of outbreeding depression occur when individuals from previously genetically isolated populations (usually subspecies) mate. The vast majority of naturally occurring primate dispersals are to nearby (often contiguous) groups (MOORE, 1992). Thus, most primate group transfers occur between groups that cannot be considered genetically isolated. However, outbreeding depression remains a possibility in a few specialized cases in wild populations, such as in subspecies hybridization (e.g. *Papio h. hamadryas* and *P. h. anubis* hybrids in Awash National Park, Ethiopia: SZMULEWICZ et al., 1999).

A few primate species may profit from benefit number four, the promotion of within species variation among populations. For example, in *Theropithecus gelada*, gene flow between bands (a group of harem like reproductive units which share the same home range) is only about five per cent per generation (SHOTAKE, 1980). Thus, members of each band are considered to be closely related (DUNBAR, 1993). In this situation, the low level of gene flow between bands creates populations of relatively reproductively isolated demes (bands), which results in greater genetic variation at higher levels of organization (i.e. metapopulation, species). However, because this benefit accrues through group selection, and would have to overcome the cost of inbreeding depression to individuals, it is expected to be a weak selective factor.

For inbreeding to become a favored strategy, its benefits must be greater than its costs. In the previous section, we demonstrated that inbreeding is costly to a wide array of organisms, including primates. In the few cases where inbreeding appears to have possible benefits in primates, empirical evidence is either lacking or is significant in only a few cases. It therefore seems that in most species the usually deleterious effects of inbreeding will outweigh its potential benefits. Therefore, behavioral mechanisms that enable primates to avoid inbreeding are expected to have evolved and these are discussed in the next section.

Assumption 3: Mechanisms to avoid inbreeding

Mating with close relatives occurs less often than expected by chance, indicating that there exist aspects of primate behavior preventing inbreeding (PUSEY and WOLF, 1996). The third assumption of the inbreeding avoidance hypothesis is that if the costs of inbreeding are greater than its benefits, natural selection will favor mechanisms that prevent it. Several proposed inbreeding avoidance mechanisms are discussed in the literature: behavioral avoidance of inbreeding, extragroup copulations, reproductive suppression, and, finally, dispersal. It is important to note that the existence of these behaviors does not necessarily imply that they are evolved mechanisms for inbreeding avoidance, but that, rather, inbreeding avoidance is a consequence of them, regardless of their ultimate evolutionary origins.

Behavioral avoidance of inbreeding

In some species, inbreeding is avoided because individuals prevent themselves from mating with relatives. Evidence for this "behavioral avoidance of inbreeding" has been found in a wide variety of animals, including mammals, reptiles, and fish (e.g. ARNOLD, 2000; BULL and COOPER, 1999; ISHIDA et al., 2001). Note that females are expected to avoid inbreeding more actively than males (CLUTTON-BROCK and HARVEY, 1976; WASER et al., 1986) because of their greater investment per offspring (TRIVERS, 1972). This is especially so in female mammals, who invest substantial time and energy in each offspring through their biological commitment to gestation and lactation.

Selectively avoiding breeding with relatives appears to occur through two mechanisms: the Westermarck effect and phenotype matching. According to the first of these, originally described by Edward WESTERMARCK in 1891, there "is a lack of inclination for, and a feeling of aversion associated with the idea of, sexual intercourse between persons who have lived in a long-continued relationship from a period of life when the idea of sexual desire, in its acuter forms at least, is naturally out of the question" (1922, p. 198). In other words, individuals are less likely to interact sexually with others with whom they were intimately familiar during development, namely siblings and parents. This effect is expected to occur regardless of the genetic relatedness of the individuals involved. For example, mandarin voles (*Microtus mandarinus*), display a significant preference for individuals raised by other parents over those raised by the same parent (FADAO et al., 2000). In naked mole rats (*Heterocephalus glaber*), reproductively active females were found to prefer to associate with unfamiliar males. However, reproductively inactive females do not discriminate. Neither set of females discriminate between kin and non-kin suggesting that recognition and sexual aversion is based on familiarity and not on genetics

(CLARKE and FAULKES, 1999). In humans, the Westermarck effect has been noted in such studies as SHEPHER's well-known 1971 study of age-mates in Israeli kibbutzim. In this study, SHEPHER noted that children reared together in kibbutzim lacked sexual interest in one other, presumably due to close familiarity during childhood.

In addition to an aversion to familiar individuals as mates, this effect also accounts for attractions to unfamiliar or novel individuals as mates. For example, in montane voles (*Microtus montanus*), when litters were cross-fostered at birth, males mated with biological daughters that were separated from them at birth, but not familiar foster daughters (BERGER et al., 1997).

In recent years, the concept that organisms avoid inbreeding based on phenotype matching according to their major histocompatibility complex (MHC) makeup has been widely discussed (reviewed in PENN, 2002). The MHC is a highly polymorphic set of genes that controls self/non-self discrimination in the immune system. In 1975, Lewis THOMAS proposed that the MHC is associated with chemosensory signals emitted and interpreted by certain organisms. In particular, these chemosensory signals are related to individual specific body odors and organisms use these olfactory cues to select mates with particular MHC makeups (EGGERT et al., 1999). PENN and POTTS (1999) explain that individuals choose mates with MHCs dissimilar to their own because offspring with high levels of MHC heterozygosity have greater resistance to parasites and pathogens.

Of course, the mechanisms of the Westermarck effect and phenotype matching are not mutually exclusive. Evidence for both mechanisms existing in the same species has been found in house mice (*Mus musculus domesticus*). In one study, PENN and POTTS (1998) found that females avoided mating with males carrying MHC genes of their foster family, consistent with the familiarity hypothesis. In another study (1999) these researchers found that individuals prefer mates genetically dissimilar to themselves at the MHC, supporting the phenotype matching hypothesis.

Extragroup copulations

Another way in which individuals can limit the possibility of inbreeding depression is through extragroup copulations. By finding mates outside of its social group, an individual can enjoy the benefits of kin-directed altruism, but still avoid the costs of inbreeding depression. The ability to recognize kin and avoid mating with them is but one component of this mechanism. Individuals must also be able to find unrelated extragroup individuals with whom to mate. Thus, using extragroup copulations to avoid inbreeding is a more complicated process than the mechanism described above. However, STOCKLEY et al. (1993) noted that females can still reduce the probability of inbreeding by seeking multiple mates, regardless of the ability to recognize kin, because by so doing they increase their chance of producing at least some outbred young. This would be especially important in cases where females cannot avoid copulating with close relatives. Evidence of extragroup copulations has been found for many types of birds and primates (e.g. Montagu's harriers: MOUGEOT et al., 2001; shorebirds: BLOMQUIST et al., 2002; Fairy wrens: DUNN and COCKBURN, 1999; for primates see Table 1).

Table 1: Inbreeding: Consequences and nondispersal mechanisms of avoidance.

Species	**Cases of Inbreeding**	**Fitness consequences of inbreeding**	**Behavioral avoidance of inbreeding**	**Extragroup Copulation**	**Reproductive suppression**	**Citation**
Pan troglodytes	1 offspring	no data	X	X[a]		CONSTABLE et al., 2001; GAGNEUX et al., 1999; GOODALL, 1986
Hylobates lar				X		BROCKELMAN, 1996; REICHARD, 1995
Colobus badius	possible cases[b]		X	X		STARIN, 2001
Erythrocebus patas				X		CARLSON and ISBELL, 2001
Macaca mulatta	possible cases[c]		X			LOY, 1971; MANSON and PERRY, 1993; SADE, 1968; MANSON, 1995; HAMBRIGHT, 1993
Papio cynocephalus	3 offspring	all died before one month	X[d]			ALBERTS and ALTMANN, 1995; ALBERTS, 1999; ERHART et al., 1997
Semnopithecus (Presbytis) entellus				X		RAJPUROHIT and SOMMER, 1993
Alouatta seniculus				X		AGORAMOORTHY and HSU, 2000
Brachyteles arachnoides	possible case[e]		X	X	not observed	STRIER, 1997, 2000; STRIER and ZIEGLER, 2000
Callimico goeldii			X			PORTER et al., 2001
Callithrix jacchus			X	X	X	DE OLIVEIRA, 2001; DIGBY, 1999; LAZARO-PEREA, 2001; SALTZMAN et al., 2001
Leontopithecus rosalia	14 offspring	all died before weaning		X		BALES et al., 2001; DIETZ and BAKER, 1993; DIETZ et al., 2000
Saguinus oedipus					X	SAVAGE et al., 1996
Hapalemur griseus				X		NIEVERGELT et al., 2002

No data: the variable was not explored in the study
Not observed: the variable was explored in the study, but evidence of it was not found

[a] Extragroup copulations were observed in a study group at Tai, Cote d'Ivoire, but not observed at GomBe, Tanzania

[b] Two females remained in their natal troop and mated with potential half-sibs

[c] 8/26 mother-son dyads mated

[d] Has been experimentally found to be based on Westermarck effect (ERHART et al., 1997). ALBERTS (1999) noted that paternal siblings lower levels of affiliative and sexual behavior and suggested that it may be based on phenotype matching and age proximity avoidance

[e] One mother-son copulation

Reproductive suppression

Reproductive suppression of certain members of a social group can also reduce the probability of inbreeding. Similar to the other two mechanisms described above, individuals still experience the kin selected benefits of remaining with relatives in a social group. However, individuals who are being reproductively suppressed forfeit breeding opportunities. Note that, although inbreeding depression does result in such effects as increased offspring mortality, inbred offspring often do survive. Thus, theoretically, there exist situations in which an individual could increase its fitness more by inbreeding than by remaining reproductively suppressed. Young females are typically those reproductively suppressed and are thus prevented from inbreeding with their brothers and father (see Table 1 for examples of marmosets and tamarins). However, bisexual reproductive suppression has also been found in birds. For example, in acorn woodpeckers (*Melanerpes formicivorus*), groups whose membership consists of only closely related members of the opposite sex might forego breeding for up to three years if membership remains unaltered (KOENIG et al., 1998). In small mammals, a majority of the evidence for inbreeding suppression has been from the release of such suppression through the introduction of novel (unrelated) mates. Some recent examples of this include cooperatively breeding meercats (*Suricata suricatta*: O'RIAIN et al., 2000) and Damarland mole-rats (*Cryptomys damarensis*: COONEY and BENNETT, 2000).

Non dispersal mechanisms of inbreeding avoidance in primates

As shown in Table 1, primates exhibit all of the nondispersal mechanisms of inbreeding avoidance described above (see introduction to Part II in which species-selection criteria are explained). Note that more than one of these mechanisms is present in several species. In addition, despite the various non-dispersal mechanisms that limit inbreeding, there are cases in which inbred offspring have been produced. For the vast majority of inbred primate offspring, infant mortality rate is very high, often approaching 100 % (see Table 1 for examples). Behavioral avoidance of inbreeding and extragroup copulations appear to be the most common nondispersal mechanisms, with few cases of reproductive suppression, notably in marmosets and tamarins (e.g. SALTZMAN et al., 2001; SAVAGE et al., 1996).

Dispersal

The final mechanism of inbreeding avoidance that is discussed here, and the mechanism that is the primary focus for the remainder of this paper, is dispersal. Unless otherwise noted, discussion of dispersal will refer to primary dispersal from the natal group. Dispersal has been found in all primate species and is also widespread in mammals, birds, reptiles, fish, amphibians, and insects (PUSEY and WOLF, 1996). Dispersal functions to limit inbreeding by physically separating relatives. However, the ability of dispersal to limit inbreeding depends on the distance that the individual disperses and the amount of interaction that the disperser has with its natal group after dispersal, which includes the possibility of return to the natal group.

While dispersal benefits individuals by reducing the probability of inbreeding, it is not without costs. Unlike the other three mechanisms of inbreeding avoidance noted above, the dispersing individual loses the benefits of kin-directed altruism experienced in the natal group, unless it manages to transfer with, or to a group containing, relatives. Of course, dispersing with or to relatives also affects an individual's ability to avoid inbreeding. Other costs of dispersal involve the mortality risk it imposes on the disperser by exposing it to increased predation, and unfamiliar habitats and conspecifics. However, these costs are dependent on the age of the disperser, the number and type of predators in the area, the home range saturation of the area, the distance of dispersal, physical barriers to dispersal, and the willingness of new group members to accept the disperser. Dispersal costs can also be reduced by dispersing with or to a group containing relatives. Thus, the costs of dispersal are both species and situation dependent.

Quantifying the variable cost of dispersal is extremely difficult. However, there have been recent studies describing variation in the cost of dispersal for a few species. For example, in theridiid spiders (*Anelosimus studiosus*), individuals who delayed dispersal acquired more resources and acquired them more consistently, thus reducing the costs of dispersal (JONES and PARKER, 2000). And in arctic ground squirrels (*Spermophilus parryii plesius*), those who dispersed farther experienced higher mortality than more local dispersers (BYROM and KREBS, 1999).

Critics have argued that dispersal is unlikely to have evolved as an inbreeding avoidance mechanism because it is biologically costly and because other, less costly, mechanisms for preventing inbreeding, such as behavioral inbreeding avoidance, are available (e.g. MOORE and ALI, 1984). However, we again note that the costs and benefits of both inbreeding and dispersal are situationally dependent. Dispersal costs in particular are highly variable. For example, in red howler monkeys (*Alouatta seniculus*), females disperse at a much younger age than do males and can only join newly forming groups. Thus, females have a much higher mortality rate than do males during dispersal and therefore, their dispersal cost-benefit ratio greatly differs from that of the males (POPE, 1992; CROCKETT and POPE, 1993). Also, individuals are expected to exhibit trade-offs in their attempts to avoid inbreeding. If dispersal costs are high, non-dispersal mechanisms are more likely to be used to avoid inbreeding than dispersal. However, if dispersal costs are low, then dispersal becomes a viable behavioral option for avoiding inbreeding.

We note that the presence of particular inbreeding avoidance mechanisms in species is based on historical contingency during evolution. In other words, because of differences in the relationship of a species to its environment and the random nature of historical contingency, one would expect to see an array of mechanisms for avoiding inbreeding among species. In addition, it is likely that multiple inbreeding avoidance mechanisms can co-exist within a single species if a variety of mechanisms are required to insure that inbreeding is avoided. PUSEY and WOLF (1996) have noted that the type (or types) of mechanism that evolves appears to be dependent on the social system of the species and the probability that individuals will encounter kin. For example, behavioral avoidance of inbreeding is expected only among individuals who have been intimately associated. In the event that situations engendering sexual aversion were bypassed (such as cross-fostering), other mechanisms can evolve as "back up" systems (such as the additional presence of MHC discrimination in *Mus musculus domesticus*, noted above). In summary, whether or not dispersal is favored as a mechanism for the avoidance of inbreeding depends on the historical circumstances of individual species. Whether an individual's present circumstances override this tendency depends on relative cost/benefit values for the individual.

PART II: EMPIRICAL ASSESSMENT OF DISPERSAL CAUSES ACROSS THE PRIMATE ORDER

The remainder of this paper focuses on the primate dispersal literature, examining within which primate species dispersal may be related to inbreeding avoidance, sexual selection (mate competition/mate selection), or resource competition. First, we outline predictions for dispersal patterns that these three primary proposed ultimate causes of primate dispersal entail. Then we examine profiles of dispersal behavior as described in the primate literature in order to determine which characteristics of dispersal may be related to these major causes. Finally, by compiling the data from the literature on the various mechanisms of inbreeding avoidance in primates from the previous section (Table 1) with dispersal data from this section (Table 3), we attempt to identify social and environmental conditions under which dispersal is a viable means of avoiding inbreeding.

The three primary causes and their predictions

Three major ultimate causes have been proposed for why primates disperse from their natal groups: intrasexual competition for mates/mate selection, intragroup competition for resources, and inbreeding avoidance (PUSEY and PACKER, 1987). By examining the characteristics of each species' dispersal patterns, it is in some cases possible to resolve which of these causes is/are operating. These characteristics include sex bias (one sex dispersing more often or farther than the other), the stage of sexual maturation of the disperser, the presence or absence of aggression to the disperser prior to and after dispersal, differences in mate and/or resource access for those who disperse versus those who don't disperse, the seasonal pattern of dispersal, and what type of group the dispersers choose to enter. Below, we discuss the characteristics of dispersal implied by each of the three major causes and list them in summary form in Table 2.

