

Secondary transfer of adult mantled howlers (*Alouatta palliata*) on Hacienda La Pacifica, Costa Rica: 1975–2009

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Abstract Natal emigration by male and female mantled howlers (*Alouatta palliata*), and subsequent immigration into breeding groups, is well documented for the free-ranging population on Hacienda La Pacifica, Costa Rica, but secondary transfer was considered rare (Glander in *Int J Primatol* 3:415–436, 1992). Population surveys in 1998 and 2006 caused us to question our assumptions and to re-evaluate our long-term data set from a post hoc perspective. We first identified all animals observed or captured as adults in more than one non-natal group anywhere in the population. We then systematically analyzed joining or leaving by adults in seven groups tracked for various times from 1975 to 2005 for patterns suggesting secondary transfer. Fourteen adults (nine females, five males) were found in two different non-natal groups as adults. In addition, one male and one female that became dominant and reproduced in their natal group

later transferred to a second group, and one female was known to be a tertiary transfer. Data from the seven tracked social groups indicate that 35% of all the males and 29% of all the females were potential secondary transfers. In these groups, males leaving or joining was not associated with group size or absolute number of females. Females leaving or joining was not associated with group size or absolute number of males, but females left groups with more females and joined groups with fewer females. Both sexes left groups with unfavorable sex ratios for their sex and joined groups with sex ratios more favorable for their sex. Since a favorable sex ratio is associated with reproductive success in other howler populations, this suggests secondary transfer as a reproductive strategy. Other factors could also influence secondary transfer.

Keywords Secondary transfer · Sex ratio · Dispersal · Reproductive strategies · Howlers

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Introduction

Greenwood's (1980) landmark analysis greatly influenced the direction for thinking about dispersal patterns in free-ranging animals, concluding that in mammals, females were philopatric and males dispersed. Early fieldwork on ground-dwelling cercopithecids reinforced the dogma of female philopatry and male dispersal in primates (see Pusey 1992), although over the years a wealth of field data has accumulated, including long-term data sets on different species of primates in Africa, Madagascar, Asia, and the Americas (see Moore 1992; Isbell and VanVuren 1996; and below) that reveal very different patterns in both natal dispersal (leaving the group in which one was born and joining a new one for breeding purposes) and secondary

(and tertiary) dispersal (leaving a non-natal group in which one has had breeding opportunities).

Several colobine species and gorillas exhibit female natal dispersal (e.g., Harcourt et al. 1976; Marsh 1979; Sterck 1997; Korstjens and Schippers 2003; Robbins et al. 2004; Sterck et al. 2005; Douadi et al. 2007), as do a number of new world atelins (Strier 1994, 2000; Martins and Strier 2004). Genetic data from *Colobus guereza* (Harris et al. 2009), *Papio hamadryas* (Hammond et al. 2006), and *Gorilla gorilla beringei* (Guschanski et al., 2008) indicate both male and female natal dispersal, and most species of howlers have been observed to exhibit both male and female natal dispersal (Mendes 1989; Agoramorthy and Rudran 1993; Crockett and Pope 1993; Kowaleski et al. 1995; Calegario-Marques and Bicca-Marques 1996; Arroyo-Rodriguez et al. 2008; Clarke and Glander 2008). Secondary dispersal has been documented for males in *Lemur catta* (Parga and Lessnau, 2008), *Cebus capucinus* (Jack and Fedigan 2004a, b; Fedigan and Jack 2004), *Papio cynocephalus* and *P. ursinus* (Packer 1979; Alberts and Altmann, 1995), *Cercopithecus aethiops* (Isbell 2004), *Macaca thibetana* (Zhao 1994) and *Lophocebus albigena* (Olupot and Waser 2005). It has also been documented in female *Presbytis thomasi* (Sterck et al. 2005), *Saimiri scuriei* (Boinski et al. 2002) and *G. gorilla* (Bradley et al. 2007; Stokes et al. 2003). Secondary dispersal by both sexes has been documented in *Eulemur fulvus* (Erhart and Overdorff 2008) and in *Procolobus verus* (Korstjens and Schippers 2003), with suggestive data for *Alouatta palliata* in Mexico (Arroyo-Rodriguez et al. 2008).

