

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).

<i>Species</i>	DP	Age at Natal Dispersal	Secondary Dispersal (Y or N plus any details)
<i>Macaca fascicularis</i> *	♂	5 yrs (1)	Yes – adult males change groups ~ every three years (1)
<i>M. fuscata yakui</i> *	♂	5 yrs (2)	Yes – complete changeover in male membership every four years (3)
<i>M. mulatta</i>	♂	~ 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)
<i>M. silenus</i>	♂	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)
<i>M. sinica</i>	♂	NA	Yes – most males will reside in numerous groups throughout their lives (7)
<i>Papio cynocephalus</i> *	♂	8.45 yrs (7)	Yes – males disperse repeatedly throughout their lives (8) even in old age (9)
<i>Chlorocebus aethiops</i> *	♂	5 – 7 yrs (9)	Yes – complete changeover in male group membership over a four year study of three groups (10)
<i>Alouatta palliata</i>	♂♀	1.8 yrs (juveniles) (11)	No – based on >30 yrs of observation on marked animals (GLANDER, personal communication)
<i>Alouatta seniculus</i> *	♂♀	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)
<i>Cebus capucinus</i> *	♂	4.5 yrs (14)	Yes – males disperse continuously throughout their lives with complete changeover in group males every four years (15)
<i>Saimiri sciureus</i>	♂	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)
<i>Lemur catta</i> *	♂	3-5 yrs (18)	Yes – prime age males (5-7 yrs) disperse every 3-4 years (19)
<p>(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.</p> <p>* Indicates species included in further analyses in this review.</p>			

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; BENGSTON, 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 1 st Birth (~gestation length)	Notes
<i>Macaca fascicularis</i>	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)
<i>M. fuscata yakui</i>	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)
<i>Papio cynocephalus</i>	2 yrs (range 1 mo – 11.5 yrs with peaks in the 1 st and 6 th years) (5)	6 yrs (5) (5.8 mos)	Most cases of secondary dispersal occurred in the 1 st or 6 th year of residency; first year if unsuccessful at gaining mates, in the 6 th year if successful (5)
<i>Chlorocebus aethiops</i>	2.7 yrs (6)	4.5 yrs (5.4 mos)	Complete changeover in group males over a four year study of three groups (6)
<i>Alouatta seniculus</i>	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)
<i>Cebus capucinus</i>	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)
<i>Lemur catta</i>	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 SCHAİK, 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 oerstedii*), 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
<i>Brachyteles arachnoides</i>	♀	No: females transfer into neighboring groups, breed, and appear to remain there for life (1). Females disperse prior to reaching sexual maturity (2)
<i>Pan troglodytes</i>	♀	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)
<i>Saimiri oerstedii</i>	♀	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)
<i>Alouatta palliata</i>	♂ ♀	Rare; 5 of 52 female emigrations were secondary (32 years of observing marked animals) (6)
<i>Alouatta seniculus</i>	♂ ♀	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 arachnoides*: 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 intra-sexual 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
<i>Macaca fascicularis</i>	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)
<i>M. fuscata yakui</i>	No correlation Captive study of <i>M. f. fuscata</i> . 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)
<i>Papio cynocephalus</i>	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
<i>Papio cynocephalus</i>	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)
<i>Chlorocebus aethiops</i>	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.
<i>Alouatta seniculus</i>	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
<i>Alouatta seniculus</i>		Alphas never voluntarily emigrate (16) Subordinates in unrelated coalitions disperse in 2.3 yrs (see notes)			(18). Breeding males are prime age adults.
<i>Cebus capucinus</i>	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)
<i>Lemur catta</i>	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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References

- ALBERTS, S.C.: Paternal kin discrimination in wild baboons. *Proc. Roy. Soc. Lond. Ser. B* (1999) 266: 1501-1506.
- ALBERTS, S.C. and ALTMANN, J.: Balancing costs and opportunities: Dispersal in male baboons. *Am. Nat.* (1995a) 145: 279-306.
- ALBERTS, S.C. and ALTMANN, J.: Preparation and activation: Determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol.* (1995b) 36: 397-406.
- ALTMANN, J., ALBERTS, S., HAINES S.A., S.C., DUBACHH, J., MURUTHI, P., COOLE, T., GEFFEN, E., CHEESMAN, D.J., MUTUTUA, R.S., SAIYALEL, S.N., WAYNE, R.K., LACY R.C. and BRUFORD, M.W.: Behavior predicts genetic structure in a wild primate group. *Proc. Nat. Acad. Scis. USA* (1996) 93: 5797-5801.
- ALTMANN, S.A.: A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. *Ann. N.Y. Acad. Scis.* (1962) 102: 338-435.
- ASQUITH, P.J.: Provisioning and the study of free-ranging primates: history, effects and prospects. *Yearb. Phys. Anthropol.* (1989) 32: 129-158.

