RESEARCH ARTICLE

Characteristics of Alpha Males in Nepal Gray Langurs

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In species with strong male-male competition, access to females in multimale-multifemale groups is usually regulated via a dominance hierarchy. The highest ranking (alpha) male often has priority of access and sires most offspring. The alpha male can change in three basic ways: (i) a recent immigrant or a resident challenges and becomes the new alpha; (ii) formation of a new group; (iii) succession—becoming alpha after higher ranking males have left. When, in a given primate population, the alpha male changes in different ways, two questions arise: (a) which is the most successful tactic and (b) do male attributes, such as age, aggressiveness or propensity to commit infanticide, affect the outcome? We examined these questions in the seasonally breeding Nepal gray langurs (Semnopithecus schistaceus) at Ramnagar, where new alpha males were either recent immigrants or residents. Success was measured as alpha tenure, residency duration, and the number of offspring sired (paternity exclusion based on DNA analysis, 28 infants). We documented 12 alpha-male tenures across two multimale-multifemale groups between 1991 and 1997. The predominant mode of change was the immigrant tactic. Age had no effect perhaps because alpha males were among the youngest adult males in their group. As expected, infanticidal males performed similarly to non-infanticidal ones. Alpha tenure was highly variable and longer for immigrant alphas and hyper-aggressive ones. However, none of the tactics or attributes examined resulted in significantly longer residencies or more offspring, likely because of the timing of immigrations and stochastic effects (i.e., the number of conceptions occurring per alpha tenure). The influence of female mate choice on male reproductive success requires further investigation. Furthermore, it remains to be examined why resident alpha males—with their presumed better knowledge of their opponents — performed so poorly. Am. J. Primatol. 79:e22437, 2017. © 2015 Wiley Periodicals, Inc.

INTRODUCTION

Like other mammals, most nonhuman primate males compete for access to females because it is the main factor determining their reproductive success [Trivers, 1972]. Within multimale groups, access to females often follows a priority-of-access model [Altmann, 1962], with the highest ranking male (alpha male) siring the majority of the offspring [Alberts, 2012]. Consequently, this position is highly contested.

In species in which males disperse from their natal group, changes in the highest ranking position can be assigned to three basic scenarios [following van Noordwijk and van Schaik, 2004]. (i) An aggressive challenger, who can be a recent immigrant or a resident male, defeats the current alpha male. (ii) A male disperses and is joined by females so that a new group forms, or an established group splits. (iii) A resident male attains the alpha position by default, also called succession, because all higher ranking males left the group. The last scenario may include extended waiting periods (i.e., queuing for

rank). The few cases when a male immigrates into a group of females that has no adult male [e.g., mantled howler monkeys, Glander, 1992; Thomas' langurs, Steenbeck, 1996; white-faced capuchins, Fedigan & Jack, 2004] can be seen as a special form of succession.

Tactics differ in their level of risk and should vary with a male's resource holding potential. This is supported by the finding that across primates, when resource holding potential is presumably high and paternity skewed (>43% sired by alpha), changes in alpha male follow a high risk tactic, that is immigration rather than succession [van Noordwijk & van Schaik, 2004]. In contrast, succession occurs mainly in very large, often provisioned groups [Sprague et al., 1996; Alberts, 2012], which tend to have a large number of males and a low reproductive skew. These males form agonistic coalitions, which may prevent other males from using the immigrant tactic and alter the influence of dominance rank on mating behavior [Young et al., 2013], although there are exceptions [Alberts et al., 2003]. In the absence of coalitions, dominance rank usually directly reflects the asymmetry in physical strength and, with it, the difference in fighting ability between individuals [i.e., their resource holding potential, Parker, 1974]. The relationship between rank and age will be inverted, with the youngest adult individuals occupying the highest rank positions and the oldest ones holding the lowest ranks [Packer, 1979a; Alberts et al., 2003; Setchell et al., 2006].

Besides dominance rank and age, additional male attributes, such as aggressiveness, have been shown to influence male reproduction [Packer, 1979b]. For example, in chimpanzees, aggressive males who charge at females more frequently and use contact aggression toward these females also mate more frequently [Muller et al., 2007] and sire more offspring [Feldblum et al., 2013], especially when forming coalitions [Gilby et al., 2013]. More generally, most of the aggression received by adult female primates from males is connected to receptivity and interpreted as sexual coercion [Muller et al., 2009], which means it increases the likelihood that a female, when fertile, mates with the coercive male [Smuts & Smuts, 1993]. Outside of this context, male aggression toward females seems to be rare [Muller & Wrangham, 2009].

Circumstances are different for infanticidal males because aggression is specifically targeted at unweaned individuals [van Schaik, 2000] rather than at adult females or all group members. Females who have lost an infant to infanticide will not benefit by avoiding the perpetrators thereafter and are expected to, and indeed often do mate with them [Hrdy, 1979; Ebensperger, 1998]. The reproductive success of infanticidal males is difficult to predict because, in order for it to be an adaptive male reproductive tactic, the male does not need to sire more offspring than a non-infanticidal male. He should only, on average, sire more offspring than he would have without committing infanticide [Broom et al., 2004]. This hypothetical comparison of the reproductive output of the same male under alternative scenarios (infanticidal *versus* non-infanticidal) can only be modeled. The closest practical test would be a comparison of the reproductive success of males who attacked infants with those who did not, expecting no difference between the two types. In other words, infanticidal males should not perform worse than non-infanticidal ones.