Table 2: Dispersal characteristics and their hypothesized relationship to the three major causes of natal dispersal.

	Inbreeding Avoidance	**Intrasexual competition for mates**	**Intragroup competition for resources**
State of maturation	Prior to or during sexual maturation	During or after sexual maturation	No clear relationship
Sex bias	Yes	Possible	Possible
Behavioral avoidance of inbreeding prior to dispersal	Yes	No	No
Aggression	1. No aggression in natal group 2. Dispersal to groups regardless of high and/or extended aggression	Aggression in natal group from same sex members	1. Aggression in natal group 2. Low aggression (or short in duration) in receiving group

	Inbreeding Avoidance	**Intrasexual competition for mates**	**Intragroup competition for resources**
Differences in resource access between dispersers and nondispersers	No clear relationship expected	Individuals with lower reproductive access should be those who disperse	Individuals being displaced from resources should be those who disperse
Dispersal related to seasonality	No clear relationship expected	Dispersal related to breeding seasonality	Dispersal related to resource seasonality
Pattern of choice of receiving group	1. Dispersers should not return to natal group 2. Should choose groups with unfamiliar mates	Attraction to groups with more or higher quality mates	Attraction to smaller groups or groups with larger resource/size ratios
Possible male bias due to a proposed focus on mate acquisition in this sex (see text). Possible female bias due to a proposed focus on resource garnering in this sex (see text).			

Intrasexual competition for mates / mate selection

Dispersal may be related to mate competition and mate selection. In this case, dispersers are expected to leave groups where competition for mates is high and choose groups in which competition is either lower, or groups in which the disperser can attain a more competitive position. This cause is more often related to male dispersal, resulting from male-male mate competition. Males compete for the limited reproductive output of females (TRIVERS, 1972), and, as a consequence, males who are prevented from mating are expected to leave the group to try to obtain mates elsewhere. In a review of male dispersal, DOBSON (1982) suggests that male-biased dispersal in mammals arises from the predominantly polygynous mammalian mating system. Note that intrasexual competition for mates does not exclusively concern males, if the males of a species provide benefits of a high enough quality to cause females to compete for them or to select them on the basis of particular attributes (e.g. predator defense, territorial defense, infanticide protection: TRIVERS, 1972; STEENBEEK, 1999; STERCK and KORSTJENS, 2000). Dispersals with the following characteristics are likely to be motivated by intrasexual competition for mates or mate selection.

- Individuals leave their natal groups either during or after the period of sexual maturation. This is the period during which group members begin to challenge each other for mating positions in the group (e.g. RAJPUROHIT et al., 1995).
- Dispersers are expected to be those individuals who are being aggressed against or are those who are often the "losers" in aggressive interactions (MOORE and ALI, 1984).
- Dispersers receive some aggression in the group to which they transfer, however this aggression is of low intensity or short duration (MOORE and ALI, 1984). This is predicted because dispersers are expected to select groups in which there are lower levels of mating competition.
- Dispersers are those with the least access to mating opportunities in their groups, often owing to rank or age differences. Male rank has been correlated with mating

success in a number of species (but see BERARD, 1999). Low rank with diminished mating success can stimulate dispersal if higher rank and increased mating opportunities can be obtained in the receiving group.
- In seasonally breeding species, dispersal events are concentrated during the breeding season (e.g. BOELKINS and WILSON, 1972; SUGIYAMA, 1976).
- Dispersers are attracted to groups with more or better quality mates (HARCOURT, 1978). These groups may either contain a larger number of available mates or a skewed sex ratio (DRICKAMER and VESSEY, 1973; BOELKINS and WILSON, 1972). In this scenario, a potential disperser would be expected to stay in its natal group if that group has more potential mates.

Intragroup competition for resources

Dispersal related to population densities and/or resource access results from intragroup competition for resources (usually food). In general, dispersers are expected to leave groups where competition for resources is high and/or they are not in competitively advantageous positions. Dispersers are also expected to choose groups in which competition is either lower, or in which they will be more competitive. This type of dispersal should be seen more often in cases where females disperse, because females require sufficient amounts of high quality resources in order to satisfy the substantial biological costs of gestation and lactation (TRIVERS, 1972; WRANGHAM, 1980). However, resource competition as a cause for dispersal is not necessarily limited to females. Dispersal with the following features can be considered to result from intragroup competition for resources.
- Dispersers are frequently recipients of aggression in their natal groups, particularly in feeding contexts, thus prompting dispersal. Dispersals of this nature are periodically referred to as "forceful evictions" in the literature. However, there have been suggestions (e.g. PUSEY and PACKER, 1987; PRINTES and STRIER, 1999) that individuals will voluntarily migrate in order to avoid pending aggression related to competition, thus avoiding a forced eviction (see also LIDICKER's 1975 discussion on pre-saturation dispersers). However, this type of relationship is difficult to establish because aggressive displays are absent.
- Dispersers are expected to select groups with lower levels of resource competition, and thus are also expected to receive less aggression (or a shorter duration of aggression) (MOORE and ALI, 1984).
- Individuals disperse during periods related to resource seasonality, particularly scarcity, because of the heightened competition for resources within groups during these periods. This pattern is similar to that noted above for breeding seasonality effects.
- Dispersers are those who garner insufficient resources because of focused aggression or displacement by other group members. Thus, lower ranking individuals are expected to disperse more often than higher ranking ones, as would those who are otherwise noticeably blocked from obtaining resources (e.g. STRIER, 2000).
- Individuals are expected to disperse from larger groups to smaller groups or from groups with fewer resources to those with more resources (e.g. STEENBEEK and VAN SCHAIK, 2001).

Inbreeding avoidance

Based on the earlier discussion (in Part I of this paper), dispersal related to inbreeding avoidance should have the following characteristics.

- There should be a degree of sex bias. In other words, only one sex should disperse, with few exceptions, or one sex should disperse farther than the other in order to limit the possibility that relatives will mate. This argument is based on that proposed by GREENWOOD (1980), who stated that if there are costs associated with dispersal and dispersal is the means by which inbreeding is avoided, only one sex should transfer. This is because inbreeding costs are reduced by the same amount if both sexes transfer, but dispersal costs are doubled (CLUTTON-BROCK and HARVEY, 1976). The sex that transfers is determined by whether or not females form stable cooperative groups. That is, if females form stable cooperative groups, then males should transfer, and if males form such groups, then females should transfer (GREENWOOD, 1980).
- Dispersers are expected to leave prior to or during sexual maturation. By doing so, the possibility of producing inbred offspring with close relatives in the natal group is diminished (PUSEY and PACKER, 1987). Note that this prediction partially overlaps with that for mate competition regarding the timing of dispersal with respect to sexual maturation.
- Individuals leave natal groups voluntarily, having received little aggression, and transfer to new groups despite resulting high and/or extended aggression. This is the opposite of what is expected in competition situations (PUSEY and PACKER, 1987).
- There should be no differences in access to resources between those who disperse and those who don't (PUSEY and PACKER, 1987). However, this expectation can be confounded by the fact that individuals dispersing in order to avoid inbreeding are often very young individuals who tend to be unsuccessful competitors.
- Dispersing individuals should not come back to the natal group during the process of natal dispersal or any type of secondary dispersal (PACKER, 1985; PUSEY and PACKER, 1987). Evidence for return to the natal group is scarce in the primate literature (e.g. HENZI and LUCAS, 1980; PACKER, 1979).
- Dispersers should exhibit sexual disinterest in familiar individuals and choose groups because of attraction to novel mates (HARCOURT, 1978). This is related to the Westermarck effect and MHC selection (see discussion in Part I).

Overlapping causes of dispersal

Note that these three ultimate causes of dispersal are not mutually exclusive. For example, an individual may disperse to avoid competition for mates as well as to avoid inbreeding. In addition, individuals may disperse primarily for one reason, but enjoy additional benefits linked to the other two causes. For example, if an individual disperses because of competition for resources, it may still manage to avoid inbreeding by breeding in the receiving group rather than within the natal group.

Results of primate literature survey

We carefully surveyed the primate literature for cases of dispersal and profiled them in Table 3. Use of all of the available data on primate dispersal in Table 3 would have biased our results towards species-rich genera (PAGEL and HARVEY, 1988). To minimize this bias, we selected a single species to "represent" each genus. While we realize that we lose data in this process, we believe that we gain a perspective on dispersal across the primate order that is less affected by phylogenetic inertia than are comprehensive surveys that treat each species as a unique data point. The sole criterion for selecting a representative species was the completeness of information about dispersal available in the literature (i.e., we selected species for which we could obtain the most data). Thus we believe that we have avoided subjective bias in selecting species and are not merely selecting cases to support our claims, a criticism some have made (e.g. PUSEY, 1988) of previous reviews of dispersal. Our approach was to examine the predictions of each cause for each representative species and to provide a summary assessment at the end of our survey.

Most of the column headings in Table 3 are characteristics of dispersal that are based on the predictions listed in Table 2. The only column heading not based on Table 2 is "cost of dispersal", the importance of which was discussed in Part I of this paper. In the "possible causes of dispersal" column, we attribute the various dispersal characteristics to resource competition (RC), mate competition/mate selection (MC), or inbreeding avoidance (IA) as ultimate causes of dispersal.

For many species, we found no published literature describing dispersal habitats. These include a few new world and old world monkeys (*Cacajao* spp., *Chiropotes* spp., *Pygathrix* spp., *Rhinopithecus* spp.), and most of the prosimians (*Allocebus* spp., *Arctocebus* spp., *Cheirogaleus* spp., *Daubentonia* spp., *Lepilemur* spp., *Loris* spp., *Nycticebus* spp., *Perodicticus* spp., and *Phaner* spp.). Many other species are lacking sufficient information to make any sort of evaluation regarding the causes of dispersal. These include *Pongo pygmaeus*, *Nasalis larvatus, Ateles paniscus, Callithrix jacchus, Lagothrix lagotricha*, *Leontopithecus rosalia*, *Pithecia pithecia*, *Avahi laniger*, *Galago senegalensis*, *Indri indri*, *Mirza coquereli*, *Tarsius spectrum* and *Varecia variegata.* However, with increasing data available on a wide array of species in recent years, several species' dispersal patterns can be identified as consistent with at least one, if not several, of the three proposed ultimate causes of dispersal.

Even a cursory glance at Table 3 reveals that for most species (for which there is sufficient information to ascertain dispersal characteristics relevant to the three hypotheses) there is some form of competition occurring. However, in a few species, dispersal characteristics appear to be more clearly related to inbreeding avoidance (described below). Unfortunately, in a number of cases where competition is occurring, it is difficult to say that inbreeding avoidance is not operating, owing to the overwhelming effect of competition avoidance on behavior. And, finally, there are several species for which the data are consistent with the predictions of more than one cause of dispersal.

The next section examines case studies for each of the three causes and includes lists of other species for which these causes may be implicated.

Case studies

Hanuman langurs: A case study of dispersal and intrasexual competition for mates

Hanuman langurs (*Semnopithecus entellus*) in Jodhpur, India as reported by RAJPUROHIT and SOMMER (1993) will be used to illustrate dispersal that is clearly linked to intrasexual, specifically male-male, mate competition. In this species, the vast majority of females are philopatric and males disperse from their natal groups as juveniles, joining intermediate all male groups prior to migrating into a one male bisexual group. The polygynous group system of these langurs entails high variance in male reproductive success and high levels of competition among them. The high level of mating competition is indicated in the aggressive eviction of two-thirds of the dispersers from their natal groups, the scarcity of mating opportunities other than for the breeding male of a bisexual group, and the inability of a displaced breeding male to regain possession of his previously held group.

Most dispersals of natal group males occurred during the replacement of the breeding male in the bisexual group, indicating intolerance of the replacement male for other, unrelated males. However, many dispersals occurred during periods when the dispersers' fathers held the breeding male position of the group. These dispersers tended to be older, usually approaching sexual maturity, and were also often allowed to return to the natal group after initial dispersal to the all male band. However, despite being able to return to the natal group, none were known to obtain the breeding position in the group. This indicates that, although there is mate competition between fathers and sons, fathers are more likely to tolerate the presence of their sons in the breeding group than they would unrelated males. The high level of mate competition, the presence of aggressive evictions by breeding males (including evictions of sons by fathers), and the fact that males who were forced to disperse during undisturbed breeding male reigns were those approaching sexual maturity and thus entering the mate competition arena, all indicate that natal dispersal by young male Hanuman langurs is motivated primarily by intrasexual competition for mates.

Other cases involving intrasexual competition for mates/ mate selection

Referring to the data from Table 3, other species whose dispersal is definitely caused (at least in part) by intrasexual competition for mates include: *Gorilla gorilla*, *Hylobates lar, Cercocebus albigena*, *Cercopithecus aethiops*, *Macaca mulatta*, *Papio cynocephalus*, *Theropithecus gelada*, *Alouatta seniculus, Callicebus* spp., *Saguinus oedipus, Eulemur fulvus*, *Hapalemur griseus* (males), and *Propithecus verreauxi* (males). *Gorilla gorilla* dispersal is based on female mate selection for males who can successfully protect them from infanticide (WATTS, 1996a). *Hylobates lar* is an example of both sexes competing for mates (BROCKELMAN et al., 1998). The other species' dispersals are caused by male-male mate competition (see Table 3 for references).

Additional species whose dispersal is likely to be caused at least in part by mate competition/ selection include *Pan troglodytes*, *Colobus badius*, *Erythrocebus patas*, *Aotus azaria*, *Cebuella* spp., *Lemur catta*, and *Microcebus murinus*. NOË (1999) has proposed that *Colobus badius* female dispersal is based on female mate selection for males who possess high quality home ranges. *Alouatta seniculus* female dispersal has been attributed to female mate selection for males who can protect them and their offspring from aggression from conspecifics (CROCKETT, 1984; CROCKETT and JANSON, 1993). *Aotus azaria* is a possible example of both sexes competing for mates (HUNTINGTON and FERNANDEZ-DUQUE, 2001; FERNANDEZ-DUQUE and HUNTINGTON, 2002). The rest of the species' dispersals are believed to be caused by male-male mate competition (see Table 3 for references).

Muriquis: A case study of dispersal and intragroup competition for resources

Natal dispersal in muriquis (*Brachyteles arachnoides*) reported by PRINTES and STRIER (1999) at Estacao Biologica de Caratinga in Minas Gerais, Brazil will be used as an example of dispersal caused by intragroup (female-female) competition for resources. In this 12-month study, four adolescent females dispersed. Natal group adolescent females were frequently displaced from food sources by adult females. These adolescents never displaced other group members, indicating their inability to be highly competitive for these resources. Most displacements occurred during the dry season, when resources were scarcer. There was no evidence of directed aggression toward the dispersers prior to dispersal. However, most of the time, these adolescent females were peripheralized in the group.

Adolescent females were not only displaced prior to dispersal, but were also displaced after immigration (twice as often as residents). This is contrary to what would be predicted for dispersal caused by intragroup competition. Females are expected to select groups in which competition is lower and therefore, displacements should be infrequent. However, displacement behavior by residents toward these immigrants was short lived, only occurring during the seasonal sampling period during which the immigration took place.

The inability of natal group adolescent females to compete with adult females for resources, especially during the dry season when resources are scarce, and peripheralization of these same individuals prior to dispersal, indicates that this species is one in which dispersal is at least in part motivated by intragroup competition for resources. This argument may apply, as well, to other atelines, all of which display dispersal by females.

