UNUSUAL INTERGROUP MOVEMENT OF YOUNG MALES IN A MALE PHILOPATRIC SOCIETY

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Abstract

Deviations from sex-biased dispersal patterns of primate species have often been attributed to local demography, particularly in cases of dispersal by males in what are typically male philopatric societies. Here, we evaluate the demographic conditions associated with novel observations of intergroup movements by two male northern muriquis, *Brachyteles hypoxanthus,* monitored since their births at the Reserva Particular do Patrimônio Natural - Feliciano Miguel Abdala, in Caratinga, Minas Gerais, Brazil. Specifically, we compare the size and operational sex ratios (OSR) of all four muriqui groups in the study population at the time the two males, aged 5.4 and 7.9 years, left their natal group to associate with members of a non-natal group, and again 3 months later, when the older male, ZS-J, returned to his natal group. We also use Association Indices to evaluate the males' spatial relationships in their natal and non-natal groups to better understand the social conditions that may have also affected their unusual movements. The two males initially moved from their natal group (Jaó), which had the highest OSR in the population, into the smallest group with the most favorable OSR (M2). However, ZS-J subsequently returned to his natal group despite its much higher OSR. Both males had strong spatial associations in their natal group prior to their departures, but only the younger male achieved similar spatial associations in M2 group, where he remained. ZS-J's extreme spatial peripheralization in M2 group may have contributed, at least in part, to his return to Jaó group, where his earlier strong spatial associations were restored. These findings suggest that social and demographic factors may be involved in individual deviations from a species or population's normative dispersal patterns. They also demonstrate the value of long-term field studies of recognized individuals over the duration of their lives for documenting behavioral flexibility.

Keywords: *Brachyteles hypoxanthus*, male dispersal, male philopatry, demography, operational sex ratio, association index.

Resumen

Desviaciones de patrones de dispersión ligados al sexo de especies de primates han sido a menudo atribuidas a la demografía local, particularmente en casos de dispersión de machos en lo que son típicamente sociedades filopátricas de machos. Aquí, evaluamos las condiciones demográficas asociadas con observaciones novedosas de movimientos intergrupales de dos machos de muriquis del norte, *Brachyteles hypoxanthus,* monitoreados desde sus nacimientos en la Reserva Particular do Patrimônio Natural - Feliciano Miguel Abdala, en Caratinga, Minas Gerais, Brasil. Específicamente, comparamos el tamaño y proporciones de sexo operacional (OSR) de todos los grupos de muriquis en la población de estudio en el momento en que los dos machos, de 5.4 y 7.9 años de edad, dejaron su grupo natal para asociarse con miembros de otro grupo, y de nuevo 3 meses después, cuando el macho mayor, ZS-J, regresó a su grupo natal. También usamos Indices de Asociación para evaluar las relaciones espaciales de los machos en sus grupos natales y no natales para entender mejor las condiciones sociales que pueden también haber afectado sus inusuales movimientos. Los dos machos inicialmente se movieron de su grupo natal (Jaó), que tenía el más alto OSR en la población, hacia el grupo más pequeño con el más favorable OSR (M2). Sin embargo, ZS-J después regreso a su grupo natal a pesar de su más alto OSR. Ambos machos tenían fuertes asociaciones espaciales en su grupo natal antes de partir, pero solamente el macho más joven logró similares asociaciones espaciales en el grupo M2, donde permaneció. La extrema periferalización espacial de ZS-J en el grupo M2 pudo haber contribuido, por lo menos parcialmente, a su retorno al grupo Jaó, en donde sus anteriores fuertes asociaciones espaciales fueron restauradas. Estos hallazgos sugieren que factores sociales y demográficos pueden estar involucrados en desviaciones individuales de aquellos patrones de dispersión normales de una especie o una población. También demuestran el valor de los estudios a largo plazo de individuos reconocidos durante la duración de sus vidas para documentar la flexibilidad comportamental.

Palabras Clave: *Brachyteles hypoxanthus*, dispersión de machos, filopatría de machos, demografía, proporción de sexo operacional, índice de asociación.