With the exception of inbreeding avoidance, which is most appropriate for natal dispersal of one sex only, the same hypotheses that are tightly coupled with social structure, resource availability, and reproductive success are postulated for secondary as well as natal dispersal, i.e., access to resources (mates or food), predation avoidance, or infanticide avoidance (Packer 1979; Davies 1982; Moore and Ali 1984; Pusey and Packer 1987; Sterck 1997; Crockett and Janson 2000; Steenbeek and van Schaik 2001; Isbell and Young 2003). In general, male secondary transfer seems to be competitive, as it is associated with aggression (e.g., baboons, macaques), whereas female secondary transfer is not associated with aggression and is interpreted as “easy” (e.g., colobines, gorillas) (see review by Lawson Handley and Perrin 2007). Recent analyses indicate that the timing and events associated with dispersal are much more variable than previously thought, and it is likely that these explanations are too simplistic (Travis and French 2000; Lawson Handley and Perrin 2007) and that alternative modes of thinking are necessary (Cunningham and Janson 2007; Thierry 2008).

In a species such as mantled howlers, where there is both male and female natal dispersal and entry into a breeding group is a highly competitive event, leaving a group once a breeding position had been achieved would not be expected, and indeed this was reported for the La Pacifica population (Glander 1980, 1992). The population surveys of 1998 and 2006 caused us to re-evaluate our thinking and our data set. From a totally post hoc perspective, we first identified all of the animals that we had seen or captured as adults in more than one non-natal group anywhere in the population. Then we systematically examined the records for animals leaving or joining the seven groups for which we had sufficient data to determine if there were patterns that suggested secondary dispersal, and if so, whether any of the previously stated hypotheses might be plausible explanations.

Methods

Study site

La Pacifica is a 1,330 ha working cattle ranch/rice farm/tilapia farm in the dry tropical forest zone of Guanacaste Province, Costa Rica (Holdridge 1967), which was moderately deforested in the early 1950s. The site is fully described in Glander (1992) and changes in land use are documented in Clarke and Glander (2008), including the fact that areas deforested for the construction of the large canal have regrown extensively since the completion of the canal.

Study subjects

The subjects for this study are the free-ranging population of about 350 mantled howlers (*Alouatta palliata*) that live on Hacienda La Pacifica. This population has been studied by various researchers since the late 1960s.

Data collection

A timetable for all group contacts between 1975 and 2005 can be found in Clarke and Glander (2008). An additional timetable for contacts with group 30 can be found in Electronic supplementary material 1. For both of these supplementary materials, all contacts for each group are listed. Shaded areas indicate time spans that were specifically included in this analysis, which are also indicated in the data tables.

Data were collected in the following ways:

Surveys

This population was initially surveyed in the 1960s (Heltne et al. 1976) and again as part of a capture-and-mark project between 1974 and 1976 (Scott et al. 1978). The population was formally surveyed in 1984, 1991, 1998 and 2006 (Clarke et al. 1986, 2002, 2007; Clarke and Zucker 1994).

Observations

Seven groups have been under behavioral observation for various amounts of time since 1972. These same groups were also informally surveyed at six- to twelve-month intervals from 1998 through 2005 (see Electronic supplementary material and tables for specific dates included in this analysis). This represents a total of 48 adult males and 142 females as group residents during the time of this analysis.

Capture sessions

Animals in this population have been intermittently captured from 1972 through 2009 and marked with collars or legbands (Glander et al. 1991). Detailed drawings of identifying characteristics are done, and animals are also permanently identified with unique tattoos and/or Avid[®] microchips. Over 850 animals have been captured, and over 300 have been captured more than once. All information from capture sessions are maintained in a master database.

Data analysis

Documented secondary transfer

The master database (1975–2009) was searched for adult animals that had been captured or positively identified as adults in two or more non-natal groups.

Inferred secondary transfer

In order to evaluate the potential for secondary transfer, we identified all animals leaving or joining a group by age. Animals that were still reproductive that joined at an older age, or that joined when young and subsequently left at an older age while still reproductive, were considered potential secondary transfers.

Joining and leaving patterns Animals were classified according to the following rules. Adult animals new in the group were determined to have joined a group if they were identified during two consecutive observation/capture sessions. Animals were determined to have left

groups if they were not observed in the group over two observation/capture sessions, with the date of the first time not seen as the date of leaving. Animals of advanced age (24 plus years) that were not observed twice were presumed dead, and were eliminated from the data set. Transients were animals that were identified in the group during one observation/capture session but were not seen again with that group. Several animals were eliminated for various reasons (e.g., untimely death, uncertain identification, etc.). Since subadults are forced out between one and three years of age (Clarke and Glander 2008), males six years of age or less and females five years of age or less or nulliparous were considered “young” and presumably joining a breeding group for the first time. While the codes are defined in detail in the data tables, in brief, “old immigrant stays,” “resident leaves,” “young immigrant leaves,” and “old immigrant leaves” would be inferred secondary transfer. A complete list of animals included in the data set, identified by group number and emigration code, is listed in Electronic supplementary material 2.

