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# Dominance Relationships in Male Nepal Gray Langurs (*Semnopithecus schistaceus*)

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**KEY WORDS** despotism; dominance hierarchy; male age; physical condition; resource holding potential

## ABSTRACT

**Objectives:** Reproductive skew is proposed to link to despotism in dominance hierarchies. While studies illustrating male skew are plentiful, demonstrating the link to despotism is rare. Likewise, it is often unknown which factors (e.g., resource holding potential, age, physical condition) affect a male's dominance rank. Here we investigated correlates of male rank and hierarchy characteristics in Nepal gray langurs (*Semnopithecus schistaceus*), a population with high male reproductive skew, and compared the results to other multi-male groups of nonhuman primates.

**Methods:** We collected dyadic displacement interactions from two groups (mean 3.0 and 4.1 adult males) for five years each. We assessed dominance ranks for demographically stable phases ( $n = 11$ ,  $n = 28$ ) and analyzed the effects of age and physical condition through linear mixed models (LMM). We analyzed hierarchy characteristics via the program MatMan. We used data from 27 primate groups (cercopithecines, colobines, hominoids) as a comparative sample.

**Results:** The highest ranks were attained by adults in one group (LMM,  $P < 0.091$ ) and by young adults in the other group (LMM,  $P < 0.001$ ). With some exceptions, rank was highest for males with higher physical condition scores (LMM,  $P < 0.05$ ). Hierarchies had high directional consistency (mean  $> 0.93$ ) and linearity (mean  $> 0.81$ ) and were relatively steep (mean  $> 0.66$ ) when compared with other species.

**Discussion:** Dominance rank followed a pattern predicted by resource holding potential, but other individual attributes and group composition also seemed important. As predicted, hierarchy characteristics indicated a despotic system in line with the strong reproductive skew. Across primates, however, the degree of despotism did not appear to match the degree of reproductive skew. *Am J Phys Anthropol* 160:208–219, 2016. © 2016 Wiley Periodicals, Inc.

Individuals should favor group-living when the net benefits exceed those gained from a solitary existence (Alexander, 1974; Krause and Ruxton, 2002). While sociality may have direct benefits (e.g., increased safety from predators: Alexander, 1974; van Schaik, 1983; Krause and Ruxton, 2002), group-living also entails costs, because individuals may face increased competition for access to resources (e.g., food, mates: Krause and Ruxton, 2002). Likely in response to this potential for increased interference, many animals and humans form dominance relationships in which one individual consistently wins, regulating access to contested resources (Bernstein, 1970; Drews, 1993). Predictable and stable relationships can be beneficial because they may reduce the risk, energy, stress, and time associated with physical aggression and escalated competition (Maynard-Smith and Price, 1973; Drews, 1993).

In social animals, as in many nonhuman primates, these dominance relationships are the outcome of repeated competitive interactions resulting in complex dominance hierarchies (e.g., Chase and Seitz, 2011). The rank position that an individual occupies is commonly thought to be affected by its “attributes” (e.g., physical, genetic, and physiological characteristics) (Chase and Seitz, 2011). Among individual attributes, differences in dominance rank within a group are often related to asymmetry in fighting ability, or resource holding potential (RHP; Parker, 1974). When RHP influences rank,

intrinsic differences exist between individuals in size, strength, or weaponry (Galbany et al., 2015). Under such conditions, rank and age will have an inverted U-shape, reflecting age-related changes in fighting abilities: low ranks among subadults, highest ranks at prime age, and ranks falling thereafter with age. In several primate species, male dominance ranks have been shown to follow this inverted U-shape pattern with age (long-tailed macaques, *Macaca fascicularis*: van Noordwijk and van Schaik, 1985; chimpanzees, *Pan*

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*troglydytes*: Boesch and Boesch-Achermann, 2000; savannah baboons, *Papio cynocephalus*: Alberts et al., 2003; mandrills, *Mandrillus sphinx*: Setchell et al., 2006).