Here we examined different measures of success of alpha males in multimale groups of Nepal gray langurs (*Semnopithecus schistaceus* formerly called *Semnopithecus entellus* or *Presbytis entellus*). Females were philopatric [exceptions in Koenig et al., 1998] while natal males dispersed as subadults [Borries, 2000]. In this population, adult males maintained a steep, linear dominance hierarchy that changed mostly by immigrations and emigrations [Perlman et al., in prep.]. We did not observe male-male coalitions. Reproductive skew was pronounced, with alpha males siring 57% of all infants born [three groups, Launhardt et al., 2001] or 74% of all infants sired by *resident* males, which is a better measure of the within-group monopolization potential [Gogarten & Koenig, 2013]. As predicted by the high alpha paternity and relatively small average group size [means: 20.5 individuals, 3.1 adult males in multimale-multifemale groups, Borries, 2000:147] the predominant mode of alpha male change was the immigrant tactic, but occasionally a resident would became alpha [Borries, 2000]. What remained unclear is whether the two tactics differ in their success. Here, we measured success as the duration of alpha tenures, the duration of residencies, and as the number of offspring produced (details below). Furthermore, we examined how male aggressiveness modified success and whether it differed for infanticidal males [Borries, 1997]. Similar to other primates (see above), we expected (i) the youngest adult alpha males to be more successful than older ones, (ii) immigrant alpha males to be more successful than resident ones, (iii) hyper-aggressive males to be more successful than less aggressive ones, and (iv) infanticidal males to be as successful as non-infanticidal ones.

METHODS

The study was conducted at Ramnagar, Nepal (latitude 27°44′ N, longitude 84°27 E, 300 m a.s.l.) in a semi-evergreen forest [Borries, 2000]. The climate varied seasonally (92% of the average annual precipitation of 2279 mm fell between May and September), and, consequently, the Nepal gray langurs reproduced seasonally. Conceptions were confined to the period from July to November with 49% of cases ($N = 51$) during August alone [Koenig et al., 1997]. The study population is characterized by a slow life history compared to other populations. Offspring age at last nipple contact averaged 24.9 months [range: 18.8–32.1 months, Borries et al., 2001]. Females had their first offspring at a mean age

of 6.7 years [minimum 6.0 years, Borries et al., 2001] and the interbirth interval after a surviving offspring averaged 2.7 years [minimum 2.0 years, Borries & Koenig, 2000].

In this wild, unprovisioned population, 72% of the groups were multimale-multifemale and the remaining groups were one-male multifemale. Mean group size for multimale-multifemale groups was 20.5 individuals, including 7.2 adult females and 3.1 adult males [Borries, 2000]. Here we present data for two multimale-multifemale groups. P group was a medium sized group (mean about 20 individuals) with 3.0 adult males on average (range: 1–7; eight different males) and 6.9 adult females ($N = 58$ months of study). P group was observed from July 1991 through April 1996 during 1866 contact days representing 81% of all days during the study period. This amounted to a total observation time of 13581 hours, averaging 9 hours and 15 minutes per observation day. O group was a larger than average group (mean about 30 individuals) and contained 4.1 adult males on average (range: 2–10; 22 different males) and 13.6 adult females ($N = 66$ study months). O group was observed from January 1992 through June 1997 during 1491 contact days or 84% of all days. This amounted to 13814 contact hours, and averaged 9 hours and 19 minutes per observation day. On each contact day, we recorded any births and deaths, as well as the presence and absence of group members, all of which were recognized individually.

We determined male rank based on 3807 dyadic displacement interactions [Perlman et al., in prep.] collected using focal animal and *ad libitum* sampling techniques [Altmann, 1974] by 22 observers during all contact hours. Dominance ranks were based on the I&SI method [de Vries, 1998] which placed the alpha male at rank one. For details of rank assessments see Lu et al. [2013] and Perlman et al. [in prep.]. For each group, we broke down the study period into periods during which the alpha male remained the same even if membership and rank positions of the other resident males changed more frequently. During the study, none of the 30 adult males residing in the two study groups attained the alpha position in more than one group, even though some males resided in several groups in succession [Borries, 2000]. However, two males (M69 and M70) became alpha male twice in the same group. These cases were counted as separate tenures but were also combined to determine each male's total alpha tenure duration. Consequently, some measures were calculated once for all alpha tenures ($N = 12$) and once for all alpha males ($N = 10$). In contrast to an earlier analysis [Borries, 2000], we considered only 12 alpha tenures for the two groups combined, omitting brief periods for which data were insufficient to reliably assess the respective alpha male [Perlman et al., in prep.].