Demographic variables associated with dispersal events

Social group factors potentially associated with secondary transfer were tested. “Resident stay” and “transients” clearly were not secondary transfer and were eliminated from this analysis. Independent *t* tests were used to test the association between individuals joining versus leaving by chronological age, group size, number of adult females, sex ratio, and, for females, number of group males. There were not enough data to statistically test the effect of number of males on males joining or leaving. Only emigration data were used for the animals that joined and subsequently left the same group.

Population group size and sex ratio

To evaluate the number of adults, the number of adult females, and the male to female sex ratio in one-male groups versus multi-male groups, results from each of the surveys at seven-year intervals (1984, 1991 and 1998) were evaluated using independent *t* tests (Anderson-Bell Corp. 1993).

Results

Documented secondary transfer

There were 14 animals that were identified in more than one group as a breeding adult, nine females and five males (see Table 1). In addition, there was an adult male (Jitney) and an adult female (Schweppes) that became

dominant and bred in their natal groups for a number of years before leaving and joining a different group (Jitney became dominant in natal group 2 in 2001 and left and joined group 42 in 2004; Schweppes became dominant in natal group 33 in 1998 and joined group 2 in 2006). One of the females listed in Table 1 (Jamaica) left group 2 after 2005 and was a tertiary transfer into a different group in 2009. If these three are included, there are 17 documented cases of animals moving between groups as breeding adults.

Of these animals, only Chaya and Schweppes were actually observed entering a new group. They received aggression from group females (Crockett, personal communication; Ford, personal communication) but remained in the group as low-ranking females (Clarke, personal observation). Turquoise, Jamaica and Rambo II were also low-ranking after they had joined group 2 (Clarke, personal observation). Turquoise and Jamaica each left the group after two years (Jamaica reproduced twice in group 2), Chaya died of old age in group 19, and Schweppes and Rambo II were still low-ranking in group 2 in 2007 (Ford, personal communication).

Inferred secondary transfer

Patterns of joining and leaving

The total number of animals in each age/dispersal category are presented in Table 2 for males and in Table 3 for females for the seven groups that were tracked through 2005. For males, 35% of the animals who were group

members at any time were potential secondary transfers (17 of 48—older immigrant, resident emigrant, younger immigrant who emigrates; see Table 2, in bold), and for all females, 29% were potential secondary transfers (41 of 142—older immigrant, resident emigrant, and both younger and older immigrants who emigrate; see Table 3, in bold). Of the animals included in the inferred secondary dispersal analysis, only one male joined as an older male, while nine older females joined and seven left.

Demographic correlates of dispersal events

Males Independent *t* tests revealed a significant difference in males joining or leaving by chronological age and by group sex ratio. Younger males joined and older males left ($t_{32} = 4.91$, $p < 0.001$; join: mean 5.3 years, SD 2.0; leave: mean 12.1 years, SD 5.4). Males joined groups with a statistically significant higher number of females to males and left groups with a lower number of females to males ($t_{32} = -3.2$, $p < 0.002$; join: mean 1 male:5.3 females, SD 3.5; leave: mean 1 male:2.4 females, SD 0.9). There were no significant differences in joining or leaving for males by the size of groups or the absolute number of females.

Females Independent *t* tests also revealed that chronologically younger females joined groups and older females left groups ($t_{80} = -8.38$, $p < 0.001$; join: mean 5.1 years, SD 2.6; leave: mean 12.6 years, SD 5.4). There was no effect of group size or absolute number of males, but there were significant effects associated with sex ratio and with

Table 1 Adults identified in different groups

Name	Tattoo no.	Estimated birth	Old group	Date	New group	Date
Females						
Turquoise	82	1965	1	1983 ^{a,c}	2	1986 ^a
Bry	167	1973	8	1986 ^c	34	1993 ^c
Clementine	168	1981	8	1987 ^c	34	1994 ^c
Chaya	702	1972	30	1992 ^{a,c}	19	1996 ^{a,c}
Jamaica	535	1986	12	1992 ^{a,c}	2	2003 ^c
Morgana	692A	1988	34	1993 ^c	12E	2004 ^c
Zirconia	592B	1995	19	2001 ^{a,d}	30	2005 ^b
Emerald	821	1998	19	2002 ^d	30	2005 ^b
Courtney	38A	1989	7	2003 ^{a,d}	37	2005 ^{a,d}
Males						
Thames	175	1982	18	1993 ^{a,c}	39	1998 ^{a,c}
Haw	186	1982	18	1995 ^{a,c}	24	1998 ^{a,c}
Rambo II	617	1987	33	1994 ^{a,c}	2	2004 ^{a,b}
Hamilton	749	1996	7	2003 ^{a,d}	37	2005 ^a
Colby	843	1994	40	2006 ^d	41	2009 ^{b,d}