Other cases involving intragroup competition for resources

Other species whose dispersal is at least in part caused by intragroup competition for resources include *Hylobates lar*, *Macaca mulatta*, *Alouatta seniculus*, *Aotus azaria*, M*icrocebus murinus*, and *Propithecus verreauxi* (females). *Hylobates lar* is an example of both sexes competing for territories in a saturated environment (PALOMBIT, 1994). The other species' dispersals are either related to increasing population densities (*Macaca mulatta, Aotus azarai*, *Propithecus verreauxi*), dispersers receiving fewer resources prior to dispersal (*Alouatta seniculus*) or are related to seasonal scarcity of resources (*Microcebus murinus*) (see Table 3 for references). Other possible cases include *Colobus badius* (females selecting males based on territorial quality) and *Lemur catta* (see PEREIRA, 1993).

Chimpanzees: A case study of dispersal and inbreeding avoidance

A brief review of PUSEY's 1980 study on inbreeding avoidance in chimpanzees (*Pan troglodytes*) demonstrates a close fit of PUSEY's observations to inbreeding avoidance predictions. Males are philopatric and females disperse at adolescence. According to PUSEY, intergroup transfer by females is the result of attraction to unfamiliar males. Only females migrate, presumably because males form cooperative stable groups (see discussion of sex bias and GREENWOOD, 1980 above). Transfer is voluntary and not due to eviction. Females prefer to mate with strange males and actual occurrences of close inbreeding are rare. Further evidence that sexual attraction to unfamiliar mates governs female transfer in chimpanzees comes from the association of changes in a female's behavior with her reproductive status. After the first estrous period, females no longer associate with their siblings and females transfer only when they are in estrus. Moreover, females only return to their natal groups between estrous periods or when they are pregnant. High sex bias, voluntary dispersal by females, change in behavior with sexual maturation by females and attraction by females to unfamiliar mates all indicate that dispersal is motivated at least in part by inbreeding avoidance in this species.

Other cases involving inbreeding avoidance

Other species whose dispersal is at least in part caused by inbreeding avoidance include *Callimico goeldii*, *Colobus badius*, *Cercopithecus aethiops, Cercocebus albigena*, *Cebus capucinus*, *Samiri oerstedi*, *Lemur catta*, and *Microcebus murinus*. For *Callimico goeldii*, a case of inbreeding avoidance motivated dispersal has been described by PORTER et al. (2001). A male who lived in a social group containing only himself and his mother dispersed to another group containing sexually mature females. If inbreeding avoidance had not been the cause for his dispersal, he would have stayed in his natal group and mated with his mother. Dispersal in the remainder of the species listed above appears to be related to inbreeding avoidance because dispersal is sex biased and voluntary in these species (see Table 3 for details and references).

Discussion

Historically, there has been much debate in the primatological literature as to which is the primary or fundamental cause of primate dispersal: mate competition/mate selection, resource competition, or inbreeding avoidance (e.g.. MOORE and ALI, 1984; PUSEY and PACKER, 1987; MOORE 1988; PUSEY 1988). MOORE and ALI (1984) argued for the primacy of mate and resource competition, and the data presented in Table 3 support their argument. On the other hand, dispersal characteristics of several species in Table 3 are most consistent with the inbreeding hypothesis. Thus, the data presented in this paper support what seems to be the current consensus—that primate dispersal results from a combination of these causes, both among as well as within species, creating the variation in dispersal patterns that we see in primates.

In terms of the overall prevalence of dispersal specifically related to inbreeding avoidance, much variation is to be expected owing to the variable nature of inbreeding, and especially dispersal, costs and benefits. There is sufficient evidence to suggest that inbreeding is usually costly in primates. However, if inbreeding avoidance mechanisms (including dispersal) are either costly or limited in availability within a species (see "costs of dispersal" column in Table 3), there should be higher frequencies of inbreeding (e.g. *Hylobates lar* parent replacements: PALOMBIT, 1994). If inbreeding costs are high and dispersal costs are also high, but other inbreeding avoidance mechanisms are available, then nondispersal mechanisms should be favored. A possible example of this occurs in *Callithrix jacchus*. Although dispersal costs have not been quantified for this species, its small size and accompanying risk of predation (STAFFORD and MURAD FERREIRA, 1995) makes dispersal costly. This high dispersal cost is likely to be related to the variety of nondispersal mechanisms of inbreeding avoidance in this species (see Table 1). However, if inbreeding costs are high in a species and dispersal costs are low (see Tables 1 and 3), individuals should disperse in order to avoid inbreeding (depending also on the cost and availability of nondispersal mechanisms of inbreeding avoidance). For example, *Pan troglodytes* females experience low cost dispersal, and it appears that their dispersal is a direct result of their disinclination to mate with familiar individuals (GOODALL, 1986; PUSEY, 1980).

Future research

Future studies should focus on teasing apart the various causes of dispersal. For many species in Table 3, more than one cause is implicated, and there is no suggestion of which mechanism is the primary cause of dispersal. This is particularly true for those species in which there is a large data set but clear indications of overlapping causes. In particular, studies need to be developed to test all of the proposed causes for each case, rather than assuming that one, when it is present, is the primary or even the only cause of dispersal.

Excellent examples of these types of studies can be found for non-primate species. One example is a study by BYROM and KREBS (1999) on arctic ground squirrels (*Spermophilus parryii plesius*). The goals of this study were to measure mortality costs of dispersers versus philopatric individuals and also to determine which of the three primary ultimate causes of dispersal is/are operating in this species. These researchers radio-collared 150 juveniles when they emerged from their natal burrows. The various burrows were spread across several experimental plots including two control plots, a predator enclosure, a food supplemented plot, and a predator exclosure plot with food supplementation. The authors determined that dispersers experienced much higher mortality (25-40 % survivorship) than philopatric individuals (73 %). They also found that females were highly philopatric, except in one situation where population densities in that plot became very high and nonfood resources were a probable limiting factor. Thus, they determined that resource competition is responsible for female dispersal in this species. Males were much more likely to disperse, regardless of the level of resource competition in the plot, indicating that males either disperse to avoid inbreeding or to avoid intrasexual competition for mates. Although this kind of experimental study may not be feasible or justifiable for primates, it does suggest ways to discriminate among the various explanations for dispersal.

Table 3: Dispersal: Aspects of dispersal that may be either directly or indirectly related to inbreeding avoidance (IA), resource competition (RC), mate competition (MC).

Species	**Cases of inbreeding**	**Sex bias**	**Behavioral avoidance of inbreeding preceding dispersal?**	**Dispersal voluntary or preceded by aggression?**	**Stage of reproductive maturation at dispersal**	**Dispersal related to access to resource/ mates (& seasonality)**	**Receiving group choice related to size or mate availability**	**Costs of dispersal: factors**	**Possible causes of dispersal**	**Citations**
Apes										
Gorilla gorilla (*beringei*) Karisoke, Rwanda	Possible cases[a]	Slight female bias[b]			M: During and after sexual maturation; F: During sexual maturation		Group size does not appear to affect female group choice; Females choose males for infanticide defense	Direct transfer; No reproductive delay (females); Delayed breeding for many males	MC	WATTS, 1996a,b
Pongo pygmaeus Suaq Balimbing, Sumatra		Males and females with male bias for distance			Before and during sexual maturation				Not enough data to determine cause	DELGADO and VAN SCHAIK, 2000; SINGLETON and VAN SCHAIK, 2002
Pan troglodytes verus Taï, Côte d'Ivoire		Female bias (with exceptions)			During sexual maturation				Not enough data to determine cause	GAGNEUX et al., 1999
P. t. schweinfurthii Mahale, Tanzania	Possible cases[c]	Female bias (88% of females disperse)	Yes[d]		During sexual maturation			In receiving group: aggression from females, welcomed by males[e]	Possible MC	NISHIDA, 1990 NISHIDA et al., 1985

Species	**Cases of inbreeding**	**Sex bias**	**Behavioral avoidance of inbreeding preceding dispersal?**	**Dispersal voluntary or preceded by aggression?**	**Stage of reproductive maturation at dispersal**	**Dispersal related to access to resource/ mates (& seasonality)**	**Receiving group choice related to size or mate availability**	**Costs of dispersal: factors**	**Possible causes of dispersal**	**Citations**
P. t. troglodytes Gombe, Tanzania	See Table 1	Female bias (~50% of females disperse)	Yes		During sexual maturation		Females attracted to novel males		IA	GOODALL, 1986; PUSEY, 1980; PUSEY et al., 1997; CONSTABLE et al., 2001
Hylobates lar Khao Yai, Thailand	Possible case[f]	No bias		Appears voluntary	Before, during, and after sexual maturation		Some dispersers displaced same sex adults in existing territories	Most disperse nearby; Direct dispersal[g]; Area appears saturated with territories	MC RC	BROCKELMAN et al., 1998
Hylobates lar Ketambe, Sumatra	Son replaces father	No bias			Before and during sexual maturation			Some cases of two or more dispersing together	Not IA MC	PALOMBIT, 1994
Old World Monkeys										
Cercocebus albigena Kibale, Uganda		Male bias		Appears voluntary	During and after sexual maturation[h]		Receiving groups have more estrous females, but not fewer males	Dispersers mortality rate 12x that of residents; High aggression in receiving groups; Disperse to nearby groups; Associate with allospecifics during migration	MC Possible IA	OLUPOT, 1999; OLUPOT and WASER, 2001a,b

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Cercopihecus aethiops Amboseli, Kenya	Continual nonrandom transfer[i]	Male bias	Yes	Appears voluntary	During sexual maturation	88% dispersed during mating season	Group choice related to number of kin in receiving group and sexual attraction to novel females. Not related to number of females in receiving group, or habitat quality.	Disperse with others: (siblings and other familiars); Most transfer to adjacent groups; Higher mortality rate for dispersers	MC Possible IA	CHENEY and SEYFARTH, 1983; CHENEY, 1983; ISBELL et al., 1993
Cercopihecus aethiops Burman Bush, South Africa	Possible case[j]			Related to aggression	During sexual maturation	Peak during mating season; All dispersers were subordinates	No clear choice of groups according to number of females period Indication of attraction to novel mates	Direct dispersal to adjacent group; High aggression in receiving group	MC Possible IA	HENZI and LUCAS, 1980
Colobus badius Kibale, Uganda		Female bias (with male exceptions)			During sexual maturation			Low costs for females (readily accepted into groups)	Possible IA	STRUHSAKER, 1975; STRUHSAKER and POPE, 1991
Colobus badius Abuko, The Gambia	See Table 1	Males and females[k]	Yes[l]		Before sexual maturation				Possible IA	STARIN, 2001
Colobus badius Taï, Côte d'Ivoire		Female bias (with exceptions)					Appear to be attracted to the male coalition with the best territory		Possible MC Possible RC	NOË, 1999

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Erythrocebus patas		Male bias		Related to aggression					Possible MC	HALL, 1965; GUTSTEIN, 1978
Macaca mulatta Cayo Santiago, Puerto Rico	Genetic evidence for lack of inbreeding	Male bias (with exceptions)	By females not males Females attracted to mating with novel males	Related to aggression	Before sexual maturation (with adult exceptions)	Most during mating season; No evidence of increased mating success for males following dispersal; Lower ranked individuals dispersed earlier; Related to high population density	Females prefer novel males; Receiving groups do not differ in sex ratio	High mortality[m]; Less aggression in receiving group if transfer with familiars	MC RC IA	BERARD, 1990a,b, 1991; BERCOVITCH, 1997; BOELKINS and WILSON, 1972; COLVIN, 1986; DUGGLEBY in MELNICK and HOELZER, 1996; KAPLAN et al., 1995; MANSON and PERRY, 1993; WILSON and BOELKINS, 1970
Nasalis larvatus Lower Kinabatangan, Borneo		Males and females			M: Before sexual maturation; F: During sexual maturation			Juvenile males join all male groups. Solitaries of both sexes	Not enough data to determine cause	BOONRATANA, 1999
Papio cynocephalus Mikumi, Tanzania		Male bias (with female exceptions)					Choose groups with large number of estrous females		MC	RASMUSSEN, 1979, 1981; ALBERTS and ALTMANN, 1993, 1995;

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Papio cynocephalus Amboseli, Kenya		Male bias (with exceptions)	Yes		During and after sexual maturation[n]	Not seasonal Dispersers engaged in reproductive activity in natal group before dispersal		Costs of dispersal considered high[o] Disperse with familiars	MC	ALTMANN et al., 1988; CHENEY and SEYFARTH, 1977
Semnopithecus (*Presbytis*) *entellus* Jodhpur, India		Male bias (with female exceptions[p])		Most related to aggression	Before sexual maturation (with exceptions)	No seasonality effect	Transfer to all male bands for long periods; Dispersers then try to displace resident breeding male in bisexual group	Intermediate all male group between residence in bisexual groups; Majority emigrated with the displaced adult male or half brothers; Dispersal costs high[q]	MC	RAJPUROHIT and SOMMER, 1993
Semnopithecus (*Presbytis*) *entellus* Ramnagar, Nepal		Male bias				77% of all immigrations and 58% of all emigrations during the mating season	Choice of groups according to number of females unclear[r]	20-30% of males live in all male groups	MC	BORRIES, 1997
Theropithecus gelada Sankaber, Ethiopia	Possible cases[s]	Male bias			During sexual maturation		Joins all male group (long term);	Join groups which have relatives; Disperser then joins reproductive unit as subordinate	MC	DUNBAR and DUNBAR, 1975; DUNBAR, 1980, 1984, 1993

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Theropithecus gelada Sankaber, Ethiopia							follower or tries to unseat male. Dispersers attracted to large groups (with many females).	Aggression from group-holding male (receiving group)		
New World Monkeys										
Alouatta seniculus Hato Masaguaral, Venezuela	Potential cases[t]	Males and females (Slight male bias)		Most related to aggression (from same sex adults[u])	Most before or during sexual maturation (males later than females)	Dispersers had reduced access to resources and mates[v]	Some cases of increased mate availability for males	Costs very high, especially for females[w]	MC RC	CROCKETT, 1984;CROCKETT and POPE,1988, 1993; POPE, 1992; AGORAMOORTHY and RUDRAN, 1993
Aotus azaria Formosa, Argentina		No bias		Peripheralization (Lack of aggression)	Before and after sexual maturation	Dispersal delay due to lack of territory availability; Majority of dispersals around birth season; Evidence that dispersal is due to group reaching maximum size		Solitary dispersal for long periods	MC RC	HUNTINGTON and FERNANDEZ-DUQUE, 2001; FERNANDEZ-DUQUE and HUNTINGTON, 2002
Ateles paniscus Manu, Peru		Female bias			During sexual maturation				Not enough data to determine cause	VAN ROOSMALEN and KLEIN, 1988; SYMINGTON 1988, 1990

Species	**Cases of inbreeding**	**Sex bias**	**Behavioral avoidance of inbreeding preceding dispersal?**	**Dispersal voluntary or preceded by aggression?**	**Stage of reproductive maturation at dispersal**	**Dispersal related to access to resource/ mates (& seasonality)**	**Receiving group choice related to size or mate availability**	**Costs of dispersal: factors**	**Possible causes of dispersal**	**Citations**
Brachyteles arachnoides Fazenda Montes Claros, Brazil	See Table 1	Female bias		Appears voluntary	Before sexual maturation	Adolescents often displaced from food sources; No evidence of seasonality effect	Disperse to smaller group[x]	Costs considered low; Immigrants likely to join relatives in receiving group	RC	PRINTES, 1999; PRINTES and STRIER, 1999; STRIER 1990, 1993, 1996, 1997, 1999
Callicebus spp.		No bias		Appears voluntary	Before and during sexual maturation		Dispersing males sometimes challenge nearby weaker males for mate	Solitary ranging for long periods	MC	KINZEY, 1981; WRIGHT, 1996; BOSSUYT, 2002
Callimico goeldii Pando, Boliiva		No bias	Possible case[y]	Appears voluntary	Before and after sexual maturation	No available mate in natal group for disperser (except mother)	More possible mates in receiving group	Direct dispersal; Costs appear low	IA	PORTER et al., 2001
Callithrix jacchus		No bias	Yes (daughter withdraws from father); Also see Table 1		After sexual maturation			Costs believed high due to risk of predation	Not enough data to determine cause	SALTZMAN et al., 1994 FERRARI and DIGBY, 1996
Cebuella spp.		No bias		Related to aggression (From same-sex group members)	During sexual maturation				Possible MC	SOINI, 1988
Cebus capucinus Santa Rosa, Costa Rica		Male bias		Most appear voluntary[z]	Before and during sexual maturation			Dispersal with coresident males or into groups with familiar males	Possible IA Possible special case[aa]	ROSE, 1998; JACK and FEDIGAN, 2002