We did not know male age but were able to estimate the following four age classes based on physical markers [Perlman et al., in prep.]: (i) Subadult males had a head-body length at least as long as an adult female but not as long as an adult male. (ii) Young adult males had reached the head-body length typical of an adult male, but they were not yet as filled out. Once young adult, males usually acquired the full adult proportions within one year. We considered them young adult for an additional two years to capture the entire period of prime physical strength when their canines were least worn (about three years in duration). Based on our observations of the maturation of different individual males across different age classes (infant, juvenile, subadult, young adult, adult), we estimated the youngest young adult males to be about seven years of age. (iii) Adult males had adult proportions and their canines showed at least some sign of wear. They were at least ten years of age or older. (iv) Old adult males were fully grown with signs of aging such as ragged fur, wrinkled skin, often slender bodies, and a reduced speed of movements. At the beginning of each alpha tenure, we assigned all resident males to an age class.

We considered three additional male attributes, immigrant *versus* resident tactic, hyper-aggressive *versus* not hyper-aggressive, as well as infanticidal *versus* non-infanticidal. These attributes are explained in the respective results sections below.

Paternity analysis was based on DNA from fecal material for 28 infants (i.e., 70% of all 40) born into the two multimale groups. The additional 12 infants with no available DNA samples were sired during the tenures of five different alpha males: one infant each during the tenures of M11 and M69, two infants when M85 was alpha male, and four infants each during the tenures of M49 and M12, respectively [Launhardt et al., 2001]. To check for a potential bias caused by these missing data, we assigned all infants without a sample to the male at the alpha position at the time of conception and recalculated all paternity measures (see below). For paternity exclusions, we determined the genotypes at five microsatellite loci (D16S420, D17S791, D12S67, D4S2366, SCA1) reaching a mean probability of exclusion of 92.3% for the samples included here [calculated from Launhardt et al., 2001: 58]. In one case, two males could not be excluded as fathers and were assigned 0.5 infants each. In another case, although the alpha male (M13) was excluded as the father, we did not have DNA samples for three of the resident males who could have sired the offspring. Therefore, this case was not considered when determining non-alpha paternities.

We measured success as (i) the duration of the alpha tenure defined as the period during which the same male occupied the highest ranking position in the group ($N = 12$); (ii) the duration of the alpha

tenure per alpha male, because two males attained the position twice ($N = 10$); (iii) the duration of the entire residency in the group for each alpha male, including periods when they were not yet or no longer alpha (called residency in the following, $N = 10$); the number of offspring sired (iv) per alpha tenure ($N = 12$), and (v) per alpha male ($N = 10$), as well as (vi) during the entire residency ($N = 10$).

We note that our present analysis is based on only two groups and thus the results differ slightly from Launhardt et al. [2001] which included a third multimale group for which the mode of alpha male change was unknown. Because of the small sample size (12 alpha tenures), we tested the effect of male attributes on all measures of success separately with Mann–Whitney U-tests and did not correct for repeated testing. The Mann–Whitney U-test can yield significant results even for very small sample sizes, in our case two *versus* eight males [Mann & Whitney, 1947; Sokal & Rohlf, 2012]. We performed correlations as Spearman rank correlations [Sokal & Rohlf, 2012].

The data collection protocol was approved by the Research Division, Tribhuvan University, Kirtipur, and the Ministry of Education, HMG, Katmandu. It adhered to the legal requirements of Nepal and Germany, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

RESULTS

Alpha Tenure and Residency

In our two multimale study groups an average alpha tenure lasted 304 days ($N = 12$, Table I, or 364 days if every male was considered only once, $N = 10$). The range was large (10–1573+ days). Residency averaged 851 days ($N = 10$, range: 40–1573+ days, Table II). The length of the alpha tenure did not correlate with residency duration (Spearman rank correlation, $r_s = 0.200$ for $N = 12$, $r_s = 0.127$ for $N = 10$, $P > 0.05$ for both). These are minimum values because two alpha tenures and three residencies were still ongoing at the end of the study (Table II). Furthermore, these values refer only to males who became alpha male. Across all adult males, including those who did not became alpha, residency in multimale-multifemale groups lasted 356 days [calculated from Borries, 2000:149].

Paternities During Alpha Tenure and Residency

An average alpha male sired 1.3 offspring per tenure (range: 0.0–6.5, $N = 12$) or 1.6 offspring per individual alpha male (range: 0.0–6.5, $N = 10$, Table II). Most males had 0–3 offspring (Fig. 1). Only one male had a higher success (M49 with 6.5 offspring). If the four infants without DNA samples sired during his alpha tenure were his as well, the maximum reproductive success in our sample would be 10.5 offspring. When all infants without samples were counted as alpha paternities, the average number of offspring sired per alpha tenure increased to a mean of 2.3 (range: 0.0–10.5, median = 0.5, IQR = 0.0–3.5, $N = 12$), which translated into a mean of 2.8 per alpha male (range: 0.0–10.5, median = 1.5, IQR = 0.0–4.0, $N = 10$).