Identification mode: ^atag (anklet or collar), ^bdistinguishing marks, ^ctattoo (capture), ^dchip (capture)

Table 2 Adult male subjects by group and category

Years included	Group ID	Stay			Leave				
		RS	YIS	OIS	RE	YIE	OIE	TR	EL
1990–2004	1	0	1	0	0	1	0	0	0
1985–2005	2	1	4	0	3	1	0	0	0
1975–2005	7	1	8	1	1	1	0	3	2
1992–2000	18	0	1	0	4	0	0	0	0
1980–2005	19	1	1	0	0	1	0	0	2
1993–1998	30	2	0	0	2	0	0	1	1
1990–2004	33	1	1	0	1	1	0	0	0
Total		6	16	16	11	5	0	4	5

Each number represents a unique animal (see Electronic supplementary material 2). Bold entries indicate potential secondary transfer *RS*, adult resident at start of study, remains in group until end of study; *YIS*, immigrates as young animal (six years or less for males), remains in the group until end of study; *OIS*, immigrates as older animal, remains in group until end of study; *RE*, adult resident at start of study, emigrates; *YIE*, immigrates as young animal (definition above), emigrates at a later time; *OIE*, immigrates as older animal, emigrates at a later time; *TR*, transient, seen with group during one observation/capture session only; *EL*, eliminated from analysis

Table 3 Adult female subjects by group and category

Years included	Group ID	Stay			Leave				
		RS	YIS	OIS	RE	YIE	OIE	TR	EL
1990–2004	1	0	6	1	4	0	0	2	0
1985–2005	2	6	9	2	2	2	2	1	5
1975–2005	7	4	14	4	2	3	3	13	3
1992–2000	18	3	2	0	3	0	2	1	0
1980–2005	19	0	6	2^a	0	4	0	6	0
1993–1998	30	6	1	0	1^a	1	0	2	3
1990–2004	33	3	4	0	3	0	0	1	3
Total		22	42	9	15	10	7	26	11

RS, adult resident at start of study, remains in group until end of study; *YIS*, immigrates as young animal (five years or less or nulliparous for females), remains in the group until end of study; *OIS*, immigrates as older animal, remains in group until end of study; *IE*, adult resident at start of study, emigrates; *YIE*, immigrates as young animal (definition above), emigrates at a later time; *OIE*, immigrates as older animal, emigrates at a later time; *TR*, transient, seen with group during one observation/capture session only; *EL*, eliminated from analysis

^a Same individual, all others are unique individuals (see Electronic supplementary material 2). Bold entries indicate potential secondary transfer

the absolute number of females in groups. Females joined groups with a low number of females to males and left when there was a high number of females to males ($t_{80} = -2.17, p < 0.04$; join: mean 1 male:2.9 females, SD 1.5; leave: mean 1 male:3.6 females, SD 1.7). Females also joined groups with a lower absolute number of females and

left with a higher absolute number of females ($t_{80} = -2.17, p < 0.04$; join: mean 5.7, SD 2.9; leave: mean 7.0, SD 3.0).

Group size and sex ratio

While population survey results indicate a relatively stable population, there were significantly more adults (1984: $t_{13} = -3.9, p < 0.002$; 1991: $t_{25} = -3.4, p < 0.003$; 1998: $t_{32} = -4.9, p < 0.001$) and more adult females (1984: $t_{13} = -3.5, p = 0.004$; 1991: $t_{25} = -3.1, p < 0.005$; 1998: $t_{32} = -3.6, p < 0.01$) in multi-male groups than in one-male groups. Despite this, there were no differences in sex ratio (1984: $t_{13} = -0.08, n.s.$; 1991: $t_{25} = 0.4, n.s.$; 1998: $t_{32} = 1.9, n.s.$). Whether groups are small or large, one-male or multi-male, the proportion of males to females in groups remain stable over time.