BENGSTON, B.O.: Avoiding inbreeding: At what cost? *J. Theor. Biol.* (1978): 73: 439-444.

BERARD, J.: A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates* (1999) 40(1): 15-175.

BERTEAUX, D. and BOUTIN, S.: Breeding dispersal in female North America red squirrels. *Ecology* (2000) 81: 1311-1326.

BOESCH, C.: Evidence for dominant wild female chimpanzees investing more in sons. *Anim. Behav.* (1997) 54: 811-815.

BOINSKI, S. and MITCHELL, C.L.: Male resident and association patterns in Costa Rican squirrel monkeys (*Saimiri oerstedii*). *Am. J. Primatol.* (1994) 34: 157-169.

CHENEY, D. L.: Proximate and ultimate factors related to the distribution of male migration. In: HINDE, R.A. (ed.): *Primate Social Relationships*. Oxford: Blackwell Scientific Publications (1983): 241-249.

CHENEY, D.L. and SEYFARTH, R.M.: Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Am. Nat.* (1983) 122: 392-412.

CLARKE, M. and GLANDER, K.: Female immigration patterns in mantled howling monkeys (*Alouatta palliata*) on La Pacifica, Guanacaste, Costa Rica. *Am. J. Phys. Anthropol.* (2002) Suppl. 32: 54.

CLOBERT, J., DANCHIN, E., DOHNDT, A.A. and NICHOLS, J.D.: *Dispersal*. Oxford: Oxford University Press (2001).

COCKBURN, A., SCOTT, M. and SCOTTS, D. J.: Inbreeding avoidance and male biased dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Anim. Behav.* (1985) 33: 908-915.

COWLISHAW, G. and DUNBAR, R.I.M.: Dominance rank and mating success in male primates. *Anim. Behav.* (1991) 41:1045-1056.

CROCKETT, C.M.: Emigration by female red howler monkeys and the case for female competition. In: SMALL, M.F. (ed.): *Female Primates: Studies by Women Primatologists*. New York: Alan R. Liss. (1984): 259-274.

CROCKETT, C.M. and POPE, T.R.: Consequences of sex differences in dispersal for juvenile red howler monkeys. In: PEREIRA, M.E. and FAIRBANKS L.A. (eds.): *Juvenile Primates: Life History, Development, and Behavior*. New York: Oxford University Press (1993): 104-118.

DARLING, F.F.: *A Herd of Red Deer*. Oxford: Oxford University Press (1937).

DE RUITER, J.R and VAN HOOFF, J.A.R.A.M.: Male dominance rank and reproductive success in primate groups. *Primates* (1993) 34: 513-523.

DE RUITER, J.R., WOLFGANG, S., TROMMELEN, G.J.J.M., UITTERLINDEN, A.G., MARTIN, R.D. and VAN HOOFF, J.A.R.A.M.: Male social rank and reproductive success in wild long-tailed macaques. In: MARTIN, R.D., DIXON, A.F. and WICKINGS, E.J. (eds.): *Paternity in Primates: Genetic Tests and Theories*. Basel: Place Karger (1992): 175-191.

DITTUS, W.: The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour* (1977) 63: 281-322.

DITTUS, W.P.J.: Population dynamics of the toque monkey, *Macaca sinica*. In: TUTTLE, R.H. (ed.): *Socioecology and Psychology of Primates*. Paris: Mouton Publishers (1975): 125-152.

DOBSON, F. S.: Competition for mates and predominant juvenile dispersal in mammals. *Anim Behav* (1982) 30: 1183-1192.

DRICKAMER, L.C. and VESSEY, S.H.: Group changing in free ranging male rhesus monkeys. *Primates* (1973) 14: 359-368.

EMLEN, S.T. and ORING, L.W.: Ecology, sexual selection and the evolution of mating systems. *Science* (1977) 197: 215-223.

ESCOBAR-PARÁMO, P.: Inbreeding avoidance and the evolution of male mating strategies. Ph.D. Dissertation, State University of New York at Stony Brook (1999).

FEDIGAN, L.M.: Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.* (1993) 14: 853-877.

FEDIGAN, L.M.: Dominance and reproductive success in primates. *Yearb. Phys. Anthropol.* (1983) 26: 91-129.

FRAGASZY, D., BAER, J. and ADAMS-CURTIS, L.: Introduction and integration of strangers into captive groups of tufted capuchins (*Cebus apella*). *Int. J. Primatol.* (1994) 15: 399-420.