Inclusion of offspring sired outside of the alpha tenure (i.e., during the entire residency) generated a mean of 2.0 offspring (range: 0.0–6.5, median = 1.5, IQR = 0.0–3.0, $N = 10$), which increased to a mean of 3.2 (range: 0.0–10.5, median = 2.5, IQR = 1.0–4.0, $N = 10$) if we included infants without DNA samples.

The relationship between the number of offspring sired and alpha tenure had a shallow slope which was even shallower for residency duration (slope dropping from 0.0023 to 0.0011; Fig. 1 a, b). The flatter slope for residencies is related to the fact that (a) the same number of offspring sired is accounted for over the usually longer residency and (b) two males (M13 and M24) sired offspring after they had been alpha male, during the first and second conception season respectively of a hyper-aggressive male's alpha tenure (details in Launhardt et al. [2001: 58] Table III). Additional information on hyper-aggressive males is given below. Assigning infants without DNA samples to alpha males did not change the basic relationship for offspring sired during alpha tenure or residency (the slope dropped from 0.0051 for alpha tenures to 0.0020 for residencies, figures not shown).

Alpha males sired 78% ($N = 15.5$ infants) of all the offspring sired by resident males (total $N = 20$ infants). This accounted for 55% of all offspring analyzed ($N = 28$) because 26% ($N = 7$) were sired by non-resident males (whose identities could not be determined further, but all resident adult males were excluded as fathers), 16% ($N = 4.5$) by non-alpha resident males, and in one case (4%) the alpha male was excluded as father but DNA samples for most non-alpha resident males were unavailable. These numbers differ from those published previously [Launhardt et al., 2001; Gogarten & Koenig, 2013] because we used a smaller sample size here.

Alpha Tenure and Timing

In the study population, conceptions were confined to five months of each year (July–November) so that an alpha tenure that fell outside this period would not yield reproductive success. This was the case in 2 of the 12 alpha tenures (concerning 1 of 10 males, Table II). Both were comparatively brief tenures of 21 and 40 days respectively. In three

TABLE I. Age Estimates of Non-Natal Males and Number of Infants Present at the Beginning of Each Alpha Tenure Sorted Chronologically Within Each Group

Group	Alpha male	Alpha tenure		Age class of non-natal males				N adult males	Age of N infants present at beginning [months]			N infants born after°
		Start date	Duration [days]	Subadult	Young adult	Adult	Old		≤6	6≤12	12≤18	
O	M11	02-Jan-92	413		1	4		6*		3		3
O	i M49	10-May-93	502	1	1	2	1	5	2		1	
O	i M70	29-Sep-94	126		3	2		5	7	2		
O	M75	03-Feb-95	40		3	2		5		6		
O	i M69	15-Mar 95	21		2	2		4		6		1
O	M70	05-Apr-95	158		3	2		5	1	2	4	1
O	M69	10-Sep-95	10		2	2		4	1		6	
O	M24	20-Sep-95	26		4	2		6	1		6	
O	i M85	20-Oct-95	614+	1	6	2		9	1		2	4
P	i M13	26-Jul-91	67		1	1		2	1		5	
P	M14	01-Oct-91	92			4	1	6		1	5	
P	i M12	10-Jan-92	1573+		1	2		3			1	1

Gray highlights = age class of the respective alpha male; *no age estimate for one male; + = alpha tenure still ongoing at the end of the study; ° = number of infants born in the first seven months (mean gestation length) of the alpha tenure or until the end if tenure lasted only up to seven months; i = infanticidal. Brief periods during which male dominance rank could not be determined are excluded (cf. Methods)

additional cases, no conceptions occurred during the alpha tenure (Table II). The longest alpha tenure during which no conception occurred lasted 126 days (M70, Table II).

Attribute: Age

Most males were young adult (75%, $N = 12$, Table I) when they attained the alpha position. The remaining 25% were adult. In nine of the 12 cases the alpha male was in the youngest adult age class represented in the group. In all measures of success, males starting out as young adult alphas did not differ from those beginning as adult males (Table III). The result did not change if all infants

without DNA samples were assigned to the respective alpha male (Table S1).

Attribute: Alpha Tactic

The immigrant tactic observed in the study population resembled the classic cases described earlier as "bluff immigrant" [van Noordwijk & van Schaik, 1985; 2004]: an unfamiliar male would appear in a group's home range and aggressively confront the alpha male. Within hours or a few days, the new male would become the new alpha male. In contrast, the resident tactic summarizes cases in which the new alpha male had already been a resident in the group for some time (in our population

TABLE II. Alpha Tactic Used and the Resulting Length of Alpha Tenure and Residency as Well as Paternity Results [from Launhardt et al., 2001]; Tenures Sorted in Descending Order Which Places Hyper-Aggressive Males at the Top (longest Alpha Tenures) and Resident Alpha Males at the Bottom (shortest Alpha Tenures)