Discussion

Secondary transfer does occur in both adult male and adult female mantled howling monkeys in the population living on La Pacifica. The direct evidence from the master data base shows that while there were more female secondary transfers than males, the difference is not dramatic. Two male secondary transfers formed two new one-male groups, but all other secondary transfers were into established social groups. The indirect evidence from our ongoing records of seven groups indicates that an impressive 35% of all of the adult male group members are potential secondary transfers, while 29% of all of the adult female group members are potential secondary transfers. While this is an indirect measure of transfer, it does provide information on when animals join or leave, including their age and group demographics, as well as provide clues as to why an animal would leave a non-natal group in which they had had breeding opportunities, or why they would join a second or third non-natal group. While howlers have been noted to move between groups following a social disturbance such as translocation or extreme habitat disturbance following a storm (deVries 1991; Ostro et al. 1999; Pavelka et al. 2003; Behie and Pavelka 2005), there were no dramatic environmental disturbances (e.g., hurricane, volcanic eruption, earthquake, fires, etc.) at La Pacifica during the study period.

Do the patterns of joining and leaving support any of the hypotheses associated with social structure, resources and reproductive success? Because this is a post hoc study, there are limits to what we can conclude, but we can say the following. We do not have phenology data to measure resource availability, but neither habitat type nor rainfall patterns correlated with any measures tested in any of our

analyses on this population (Glander 2005; Clarke and Glander 2005, present study; Teaford et al., in prep.). We have only limited data on dominance relationships and alliances as groups were observed for different studies at different times. We can look at the predicted association of predation and group size, the prediction of infanticide avoidance, and patterns of access to mates.

The hypothesis of predation avoidance was not supported for males, as neither the number of females nor group size was related to male secondary transfer. While females left groups with larger numbers of females and joined groups with more males to females, there was no difference in the total number of males, making predator protection unlikely as an explanation (Ridley 1986; van Schaik and Horstermann 1994). The new groups, with fewer females, should be less attractive for a male takeover, a situation that could be interpreted as supporting the hypothesis of infanticide avoidance (Sterck et al. 1997; Crockett and Janson 2000; Steenbeek and van Schaik 2001). As infanticide is well documented in this population (Clarke 1983; Clarke et al. 1994), and predation is virtually unknown, infanticide avoidance for females is a viable hypothesis.

For both males and females, however, sex ratio emerges as the key feature associated with joining or leaving a group. It is essential to recognize that favorable/unfavorable sex ratios are different for adult males and females, and male and female strategies have to be analyzed as separate entities rather than as a “balance” between the two (Cooper et al. 2004). Since survey data at seven-year intervals indicate stable sex ratios in social groups at La Pacifica, it would appear that adults are regularly redistributing themselves throughout the population to optimize the proportion of males to females for each individual adult. For males, they leave groups with fewer females to males and join groups with more females to males, and females are doing the opposite. It is unlikely that they are redistributing themselves for improved access to food, as almost all secondary transfers of both sexes remained low-ranking in their new group. Group females resisted new female secondary transfers while group males remained in proximity to new transfers, and the secondary transfers eventually stayed in the group at the bottom of the female dominance hierarchy. While a group with fewer females (resisting entry) and more males (facilitating entry) might be the only groups these females could join, the end result for the female secondary transfer was joining a group with more males and fewer females, not necessarily improved access to feeding resources.

Is there an association with optimal sex ratio and reproductive success for either sex? A recent analysis showed no differences in reproductive success for males in single versus multi-male groups (Clarke and Glander

2005), but we do not have data on reproductive success by group composition over time. However, a report on several populations of *Alouatta pigra* from Mexico and Guatemala, and another on long-term records of *Alouatta palliata* at Barro Colorado Island in Panama, suggest that optimal sex ratios for males or females are indeed associated with increased reproductive success for that sex (Van Belle and Estrada 2008; Ryan et al. 2008). While these studies compared reproductive success and group size rather than sex ratio itself, the patterns mirror those at La Pacifica. In the mantled howlers of Barro Colorado Island, as groups got larger, there were more males to females, which improved female reproductive success and decreased male reproductive success (Ryan et al. 2008). In black howlers, which are only found in small groups, that same pattern was found, and the opposite pattern was found when the sex ratio was reversed, i.e., females had better reproductive success with more males in the group, and less with more females (Van Belle and Estrada 2008). Both of these analyses corroborate the interpretation of La Pacifica howlers improving reproductive success by leaving a breeding group with a disadvantageous sex ratio and joining a second breeding group with a more advantageous sex ratio. Treves (2001) came to a similar conclusion in an analysis which, among other sources, utilized data from the La Pacifica population.