GLANDER, K.E.: Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* (1992) 33: 415-436.

GREENWOOD, P. J.: Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* (1980) 28: 1140-1162.

HENZI, S.P. and LUCAS, J.W.: Observations on the inter-troop movement of adult vervet monkeys (*Cercopithecus aethiops*). *Folia Primatol.* (1980) 33: 220-235.

INOUE, M., MITSUNAGA, F., NOZAKI, M. OHSAWA, H., TAKENAKA, A., SUGIYAMA, Y, SHIMUZU, K. and TAKENAKA, O.: Male dominance rank and reproduc-

tive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. *Primates* (1993) 34: 503-511.

ISELL, L.A., CHENEY, D.L. and SEYFARTH, R.M.: Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? *Anim. Behav.* (1993) 45: 729-734.

JACK, K.M.: Life history patterns of male white-faced capuchins (*Cebus capucinus*): male bonding and the evolution of multimale groups. Ph.D. Dissertation, University of Alberta, Canada (2001).

JACK, K and FEDIGAN, L.M.: Male dispersal patterns in white-faced capuchins (*Cebus capucinus*), Part 1: patterns and causes of natal dispersal. *Anim. Behav.* (in press a).

JACK K. and FEDIGAN, L.M.: Male dominance and reproductive success in white-faced capuchins (*Cebus capucinus*) (Abstract). *Am. J. Phys. Anthropol.* (in press b).

JOHNSON, M.L. & GAINES, M.S.: Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Ann. Rev. Ecol. Syst.* (1990) 21: 449-480.

JONES, C.B.: The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous Neotropical primate. *Primates* (1980) 21(3): 389-405.

JONES, K.C.: Inter-troop transfer of *Lemur catta* at Berenty. *Folia Primatol.* (1983) 40: 145-160.

KREBS, J.R. and DAVIES, N.B. (eds.): *An Introduction to Behavioural Ecology*, 3rd ed. Oxford: Blackwell Science (1993).

KUMAR, A., SINGH, M., KUMARA, H.N., SHARMA, A.K. and BERTSCH, C.: Male migration in lion-tailed macaques. *Primate Report* (2001) 59: 5-17.

MELNICK, D.J., PEARL, M.C. and RICHARD, A.F.: Male migration and inbreeding avoidance in wild rhesus monkeys. *Am. J. Primatol.* (1984) 7: 229-243.

MITCHELL, C.L.: Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). *Behaviour* (1994) 130: 169-190.

MOORE, J.: Female transfer in primates. *Int. J. Primatol.* (1984) 5: 537-589.

MOORE, J. and ALI, R.: Are dispersal and inbreeding avoidance related? *Anim. Behav.* (1984) 32: 94-112.

NISHIDA, T., TAKASAKI, H. and TAKAHATA, Y.: Demography and reproductive profiles. In: NISHIDA, T. (ed.): *The Chimpanzees of the Mahale Mountains*. Japan: University of Tokyo Press (1990): 63-97.

- NUNN, C.L.: The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* (1999) 46: 1-13.
- PACKER, C.: Intertroop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* (1979a) 27: 1-36.
- PACKER, C.: Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.* (1979b) 27: 37-45.
- PARKER, G.A.: Sexual selection and sexual conflict. In: BLUM, S.B. and BLUM, N.A. (eds.): *Sexual selection and reproductive competition in insects*. New York: Academic Press. (1979): 123-166.
- PARR, L.A. and DE WAAL, F.B.M.: Visual recognition in chimpanzees. *Nature* (1999) 399: 647-648.
- PERRIN, N. and MAZALOV, V.: Dispersal and inbreeding avoidance. *Am. Nat.* (1999) 154: 282-292.
- PEREIRA, M.E. and WEISS, M.L.: Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav. Ecol. Sociobiol.* (1991) 28: 141-152.
- PERRY, S.E.: Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* (1998) 135: 139-172.
- POPE, T.R.: The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* (1990) 27: 439-446.
- POPE, T.R.: The evolution of male philopatry in Neotropical monkeys. In: KAPPELER, P.M. (ed.): *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge: Cambridge University Press (2000): 219-235.
- PUSEY, A.E.: Inbreeding avoidance in chimpanzees. *Anim. Behav.* (1980) 28: 543-552.
- PUSEY, A.E.: Sex-biased dispersal and inbreeding avoidance in birds and mammals. *TREE* (1987) 2: 295-299.
- PUSEY, A.E. and PACKER, C.: Dispersal and philopatry. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): *Primate Societies*. Chicago: University of Chicago Press (1987a): 250-266.
- PUSEY, A.E. and PACKER, C.: The evolution of sex-biased dispersal in lions. *Behaviour* (1987b) 101: 275-310.
- ROWE, N.: *The Pictorial Guide to the Living Primates*. New York: Pogonias Press (1996).