However, aspects other than individual RHP may play a role in determining rank. For example, males may form coalitions (Pope, 1990; Duffy et al., 2007; Bissonnette et al., 2011; Gilby et al., 2013) or female behavior may affect male rank relationships (Kappeler and Schädler, 2008). In addition, residency can be important, with older individuals maintaining high rank despite decreasing RHP. In these instances, males tend to acquire social status by queuing, with rank depending on the sequence of arrival (Kokko and Johnstone, 1999).

On an ultimate level, rank can affect various aspects of an individual's life history and fitness (e.g., age at maturity: Alberts and Altmann, 1995; growth and development: van Noordwijk and van Schaik, 2001; reproductive output: Kappeler and Schädler, 2008). High dominance rank is often associated with increased rates of reproduction and survival (self and offspring) and thus greater reproductive success (Dewsbury, 1982; Cowlishaw and Dunbar, 1991). Indeed, many studies have demonstrated that high-ranking males have higher paternity success (review in Majolo et al., 2012). However, nonhuman primates show considerable variation in the extent of male reproductive skew (Ostner et al., 2008; Gogarten and Koenig, 2013). In some species, the alpha male sires the vast majority of offspring (Pope, 1990; de Ruiter et al., 1994; Jack and Fedigan, 2005; Setchell et al., 2005), whereas in others the percentage of alpha male paternities is much lower (Widdig et al., 2004; Alberts et al., 2006; Newton-Fisher et al., 2010). Traditionally, such a variation in reproductive skew has been described along a continuum from despotic (strong skew) to egalitarian (weak skew) (Vehrencamp, 1983).

Variation in reproductive skew has been predicted to be associated with differences in dominance hierarchies along a similar continuum from despotic to egalitarian (van Schaik, 1989) represented by three dimensions of hierarchy characteristics including: 1) directional consistency (DC), 2) linearity, and 3) steepness. DC represents the frequency with which the agonistic behavior occurs in a given direction within a dyad (van Hooft and Wensing, 1987), while linearity depicts the overall transitivity (i.e., A dominates B, B dominates C, and A also dominates C) of the relationships (de Vries, 1995). Steepness reflects the degree to which individuals differ from each other in winning dyadic interactions, thus providing a measure of absolute distance between ranked individuals (de Vries et al., 2006). On the despotic-egalitarian spectrum, despotic social systems should exhibit high directional consistency and linearity, with a steep hierarchical structure while egalitarian hierarchies should have lower directional consistency and linearity, with a shallower hierarchical structure (van Schaik, 1989). Among nonhuman primates, for example, linear hierarchies have been documented in male ring-tailed lemurs (*Lemur catta*: Parga, 2009), olive baboons (*Papio anubis*: Packer, 1979), mandrills (Setchell et al., 2006), and crested black macaques (*Macaca nigra*: Reed et al., 1997). By contrast, male white-faced capuchins (*Cebus capucinus*) have a clear alpha male but lack a linear hierarchy among the other males (Perry, 1998).

Given the (potential) importance of rank, surprisingly few studies have examined its determinants among nonhuman primate males. Additionally, while the consequences of male rank (e.g., reproductive skew) in

primate multi-male groups have been studied repeatedly (overviews in: Ostner et al., 2008; Gogarten and Koenig, 2013), the proposed link to structural aspects of the dominance hierarchy has rarely been examined. Underlying this problem is the unanswered question: what constitutes an egalitarian or despotic hierarchy numerically? In other words, we still do not have an understanding of how despotism is defined based on values of hierarchy characteristics. Furthermore, the overall extent of the variation in despotism among primate males is relatively unknown.

