Male Tenure and Reproductive Success in Single-male vs. Multi-male Groups of Free-Ranging Howling Monkeys in Costa Rica

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Introduction

Male reproductive success in nonhuman primates has traditionally been measured by access to estrous females, and successful matings/inseminations are attributed either to high-ranking males in multi-male groups or to the one male in a single-male group (e.g., Fedigan, 1983; Smuts, 1987; Dixson *et al.*, 1993; Paul *et al.*, 1993). Paternity exclusion techniques and the testing of potential fathers and infants, however, have demonstrated that access, including copulation, does not always correlate with success. As group size increases, there are more females for the highest-ranking male to inseminate, and if the females are seasonal or synchronous breeders, the male is less able monopolize estrous females (Nunn, 1999; Takahashi, 2001). The discrepancy between dominance rank and mating success involves more than female availability, however. In single-male patas monkey groups, the resident male did not sire all offspring (Ohsawa *et al.*, 1993), and alternate male strategies in multi-male groups are known from rhesus monkeys (Berard *et al.*, 1993, 1994, 1999; Smith, 1993, 1994) and savannah baboons (Alberts *et al.*, 2003) which allow for reproductive success in lower-ranking males.

True reproductive success is defined as the total number of surviving offspring, which can only be measured over the lifetime of an individual male. Given the practical difficulties, this may be reduced to a pair of simple proxies: the length of time a male is fertile and has access to fertile females, and the number of other males competing for those same females. These two measures may serve as useful predictors of potential reproductive success.

Mantled howlers (*Alouatta palliata*) may form both single-male and multi-male groups within the same population. Since howler groups often experience takeovers by an outside male, there could be an advantage to living in a multi-male group, as low-ranking males would have the "protection" of the high-ranking males' competitive ability to repel newcomers (Nunn, 2000). Although all males would compete for access to estrous females, occasional reproductive synchrony could benefit low-ranking males; the dominant male can only monopolize one female at a time, which allows other males access to other fertile females. Conversely, the lone male in the single-male group would be expected to have access to all estrous females and father all offspring born in that group (Ridley, 1986), but would be at higher risk for predation or a takeover by an outside male (van Schaik and Horstermann, 1994).

To evaluate the effects of male tenure on reproductive success in both single-male and multi-male groups, we examined our records for group membership and infant survival in seven groups of howlers at Hacienda La Pacifica between 1970 and 2002. These included one group that had always had only one male, two groups that were always multi-male, and four groups that fluctuated between single- and multi-male status. As resource availability could have affected reproductive success, we carried out a similar analysis for males in riparian habitats (three groups), which could be considered richer in resources (Glander and Nisbett, 1996), vs. males in upland habitats (four groups).

We have made two important assumptions in this analysis. First, we assume that the male in a single-male group sires all offspring; and second, we assume that over a male's lifetime, males in multi-male groups have equal reproductive success. Takeovers by young males result in a reverse age-graded dominance hierarchy in this population (Glander, 1980; Jones, 1980). A young, dominant male would be expected to have high reproductive success, which would presumably decrease as the male aged and lost his status.

Methods

Study site

La Pacifica is a working cattle ranch / rice farm / tilapia farm in the dry tropical forest zone of Guanacaste Province, Costa Rica (Holdridge, 1967). Three rivers border the farm with associated riparian habitat. The farm was deforested in a comparatively conservative manner in the 1950s for cattle ranching The upland habitat was converted to pastureland, leaving strips of forest as windbreaks between pastures, and large areas of forest were left in hilly, rocky areas deemed unsuitable for grazing. Forested areas along the three rivers were untouched. The farm was originally irrigated through a low-maintenance, low-impact system operated by gravity, pulling water from the river on the north side of the farm. In 1986 the farm was sold and irrigation patterns changed: large machinery was used to clear larger ditches which increased waterflow and caused extensive soil erosion. In 1991 a substantial section was deforested for a major government irrigation canal, and in 1998 a major shift in land use occurred as pastures were converted to wet rice agriculture or tilapia tanks. Many of the forest areas were disturbed, but many others remain, and the size of the monkey population remained essentially unchanged from the 1970s to 1998 (Clarke *et al.*, 2002).