SAPOLSKY, R.M.: Why should an aged male baboon ever transfer troops? *Am. J. Primatol.* (1996) 39: 149-157.

SAUTHER, M.L. and SUSSMAN, R.W.: A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: KAPPELER, P.M. and GANZHORN, J.U. (eds.): *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press (1993): 111-121.

SAUTHER, M.L.: Reproductive behavior of free-ranging *Lemur catta* at Beza-Mahafaly Special Reserve, Madagascar. *Am. J. Phys. Anthropol.* (1991) 84: 463-477.

SAUTHER, M.L., SUSSMAN R.W. and GOULD, L.: The socioecology of the ring-tailed lemur: thirty-five years of research. *Evol. Anthropol.* (1999) 8: 120-132.

SAUTHER, M.L., SUSSMAN R.W. and CUOZZO, F.: Dental and general health in a population of wild ring-tailed lemurs: a life history approach. *Am. J. Phys. Anthropol.* (2002) 117: 122-132.

SHIELDS, W.M. : Dispersal and mating systems: Investigating their causal connections. In: CHEPKO-SADE, D. and HALPIN, Z.T. (eds.): *Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics*. Chicago: University of Chicago Press (1987): 3-24.

SHIVLEY, C. and SMITH, D.G: Social status and reproductive success of male *Macaca fascicularis*. *Am. J. Primatol.* (1985) 9: 129-135.

SMALE, L., NUNES, S. and HOLEKAMP, K.E.: Sexually dimorphic dispersal in mammals: patterns, causes, and consequences. *Adv. Stud. Behav.* (1997) 26: 181-250.

SMITH, E.O.: Dispersal in sub-Saharan baboons. *Folia Primatol.* (1992) 59: 177-185.

SMITH, D.G.: Inbreeding in three captive groups of rhesus monkeys. *Am. J. Phys. Anthropol.* (1982) 58: 447-451.

SPRAGUE, J.S.: Life history and male intertroop mobility in Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.* (1992) 13: 437-454.

SPRAGUE, D.S., SUZUKI, S, TAKAHASHI, H. and SATO, S.: Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates* (1998) 39: 351-363

STRIER, K.B.: Myth of the typical primate. *Yearb. Phys. Anthropol.* (1994) 37: 233-271.

STRIER, K.B: Mate preference of wild muriqui monkeys (*Brachyteles arachnoids*): reproductive and social correlates. *Folia Primatol.* (1997) 68: 120-133.

STRIER, K.B. and ZEIGLER, T.E.: Lack of pubertal influences on female dispersal in miqui monkeys, *Brachyteles arachnoids*. Anim. Behav. (2000) 59: 849-860.

SUSSMAN, R.W.: Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). Int. J. Primatol. (1992) 13: 395-413.

SUZUKI, S., HILL, D.A. and SPRAGUE, D.S. Intertroop transfer and dominance rank structure in nonnatal male Japanese macaques in Yakushima, Japan. Int. J. Primatol. (1998) 19: 703-722.

TAKAHATA, Y., HUFFMAN, M.A., SUZUKI, S., KOYAMA, N. and YAMIGAWA, J.: Why dominants do not consistently attain high mating and reproductive success: a review of longitudinal Japanese macaque studies. Primates (1999) 40: 143-158.

TRIVERS, R.: Parental investment and sexual selection. In: CAMPBELL, B. (ed.): Sexual Selection and the Descent of Man, 1871-1971. Chicago: Aldine (1972): 136-179.

VAN NOORDWIJK, M.A. and VAN SCHAIK, C.P.: Male careers in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour (1988) 107: 24-43.

VAN NOORDWIJK, M.A. and van SCHAIK, C.P.: Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behaviour (2001) 138: 359-395.

VAN SCHAIK, C.P.: Why are diurnal primates living in groups? Behaviour (1983) 87: 120-144.

WALTERS, J.R. and SEYFARTH, R.M.: Conflict and cooperation. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M., WRANGHAM, R.W. and STRUHSAKER, T.T. (eds.): Primate Societies. Chicago: University of Chicago Press (1987): 306-317.

WASER, P.M.: Does competition drive dispersal? Ecology (1985) 66: 1170-1175.

WASER, P.M., CREEL, S.R. and LUCAS, J.R.: Death and disappearance: Estimating mortality risks associated with philopatry and dispersal. Behav. Ecol. Sociobiol. (1994) 5: 135-141.

WASER, P.M. and JONES, W.T.: Natal philopatry among solitary mammals. Quart. Rev. Biol. (1983) 58: 355-390.

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