Species	**Cases of inbreeding**	**Sex bias**	**Behavioral avoidance of inbreeding preceding dispersal?**	**Dispersal voluntary or preceded by aggression?**	**Stage of reproductive maturation at dispersal**	**Dispersal related to access to resource/ mates (& seasonality)**	**Receiving group choice related to size or mate availability**	**Costs of dispersal: factors**	**Possible causes of dispersal**	**Citations**
Lagothrix lagotricha La Macarena, Colombia		No bias			Before sexual maturation (females)				Not enough data to determine cause	NISHIMURA, 1988
Lagothrix lagotricha Yasuni, Ecuador		No bias						Solitary males and bachelor group found	Not enough data to determine cause	DIFIORE, 2002
Leontopithecus rosalia Poco das Antas, Brazil	See Table 1	No bias						Either disperse with same sex relative or join group with same sex relative; Costs lower for males than females[ab]	Not enough data to determine cause	DIETZ and BAKER, 1993; BAKER and DIETZ, 2002
Pithecia pithecia Guri Lake, Venezuela		No bias						Disperse alone	Not enough data to determine cause	NORCONK in SUSSMAN, 2000
Saguinus oedipus Coloso, Colombia		No bias		Appears voluntary			Males choose group for mates and females don't[ac]	Temporary associations Some cases of aggression from receiving group	MC	SAVAGE et al., 1996
Saimiri oerstedi Corcovado, Costa Rica		Female bias (with special cases with males[ad])			During sexual maturation				Possible IA[ae]	BOINSKI and MITCHELL, 1994

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Prosimians										
Avahi laniger		Males and females						Solitaries of both sexes seen	Not enough data to determine cause	GANZHORN et al., 1985
Eulemur fulvus Kirindy, Madagascar		Male bias			After sexual maturation		In pair migration, they replaced the receiving groups' males	Solitaries and pairs	MC	OSTNER and KAPPELER, 2001
Eulemur fulvus Ranomafana, Madagascar		Male bias			After sexual maturation			Some long term solitaries (try repeatedly to enter various groups); Some enter groups in which there are familiar males	MC	OVERDORFF et al., 1999
Galago senegalensis		Slight male bias (distance)			During sexual maturation (female disperse later due to lack of available territories)				Not enough data to determine cause	BEARDER, 1987
Hapalemur griseus Lac Alaotra, Madagascar		No bias		Related to aggression	F: Before sexual maturation M: During sexual maturation		Male either joins solitary females or replaces neighboring male	Solitaries of both sexes seen rarely;	M: MC F: Not enough data to determine cause	MUTSCHLER, 1999; MUTSCHLER and NIEVERGELT, 1997;

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Hapalemur griseus Lac Alaotra, Madagascar								Most males direct transfers to neighboring groups		NIEVERGELT et al., 2002
Indri indri		Males and females							Not enough data to determine cause	POLLOCK, 1975
Lemur catta Berenty, Madagascar		Male bias		Appears voluntary	During and after sexual maturation	Dispersal during birth season		Dispersal sometimes in pairs; Direct dispersal to familiar, nearby groups; Aggression from receiving group males	MC Possible IA	JONES, 1983
Lemur catta Beza Mahafaly, Madagascar		Male bias				Dispersal prior to and during mating season		Dispersal in twos and threes	MC Possible IA	SUSSMAN, 1992
Lemur catta Duke University Primate Center, US		Male bias	Yes (females)		Most before sexual maturation (with adult exceptions)		Females attracted to novel mates	Aggression from receiving group	RC (per PEREIRA, 1993) IA	PEREIRA, 1993; PEREIRA and WEISS, 1991; SUSSMAN, 1991
Microcebus murinus Ampijoroa, Madagascar	Potential cases[af]	Male bias (with exceptions[ag])			Before first mating season	Most dispersals took place during the first half of the dry season			MC RC Possible IA	RADESPIEL et al., 2001a,b, 2002

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations
Microcebus murinus Kirindy, Madagascar	Not observed in genetic analysis	Male bias (with exceptions)							Possible IA	WIMMER et al., 2002
Mirza coquereli		No bias							Not enough data to determine cause	PAGES, 1978, 1980; KAPPELER, 1997
Propithecus verreauxi Beza Mahafaly, Madagascar		Male bias[ah]		Appears voluntary (males)	Before and after sexual maturation	Lowest ranking females emigrate from the largest groups[ai] 1/3 of dispersal during birth season	Males transfer to groups with higher proportion and number of females	Most males disperse to groups with overlapping home ranges; Little aggression from receiving group	F: RC M: MC	KUBZDELA, 1997; RICHARD et al., 1993; BROCKMAN et al., 2000
Tarsius spectrum		Males and females (with male bias for distance)							Not enough data to determine cause	MACKINNON and MACKINNON, 1980
Varecia variegata Ranomafana, Madagascar		Male bias							Not enough data to determine cause	WHITE et al., 1993

[a] 9 of 29 (28%) females reproduced in their natal groups (which had potential mates other than fathers).

[b] Some males disperse and some stay in the natal group where they may become the dominant males.

[c] Three cases of mother-son copulation during the final process of weaning and one case which a sexually mature son mated with his mother (intromission, but no ejaculation). Also, NISHIDA (in MITANI et al., 2002) reports that several females stay in their natal groups and reproduce, creating a situation in which inbreeding is possible.

[d] Presence of adult female and adolescent brother in the same group without mating

[e] However, females with infants were attacked by receiving group males

[f] Adult male left group and son (F1) assumed adult male role in territorial defense for 6 months. Also duetted with mother.

Species	Cases of inbreeding	Sex bias	Behavioral avoidance of inbreeding preceding dispersal?	Dispersal voluntary or preceded by aggression?	Stage of reproductive maturation at dispersal	Dispersal related to access to resource/ mates (& seasonality)	Receiving group choice related to size or mate availability	Costs of dispersal: factors	Possible causes of dispersal	Citations

[g] Gibbon studies have noted scarcity of floaters (LEIGHTON, 1987). Suggestions of high mortality rates among these (MITANI, 1990).

[h] However, these dispersals are likely to be secondary and natal dispersals combined

[i] CHENEY and SEYFARTH (1983) found that those who transfer randomly have higher risk of mating with close kin than do males who disperse nonrandomly.

[j] One male returned to the group from which he had originally dispersed.

[k] Most males return to natal group and most females join another group

[l] The only two females who bred in their natal troop were the only females in which all older males were absent or no longer chief copulators. Also, males did not breed with mothers (due to rejection by mothers) but did breed with mother's age mates (familiar females). This indicates the lack of a Westermarck effect. Secondary dispersal by adult females when their sons became the primary breeding male in the group is Also an indication of behavioral inbreeding avoidance.Two females whose sons did not become the primary breeding male did not disperse. Also, mothers threatened fathers who were attempting to mount their pubescent or prepubescent daughters.

[m] 21% of males who die upon first transfer do so within one year.

[n] Timing of dispersal influenced by individual mating success and female availability

[o] Due to missed reproductive opportunities during dispersal and mortality risk. Dispersers suffer a 2x to 10x higher mortality rate.

[p] These females left after a new and potentially infanticidal male entered the group (for a review of the effects of infanticide on female dispersal see STERCK and KORSTJENS, 2000).

[q] The differential mortality rate created by the sex bias in dispersal resulted in a sex ratio for subadult and adults of 1:4.1 (RAJPUROHIT and SOMMER, 1991)

[r] 50% of males migrated into groups with more adult females, 44% into groups with fewer adult males, and 6% into groups with more females and fewer males.

[s] Some males have joined reproductive units in their natal bands.

[t] Possibility of father-daughter inbreeding due to male tenure lengths; also 2 males became breeding males in natal groups

[u] However, some male dispersers appear to leave voluntarily.

[v] The tendency of females to disperse was related to the number of breeding females already present in the group, indicating role of resource competition.

[w] Males: Aggression from receiving groups; evidence of males dispersing together; 56% alive at 7 years. Females: Excluded from receiving groups; dispersed 6X farther than males; disperse alone; are at higher risk of dietary deficiencies; only 13% believed to reproduce (those who do reproduce have delays); 26% alive at 7 years

[x] Possible artifact: the study group is the largest in the area

[y] Pair believed to be mother-son never mated even when no other males present

[z] All immatures, subadults, and 82% of adult males dispersed voluntarily. Six adult males were evicted by new immigrants.

[aa] Dispersal possibly due to attraction to extragroup males or dispersing coresident males (proposed by JACK and FEDIGAN, 2002).

[ab] Males usually disperse in pairs, females rarely; males disperse directly into neighboring groups, females are solitary "floaters" for long periods.

[ac] Males choose groups without breeding males; Females choose groups with breeding females who defend their breeding position in the group.

[ad] Some age cohorts of males leave their natal group to take over the breeding positions of males in other groups

[ae] BOINSKI and MITCHELL (1994) state that male philopatry in this population is due to female biased dispersal. Thus, males can remain philopatric with reduced risk of inbreeding.

[af] Reported potential for inbreeding in 3.8% of mother-son dyads and 21.9% of father-daughter dyads

[ag] There is genetic evidence of low levels of female dispersal.; male dispersal is not obligate

[ah] All males natally disperse between existing groups. Females rarely natally disperse to form new groups with older males.

[ai] These females also do not manage to reproduce in their natal group.

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Correspondence to
Michelle Field, Department of Anthropology, Ohio State University, 244 Lord Hall, 124 W. 17th Avenue, Columbus, OH 43210, USA; E-mail: field.21@osu.edu

MALES ON THE MOVE: EVOLUTIONARY EXPLANATIONS OF SECONDARY DISPERSAL BY MALE PRIMATES. JACK, K.

Key words: migration, male dispersal, male transfer, secondary dispersal, breeding dispersal, dominance and reproductive success, inbreeding avoidance, intrasexual competition

Abstract

The dispersal of one or both sexes from the birth group is a trait common to all social mammals, but for many species, movement between groups does not end there. In several species of primates characterized by male dispersal, males have very short tenure within groups, and they appear to change groups throughout their lives. Much effort has been expended to explain the adaptive significance of natal dispersal, while comparatively little attention has been given to the significance of secondary dispersal. In this paper, I examine the data available on secondary dispersal in seven primate species and evaluate the inbreeding avoidance and intrasexual mating competition hypotheses as explanatory frameworks for its evolution. The data available, although limited, provide strong support for the intrasexual mating competition hypothesis. The inbreeding avoidance hypothesis is not well supported.

Introduction

Most social mammals are characterized by male emigration from the natal group at or near the time of sexual maturity, while females remain in their birth group for life (GREENWOOD, 1980; DOBSON, 1982; WASER and JONES, 1983; COCKBURN et al., 1985; PUSEY and PACKER, 1987a; but see MOORE, 1984; STRIER, 1994). Although dispersal in many mammalian species appears to be limited to a specific developmental stage (SMALE et al., 1997), this is not the case in primates, particularly species characterized by male dispersal where, in some cases, males continue to move between groups throughout their lives (see PUSEY and PACKER, 1987a, for review). Known as secondary or breeding dispersal, further movement between social or breeding groups following natal dispersal (CLOBERT et al., 2001) appears to be a common phenomenon for many male dispersed primate species, but one that has received relatively little attention in the primatology literature. While investigations into the adaptive significance of natal dispersal have been numerous, secondary dispersal has been largely ignored (BERTEAUX and BOUTIN, 2000). This discrepancy is due to the inherent difficulty of following the fates of dispersing individuals and a tendency for investigators to focus on the philopatric sex (MOORE, 1984). Because of these biases, we know relatively little about the patterns and causation of male secondary dispersal and even less about the effects of dispersal patterns on male life history patterns and reproductive success.

Dispersal is a risky undertaking. Dispersing individuals may be at a higher risk of predation, aggression from unfamiliar conspecifics, or even starvation once they leave familiar areas in search of a new social group (e.g. GARTLAN, 1975; DITTUS, 1977; van SCHAIK, 1983; JOHNSON and GAINES, 1990; ISBELL et al., 1993; ALBERTS and ALTMANN, 1995a). There are also opportunity costs associated with dispersal, in that males may lose opportunities to mate while spending time alone moving between breeding groups (ALBERTS and ALTMANN, 1995a). Given these costs, the adaptive benefits of dispersal must be high as dispersal is a trait common to all social mammals. Intrasexual competition and inbreeding avoidance are cited as the main factors influencing the evolution of dispersal, particularly male-biased dispersal. The effects of inbreeding have been well documented (see MOORE and ALI, 1984; ALBERTS and ALTMANN, 1995a, for reviews), and outbreeding is thought to lead to increased reproductive success. Intrasexual mating competition may push males to selectively transfer into groups with a higher number of cycling females (PACKER, 1979a), with a lower ratio of males to females (SUSSMAN, 1992), or where they can increase their dominance rank and, thereby, improve their access to mates (CHENEY and SEYFARTH, 1983). Although these explanations are invoked mainly to explain the adaptive significance of natal dispersal, they have also been investigated as evolutionary explanations for secondary dispersal in a number of species (e.g. DOBSON, 1982; MOORE and ALI, 1980; WASER, 1985; PUSEY, 1987; PUSEY and PACKER, 1987b; SHIELDS, 1987; JACK, 2001).

The goal of this report is to examine secondary dispersal in a wide range of primate taxa and evaluate its adaptive significance in light of current evolutionary theory. I begin with a review of the occurrence and frequency of secondary dispersal within the Primate order, followed by an evaluation of the inbreeding avoidance and intrasexual mating competition hypotheses for dispersal in a select number of species for which there are sufficient data.

Secondary Dispersal in Primates

Table 1 summarizes data available on male natal and secondary dispersal in twelve primate species. The studies reviewed here are limited to those on wild unprovisioned primates as both captivity and provisioning can have profound effects on dispersal patterns (for a discussion of the effects of provisioning see ASQUITH, 1989). The data presented here are by no means exhaustive, and additional data on male dispersal do exist; however, published reports providing sufficient detail of the fates of dispersing individuals, or even summaries of observed dispersal patterns, are very limited. These types of data are only possible after intense long-term observations of known individuals in multiple groups, although detailed reports of dispersal patterns are lacking even for some of the well-studied primate species (e.g. *Cebus apella*). It is possible that in cases where data on secondary dispersal are not available, that it does not commonly occur in the species in question. However, it is curious that for the majority of the well-studied male-dispersed species, most males are known to reside in more than two groups throughout their lives (see Table 1; ALBERTS and ALTMANN, 1995a).

Of the 12 species reviewed here, only one, *Alouatta palliata*, does not display secondary dispersal. For the past 30+ years, Glander and colleagues have been studying a large population of marked individuals of *A.. palliata* at La Pacifica, Costa Rica, and secondary dispersal by males has never been observed. This finding is explicable when we consider the way in which male *A. palliata* enter groups. After dispersing at a very young age (< 2yrs) these maturing males spend a portion of their

Table 1: Evidence of Secondary Dispersal by Male Primates Displaying Bisexual or Male-Biased Dispersal Patterns (DP).