While both males and females join groups as younger animals and leave as older animals, the age range for leaving is quite variable (1 SD = 6.6–17.4 years), suggesting the possibility of multiple social or environmental “triggers” for secondary transfer. It is highly likely that there are different proximate cues and causes during an animal’s lifetime that make the difference between staying or going. Variable reasons “why” adults disperse have been identified in other species. Sterck et al. (2005) argue that nulliparous female Thomas’s langurs transferred for inbreeding avoidance, while older multiparous females transferred to groups with young adult males that could presumably offer better protection against infanticide and predation than an older tenured male. In gorillas, female mountain gorillas preferentially transfer to larger, multi-male groups (Watts 2000), while in western gorillas, they transfer to smaller groups (Stokes et al. 2003), a pattern that is also interpreted as an adaptation to infanticide avoidance (Yamagiwa et al. 2003). Condition-dependent dispersal in male baboons was also associated with absolute numbers of females and “excess” numbers of males, with “high quality” males (those likely to achieve high dominance status) transferring to groups with a higher number of females, and “low quality” males moving out of groups with excess males to groups with fewer males (Clarke et al. 2008), a pattern that could be occurring in La Pacifica howler males. The only adult animal known to

transfer to a new group as a high-ranking animal at La Pacifica was a prime high-ranking male (Jitney) that left group 2 just after the adult composition became five males and nine females. He was seen just a few months later in a nearby group as a dominant male supplanting everyone, but his new group was now composed of four males and 12–15 females (Clarke, personal observation).

It is possible that some of our assumptions about group living, dispersal patterns, and relatedness in primates are too simplistic. Genetic analyses of chimpanzees indicate that philopatric males are only closely related in very small groups (Lukas et al. 2005), and similar studies in orangutans indicate that both males and females within a group area are more related to each other than to nonresident animals, despite the fact that males disperse and females are philopatric (Goossens et al. 2006). And in gorillas, where both sexes emigrate, dispersal patterns in females appear to associate with habitat quality and distance from natal group, while males showed no discernible patterns (Guschanski et al. 2008). Genetic analysis also revealed that gorilla females, who would be expected to be living in groups of unrelated adults, do have female relatives (Bradley et al. 2007). The dispersal patterns of both sexes emigrating in La Pacifica howlers would also predict unrelated groups of adults, and while we do not have genetic data, we have already documented exceptions to the “all juveniles emigrate” rule (Clarke and Glander 2008), and we have also documented two juvenile males that emigrated and returned after several years to become dominant in their natal group (Clarke, personal observation). Thus, a group that would be predicted to contain nonrelated adults does contain some relatives. Genetic data from howlers at Barro Colorado Island also indicate that some adult males are related (Milton et al. 2009).

Given the extent of the “exceptions to the rule” across multiple taxa, we probably should rethink our assumptions about the relationship between primate social structure, resources and dispersal patterns. Snaith and Chapman (2007) reviewed the literature and concluded that folivores and frugivores do not have different regimens, while Majolo et al. (2008) came to similar conclusions through a meta-analysis of the published literature. Indeed, the variety of dispersal patterns now being described do not neatly fit our present models and thinking (Isbell 2004; Lawson Handley and Perrin 2007), and there are calls to both make our models more complex and meaningful (Travis and French 2000) and abandon the concept of ecological determinism as a guide to understanding primate social structure (Thierry 2008). Social history, social constraints, disease processes, cognition, time allocation, and phylogeny should all be considered when trying to understand the dynamics of nonhuman primate social grouping in general (Chapman and Pavelka 2005; Snaith and Chapman 2007;

Pollard and Blumstein 2008; Cunningham and Janson 2009; Chapman and Rothman 2009), and regrouping as a result of secondary transfer in particular.

Our post hoc analysis of the howler population of La Pacifica indicates a very different pattern from the one that was observed in two social groups living in riparian habitat in the 1970s (Glander 1980; Jones 1980; Clarke et al. 1998). We argued then that all animals left their natal group and joined a new group as the dominant animal of each sex and stayed in that group for the rest of their life. With 20 years data we still thought this was the case, but with 35 years of data we know it is much more complex. It is probably safe to say (paraphrasing Wrangham 1980 and Altmann 1989) that males may still follow females, but they do it differently according to age, rank and social history. And while females still need food, it is only one facet of a wide range of social and physical challenges that they face over a lifetime.

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