General information			Alpha tenure								Residency duration	
Male	Group	InfX	Length [days]	Tactic used	N infants conceived	N paternities determined	N alpha paternities	% alpha paternities	% other resident paternities	% non-resident paternities	N paternities	Length [days]
M12	Pc	yes	1573+	IM	13	9	3	33	11	56	3	1573+
M85	O9	yes	614+	IM	8	6	2	33	50	17	2	614+
M49	O2	yes	502	IM	12	8	6.5	81	6	13	6.5	950
M11	O1	no	413	IM	2	1	1	100	0	0	1	1429
M70	O6	no	158	IM	3	3	3	100	0	0	3	285
M70	O3	yes	126	IM	0	0						
M14	Pb	no	92	IM	0	0					0	92
M13	Pa	yes	67	IM	1	1	0	0	?	?	1	1478
M75	O4	no	40	IM*	0	0					0	40
M24	O8	no	26	RM	0	0					3	1602+
M69	O5	yes	21	RM*	0	0					0	444
M69	O7		10	RM	1	0	0					

InfX = infanticide suspected, assumed or confirmed [Borries, 1997]; IM = immigrant male; RM = resident male; gray highlights = hyper-aggressive males; underlined = alpha during at least parts of the conception season (July – November), see also Table I; + = still ongoing at the end of the study; values for residency duration given once per male (two males became alpha twice); * = tenure fell outside of the conception season which lasted from July–November [Koenig et al., 1997]; subscript = sequence of alpha males per group (numbers for O group and letters for P group).
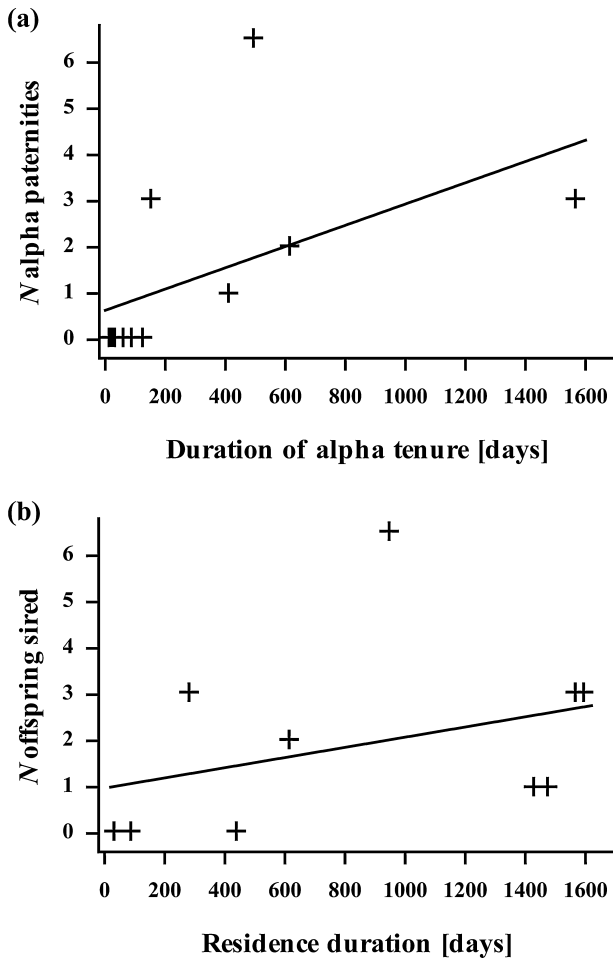
Fig. 1. Number of offspring sired as (a) alpha male and (b) during the entire residency in a group.

respectively). Just prior to attaining the alpha position, resident males were second ranking twice (M24, M69) and third ranking once (M69).

Compared to resident alphas, immigrant alphas had a significantly longer alpha tenure but similar residencies and they did not sire more offspring (Table III). The same holds true if all infants without DNA samples were assigned to the alpha male (Table S1).

Attribute: Hyper-Aggressive

Hyper-aggressive bouts by two alpha males (M85 and M12) occurred frequently and for several months at the beginning of their tenures. Females in P group continued avoiding M12 even for several years, long after he had ceased to be hyper-aggressive. Both males stalked and attacked group members at full speed. Victims fled and were often defended by other group members. These intense events were so disruptive that observers would almost certainly lose sight and track of most group members, making it impossible to document these bouts in full. Consequently, our records for hyper-aggressive males did not show a significantly higher frequency of agonistic interactions. However, because of the conspicuous character of the intense chases, there was complete inter-observer agreement on which males belonged in this hyper-aggressive category, and we used this categorization in the analysis (four observers for M12; 11 observers for M85).

Hyper-aggressive alpha males had a longer alpha tenure but not a longer residency and they did not sire more offspring than other alpha males (Table III). The P-values were lower when infants without DNA were assigned to alpha males but did not reach significance (Table S1). Given that the alpha tenure of both hyper-aggressive males was still ongoing at the end of the study it is possible that at the end of their residency they would have sired more offspring than other alpha males.