Study subjects

Animals from seven different social groups have been tracked for various periods from 1970 to the present. Thirty-three males were included in this analysis, eight in single-male groups and 30 in multi-male groups. Five of these males spent time in each type of group.

Data collection

This analysis is based on data collected during population surveys from 1974–76, 1984, 1991, and 1998 (Clarke *et al.*, 1986; Clarke and Zucker, 1994; Clarke *et al.*, 2001), yearly counts of groups by MRC, and repeated capture and mark sessions from 1970 to 2002. Behavioral studies carried out by M. R. Clarke, K. E. Glander, R. A. Nisbett and E. L. Zucker during the past thirty years have characterized group composition in detail.

Analysis

To analyze male tenure, we compared the number of years for each male in a multi-male group (n = 30) to the number of years for each male in a single-male group (n = 8) using an independent t-test. We also tested the number of years spent in a single- vs. a multi-male group for the same males in the same groups (n = 5), using a repeated measures t-test. We compared the number of years in single-male (n = 3), multi-male (n = 25), or both group types (n = 5) using an independent one-way ANOVA. We used an independent t-test to compare the number of years spent in a riparian habitat group vs. an upland habitat group. For the habitat comparison, total time for each male in the group was used regardless of male composition.

To calculate male reproductive success, we divided group history for all groups into time blocks of single- or multi-male tenure (seven blocks of multi-male, eight blocks of single-male). For each time block, the total number of "male years" was calculated and divided by the years in that time block to yield an average number of males per year. (E.g., in a four-year time block, if there were two males in the group for all four years and a third in the last year, there were 4 + 4 + 1 = 9 male-years divided by the four years of that time block, yielding an average of 2.25 males/year.) We used the same approach to calculate the mean number of females per year. We also tabulated the mean number of infants born per year and surviving per year. We calculated the potential number of infants per male (*potential infant/male*) by dividing the mean number of females by the mean for males. *Realized reproductive effort* was calculated by dividing the mean number of infants born to the mean number of males, and dividing that by *potential infant/male*, while *relative infant loss* was calculated by subtracting the mean number of infant survivors from the mean of all infants born. Each of these measures was tested by habitat (riparian vs. upland) and by male composition (single-male vs. multi-male) using independent t-tests.

Results

Male tenure

We found no significant differences in time spent in a single-male group or in a multi-male group (Table 1). For the five males which spent time in both group types, we also found no statistical differences between the length of time they spent in a single-male vs. a multi-male group (Table 1). However, when total time for specific males that alternated between group types is compared to males living exclusively in a single-male or multi-male group, males with the alternating strategy were in social groups significantly longer overall (Table 1). As before, however, we found no differences between animals living only in a single-male or in a multi-male group (Tukey post hoc test, p < 0.05, critical diff. = 6.0: single/multi = 0.45; single/both = 6.7; multi/both = 7.1). There were no differences in length of time in social groups by habitat type (Table 1).

Reproductive success

We found no difference in realized reproductive effort per male between single- and multi-male groups (see Table 2), but the potential for infant production was significantly greater in the single-male groups. Infant survivorship, when expressed as a ratio of infants born minus infants surviving, was greater in a single-male group, although it only approached statistical significance (see Table 2). More infants per female per male were born in riparian habitats, but neither the number of potential infants per male nor infant survivorship were associated with habitat type (see Table 2).

Discussion

We expected that males would reside in multi-male groups longer than in single-male groups, but this was not borne out. Residence in a larger group would presumably buffer an individual male's reproductive success against the likelihood of a male takeover, ensuring that the resident male shared group membership rather than having no membership at all. In theory, the shared group membership would be balanced by increased competition for access to fertile females, as opposed to the presumably sole access in the much smaller single-male group. The true situation, however, is apparently much more complex.