Introduction

Dispersal patterns of primates exhibit strong phylogenetic signals and are therefore often regarded as phylogenetically conservative traits in comparative models of social evolution (Lee and Kappeler, 2003; Clutton-Brock and Lukas, 2012; Lee and Strier, 2015). However, while male-biased dispersal with female philopatry appears to be a highly stable dispersal regime in cercopithecines (Di Fiore and Rendall, 1994), both bi-sexual and female-biased dispersal regimes exhibit higher levels of facultative responsiveness to local demographic and ecological conditions (Fredysted *et al.*, 2007; Strier *et al.*, 2014; Lee and Strier, 2015). Observational and genetic data have revealed cases in which same-sexed offspring of either sex have remained in their natal groups in species with normative bi-sexual dispersal regimes, *e.g.*, callitrichids: Goldizen (2003); howler monkeys: Van Belle *et al.* (2014a); Van Belle *et al.* (2014b); gibbons: Brockelman *et al.* (1998); gorillas: Robbins and Robbins (2015). Comparable exceptions to female-biased dispersal have also been reported, with cases of females remaining in their natal groups, *e.g.*, chimpanzees: Pusey and Schroepfer-Walker (2013); northern muriquis: Strier *et al.* (2006).

Exceptional cases of dispersal by males in male philopatric societies have similarly been reported (*e.g.* bonobos: Hohmann (2001); woolly monkeys: Di Fiore and Fleischer (2005); Maldonado and Botero (2009); and spider monkeys: Aureli *et al.* (2013). The observation of dispersal by a pair of bonobo males was hypothesized to be a response to the favorable adult sex ratio in the group they joined (Hohmann, 2001). Variable male dispersal was also suspected from the lack of close genetic relatedness among male woolly monkey group members (Di Fiore and Fleischer, 2005). Observations of male spider monkeys in non-natal groups have been attributed to singular circumstances, such as the small number of resident males, but the risk of aggression toward immigrant males is thought to limit the occurrence of dispersal of males in these male-philopatric societies (Aureli *et al.*, 2013).

Here, we add to this growing literature with new observations of young males traveling with a non-natal group in another ateline, the northern muriqui (*Brachyteles hypoxanthus*). We compare the size and operational sex ratios of all four northern muriquis groups in the study population to evaluate the potential demographic conditions that might have stimulated these males to leave their natal group to associate with members of a non-natal group, and in the case of the older male, to return to his natal group 3 months later. We also evaluate the males' spatial relationships with one another and with other members of their natal group and non-natal group to better understand the social correlates of their unusual movements.

Methods

The study was conducted at the Reserva Particular do Patrimônio Natural - Feliciano Miguel Abdala (RPPN - FMA), a 1,000 ha fragment of Atlantic forest in Caratinga, Minas Gerais, Brazil (19°50′ S, 41°50′ W). Climate is seasonal at this site, with an annual rainy season from November– April , when more than 80% of the mean annual rainfall of 1,134±266 mm falls, and a distinct dry season from May–October (Strier *et al.*, 2001). Annual temperatures avarage 20.6 ± 2.9ºC (Jung *et al.*, 2015). We investigated four muriqui groups (i.e. Matão, M2, Nadir and Jaó groups; Table 1), where animals were individually identified through natural marks. Data were collected from August 2014 to July 2015 on a daily basis, except from 24 December 2014 to 12 January 2015 when no observations were conducted.

Group size was calculated from the number of observed individuals in each group and summarized on a monthly basis. We calculated the Operational Sex Ratio (OSR), or the ratio of the number of breeding males to the number of sexually receptive females (Kvarnemo and Ahnesjo, 1996) in each of the groups at the start of the two months (1 December 2014 and 1 March 2015) that intergroup transfers involving at least one of the young males occurred. Our calculations of OSR included all males > 7 years of age and females > 7 years that were not carrying infants < 2 years of age and that did not give birth before September 2015, and could therefore be considered potentially sexually receptive during the months with male movements.

Following Tokuda *et* al. (2013), we used daily records of group composition, called roll-calls (RCs), of all individuals observed in the Jaó and M2 groups on each day the groups to estimate Association Indices. This index is a measure of the frequency of individuals seen with each other. This analysis was made for each of the young males and all other individuals in these groups. Also following Tokuda *et al.* (2013), we used SOCPROG (Whitehead, 2009) to construct separate clusters based on the distribution of individuals across RCs during three periods of group membership: while the males were still in their natal Jaó group (1 August-10 December 2014); during the three months in which they were both associating with M2 group (11 December 2014-29 March 2015); and after ZS-J returned to Jaó group (30 March- 31 July 2015). The validity of the subgroups represented by the clusters was evaluated with the coefficient of modulation of associations (Q) where Q ≥ 0.3 was considered to be a valid subgroup. The tendency of each of the subjects to associate with other individuals in their groups was evaluated from the sum of their association indices with all others, or *Strength* (*S*); the higher the *S* value, the stronger the individual's associations.

Results

We recorded the movements of two young males that left their natal Jaó group to live with a neighboring, non-natal group (M2). The two males were last sighted with their natal group on 8 December 2014 and first sighted with the M2 group on 11 December 2014, following an encounter between the two groups on the same and prior days. The older of the two males (ZS-J; 7.9 years) returned to his natal Jaó group 3 months later, while the younger male (FRD-J; 5.4 years) has remained in the M2 group through the present (August 2016).