The two hyper-aggressive immigrant alpha males lost paternities to other resident males and to non-resident males (Table II). Of all paternities determined during their tenure, both males sired only 33% (M12 had 3 of 9, M85 had 2 of 6). The percentage of all infants sired by *resident* males (within group) was 75% for M12 (3 of 4 offspring) and 40% for M85 (2 of 5). Conversely, the percentage of non-resident paternities (outside of the group) was higher for M12 (56% or 5 of 9 offspring) compared to M85 (17% or 1 of 6). When offspring without DNA samples were added to the alpha males, the percentage of all paternities for M12 and M85 rose to 54% and 50%, respectively (7 of 13 and 4 of 8), with other resident males siring 8% (1 of 13) and 38% (3 of 8). Non-resident paternities were 39% (5 of 13) for M12 and 13% (1 of 8) for M85, respectively. Alpha

for more than five months, see below). We assume that the resident alpha male tactic resembles the "rank turnover" described for Japanese macaques [Sprague et al., 1996], although we could not confirm that aggression played a major role during resident alpha male changes in our study population.

A previous analysis showed that immigrant males were more likely to attain the alpha position than any other lower rank position [Borries, 2000]. This is also reflected in the fact that the immigrant tactic was most common among alpha males (75%, 9 of 12 cases; 80%, 8 of 10 males). Of the two males who became alpha twice, one (M70) was an immigrant both times. After having been defeated by another immigrant, M70 left the group to re-immigrate into the same group after an absence of two months. The other male, M69, was a resident both times. He became resident alpha on day 172 and again on day 351 of continuous residency at a lower rank position. The second male using the resident tactic, M24, became alpha after 1022 days of residency, which included three brief absences (5, 9, and 13 days

TABLE III. Success Measures for Alpha Males Who Were and Were Not Young Adult, Immigrant, Hyper-Aggressive, or Infanticidal

Male attributes	Success measures	Sample size A	Sample size B	Mean A	Mean B	Median A	Median B	IQR A	IQR B	U	P
Young adult (A)	Alpha tenure	9	3	331	220	126	92	26-413	67-502	12.0	0.864
	Alpha tenure[1]	7	3	426	220	285	92	31-614	67-502	10.0	1.000
Versus	Residency[1]	7	3	855	840	614	950	285-1573	92-1478	10.0	1.000
Adult (B)	N offspring as alpha	8	3	1.1	2.2	0.5	0.0	0.0-2.5	0.0-6.5	12.0	1.000
	N offspring as alpha[1]	7	3	1.7	2.5	2.0	1.0	0.0-3.0	0.0-6.5	10.0	1.000
	N offspring overall[1]	7	3	1.3	2.2	1.0	0.0	0.0-3.0	0.0-6.5	10.5	1.000
Immigrant (A)	Alpha tenure	9	3	398	19	158	21	92-502	10-26	0.0	0.009
Versus	Alpha tenure[1]	8	2	448	29	349	29	80-558	26-31	0.0	0.044
Resident (B)	Residency[1]	8	2	808	1023	782	1023	189-1454	444-1602	5.0	0.533
	N offspring as alpha	9	2	1.7	0.0	1.0	0.0	0.0-3.0	0.0	4.0	0.327
	N offspring as alpha[1]	8	2	2.0	0.0	1.5	0.0	0.0-3.0	0.0	3.0	0.267
	N offspring overall[1]	8	2	2.1	1.5	1.5	1.5	0.5-3.0	0.0-3.0	7.0	0.889
Hyper-Aggressive (A)	Alpha tenure	2	10	1094	146	1094	80	614-1573	26-158	0.0	0.030
	Alpha tenure[1]	2	8	1094	182	1094	80	614-1573	36-349	3.5	0.267
Versus	Residency[1]	2	8	1094	790	1094	697	614-1573	189-1454	5.0	0.533
Not hyper-Aggressive (B)	N offspring as alpha	2	9	2.5	1.2	2.5	0.0	2.0-3.0	0.0-1.0	3.5	0.218
	N offspring as alpha[1]	2	8	2.5	1.3	2.5	0.0	2.0-3.0	0.0-2.0	3.5	0.267
	N offspring overall[1]	2	8	2.5	1.8	2.5	1.0	2.0-3.0	0.0-3.0	5.0	0.533
Infanticidal (A)	Alpha tenure	8	4	384	143	142	66	44-558	33-253	12.0	0.570
Versus	Alpha tenure[1]	6	4	512	143	394	66	67-614	33-253	6.0	0.257
Non-Infanticidal (B)	Residency[1]	6	4	891	791	782	761	444-1478	66-1515	10.0	0.762
	N offspring as alpha	7	4	2.1	0.3	2.0	0.0	0.0-3.0	0.0-0.5	7.5	0.230
	N offspring as alpha[1]	6	4	2.4	0.3	2.5	0.0	0.0-3.0	0.0-0.5	5.0	0.171
	N offspring overall[1]	6	4	2.6	1.0	2.5	0.5	1.0-3.0	0.0-2.0	6.5	0.257

Tenure length rounded in days; gray highlights = first option of each attribute; IQR = interquartile range;[1] = total values for the two males who became alpha twice. Final columns show Mann–Whitney U-test comparisons of alpha males with the different attributes.

paternities on all *resident* paternities rose to 88% (7 of 8) and 57% (4 of 7) respectively.