We found no differences in the mean number of infants born per male between single- or multi-male groups, but there were significantly more females available per male in the single-male group (almost double) than in the multi-male groups. Thus, males in single-male groups are not achieving all possible pregnancies, which raises several questions. Are they spending their time defending their females rather than copulating? In the absence of male-male competition, do they monitor female receptivity less carefully? Even considering the approximately two-year interbirth interval documented in this population (Glander, 1980), half of the females should give birth every year regardless of the number of available males. As reproductive success involves infant survivorship as well as number of offspring, it should be noted that infant survivorship is somewhat greater in single-male groups. Thus, a female might be less likely to conceive in a single-male group, but once she is pregnant, it would appear that her infant has a better chance of surviving its first year in a single-male group.

Table 1. Group tenure. Comparison of time in years which males spent in single-male groups, multi-male groups or both group types, and for groups in riparian vs. upland habitat.

	Mean	SD	Mean	SD	Mean	SD	t / F	df	Significance
	Single-male		**Multi-male**		**Both**				
Sample Type:									
One-multi (all)	5.6	3.0	6.2	3.6	-	-	t = 0.41	36	n.s.
Repeated	5.2	2.6	7.8	4.5	-	-	t = -1.34	4	n.s.
One/multi/both	6.3	4.0	5.9	3.4	13.0	6.0	F = 6.9	32	p < 0.01
	Riparian		**Upland**						
All males	8.1	5.4	6.1	3.7			t = 1.23	31	n.s.

Table 2. Reproductive success. Realized and potential reproductive success by year for males in single-male and multi-male groups, and by riparian vs. upland habitat type, including infant loss.

	Mean	SD	Mean	SD	t	df	Significance
	Single-male		**Multi-male**				
Sample (mean per year)							
Realized reproduction/male	0.4	0.2	0.5	0.1	-1.16	13	n.s.
Potential infant/male	4.3	1.2	2.6	0.8	3.17	13	p < 0.01
Relative infant loss	0.4	0.6	0.9	0.5	-2.05	13	p = 0.06
	Riparian		**Upland**				
Realized reproduction/male	0.5	0.1	0.3	0.1	2.68	13	p < 0.02
Potential infant/male	3.3	1.0	3.7	1.5	-0.54	13	n.s.
Relative infant loss	0.7	0.6	0.6	0.6	0.50	13	n.s.

Single-male groups are generally smaller (range = 4–12) than multi-male groups (range = 8–42), and while single-male groups occur in both habitat types, they are more common in upland habitat (Clarke *et al.*, 2002). Upland habitat is more affected by the distinct seasonality of the dry tropical forest, and upland habitat females are lighter than their riparian counterparts (Teaford and Glander, 1997; Glander, in press). These are factors which could contribute to females not conceiving, but they would not explain higher infant survivorship in single-male groups. As high-ranking females often attack the infants of lower-ranking females (Clarke *et al.*, 1998), it is possible that having fewer females in a single-male group may improve infant survivorship, an important factor unrelated to the number of males.

From the male standpoint, it might seem that the best strategy for long-term access to females is to maintain group membership, regardless of whether it is in a single-male or a multi-male group. This flexible strategy is not common, however, as only five of the 33 males in this sample were able to pursue it successfully. While males can stay in a multi-male group after a new male takes over, the sex-ratio becomes less favorable thereafter, with fewer females in proportion to males. Older males have two alternative strategies: leave a multi-male group and take over a single-male group, or form a new group with peripheral females. There is evidence that both patterns exist (Clarke and Glander, 2004).

The most surprising result is the almost complete lack of association of either tenure or reproductive parameters with habitat type. The dichotomy between the upland habitat and riparian habitat in dry tropical forest is a common analytical parameter, but it should be noted that while the groups labeled "upland" never used riparian habitat, all of those labeled "riparian" do make extensive use of upland habitat at some times of the year (pers. obs.). A confounding effect is involved because single-male groups are more common in the upland habitat, but from this analysis, it appears that the composition of social groups is a better predictor of tenure and reproductive success than the habitat alone.

This analysis is based on assumptions that need to be confirmed through paternity exclusion tests. The overall conclusion—that males have improved reproductive success through complete access to females in a single-male group, as opposed to competing for females in a multi-male group—should not be accepted without question. These results, based on long-term field records, should provide evidence that presumptions about male reproductive

success based on observations of potential access to females alone are not valid.