Group sizes and OSRs varied during the different phases of the study period due to births, migrations, and disappearances (Table 1). On 11 December 2014, the two males changed their associations from their natal Jaó group to the smallest group with one of the lowest OSRs (M2) in the population. By March 2015, however, the OSR in all but one of the groups (Nadir) had increased. By then, the OSR of the Jaó group was 46% higher than that of the M2 group.

As expected based on our observations of the groups, association patterns clearly distinguished between the M2 and Jaó groups (Q<0.3) for all three phases of male group membership (Table 2). Thus, the males' intergroup movements were not related to broader group dynamics such as group fusion.

The *S* values differed between individuals and their groups (Table 2). The high *S* values of ZS-J and FRD-J in their natal Jaó group are indicative of their strong spatial associations. In M2 group, however, the strength of FRD-J's associations remained high while ZS-J's declined. Upon his return to Jaó, ZS-J's *S* value rose again.

Discussion

The unusual movements of these males were partially consistent with predictions about male movement based on potential demographic advantages. While joining a smaller group might have been advantageous for reducing intragroup competition for both males, the return of ZS-J to his natal group 3 months later might have been a response to his weak spatial associations (low *S* value) in M2 group.

The contrast between ZS-J's intergroup movements and FRD-J's persistence in M2 group, where he has now remained for more than a year, resembles the dispersal processes of "Visit" and "Direct" described by Strier *et al.* (2015) for females in this population. Although ZS-J and FRD-J transferred together, the differences in their respective *S* values before and after their natal group departures suggest that their movement decisions may have been independent. Both males were well connected to other members of their natal group prior to their departures, but whereas FRD-J developed strong associations in his adopted M2 group, ZS-J's *S* score declined in the M2 group. Social peripheralization in the M2 group may have contributed, at least in part, to his return to Jaó group, where his earlier strong social associations were restored.

Table 1. Group size (number of individuals), Number (N) of breeding males and potentially sexually receptive females present in each group, as defined in the text, and Group OSR at the start of the months of male inter-group movements (December 2014 and March 2015). The two male subjects were included with Jaó's group size in December 2014, and with M2 group in March 2015. See text for details.

	December 2014				March 2015			
Group	**Group size**	**N Breeding males**	**N Potentially receptive females**	**OSR**	**Group size**	**N Breeding males**	**N Potentially receptive females**	**OSR**
Jaó	76	22	13	1.69	81	21	8	2.63
M2	61	17	13	1.31	62	18	10	1.80
Nadir	79	22	17	1.29	82	21	17	1.24
Matão	126	33	24	1.38	133	33	21	1.57

Table 2. Strength (*S*) of males' association and coefficient of modulation of associations (Q) in groups in differents moments.

Period of male inter-group movements	**Coefficient of modulation of associations (Q)**	**Strength (*S*)**	
		ZS-J	**FRD-J**
1 August – 10 December 2014	0.06	29.95	28.16
11 December 2014 – 29 March 2015	0.04	13.91	30.96
30 March – 31 July 2015	0.06	34.40	30.96

Being more than 2 years younger may have contributed to FRD-J's greater social assimilation in M2 group compared to ZS-J, as has been proposed for the assimilation of young dispersing male woolly monkeys (Maldonado & Botero, 2009). FRD-J also filled a vacant age class among males in the M2 group that may have contributed to his social acceptance. Although males as young as FRD-J are sexually active in this population, ZS-J may have been perceived as a competitor because he was much closer to the 8 years of age at which males in this population are known to sire offspring (Strier *et al.*, 2011).

Dispersal is fundamental to the avoidance of inbreeding in all species, yet it remains one of the most difficult behavior patterns to understand (Di Fiore *et al.*, 2009). The initial movement of males in our study into a group with a more favorable OSR also suggests that demographic conditions could be at least partially responsible for the unusual intergroup movements of the two males in our study. Indeed, favorable OSRs have previously been implicated in analyses of male group membership following group fission (Tokuda *et al.*, 2013). However, comparative OSRs do not explain why these particular males left their natal Jaó group while other male contemporaries remained. Indeed, consistent with the egalitarian relationships that distinguish males in this population (Strier *et al.*, 2011; Tokuda *et al.*, 2012), there was no evidence of overt aggression directed toward these males. Long term data on OSR influencing dispersal decisions and analyses focusing on male social networks with one another and with females may provide additional insights into the unusual dispersal patterns of individual males.

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