The siring rates of these hyper-aggressive males changed through time [Launhardt et al., 2001]. In his first mating season in the group, M12 sired none of the five infants analyzed, although no DNA samples were available for two additional infants. In his second mating season, no conception occurred. In his third and fourth mating season, M12 fathered three of the four infants for which paternity was assigned, with two more infants without DNA samples. When the other hyper–aggressive male, M85, became alpha the mating season was almost over, and he only sired the last infant conceived that year. In his second mating season, he sired one of five infants, again with no DNA samples for two additional infants. Our study did not include a third mating season for this male.

The two hyper-aggressive alpha males both used the immigrant tactic. If these two males were excluded from the analysis, the mean tenure length of the remaining immigrant alpha males was shorter (200 days for alpha tenure and 712 days for residency) and the average number of offspring sired during residency changed from 2.1 to 1.9. Of all success measures only the tenure as alpha male of non-hyper-aggressive *immigrants* was significantly longer compared to *resident* alpha males (Mann–Whitney U-test, U = 0.0, P = 0.017). This mirrors the test results when including hyper-aggressive males (Table III), indicating that results for the immigrant tactic were not driven by the two hyper-aggressive males.

Attribute: Infanticidal

In contrast to hyper-aggressive males who targeted individuals of all age-sex classes, infanticidal males specifically attacked infants. The attacking males held different rank positions (ranks 1–5) but the alpha male was over-represented [Borries, 1997]. Of the ten individual alpha males considered in this analysis, one male was observed killing an infant, two males likely killed infants (the infant died or disappeared after sustaining injuries that could have been inflicted by the canine teeth of a male and several group members avoided the particular male before and after the infant disappeared), for two males we presumed it (the male was seen to attack infants and the infant disappeared), and we observed one male attacking an infant without killing it [definitions and a list of all cases in Borries, 1997]. We distinguished these six infanticidal alpha males from the other four non-infanticidal ones. While the latter were alpha males, we did not observe them attacking even though infants were present and additional infants were born during the first seven months [i.e., mean gestation length in the study population, Ziegler et al., 2000] of their alpha tenure (Table I). Note: we considered infants up to 18 months because the infant killed in our presence was 18 months old [see also Arlet et al., 2014 for gray-cheeked mangabeys].

Infanticidal males did not differ significantly from non-infanticidal males in their alpha tenure, their residency duration, or the number of offspring

produced (Table III). When we assigned infants without DNA samples to alpha males, the results did not change (Table S1).

DISCUSSION

We found that alpha males changed primarily via immigration. Age had no effect on the duration of alpha tenures; instead, duration depended on the tactic used and on aggressiveness, with longer tenures for immigrants and hyper-aggressive males. Longer tenures, however, did not necessarily pay off *via* more offspring. As expected infanticidal males did not sire fewer infants, and were about as successful as non-infanticidal males. When interpreting these results, we need to keep in mind that, with 12 alpha tenures (ten males), the sample size is small and we can get only an initial glimpse at male tactics, attributes, and reproductive success. It would be interesting to include offspring survival, but this would reduce the sample size even further. Still, 12 changes in the alpha male position are a large number for a difficult to observe arboreal primate. In the following discussion we mainly rely on other species because even though *Semnopithecus* spp. has been studied at about 30 locations [Koenig & Borries, 2001], in most populations groups were one-male multifemale, and no study on multimale-multifemale groups span several alpha tenures.

What Influences Male Tactic and Tenure?

Immigrant was the predominant tactic used by males in the study population (75–80%) to gain the alpha position. This stands in contrast to long-tailed macaques where the resident tactic was more frequent [van Noordwijk & van Schaik, 2001] perhaps because it was executed differently. Male long-tailed macaques immigrated into a new group before reaching adult size. They later challenged the alpha male following a solitary period of several months spent within the group's home-range. In contrast, at Ramnagar, males had been continuously associated with the group for at least five months prior to using the resident tactic. Compared to resident long-tailed macaques, resident Nepal gray langurs might therefore have better information about their opponents to select the best moment for taking over the alpha position. Judged by the poor performance of resident alpha males at Ramnagar (short alpha tenure without siring offspring), it could be that the change was initiated by a weakened or disappearing predecessor. Just prior to becoming alpha male, these residents already held high-ranking positions. They could simply have been the next-in-line following the departure or weakening of an alpha male, thus resembling a chance succession process rather than a timed challenge [Sprague et al.,

1998]. We currently know too little about the exact circumstances during resident alpha male changes to resolve the issue.

Male white-faced capuchins at Lomas Bardudal used both the resident ($N = 17$) and the immigrant tactic ($N = 12$) [Muniz et al., 2010]. However, the resident tactic included challenging the current alpha, succeeding him after his death, as well as becoming alpha in a subgroup after a split. At a different site (Santa Rosa) males of the same species mainly used the immigrant tactic (79%) although, in all but one case a coalition of males ousted all resident males in the group [Fedigan & Jack, 2004]. At present it is not clear which factors determine the use of a specific tactic, and it will take time before enough data of sufficient quality will have accumulated to allow for a meta-analysis of factors influencing alpha male tactics in nonhuman primates.