Species	**DP**	**Age at Natal Dispersal**	**Secondary Dispersal (Y or N plus any details)**
*Macaca fascicularis**	♂	5 yrs (1)	**Yes** – adult males change groups ~ every three years (1)
*M. fuscata yakui**	♂	5 yrs (2)	**Yes** – complete changeover in male membership every four years (3)
M. mulatta	♂	~ 4 yrs (4)	**Yes** – males change groups every few years (4, 5) and adult males are only rarely present in groups when daughters reach sexual maturity (5)
M. silenus	♂	NA	**Yes (?)** – One documented case plus the observation of solitary males lead to the conclusion that male intertroop movement is a common feature for this species (6)
M. sinica	♂	NA	**Yes** – most males will reside in numerous groups throughout their lives (7)
*Papio cynocephalus**	♂	8.45 yrs (7)	**Yes** – males disperse repeatedly throughout their lives (8) even in old age (9)
*Chlorocebus aethiops**	♂	5 – 7 yrs (9)	**Yes** – complete changeover in male group membership over a four year study of three groups (10)
Alouatta palliata	♂♀	1.8 yrs (juveniles) (11)	**No** – based on >30 yrs of observation on marked animals (GLANDER, personal communication)
*Alouatta seniculus**	♂♀	4-6 years (some stay in natal group to help father) (12)	**Yes** – males tend to disperse more than once in their lifetime (12); coalitions of 2-4 males aggressively oust resident males (12, 13)
*Cebus capucinus**	♂	4.5 yrs (14)	**Yes** – males disperse continuously throughout their lives with complete changeover in group males every four years (15)
Saimiri sciureus	♂	4-5 yrs (16)	**Yes** – bachelor groups are common and males form alliances that last over several migrations (based on 5 yrs. of census data) (17)
*Lemur catta**	♂	3-5 yrs (18)	**Yes** – prime age males (5-7 yrs) disperse every 3-4 years (19)

(1)VAN NOORDWIJK and VAN SCHAIK, 2000; (2) SPRAGUE et al., 1998; (3) SPRAGUE, 1992; (4) DRICKAMER and VESSEY, 1973; (5) MELNICK et al. 1984; (6) KUMARA et al., 2001; (7) DITTUS, 1975; (8) ALBERTS and ALTMANN, 1995a; (9) SAPOLSKY, 1996; (10) HENZI and LUCAS, 1980; (11) GLANDER, 1992; (12) CROCKETT and POPE, 1993; (13) POPE, 2000; (14) JACK and FEDIGAN, in press a; (15) JACK, 2001; (16) ROWE, 1996; (17) MITCHELL, 1994; (18) SAUTHER et al., 1999; (19) SUSSMAN, 1992.

* Indicates species included in further analyses in this review.

lives as solitaries, usually > 3 yrs, while they attain full adult size (GLANDER, 1992). Upon reaching adult size, males may either form a new group by attracting females to them, or they can aggressively enter an established group. In the latter case, the immigrating male attacks the resident alpha male and, if successful, will join the group as the new alpha, while the deposed male becomes a subordinate member of the group. Alpha male *A. palliata* are in their prime (young adults: JONES, 1980) and, after losing their status within a group, males are no longer physically able to attempt another takeover. Given the dangers of living as a solitary animal, deposed alpha males benefit by remaining in the group as a subordinate, gaining copulations where and when they can (GLANDER, personal communication). If the immigrating male is unsuccessful in assuming the top rank within the group, he will remain solitary, and perhaps later attempt to enter a different group. GLANDER (1992) describes immigrating males as trailing a number of established groups before attempting to enter one as an alpha male; it seems that they spend a period assessing the ability of resident alpha males and try to enter a group where they have the best chance of succeeding. Given that alpha males are the youngest adult males in the group (i.e., male rank is determined by age: JONES, 1980), male *A. palliata* work within a very limited timeframe in gaining group entry.

For the remaining 11 species reviewed here, secondary dispersal appears to be a common occurrence, although data are limited. For this reason, the remainder of this report will focus on the seven species for which there are sufficient data available to address the evolutionary significance of dispersal. These species are indicated by an * in Table 1 and include: *Macaca fascicularis*, *M. fuscata yakui*, *Papio cynocephalus*, *Chlorocebus aethiops*, *Alouatta seniculus*, *Cebus capucinus*, and *Lemur catta.*

Evolutionary Explanations for Secondary Dispersal

Inbreeding Avoidance

The inbreeding avoidance hypothesis is by far the most commonly cited evolutionary explanation for the universality of dispersal among animal species and it has a very long history of investigation (e.g. DARLING, 1937; BENGSSTON, 1978; PARKER, 1979; WASER et al., 1986; ALBERTS, 1999). Many of these studies have concluded that dispersal, particularly male-biased dispersal, is an adaptation for inbreeding avoidance (see MOORE and ALI, 1984 for review). Inbreeding has been shown to result in decreased fertility and viability of offspring in a number of species, including insects, fish, rodents, baboons, and domesticated farm animals (see PACKER, 1979a, for review; ALBERTS and ALTMANN, 1995a). According to the inbreeding avoidance hypothesis, dispersal of one or both sexes from the birth group has evolved as a means of avoiding consanguineous matings and its fitness-reducing consequences (see MOORE and ALI, 1984). Although most often invoked as an evolutionary explanation for natal dispersal, the inbreeding avoidance hypothesis has been suggested as an explanation for secondary dispersal by males in a number of species (e.g. CHENEY and SEYFARTH, 1983; PUSEY and PACKER, 1987b; JACK, 2001). SMITH (1982) suggested that because of the promiscuous mating systems characteristic of most primate species, it is unlikely that males are able to recognize their daughters; given the potential costs of inbreeding, it would be advantageous if male tenure length had an upper limit imposed. This upper limit for group residency would be determined by the age at which females reach reproductive maturity for a given species (CHENEY and SEYFARTH, 1983).

If male tenure length does have a limit, then males will need to transfer between groups more than once, and, given the longevity of primates in general, it would be expected that males should continuously disperse throughout their lives. It has also been suggested that dispersal, as a means of inbreeding avoidance, should be voluntary (e.g. PUSEY and PACKER, 1987a), although HENZI and LUCAS (1980) argue that the proximate cause of frequent dispersal is inconsequential in evolutionary terms as the end result is the same: males will not reside in the group when their daughters are old enough to reproduce, and inbreeding will be avoided.

Table 2 presents data on group tenure length for nonnatal males, female age at first birth and gestation lengths for each of the seven species reviewed here. The inbreeding avoidance hypothesis for secondary dispersal predicts that male tenure lengths within groups will be shorter than female age at reproductive maturity (age at first birth – gestation length). This hypothesis was supported in four of the seven species: *Macaca fuscata yakui*, *Papio cynocephalus*, *Chlorocebus aethiops*, and *Cebus capucinus*. The proximate reasons for male dispersal in these species are variable, with either voluntary or forced dispersal, and largely unknown/unreported for *Chlorocebus aethiops*. For example, male dispersal appears to be voluntary in *Macaca fuscata yakui*, even for high-ranking males, and it has been reported that female choice for novel mates is the proximate factor driving male mobility in this species (SPRAGUE, 1992; see BERARD, 1999 for similar findings in *M. mulatta*). Male *Cebus capucinus* also display tenure lengths that are much shorter than female age at reproductive maturity, and male emigration is often voluntary even by top-ranked males (JACK, 2001), although evictions following aggressive group takeovers by extragroup males are also common (FEDIGAN, 1993). In their long-term studies of *Papio cynocephalus*, ALBERTS and ALTMANN (1995a) found two peaks in the timing of male secondary dispersal. The first peak occurs around the end of the first year of residency, when males who have been unsuccessful in obtaining mating opportunities within a group disperse and seek opportunities elsewhere. The second dispersal peak occurs in a male's sixth year of tenure, which coincides with the age that female offspring would attain reproductive maturity. Unfortunately, there is no discussion of the proximate reasons for why males disperse (i.e., forced or voluntary).

Although the social system of *Alouatta seniculus* is typically multimale or age-graded, the mating system is unimale in the sense that the dominant male is responsible for all copulations and for siring all offspring (POPE, 1990). POPE (2000) reported that in *A. seniculus*, breeding males frequently remain in groups long enough to mate with potential daughters, as the mean breeding tenure is 5-7.5 yrs while female age at reproductive maturity is approximately 4 years. However, *A. seniculus* is characterized by bisexual dispersal, with females dispersing from the natal group at 2-3 years of age (POPE, 2000; also see CROCKETT, 1984). It could be argued, then, that the natal dispersal of female *A. seniculus* is an adaptation for inbreeding avoidance, although it should be noted that it is not uncommon for either males or females in this species to remain and breed within the natal troop (CROCKETT and POPE, 1993). Female natal dispersal in *A. seniculus* appears to be dependent upon

Table 2: Nonnatal Male Tenure Length and Female Age at First Reproduction*.

Species	**♂ Tenure Length**	**♀ Age at 1st Birth (~gestation length)**	**Notes**
Macaca fascicularis	3.5-3.8 yrs (Adult tenure ~ 3 years) (1)	3.4 yrs (5.5 mos)	Alpha male tenure was ~ 2 years although deposed males may stay on in group for another .5 – 3 years as a subordinate (average tenure for males who reach top dominance was ~ 5yrs) (1); Alphas are siring the majority of infants with betas siring most of the remaining offspring. Beta males sire the offspring of daughters of alpha males (2)
M. fuscata yakui	3 years (3, 4)	4.5 yrs (5.8 mos)	Migrations are concentrated in the mating season; voluntary and thought to be in response to decreased mating success with increased length of group tenure (3, 4)
Papio cynocephalus	2 yrs (range 1 mo – 11.5 yrs with peaks in the 1st and 6th years) (5)	6 yers (5) (5.8 mos)	Most cases of secondary dispersal occurred in the 1st or 6th year of residency; first year if unsuccessful at gaining mates, in the 6th year if successful (5)
Chlorocebus aethiops	2.7 yrs (6)	4.5 yrs (5.4 mos)	Complete changeover in group males over a four year study of three groups (6)
Alouatta seniculus	5-7.5 yrs (7) (breeding tenure)	4.7 yrs (6.3 mos)	Male dominance and residency changes most often through aggressive takeovers by male coalitions; infanticide common; 32% of breeding males (only dom. male breeds) remain in group long enough to mate with maturing daughters (8); breeding males never leave voluntarily (POPE, personal communication)
Cebus capucinus	3.5 yrs (all ages); 4 yrs (adults) (9)	7 yrs (11) (5.4 mos)	Aggressive male takeovers and infanticides common (10); voluntary secondary dispersal is also common, even for alpha male (11)
Lemur catta	3.5 yrs (12)	3 yrs (13) (4.5 mos)	Several alpha males have retained top rank for 6 years (14) so inbreeding is possible. However, evidence of female avoidance of mating with offspring or maternal relatives in captivity has been reported (15)

*Unless otherwise noted, age at first reproduction and gestation length have been taken from ROWE, 1996.
(1) VAN NOORDWIJK and VAN SCHAIK, 2001; (2) DE RUITER et al., 1992; (3) SUZUKI et al., 1998; (4) SPRAGUE et al., 1998; (5) ALBERTS and ALTMANN, 1995a.; (6) HENZI and LUCAS, 1980; (7) CROCKETT and POPE, 1993; (8) POPE, 2000; (9) JACK and FEDIGAN, in press a. (10) FEDIGAN, 1993; (11) JACK, 2001; (12) SAUTHER et al, 1999; (13) SUSSMAN, 1992; (14) SAUTHER and SUSSMAN, 1993; (15) PEREIRA and WEISS, 1991.

the number of breeding females in the natal group (POPE, 2000), and additional data are necessary to determine if the tenure of breeding males influences female dispersal and if inbreeding actually occurs in this species.

Average male tenure lengths for *Macaca fascicularis* and *Lemur catta* exceed female age at reproductive maturity and do not provide general support for the inbreeding avoidance hypothesis. Even in those species where average male tenure length is shorter than age at female reproductive maturity, some questions arise as to how well these data support the inbreeding avoidance hypothesis. For example, in *Cebus capucinus*, adult male tenure length is 4 years while female age at sexual maturity is approximately 6.5 years. A similar pattern exists for *Macaca fuscata yakui*, *Papio cynocephalus,* and *Chlorocebus aethiops*. If secondary dispersal is an adaptation for avoiding inbreeding, we should see male tenure lengths very closely timed to female reproductive maturity, rather than occurring years before, as is the case for several of the species reviewed here. In addition, if dispersal has evolved as a mechanism for inbreeding avoidance, we should see most, if not all, males dispersing before their daughters reach reproductive maturity. There are, however, many examples of males remaining in a group well past the age at which female offspring reach reproductive maturity. For example, in *Cebus capucinus,* alpha males are responsible for the majority of the group's reproduction (JACK and FEDIGAN, in press b) and their breeding tenure ends either through eviction by invading male coalitions or through voluntary dispersal (abdication). However, in one of our long-term study groups at Santa Rosa National Park, one alpha male has experienced a very long tenure (> 8 yrs) and has been observed to mate with his mature daughters (personal observation). We await paternity analysis to determine if these males are producing offspring with their daughters (see ALBERTS and ALTMANN, 1995a for similar examples in *Papio cynocephalus*).

Additional evidence against the inbreeding avoidance hypothesis is provided through an examination of secondary dispersal in female-dispersed species. If dispersal is an adaptation for inbreeding avoidance, and the age at reproductive maturity of offspring imposes an upper limit for tenure length, female-dispersed species should also have limited tenure length to avoid mating with maturing sons. Table 3 presents data on female dispersal in five primate species traditionally residing in multimale-multifemale groups. Very few data are available on females in species characterized by female-biased dispersal, again demonstrating the bias in primatological studies towards the philopatric sex. Given this bias, it is not surprising that studies of species displaying bisexual dispersal (e.g., *Alouatta seniculus* and *A. palliata*) provide a much more complete picture of primate dispersal and life history patterns (e.g., see CROCKETT and POPE, 1993; GLANDER, 1992). Even for *Pan troglodytes*, one of the best-studied primate species, there is surprisingly little information on the fates of dispersing females. Strier's long-term studies of *Brachyteles arachnoids* are an exception, and her data set provides one of the most complete life history portraits for both males and females of any species. Although the data on female dispersal patterns are limited, it appears that none of the well-studied species (i.e., excluding *Saimiri oerstedi*), displaying either bisexual or female-biased dispersal, show a tendency towards secondary dispersal of females, nor do we see any species in which females continuously transfer between social groups throughout their lives (see Table 3). Although adult females might benefit from secondary dis-

Table 3: Evidence of Secondary Dispersal by Female Primates Displaying Bisexual or Female-Biased Dispersal Patterns (DP).

Species	**DP**	♀ **Secondary Dispersal**
Brachyteteles arachnoides	♀	**No**: females transfer into neighboring groups, breed, and appear to remain there for life (1). Females disperse prior to reaching sexual maturity (2)
Pan troglodytes	♀	**Rare** to absent; Nishida et al. noted secondary dispersal between study groups following the disappearance of most of the group's males (only two males remained when females transferred) (3, 4)
Saimiri oerstedi	♀	**Yes** but data are limited; Pregnant females and females with offspring have been observed to enter established groups; adult females have been observed to emigrate from study groups but no transfer data are available. Male transfer has been observed but may be rare. These data are based on a 11-month study of one social group (5)
Alouatta palliata	♂ ♀	**Rare**; 5 of 52 female emigrations were secondary (32 years of observing marked animals) (6)
Alouatta seniculus	♂ ♀	**No**; once females breed in a group they remain for life; emigration of a parous female has not been observed (7, 8)
(1) STRIER, 1997; (2) STRIER and ZEIGLER, 2000; (3) NISHIDA et al., 1990; (4) BOESCH, 1997; (5) BOINSKI and MITCHELL, 1992; (6) CLARKE and GLANDER, 2002; (8) POPE, 2000; (7) CROCKETT and POPE, 1993		

persal as a means of avoiding breeding with maturing sons, it appears that inbreeding is avoided through mechanisms other than secondary dispersal (e.g. *Pan troglodytes*: PUSEY, 1980; PARR and DE WAAL, 1999; *Brachyteles arachnoids*: STRIER, 1997).