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CARACTERIZACIÓN DE LOS DORMIDEROS USADOS POR *ATELES BELZEBUTH* EN EL PARQUE NACIONAL YASUNÍ, ECUADOR

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Introducción

En general, la mayoría de los primates duermen en árboles, pero algunas especies del Viejo Mundo, como los hamadrias (*Papio hamadryas*), duermen en peñascos (Stammbach, 1987), los orangutanes (*Pongo pygmaeus*) pernoctan en plataformas construidas sobre el suelo con ramas y hojas (Rodman y Mitani, 1987) y los gorilas (*Gorilla gorilla*) pasan la noche en nidos construidos en los árboles o sobre el suelo (Schaller, 1963; Morris, 1991).

En los bosques Neotropicales, todos los primates duermen en árboles, cuyas características difieren de una especie a otra. Así, por ejemplo, los monos nocturnos (*Aotus* spp.) utilizan diferentes tipos de dormideros, tales como huecos en troncos y ramas de árboles secos o envejecidos (obs. pers.), sitios complejos formados por una masa vegetal de epífitos, trepadoras y enredaderas, o sitios simples de un follaje denso (Aquino y Encarnación, 1986). Los escasos estudios de campo respecto a primates del género *Callithrix* sugieren diferencias entre sus especies, pero la mayoría de ellas aumentan el número de árboles utilizados como dormideros con el tamaño de sus ámbitos hogareños, pudiendo también usar el mismo dormidero por varias noches consecutivas (Stevenson y Rylands, 1988). Los monos chichicos (*Saguinus* spp.) acostumbran cambiar frecuentemente sus dormideros, los mismos que son seleccionados estratégicamente a fin de minimizar el contacto con sus predadores (Snowdon y Soini, 1988). Especies del género *Leontopithecus* presentan la tendencia de dormir en huecos de árboles (nidos) abandonados por otras especies (Kleiman *et al.*, 1988).

Monos de tamaño más grande, como los aulladores (*Alouatta* spp.), duermen en las ramas horizontales de árboles de mediano a gran tamaño; casi siempre estos árboles son forrajeados antes de ser usados como dormideros (Neville *et al.*, 1988). Los chorongos del Yasuní (*Lagothrix lagothricha*) forman grandes agrupaciones sociales (Di Fiore, 1997). Estos grandes grupos forrajean juntos y al final del día se dividen en subgrupos que duermen muy cercanamente, usando varios árboles de características diferentes (obs. pers.). Observaciones de campo realizadas por Ramírez (1988) en la Amazonía peruana indican que un subgrupo de cinco individuos escogió para dormir un gran árbol completamente lleno de hojas. Los muriquís del Brasil (*Brachyteles arachnoides*) generalmente duermen en el estrato medio del bosque, utilizando las ramas bifurcadas de sus árboles dormideros (Nishimura *et al.*, 1988).

Existe escasa información que caracterice los dormideros que usa *Ateles belzebuth*, probablemente debido a la dificultad que representa seguir a individuos de esta especie. Sin embargo, van Roosmalen (1985) y Chapman (1989) han reportado que los monos araña (*Ateles paniscus paniscus* y *Ateles geoffroyi* respectivamente) prefieren dormir en árboles de los estratos altos del bosque, usando entre 11 y 43 individuos arbóreos y que muchos de estos árboles suelen utilizarse para dormir en múltiples ocasiones. Generalmente, estos primates duermen en subgrupos que ocupan uno o varios árboles dormideros y el tamaño de los subgrupos se relaciona con las necesidades forrajeras de sus individuos (Chapman, 1989).

En este artículo se describen las características de los sitios y árboles utilizados como dormideros por parte de un grupo de *Ateles belzebuth* en el Parque Nacional Yasuní (PNY), Ecuador, durante un seguimiento realizado entre diciembre de 1994 y febrero de 1996, con el fin de estudiar el comportamiento social y las costumbres alimenticias de la especie (Pozo, 2001, 2004a).