The mean duration of alpha tenures of Nepal gray langurs (12 months, $N = 10$ males) was similar to white-faced capuchins [Perry, 2012] but shorter than in long-tailed macaques [25 months, van Noordwijk & van Schaik, 2001]. However, for example in baboons [chacma baboons 5.5 months, Palombit et al., 2000; savannah baboons: 8 months, Alberts et al., 2003] alpha tenures were even shorter. Similar to the choice of alpha tactic, it is currently unclear what determined tenure length. It may be related to group size and whether coalitions occurred [Alberts, 2012]. Even within a given population the range of alpha tenures is often large. Arguably one of the extreme cases are white-faced capuchins at Lomas Barbudal where alpha tenure averages 12 months but the median is 14 days and the range 1 day to 18+ years [$N = 86$, Perry, 2012; Perry et al., 2012]. At Santa Rosa the same species has a mean alpha tenure of 2.8 years and a range of 4 months to 14.6 years [$N = 26$, Jack et al., 2013]. Some of the differences may be related to observation densities which allow determining an alpha tenure of 1 day at one site but not the other. These logistic differences currently hamper comparisons across sites and species.

There are several indications that becoming and staying alpha male in Nepal gray langurs is a reflection of individual strength. First, there was little variance in age at the beginning of an alpha tenure. Most males were very young and presumably at the height of their physical abilities [Packer, 1979a] similar to mandrills [Setchell et al., 2006] and chimpanzees [Boesch & Boesch-Achermann, 2000]. Second, most males used the immigrant tactic to become alpha male which included direct, aggressive challenges. The fact that males almost always came and challenged alone and that other males did not form coalitions could have facilitated this tactic. Third, hyper–aggressive males had the longest alpha tenures suggesting that aggressiveness may reflect a strong resource holding potential.

What Influences Male Reproductive Success?

Similar to other primates [Dittus, 1975; van Noordwijk & van Schaik, 2001], male reproductive success in the study population depended on the timing of alpha tenures [Borries, 2000]. In 42% (five of 12 alpha tenures), conceptions were either not possible (outside of the 5-month long conception season), or did not occur. In addition, the number of conceptions per mating season varied between 0–7 in the medium-sized P group and between 2–9 in the larger-than-average O group [Launhardt et al., 2001] adding a stochastic element to the timing. Years with a high number of conceptions could alternate with few or no conceptions because the minimum interbirth interval after a surviving offspring was two years and the median three years [Borries & Koenig, 2000].

In the long run, inbreeding avoidance will limit male reproductive success in primate populations with extended male residencies [white-faced capuchins, Muniz et al., 2006; review in Tennenhouse, 2014]. At Ramnagar, the youngest age at first conception was 5.4 years [Borries et al., 2001] while the longest documented tenure of an alpha male was 4.3+ years (or 1573+ days), which suggests that our results for alpha males should not be impacted by inbreeding avoidance. However, because this longest alpha tenure and the longest residency [2146+ days or 5.9+ years, Borries, 2000] were still ongoing at the end of the study, inbreeding avoidance could soon become an issue.

It seems unlikely that the number of resident males played a major part in paternity distributions because at the time of each conception the male with the highest alpha paternity (M49) resided with 3.8 other adult males, while the hyper-aggressive males with the lowest realized paternities averaged 2.0 (M12) and 2.5 (M85) other resident males, respectively [calculated from Launhardt et al., 2001: 58]. This stands in contrast to the general notion that the number of adult males has a large impact on the relationship between male dominance rank and mating or reproductive success [Cowlishaw & Dunbar, 1991; Gogarten & Koenig, 2013].

The result that neither tactic nor any of the other male attributes affected male reproductive success could be an indication for female choice. In Nepal gray langurs, females have no external signs of receptivity [Hrdy, 1977] making it difficult to assess their exact reproductive state. Nevertheless, there were behavioral indications that males in the study population distinguished pregnant from cycling females and among receptive females between non-conceptive and conceptive receptive periods [Ostner et al., 2006], but not the exact timing of ovulation within receptive periods [Heistermann et al., 2001]. This scenario leaves room for females to influence paternity which could have contributed to the low percentage of paternities realized for hyper-aggressive males. We would like to emphasize that hyper-aggressive males targeted all group members for many months and did not concentrate on receptive females. These cases are, therefore, fundamentally different from reports of male aggression toward females in other species which fit the predictions of sexual coercion [Muller et al., 2009] and may improve male mating and reproductive success [chacma baboons, Kitchen et al., 2009; chimpanzees, Gilby et al., 2013].

In sum, we found that, similar to other primates, alpha tenure was highly variable. The exact determinants of tenure length are often unclear, but in the study population they seem to relate to the immigrant tactic and the aggressiveness of the male. This is supported by the fact that neither tactics nor any of the attributes resulted in longer residencies or more offspring, which was likely due to the timing of immigrations and stochastic effects, but female mate choice might have played a role as well.

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Supporting Information

Additional supporting information may be found in the online version of this article.