The possibility of interbreeding among close kin, either as a result of delayed natal dispersal or long tenure of breeding males, is frequent enough that some authors have suggested that there are mechanisms in place to avoid consanguineous matings (see ALBERTS, 1999 for review) and there is mounting evidence in favor of this proposal. For example, DE RUITER et al. (1992) found that in *Macaca fascicularis,* alpha males sire the majority of offspring born into their groups (60-90 %), and in cases where they experience long breeding tenure, it is the beta males who are responsible for siring the offspring of the alpha's daughters. ESCOBAR-PARÁMO (1999) found similar results in her study of paternity in wild *Cebus apella*, while ALBERTS (1999) found strong evidence of kinship discrimination among paternal siblings based on both familiarity and recognition of paternal phenotypic characteristics in *Papio cynocephalus*. There appear, therefore, to be a number of different proximate explanations for how inbreeding is avoided in a wide range of species: female choice, breeding concessions to coresident males, voluntary dispersal of males, eviction due to aggressive takeovers, etc. These means of avoiding inbreeding do not, however, always involve dispersal. Together, these data indicate that dispersal, particularly continuous dispersal in species where multiple fathers are possible, is not necessary for outbreeding to occur and that inbreeding avoidance alone does not provide a convincing evolutionary explanation for secondary dispersal (see MOORE and ALI, 1984 and PERRIN and MAZALOV, 1999 for similar conclusions).

Intrasexual Mating Competition

Male reproductive success is regulated by male access to mates (NUNN, 1999; KREBS and DAVIES, 1993; EMLEN and ORING, 1980; TRIVERS, 1972), and it has been suggested that male secondary dispersal is not timed to avoid mating with close kin (i.e., maturing daughters) but, rather, to increase mating opportunities, (PACKER, 1979a; MOORE, 1984; MOORE and ALI, 1984) and is ultimately the result of intrasexual competition for mates (WASER, 1985; PUSEY, 1987; SHIELDS, 1987). The intrasexual mating competition hypothesis predicts that (a) males should transfer into groups with lower numbers of same-sex competitors and a higher number of available mates (lower ratios of males to females or an increased proportion of cycling females), (b) males should experience increased mating success with group transfers, and (c) in species where male dominance rank and reproductive success are related, males should engage in secondary dispersal as a means of increasing their dominance ranks. Note that these predictions are not mutually exclusive, and each prediction need not be accepted to support the intrasexual mating competition hypothesis. Published data on secondary dispersal are not complete enough to assess all three of these predictions for each of the seven species reviewed here, however, collectively the predictions and the data set do provide some insight into this explanatory hypothesis.

Mate availability and mating success. If dispersal functions to increase male access to mates, then we should see males transferring into groups with more favourable sex ratios. Data on the ratio of adult males to females in groups before and after male transfers are, unfortunately, very limited and are unavailable for *Macaca fuscata yakui*. These data are also unavailable for *A. seniculus*; however, given that this species is characterized by a single breeding male, if transferring males are able to attain alpha male status within their new groups, they will be increasing their reproductive opportunities through their transfer. Although changeovers in breeding males do occur from challenges within the group (CROCKETT and POPE, 1993), takeovers by subordinate males from neighboring groups have also been observed. POPE (1990) suggests that males move between neighboring groups because this better enables them to assess their opportunities of attaining breeding status before staging a takeover.

For the remaining five species for which data on sex ratios are available, the results are far from straightforward. In *Macaca fascicularis* and *Chlorocebus aethiops*, males do not preferentially transfer into groups with more favourable sex ratios, although it appears that males may move towards groups where they can attain a high dominance rank, which is tied to mating success in both of these species (see "Male rank and secondary dispersal" below). Male *Papio cynocephalus* show a tendency to move towards groups with a lower number of same-sex competitors and in *Cebus capucinus* and *Lemur catta*, males transfer into groups with lower ratios of males to females. The most complete data on group composition before and after male transfer come from the long-term study of *Cebus capucinus* in Santa Rosa National Park, Costa Rica. In this species we were able to track the fates of 16 nonnatal males as they moved between study groups; all 16 of these males transferred into groups with significantly lower ratios of adult males to females (JACK, 2001; JACK and FEDIGAN, unpublished ms.).

Although it has been suggested that secondary dispersal of male *Papio cynocephalus* is influenced by the number of cycling females to males (PACKER, 1979b; SMITH, 1992), long-term data on this species in Amboseli indicate that male transfer is largely related to their mating success within a particular group. ALBERTS and ALTMANN (1995a) found that males who were unsuccessful at mating in one group were successful in the next group. In *P. cynocephalus* male tenure length appears to be largely dependent upon their mating success, with unsuccessful males transferring groups after only one year, while successful males remained in groups for an average of six years. Although comparative data on transfer groups in *Macaca fuscata yakui* are not available, the proximate explanation for male secondary dispersal in this species strongly suggests that mating success is also the main motivator. In this species, female choice for novel mates appears to be the proximate factor driving male dispersal, as dispersal appears to be voluntary, even for males at high ranks, and occurring in response to declining mating success (SPRAGUE, 1992; see BERARD, 1999 for similar findings in *M. mulatta*). Male *M. f. yakui* are reported to experience a peak in mating success during the first few years of group residency (SPRAGUE et al., 1998; SPRAGUE, 1992) and would, therefore, increase their mating success by transferring frequently between groups.

Male Rank and Secondary Dispersal

In the majority of primate species, male intrasexual competition within groups results in agonistic dominance hierarchies (WALTERS and SEYFARTH, 1987) and there is considerable debate over the correlation between high dominance rank and increased reproductive success. Widely known as the "priority of access" model (ALTMANN, 1962), the question of the reproductive benefits of high rank has had a long history of investigation in primate studies (e.g. TAKAHATA et al., 1999; see DE RUITER and VAN HOOFF, 1993; COWLISHAW and DUNBAR, 1991; FEDIGAN 1983 for reviews). Although the debate is far from settled, the relationship between these two variables may shed light on male dispersal patterns, as dispersal for many species is associated with a change in dominance rank. As predicted by the intrasexual mating competition hypothesis, if high rank provides males with increased access to mating opportunities and/or increased reproductive success, then males should be dispersing in an attempt to increase their dominance rank. To investigate this prediction, it is first necessary to determine if there is a correlation between dominance rank and reproductive success, and then examine male dispersal patterns and rank changes that occur with group transfers.

Data on male dominance rank and reproductive success are available for six of the seven species reviewed here (excluding *Chlorocebus aethiops*) (see Table 4). A positive correlation between male dominance rank and reproductive success has been reported for *Macaca fascicularis*, *Papio cynocephalus*, *Alouatta seniculus*, and *Cebus capucinus*. For the remaining two species, *Macaca fuscata fuscata* (no data are available for *M. f. yakui*) and *Lemur catta*, there was no significant correlation between male dominance rank and reproductive success. Interestingly, these latter two studies were based on captive populations, while the four studies reporting a positive correlation between male rank and reproductive success were from wild populations. ALTMANN et al. (1996) suggest that captive conditions may account for the lack of correlation between dominance and reproductive success in some species, and paternity data on both wild and captive *Macaca fascicularis* provide strong support for this suggestion. DE RUITER et al. (1992) found a significant positive correlation between dominance rank and reproductive success in their study of wild *M. fascicularis*, while SHIVELY and SMITH (1985) reported a negative correlation in their study of a captive population of the same species. The lack of correlation between male rank and reproductive success in captive populations may be related to the fact that in captivity, male dominance rank is generally much more stable over the long-term than it is in wild populations. This stability of male rank in captivity is likely due to the complete absence of either emigrations or immigrations characteristic of many captive groups, or the controlled conditions under which new individuals are introduced (e.g. FRAGASZY et al., 1994). ALTMANN et al. (1996) found that although there is a strong correlation between male rank and reproductive success in *Papio cynocephalus*, long-term variance in male reproductive success is low due to the instability of rank over time. Moreover, in wild populations, male rank is generally dependent on age and for all seven of the species reviewed here, dominant males are described as being "prime age" (see Table 4). In captive or provisioned groups, on the other hand, high rank is often based on tenure length and aged alpha males are common (see WALTERS and SEYFARTH, 1987 for review). Although the possibility remains to be tested, it would be of interest to see if studies of captive populations found an initial correlation between dominance rank and reproductive success that wanes with time, similar to what has been reported for wild groups of *Macaca fuscata yakui* (SPRAGUE et al., 1998). In this species, high-ranking males do ini-

Table 4: Correlation Between Male Dominance Rank (DR) and Reproductive Success (RS), Tenure Length According to Rank, and Changes in Male Rank and Group Sex Ratios Experienced With Group Transfers.

Species	Correlation Between Dominance Rank and Reproductive Success*	Alpha /Subordinate Tenure	Rank ↑↓ With Transfer	Sex Ratio (M:F) ↑↓ With Transfer	Notes
Macaca fascicularis	Positive correlation Alphas sire 60-90 % of all infants with betas siring ~ 50 % of the remaining infants (2)	25.4 ± 3.7 mos although total tenure of males who achieve top dominance is 61.6 ± 5.6 mos as they often remain as betas after losing alpha position (1) Sub. Tenure: 38.2 ± 3.9 mos. (1)	↑↓ Males benefit from entering groups at low ranks as internal challenges for top rank are more successful (84 %) than external challenges (34%). Males move into neighboring groups and may be assessing the possibilities of obtaining high rank in various groups prior to joining (1)	NS differences in sex ratios within emigration and immigration groups (1)	Alpha males are always prime age adults (~9 yrs). Top rank is only achieved though active challenges and usually held for at least one mating season (1). Deposed alphas never attain top rank again but take up mid to high rank in next groups (3)
M. fuscata yakui	No correlation Captive study of *M. f. fuscata*. Male rank and ejaculatory success were correlated but not with reproductive success (6). In wild groups there is an initial correlation between rank and mating success but this declines with troop tenure length.	NA Complete changeover in male membership every four years, although not simultaneous (4)	↑↓ Adult males may aggressively enter groups and assume top rank, although most join peacefully at low ranks (4)	NA No data on the fates of migrating males but emigrations seem to be related to mating success rather than rank (7)	Male rank can be increased through death/dispersal of higher ranking males or through dispersal and aggressive entry into new group (4, 5, 8). In unprovisioned groups male rank is related to age, with males attaining their highest rank in prime adult stage (10-15 yrs) (8)
Papio cynocephalus	Positive correlation Dominant males have reproductive priority, but	67 mos for top half hierarchy; 18 mos bottom half of hierarchy (12)	↑ (see notes)	↓ Males moved into groups with lower numbers of "excess males" (9)	No direct reports of male DR changes with transfer. However, male DR is

Species	**Correlation Between Dominance Rank and Reproductive Success***	**Alpha /Subordinate Tenure**	**Rank ↑↓ With Transfer**	**Sex Ratio (M:F) ↑↓ With Transfer**	**Notes**
Papio cynocephalus	male dominance rank is unstable over time (11)	Rank (12) and mating success (9), which are correlated in this species (11), are excellent predictors for male tenure length.			+ correlated to male mating and reproductive success (11) and males who were unsuccessful in mating in one group were successful in the next (9) indicating a rise in DR with group transfer. High ranked males are in prime adult stage (11)
Chlorocebus aethiops	Not measured + correlation between male rank and mating success (13, 14, 15)	20.7 mos for alpha males (N=3) (15) 2.68 yrs for all males; range 2 - 26 mos (15)	↑ Male rank is reported to increase with dispersal (13, 14). Nine of 12 males for which rank was known before and after transfer, rose in rank within three months of their transfer (14) and no alpha males emigrated until they lost their status (15)	Males did not consistently transfer into groups with greater numbers of females (14; 15) or those with more favorably skewed sex ratios (14)	Alpha status is agonistically attained and achieved, males are assumed to attain highest ranks in their prime.
Alouatta seniculus	Positive correlation Alpha males have exclusive access to copulations and reproductions; females refuse matings with subs. to avoid infanticide (17)	Breeding/alpha male tenure is 5-7.5 yrs. Alpha male is evicted by outside males or challenged by subordinates within the group. If males are related, the deposed alpha will sometimes remain as a subordinate.	↑ Sub. males will disperse and attempt to take over breeding position in a neighboring group.	NA. Subs. that transfer and attain alpha status will always be experiencing an ↑ in access to mates as only the dominant male reproduces	↑ rank and ↑ in available mates is only applicable to those males able to become the breeding male within a group. Note: coalitions between related males last 8.2 yrs, although these may include multiple transfer

Species	**Correlation Between Dominance Rank and Reproductive Success***	**Alpha /Subordinate Tenure**	**Rank ↑↓ With Transfer**	**Sex Ratio (M:F) ↑↓ With Transfer**	**Notes**
Alouatta seniculus		Alphas never voluntarily emigrate (16) Subordinates in unrelated coalitions disperse in 2.3 yrs (see notes)			(18). Breeding males are prime age adults.
Cebus capucinus	Positive correlation Alphas siring > 80 % offspring (20)	Alphas: 47.9 mos Subs.: 51.4 mos (21) (see notes)	↑ (21) Male rank significantly increased with troop transfer (N=16)	↓ Ratio of M:F was significantly lower in immigration vs. emigration groups (N=16) (21)	Alpha males lose rank through takeovers by extragroup males (22); rank reversals within group (23); voluntary dispersal (21). High ranking individuals are adults in their prime (~11-16 yrs)
Lemur catta	No correlation Captive study (27); In the wild alpha males are the first to mate and they actively guard females as long as possible following copulation (28); mating order appears to influence paternity in captive lemurs, although there was no correlation between DR and RS (27).	3.5 yrs for all mature males (28); 3 of 9 dominant males maintained their position for 6 yrs (26)	NA Males usually enter groups at low ranks (26) but they may be preferentially moving towards groups where they can eventually attain dominant, central position (25)	↓ Most males transfer into groups with fewer males (no mention of sex ratio) (30); males show a tendency to leave groups with higher M:F sex ratio (25);	Females preferentially mated with newly introduced, but low ranking males, while actively avoiding close maternal relatives (27); groups are characterized by one agonistically dominant male who has priority of access to resources (29); top ranked males are prime adult age (25)

*Unless otherwise noted, all assessments of reproductive success are based on genetic studies of wild populations.

(1) VAN NOORDWIJK and VAN SCHAIK, 2001; (2) DE RUITER et al., 1992; (3) VAN NOORDWIJK and VAN SCHAIK, 1988; (4) SPRAGUE et al., 1998; (5) SPRAGUE, 1992; (6) INOUE et al., 1993; (7) TAKAHATA et al., 1999; (8) SUZUKI et al., 1998; (9) ALBERTS and ALTMANN, 1995a; (10) ALBERTS and ALTMANN, 1995b; (11) ALTMANN et al., 1996; (12) SMITH, 1992; (13) CHENEY and SEYFARTH, 1983; (14) CHENEY, 1983; (15) HENZI and LUCAS 1980; (16) POPE, 2000; (17) POPE, 1990; (18) CROCKETT and POPE, 1993; (19) JACK and FEDIGAN, in press a; (20) JACK and FEDIGAN, in press b; (21) JACK, 2001; (22) FEDIGAN, 1993; (23) PERRY, 1998; (24) SAUTHER et al., 1999; (25) SUSSMAN, 1992; (26) SAUTHER et al., 2002; (27) PEREIRA and WEISS, 1991; (28) SAUTHER, 1991; (29) SAUTHER and SUSSMAN, 1993; (30) JONES, 1983.

tially experience higher copulatory success, but this success decreases with increasing time spent in any one group, possibly an effect of decreased novelty of males to females over time.

PEREIRA and WEISS (1991) found no correlation between male dominance rank and reproductive success in their study of captive *Lemur catta*; however, a closer examination of their findings, in combination with data gathered from studies of wild populations of the same species, provides interesting results. In their study of mating behavior in wild *L. catta*, SAUTHER and SUSSMAN (1993) found that one of the adaptive advantages of becoming a central, top-ranking, male is that they are able to form relationships with females year-round and this enables them first access to females during the mating season. Interestingly, PEREIRA and WEISS (1991) found that those males who mated first were successful in reproducing (according to paternity testing); however, in their captive study group, high ranked males did not get first access to females. Instead, females showed a tendency for mating with a newly introduced "immigrant" male. These results provide good evidence that captive conditions, which block natural dispersal patterns, influence the mating system, at least within this species.

Given the finding that dominance rank and reproductive success are positively correlated in four of the species reviewed here, we can now test the prediction that if secondary dispersal functions to increase male access to mates, then males should be trying to increase their dominance rank with troop transfer. Unfortunately, very few studies are following the fates of dispersing males and even those with impressive datasets, such as the long-term studies of *Papio cynocephalus* in Amboseli (e.g. ALBERTS and ALTMANN, 1995a), do not report data on male rank before and after group transfers. Data presented in Table 4 indicate that, overall, the species reviewed here do show a tendency for males to increase their dominance rank with group transfers, but no generalizations can be made with the limited evidence available. The most complete data available again come from the long-term studies of *Cebus capucinus* in Santa Rosa National Park, Costa Rica, where the fates of 16 non-natal males were tracked between 1984 and 2000 (JACK, 2001; JACK and FEDIGAN, unpublished ms.). We found that male *C. capucinus* experienced a significant increase in rank with group transfer and although several males maintained their same rank (namely alpha males moving between groups), none of the males experienced a decline in dominance rank. As male rank and reproductive success are positively correlated in this species, the finding that dispersal is either voluntary or forced, and that males experience an increase in rank with group transfer, provides very convincing evidence for the intrasexual mating competition hypothesis, for this species.

Similar results can be extrapolated from the data available on *Papio cynocephalus*. In this species, male dominance rank is correlated with both mating and reproductive success (ALTMANN et al., 1996), and male tenure length appears to be determined by his mating success, with unsuccessful males dispersing sooner than successful males (see SMITH, 1992; ALBERTS and ALTMANN, 1995a). ALBERTS and ALTMANN (1995a) found that males who were unsuccessful in mating in one group were usually successful in the subsequent group. Collectively, these data provide good evidence that male dispersal is the result of intrasexual mating competition and functions to increase male mating success. In fact, ALBERTS and ALT-

MANN (1995a, p. 281) suggest that "[d]ispersal therefore influences every component of lifetime reproductive success, and variability in dispersal patterns may be a crucial source of variance in fitness for male baboons".

DE RUITER et al. (1993) found a positive correlation between male dominance rank and reproductive success in *Macaca fascicularis*; however, it does not appear that males experience a rise in dominance rank with troop transfer. In fact, van NOORDWIJK and van SCHAIK (2001) suggest that males may benefit from entering groups at low ranks and then making internal challenges for the dominant positions within the group, as 84 % of internal challenges for top rank were successful, compared to only 34 % of external challenges. van NOORDWIJK and van SCHAIK (2001) found that males transfer into groups where they have a better chance of attaining high ranks in the future and that a male's lifetime reproductive success is largely determined by his ability to attain high dominance rank. Similar findings have been reported for *Lemur catta*, where, although males enter groups at low ranks, they seem to move towards groups where they have a chance of eventually attaining a dominant, central position (SUSSMAN, 1992). Because, in wild populations, dominant, central, males have priority of access to estrous females, it could be argued that dispersing males may be attempting to increase their dominance rank and their access to mates, but additional data are needed before conclusions can be made. Although no paternity data are yet available for *Chlorocebus aethiops*, a positive correlation between male dominance rank and mating success has been reported (CHENEY, 1983; CHENEY and SEYFARTH, 1983; HENZI and LUCAS, 1980). Male transfer in *C. aethiops* is usually associated with a rise in dominance rank (HENZI and LUCAS, 1980), which would in turn lead to an increase in mating success for these males.

Conclusions

Our understanding of dispersal patterns in nonhuman primates, in particular their reproductive consequences, is extremely limited. Although data on male secondary dispersal are scant, it does appear to be the norm for most of the well-studied species and is not restricted to a single life stage. The inbreeding avoidance hypothesis for secondary dispersal predicts that male tenure length should not exceed female age at reproductive maturity and that males disperse to avoid mating with maturing female offspring. Although average male tenure length is shorter than female age at reproductive maturity in four of the seven species investigated, collectively, the data reviewed do not support the inbreeding avoidance hypothesis. Inbreeding avoidance may be better described, as MOORE and ALI (1984) have suggested, as an epiphenomenon of dispersal rather than an adaptation for it. MOORE and ALI (1984) argue that the logic behind the assumption that dispersal is an evolved response to the occurrence of inbreeding depression is faulty. This logic 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" (MOORE and ALI, 1984; p.94). As outlined above, there are other mechanisms for avoiding inbreeding, such as female choice for novel mates, kin recognition, and breeding concessions to coresident males, and dispersal is not the only mechanism for preventing inbreeding. This review found that inbreeding avoidance alone does not explain the occurrence of secondary dispersal in the species investigated here.

Although additional data detailing the fates of known individuals moving between groups are needed, the data reviewed here provide strong support for the intrasexual mating competition hypothesis. The intrasexual mating competition hypothesis predicts that males should transfer into groups with more favorable sex ratios or a greater number of cycling females, males should experience increased mating success with group transfers, and if male dominance rank is linked to mating and/or reproductive success, males should disperse in an attempt to increase their dominance rank. Although data availability precluded the power to assess each of these predictions in all seven species, the intrasexual mating competition hypothesis was supported in each of them. It does appear that male dispersal functions to increase male mating success, be it through transfer into groups with more favorable sex ratios and/or into groups where a higher dominance rank can be realized.

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Correspondence to:
Dr. Katharine Jack, Department of Anthropology, Tulane University, 1021 Audubon Street, New Orleans, LA 70118, U.S.A.; E-mail: kjack@tulane.edu

THE EFFECTS OF DISPERSAL COSTS ON REPRODUCTIVE SKEW AND WITHIN-GROUP AGGRESSION IN PRIMATE GROUPS. HAGER, R.

Key words: reproductive skew, models, dispersal costs, within group aggression, philopatry, primates

Abstract

The study of primate dispersal and philopatry has revealed greater variation between species and higher taxonomic groups than previously assumed. While it is clear that both behavioral patterns incur costs and benefits that need to be weighed against each another, it remains very difficult to assess the relative importance of individual factors both in empirical and theoretical studies. Models of reproductive skew have recently been developed that offer a framework linking the costs and benefits of dispersal and philopatry to subordinates and dominants to the distribution of reproduction in a group ("reproductive skew") and to levels of within-group aggression. Specifically, these models investigate the degree of reproductive skew given certain costs of dispersal. In this paper, I present examples of primate dispersal patterns and philopatry that can be analyzed using skew models. Further, I show that levels of within-group aggression can be expressed as the result of constraints on dispersal that will affect the distribution of reproduction in the group.

Introduction

Primate societies are characterized by high rates of dispersal of individuals (GREENWOOD, 1980; STRIER, 1994). The evolutionary causes of why animals disperse have invoked much discussion about the costs and benefits associated with dispersal (see e.g. GADGIL, 1971; CLOBERT et al., 2001; PUSEY and PACKER, 1987; SHIELDS, 1983). Theoretical studies have mainly focused their analysis on either the costs incurred by dispersal ("ecological constraints models": e.g., EMLEN, 1982) or on the benefits of philopatry (e.g., STACEY and LIGON, 1987). However, the issue of whether a behavior will be selectively advantageous or not will clearly depend both on costs and benefits that need to be weighed against each other. Only recently have models identified that costs and benefits of staying in the group versus dispersing need to be considered together when analyzing this tradeoff (EMLEN, 1995; KOKKO and JOHNSTONE, 1999). A key predictor in this tradeoff will be the potential reproductive success of an individual inside and outside the group. The difficulty in discerning the adaptive value of dispersal behaviour is to decide what the consequences are for an individual's fitness (measured in its lifetime reproductive success) given specific ecological constraints.

Using the common currency of inclusive fitness for both costs and benefits, several reproductive skew models have been developed that analyze under what genetic and ecological conditions dispersal of individuals is to be expected. In this article, I discuss how reproduction between group members is distributed given specific costs of dispersal and under what conditions some individuals are expected to remain in the group and when to leave. The use of reproductive skew models in primatology has only recently been identified (e.g., HAGER, 2003) and yields an interesting and new framework with which to explore several patterns of dispersal in primates.

Two types of dispersal patterns can be distinguished. Leaving the natal group has been referred to as natal emigration while any further movement from a group is termed secondary dispersal (PUSEY and PACKER, 1987). In most Old World monkeys, with the exception of hamadryas baboons (*Papio hamadryas*) and red colobus monkeys (*Procolobus badius*), males disperse (natal and secondary dispersal). Both sexes disperse in red howling monkeys (*Alouatta seniculus*), mantled howlers (*A. palliata*), gorillas (*Gorilla*), and hamadryas baboons, whereas in groups of red colobus and chimpanzees (*Pan troglodytes*) females appear to disperse at a higher rate than males (PUSEY and PACKER, 1987; STRIER, 1994).

After leaving their group, individuals may either join other bisexual groups, remain solitary, or join single sex groups. In particular, emigrated males will often associate and form male-male coalitions to gain access to bisexual groups or to evict the dominant male (e.g., Hanuman langurs, *Semnopithecus entellus*: MOORE, 1984). The most common proximate causes of male dispersal are eviction by the dominant male or leaving voluntarily, but these patterns of response may vary even within species (PUSEY and PACKER, 1987; DIXSON, 1998; HORWICH et al., 2000). Several hypotheses about costs and benefits have been proposed to explain the ultimate causes of why individuals disperse.

Forms of Costs and Benefits of Dispersal and Philopatry

To investigate the ultimate causes of dispersal versus philopatry one first needs to consider what the costs and benefits of each behaviour are. Several factors have been proposed to play a key role in determining whether an individual should stay or leave the group. A major advantage of dispersal is said to be inbreeding avoidance (e.g. PACKER, 1975; PUSEY and PACKER, 1987). If offspring remain in the natal group and mate with parents or siblings, deleterious mutations will accumulate in following generations and hence lower the fitness of the parents (FALCONER and MACKAY, 1996). Characters that are not closely related to the fitness of an individual are considerably less affected by inbreeding. Support for this interpretation comes from the observation that normally one sex disperses from the natal group while the other stays (GREENWOOD, 1980; MOORE and ALI, 1984; PACKER, 1985), thus avoiding, for instance, the consequence that fathers might mate with their reproductively mature daughters. However, in many species both sexes disperse, so this hypothesis alone cannot account for the observed patterns (MOORE and ALI, 1984). In particular, male dispersal has been explained by the fact that male reproductive success depends highly on access to females (KREBS and DAVIES, 1993; TRIVERS, 1972). Therefore, males are selected to move to groups where there are potentially more mates (CLUTTON-BROCK and HARVEY, 1976; PACKER, 1979). This could take the form of natal or secondary dispersal.

Missed reproductive opportunities are commonly cited as a cost of dispersal of particular relevance to males (EMLEN, 1995). On the other hand, female reproductive success is more dependent on RESOURCE availability (KREBS and DAVIES, 1993; STERCK et al., 1997) which might predispose them to remain in familiar habitat or to remain where resources can be cooperatively defended (WRANGHAM, 1980). Staying in the natal group might also increase chances of inheriting a breeding position in the future (KOKKO and JOHNSTONE, 1999; STACEY and LIGON, 1987). It has generally been argued that philopatry increases the inclusive fitness benefits from helping close kin (HAMILTON, 1964, 1972). However, it should be noted that recent theoretical work has suggested that philopatry might also lead to increased competition among relatives (WEST et al., 2002; also see PEREZ-TOME and TORO, 1982). As a consequence, the benefits gained from helping close kin can be offset by increased competition (WEST et al., 2002). Specifically, within group competition for food is to be expected and is likely to be a major cost of group living (JANSON, 1988; ALEXANDER, 1974).

Several other factors have been identified as possible costs of dispersal. Among the key factors are increased predation risk or general risks associated with migration, difficulties in setting up a new territory and finding a potential partner as well as problems when attempting to join a different group (MOORE and ALI, 1984; VAN SCHAIK, 1989; VEHRENCAMP, 1983a,b). Support for these hypotheses comes from evidence of high mortality among dispersing individuals (e.g. GAINES and MCCLENAGHAN, 1980). In a long term study on the costs of dispersal for male baboons, ALBERTS and ALTMANN (1995) demonstrated that costs of philopatry were high mortality of offspring sired by males that remained in the natal group while dispersal incurred serious costs in terms of higher mortality risks for solitary individuals and missed reproductive opportunities. It should be noted that there are numerous exceptions to these general observations (see, for example, STRIER, 1994)

It shows that often costs of dispersal behaviour can be expressed as benefits of staying in the group. Here, I propose that under specific conditions animals may disperse either because they are not granted a share of reproduction in the group or that they are evicted because they lower the reproductive share of the dominant group member. Thus, costs of dispersal that affect whether a given share of reproduction is favorable—over potential chances outside the group—will determine how reproduction is shared among the same sex in a group. This tradeoff is formally analyzed by models of reproductive skew (e.g., HAGER, 2003). In the next section, I introduce the most relevant skew models and assess their potential to explain dispersal and its effects on the reproductive success of dominant and subordinate group members.

Dispersal, Reproductive Success, and Models of Reproductive Skew

Models of reproductive skew have been developed to investigate how dispersal costs, relatedness among group members and costs and benefits of subordinates to group productivity interact and what the fitness consequences for the individuals are (e.g. CLUTTON-BROCK, 1998; HAGER, 2003; VEHRENCAMP, 1983a,b). The principal measure of fitness in these models is the share of reproduction obtained by individuals, or, simply, how many offspring individuals can be expected to produce given specific conditions. Reproductive skew refers, then, to the differences in reproduction among group members of the same sex. Skew is high where one or a few individuals monopolise reproduction while there is no skew when reproduction is egalitarian.

Most reproductive skew models apply a game theory approach in that the predicted reproductive success of individuals depends on what others in the group do ("frequency-dependence"). One class of these models can be applied to primates because many of the underlying assumptions hold (HAGER, 2003). These so called concession models derive fitness payoffs to dominant and subordinate group members and determine what proportion of reproduction can be claimed by individuals depending on costs of dispersal and relatedness of group members. Thereby, one can predict under what conditions an individual is expected to disperse either voluntarily or through eviction by the dominant. The term, concession model, refers to the assumption that dominant individuals will have to concede a share of reproduction to other group members in order to prevent them from dispersing. Thus, these models analyze the tradeoff between staying (and obtaining a certain share of reproduction) or dispersing and attempting to breed somewhere else. Other assumptions are that a dominant in the group is able to expel individuals from the group and decides who can join the group. Subordinates should be prevented from dispersing when their contribution to group productivity is positive and outweighs negative effects of their presence. The share of reproduction that needs to be conceded, as well as deleterious effects from increased competition for resources, are negative effects on the dominant's fitness.

Further, several skew models make predictions about the level of aggression that is to be expected in a group given specific costs of dispersal and benefits from aggressive behavior. An individual is expected to leave the group when its breeding chances and its prospective reproductive success are greater than when remaining in the group. This may depend on several factors such as its relative fighting ability (used to gain breeding status in the group), costs of dispersal, and chances to inherit the breeding position.

In the following section I present several skew models that make testable predictions about how these factors interact and what the consequences are for the reproductive success of individuals.

Concession Models of Reproductive Skew Applied to Primate Dispersal

Most of the discussed models take the form of concession based models in that they assume a dominant individual may benefit from the subordinate's presence (see above). Here, the subordinate's strategy to is to leave the group when it is not granted a share of reproduction. The models show that when costs of dispersal are high, the subordinate will be granted only a low share of reproduction (resulting in high skew in the group) because only a small staying incentive is required to render a positive tradeoff for staying (i.e., benefits>costs= stay in group). In other words, the subordinate would have a lower inclusive fitness if it left the group. When the breeders are related, skew is also expected to be high because the inclusive fitness benefits the dominant gains through the subordinate's presence also increase the subordinate's fitness; thus, the latter is willing to accept a lower share of reproduction.

It has been found that concession models of reproductive skew offer a good framework to investigate the tradeoff between leaving or staying, or between joining or not joining a group, that primates encounter (HAGER, 2003). Male-male associations are of particular interest here. These all male groups are normally composed of related and unrelated individuals of either young males that left (or were expelled from) their natal group and/or older males that lost their dominant position. Male-

male coalitions might attempt to gain access to females or membership to other groups or cooperatively defend their group against extra group males (SMUTS, 1987; BOINSKI and MITCHELL, 1994; HORWICH et al., 2000). The question at issue is how reproduction is shared among these males. Do subordinate males fare better when staying in such groups and accepting their share of reproduction granted by the dominant or do they stand a chance to increase their reproductive success from dispersal?

In chimpanzees, males normally stay in their natal group and are thus related (NISHIDA and HIRAIWA-HASEGAWA, 1987). The dominant male tolerates some, but not all subordinate matings and skew is presumably high, taking the number of copulations as a measure (NISHIDA, 1983). Clearly, the dominant lowers his direct reproductive success by sharing reproduction in the group. Concession models explain this by the benefits of the subordinates' presence in the group. Because these males help defend the group against extra group males, the dominant benefits and thus concedes a share of reproduction in order to retain the subordinates. In turn, they are related to the dominant and increase their inclusive fitness. Their share of reproduction thus will favor staying in the group compared to leaving the group. In other words, dispersal costs (costs of migration as well as those associated when immigrating into other groups) render staying in the group a better option for these subordinate males. While the general prediction of concession models appears to hold for chimpanzees, several variables remain unexplained. For instance, it is not clear whether subordinate reproduction is the result of the dominant conceding a share of reproduction or because the dominant has simply incomplete control over group productivity (CLUTTON-BROCK, 1998).

An important advantage of philopatry is the possibility of inheriting breeding status in the future (STACEY and LIGON, 1987). This has been formally modelled by KOKKO and JOHNSTONE (1999) in a concession based model comparing the delayed benefits of philopatry with the immediate opportunities for independent breeding by using the common currency of lifetime inclusive fitness for both costs and benefits. This approach appears to be very useful when comparing current benefits and future benefits of staying versus leaving, in particular, when the benefits of the association are asymmetrical or unequal for the members. The model demonstrates that chances to inherit breeding status can greatly reduce the reproductive share required to keep subordinates from dispersing, thus increasing reproductive skew. In addition, the dominant benefits, also, from tolerating subordinates in the group, even if their presence lowers the group productivity. This is because the dominant will benefit, too, if a relative takes over the breeding position. Only if a cost is incurred from inbreeding are higher dispersal rates expected. The model predicts, further, that groups are more stable in long lived species because greater survival prospects enhance the benefits of queuing ("persistence").

The social queuing model (KOKKO and JOHNSTONE, 1999) may be applied to explain dispersal patterns in several primate species, specifically, in those with age-graded groups. For instance, in Thomas's langurs, *Presbytis thomasi*, age-graded groups occur when young males born in the group are tolerated by the dominant male after they have reached sexual maturity (STEENBEEK et al., 2000). Because both sexes emigrate in this species, there are chances to establish new groups with other emigrated individuals. Thus, the costs of dispersal can be assumed to be less than in species where only one sex emigrates. This, together with the chance that the subordinate males may take over the breeding position, should lead to high reproductive skew in age graded groups. While so far no study has measured skew directly, low reproductive competition in such groups has been reported (STEENBEEK et al., 2000), which might indicate high skew. However, this possibility remains to be tested.

Despite their usual classification as a one male ("harem" or "polygynous") society, more than 40 % of all mountain gorilla (*G. gorilla beringei*) groups comprise several males (ROBBINS, 1995) and are most likely age-graded in the sense that the dominant male monopolizes reproduction. Male emigration into other groups is rare so that all males can be assumed to be close relatives. Reproductive skew has been shown to be high, but subordinates sire some young in the group (BRADLEY et al., 2001). Levels of within group aggression are high among males (WATTS, 1989), which can be taken as a measure of the dominant's attempts to monopolize reproduction. The combination of high skew, little dispersal, and high relatedness can be explained by the concession model of social queuing (KOKKO and JOHNSTONE, 1999). Here, the key benefits of staying to subordinate males are chances to inherit the breeding position. It should be noted that where there is only one breeding male, inheritance will also succeed to only one male. Therefore, it would be appropriate to consider differential chances for succession for several subordinates in future skew models. Subordinates may also benefit indirectly by prolonging the tenure of the (related) dominant male. Nothing is known yet about the costs of dispersal, but, as shown by the queuing model, these need not necessarily be high in order to render dispersing unprofitable compared to staying.

A similar example of social queuing can be found in the cooperatively breeding marmosets, *Callithrix* spp. Here, subordinates remaining in their natal group, often help to rear the dominant's young (GOLDIZEN, 1987). In this study, a high proportion of subordinate females that stayed in their group eventually inherited the breeding position, increasing the delayed benefits of staying. From KOKKO and JOHNSTONE'S (1999) model, we predict high skew in such groups because the limited availability of territories is expected to yield high dispersal costs and, consequently, few individuals would attempt to leave (DIETZ and BAKER, 1993). It would be of interest to compare groups that differ with respect to the proportion of subordinate females inheriting the dominant status. Skew in groups with a high proportion of females should be greater than skew in groups in areas with a higher chance of establishing a new breeding group since both high dispersal costs and delayed benefits will increase the chances that the subordinate stays, also increasing reproductive skew.

In cooperatively breeding marmosets, helpers are essential to assist the dominant to raise her offspring. Therefore, one might expect competition for helpers in these species. A concession model by REEVE (1998) allows subordinates to move between groups and assess the share of reproduction that the dominant is willing to concede to make staying in the group advantageous to subordinates. In general, where helpers are rare, the model predicts low skew because the benefits gained from the subordinate's presence will outweigh the costs from conceding a share of reproduction. It shows that under conditions of good chances for inheriting a breeding position (with the consequence of high skew), but high benefits from the subordinate's presence and helping (with the consequences of low skew), effects may cancel out, and the actual degree of skew will then depend on the relative importance of these factors.

Skew models may also be useful in helping to understand how male philopatry affects reproductive patterns in species in which males are born and stay (e.g., woolly monkeys, *Lagothrix*; muriquis, *Brachyteles*: STRIER, 2000). In these species, groups with more males will be more attractive to females. Therefore, the dominant breeding male benefits from additional males. Moreover, maturing males born in the group were observed to replace older breeding males later. Under these conditions, concession models predict strong reproductive skew in large groups and more egalitarian reproduction in small groups. Since the attractiveness to females depends on group size, smaller groups will be more tolerant of maturing males or, possibly, immigrants and these males should obtain their share of matings as a concession to retain them. This effect will be much smaller in larger groups; hence, skew should be higher.

Alternatives to Concession Models

The critique has been made that the presence of subordinates is not always beneficial to the dominant individual, as assumed by concession models (CLUTTON-BROCK, 1998). Observations in vervet monkeys, *Cercopithecus aethiops* (HENZI and LUCAS, 1980), and black tufted-ear marmosets, *Callithrix kuhlii* (SCHAFFNER and FRENCH, 1997), showed that subordinates were clearly unwilling to leave the group while dominants attempted to expel them. This led to the development of a different skew model which assumes that the dominant is unable to control reproduction (but controls group membership) and that subordinates are able to claim unsanctioned reproduction. Subordinates are restrained from monopolizing reproduction by the dominant's threshold of tolerance for evicting them. This so called restraint model (as opposed to a concession model) predicts that when costs of dispersal are low, the subordinate should receive a smaller share of reproduction (leading to higher skew in the group) because it will suffer less when dispersing. This, in turn, will lower inclusive fitness costs to dominants (if they are related), and, hence, they will be more likely to tolerate reproduction by subordinates. In other words, with high costs of dispersal, reproductive skew is expected to be lower. When costs of dispersal are so weak that breeding success outside the group is greater than inside the association, then the dominant is more likely to eject a close relative because it gains more through the breeding success of a related subordinate. These predictions are in contrast to concession based models because the same factors render the association profitable for both the subordinate and the dominant (such as high dispersal costs, high relatedness).

While observations in vervet monkeys and black tufted-ear marmosets suggest that a different approach to the concession models is needed, I was unable to find a primate species in which the basic assumptions of the restraint model holds: that the dominant controls group membership but the subordinate controls the distribution of reproduction. It seems, rather, that, in most primate species, the definition of "subordinate" encompasses their inability to control reproduction (HAGER, 2003).

Effects of Costs of Dispersal on Within Group Aggression and Skew

The analysis of effects of dispersal costs on reproductive skew also yields interesting predictions for levels of within group aggression. Basically, models of reproductive skew assume that within group aggression results from a conflict between individual group members attempting to increase their share of reproduction. While it is clear that not all within group aggression is about reproductive opportunities but, for instance, about access to food or space, it seems reasonable to assume that conflicts over reproduction will account for many agonistic interactions. It should be noted that skew models analyze how reproduction is shared among group members of the same sex. Thus, these models do not directly offer a formal explanation of aggression *between* the sexes. In addition to the key parameters of other skew models (relatedness, costs of dispersal, and contribution to group productivity by individuals), models that analyse within group aggression also include individual fighting ability. Below, I discuss two skew models that explore within group aggression and show how they can relate to within group aggression in some primate species.

A concession model that analyses how costs of dispersal affect the level of within group aggression has been developed by CANT and JOHNSTONE (2000). Here, a dominant controls reproduction and group membership, while a subordinate has the option to challenge the dominant or to disperse. Generally, the expected fitness of a dispersing individual is assumed to be inversely proportional to ecological constraints. The model demonstrates that high costs of dispersal should lead to an increase of within group aggression if there is a chance that the subordinate receives a share of reproduction. The reason is that dispersal costs are too high to render leaving the group profitable. The alternative is to stay, and the potential gain from increased aggression is expected to yield a higher share of reproduction. Thus, high costs of dispersal are expected to lead to an increase in within group aggression. The effects of this on how reproduction is shared in the group will depend on the relatedness among members and on the effects of aggression on group productivity. The model shows that while higher relatedness will cause reduced aggression and higher skew, increasing dispersal costs are expected to cause elevated levels of aggression and also higher skew. In other words, two factors may have the same overall effect on reproductive skew but lead to different levels of aggression. Further, for different groups consisting of related individuals, this model predicts a positive relation between skew and level of aggression when costs of dispersal vary among these groups. However, if groups differ with respect to within group relatedness but are subject to similar costs of dispersal, the relation between skew and aggression becomes negative.

REEVE (2000) developed a concession model in which the level of aggression of within group aggression can be explained as a result of dispersal costs. Here, aggression was defined as the difference between the maximum share of reproduction a subordinate can claim without being evicted by the dominant and the minimum share that the dominant needs to concede to retain the subordinate in the group. Because the level of reproduction a subordinate can claim without being evicted depends on the costs of dispersal, levels of aggression can be related to the latter. Further, it is assumed that the dominant benefits from the subordinate's presence in the group, which is why a share of reproduction needs to be conceded to subordinates to retain them (otherwise they would depart). This model predicts that in groups in which joining is an alternative to solitary breeding (so called unsaturated groups), aggression increases as dispersal costs increase. The reason is that the difference between the minimum share the dominant is willing to concede and the maximum share that the subordinate can claim increases.

In saturated groups, joining by subordinates is no longer advantageous because either the dominant is favoured to eject the subordinate, or subordinates fare better by leaving the group voluntarily. Any further subordinate in the group would lower the overall group productivity and, hence, the dominant's benefits. Therefore, the dominant is expected to expel any subordinates. In such saturated groups, no aggression is expected. The size of these groups is expected to increase with dispersal costs because subordinates are forced to accept a lower share of reproduction, which is still better than dispersing. In other words, the dominant needs to concede less reproductive opportunities to subordinates (higher skew) when conditions of dispersal are harsh.

In an extension of this model, REEVE and EMLEN (2000) make the interesting prediction that parent-offspring associations (in which the dominant is a parent of the subordinate and, thus, is asymmetrically related to his/her own and subordinate offspring) are predicted to break up by voluntary departure of subordinate offspring. On the other hand, in groups composed of symmetrically related or unrelated individuals, dispersal is the result of eviction by the dominant. Reproductive skew is, thus, expected to be higher in groups with asymmetrically related individuals and should increase with costs of dispersal (REEVE and KELLER, 1995).

Observed patterns of within group aggression in several primate species may be explained by the models outlined above. In chimpanzees, aggressive encounters between males are frequent and occur in the context of conflict over rank position (NISHIDA and HIRAIWA-HASEGAWA, 1987). Males are said to be close relatives because of male philopatry, and skew is high (see above). Subordinate males help to defend the group against extra group males, thus increasing the dominant's tenure and, ultimately, his fitness. Concession models predict high levels of male-male aggressive encounters in such groups because a dominant individual benefits greatly from his breeding position (high reproductive skew in these groups) and, thus, is expected to defend it vigorously. Similarly, because high skew is associated with high reproductive success of the breeding individual, subordinates will attempt to challenge the dominant frequently.

A comparative study of aggression among female rhesus monkeys, *Macaca mulatta*, and hamadryas baboons has been conducted by GORE (1994). Aggression between female rhesus monkeys was shown to be higher than between baboon females, and, in both species, most aggressive behaviors were directed to other females. While, in *P. hamadryas*, females emigrate to single male units and are, thus, unlikely to be related (SIGG et al., 1982), in *M. mulatta*, females are matrilocal and are close relatives (VEHRENCAMP, 1983a). According to concession models, higher aggression is to be expected among closely related individuals, and these models predict further that skew in female rhesus monkeys will be higher than in female baboons, offering a good opportunity to test predictions of the model.

While skew models analysing within group aggression focus on agonistic encounters between individuals of the same sex, a biased distribution of reproduction may affect levels of aggression among members of the other sex. For instance, in rhesus monkeys, females are philopatric and males disperse, with strong reproductive skew among males (BERCOVITCH et al., 2000). Consequently, females are more likely to be paternal than maternal siblings. A study by WIDDIG et al. (2002) demonstrated that levels of aggression towards other females depended upon whether they were maternal or paternal kin. Maternal kin were shown to be more aggressive and affiliative towards each other than to either paternal half siblings or non-kin (WIDDIG et al., 2002).

Conclusions

Dispersal patterns in primates are highly variable, and multiple reasons account for why some individuals stay and others leave the group (e.g. STRIER, 1994). Models of reproductive skew, in particular, concession models, offer a formal analysis for specific situations in that they explore what the effects of costs of dispersal are on the distribution of reproduction in a group and, thus, ultimately, on the fitness of group members. Clearly, the explanatory value of these models is limited to conditions that meet the assumptions of the models. Control of reproduction and group membership should be attributable to a dominant individual, and the presence of subordinates should potentially be beneficial to the dominant (in the case of concession models). These conditions are met in several examples of male-male coalitions and age-graded groups, such as in chimpanzees and gorillas. Moreover, in many primate species, individuals have the chance to inherit the breeding position if they stay in their group. This advantage of philopatry and the consequences for reproductive skew in the group and the inclusive fitness of individuals is analyzed by the social queuing model (KOKKO and JOHNSTONE, 1999). Marmosets, Thomas's langurs, and some other species in which inheritance of dominance status occurs offer good opportunities to test this model.

A problem when testing predictions of skew models arises because they assume a common currency—both for costs and benefits of dispersal versus philopatry—but do not quantifiy these. Ideally, models of reproductive skew assume that, for instance, chances to establish a new group, predation risk when dispersing, inbreeding depression, and other factors influencing the trade-off of leaving versus staying have been measured in their effects on an individual's inclusive fitness, which can then be used when calculating overall costs and benefits. This very difficult task remains the work of field biologists who will most likely object to the idea that this is feasible at all for primates. For the moment, the models presented above offer valid explanations for patterns of dispersal and philopatry given specific assumptions. To date, such models have not been considered when investigating evolutionary causes of these behaviours. Future empirical and theoretical studies on dispersal should, thus, focus on reproductive opportunities, both within and outside the group.

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Correspondence to:
Dr. Reinmar Hager, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK; E-mail: rh244@am.ac.uk.