In our present study, we examined the determinants of rank and the link between skew and hierarchy characteristics in male Nepal gray langurs (*Semnopithecus schistaceus*) and then compared the latter with values across a number of primate species with multi-male social organization. *Semnopithecus* spp. vary in male group composition across populations, ranging from 100% one-male groups to 100% multimale groups (Koenig and Borries, 2001). Females are philopatric and males disperse. Nepal gray langurs exhibit substantial sexual dimorphism in body mass and canine size (Smith and Jungers, 1997; Plavcan, 2001), suggesting strong intrasexual competition among males over access to mates (Plavcan and van Schaik, 1997). Generally, reproductive skew is unknown in *Semnopithecus* spp. However, in the study population, the alpha males fathered significantly more infants than all other resident males (Launhardt et al., 2001). The high reproductive skew (alpha paternity 73.9%; Gogarten and Koenig, 2013) suggests strong contest competition and a resulting despotic hierarchical system. Furthermore, while male coalitions can influence male-male competition and resulting dominance relationships (Bissonnette et al., 2011), male Nepal gray langurs do not form coalitions and we expected the dominance hierarchies to be individualistic.

Given these conditions and following Parker (1974), we predicted that an individual's dominance rank reflects its fighting ability (RHP) assessed via age and nutritional status. We expected higher dominance ranks in young adult males and in males in the best physical condition. Furthermore, given the strong reproductive skew, we predicted that male dominance hierarchies would have high directional consistency, linearity, and steepness. In comparison with other primates, we thus expected Nepal gray langurs to range numerically at the upper (despotic) end of the indices.

## METHODS

### Study population

We collected data from a wild population of Nepal gray langurs (*Semnopithecus schistaceus*) located in Southern Nepal, near Ramnagar (300 m a.s.l., 27°44'N, 84°27'E). Details on the habitat and climate have been described elsewhere (Koenig et al., 1997). Most groups in the population were multi-male, multi-female (72%), with the remainder being one-male, multi-female (Koenig, 2000). In Nepal gray langurs, females were generally philopatric (for exceptions, see Koenig, 2000). Males dispersed from their natal groups at maturity and secondary dispersal was common (Borries, 2000).

### Study periods and groups

Data were collected on two fully habituated groups: from July 1991 to April 1996 (P group: 1,733 contact

days) and from January 1992 to June 1997 (O group: 1,491 contact days). The groups occupied neighboring home ranges. P group was of medium size compared with the population mean, averaging 20 individuals, including two to seven adult males (mean:  $3.0 \pm 1.5$ ). O group was larger with an average of 30 individuals and two to nine adult males (mean:  $4.1 \pm 1.4$ ). Because natal males were always found at the bottom of the male hierarchy, we included only non-natal males in the analysis (for age classification, see below): eight males in P group and 22 in O group. Two individuals, M9 and M11, were members of both groups during the study period (Supporting Information Tables S1 and S2).

### Data selection

We determined dominance relationships from the outcome of dyadic displacement interactions (Hrdy and Hrdy, 1976), i.e., interactions in which at the end of the interaction one individual physically displaced another. Two distinct patterns were considered (Borries et al., 1991): 1) Male A approached male B whereupon B moved away and A usurped the location of B. Aggression did or did not occur in this pattern. 2) Male A and male B were already situated in close proximity. Aggressive behavior by A towards B led to the departure of B, while A remained. The outcome of dyadic displacement interactions was collected using focal animal and ad libitum sampling techniques (Altmann, 1974).

We compiled all dyadic interactions into actor-receiver matrices for each group separately. In order to avoid structural zeroes (de Vries, 1998), we subdivided the study period into phases during which the identity of all non-natal males within a group remained the same. Because most rank changes were due to immigrations and emigrations (Borries, 2000), this method resulted in phases with stable ranks with four exceptions. In these four periods without demographic change, rank changes occurred between resident males. We subdivided each of these phases into stable periods without rank changes (phases 18–19 in P group, phases 9–10, 13–14, 27–28 in O group; see Supporting Information Tables S1 and S2). In total, we identified 20 phases for P group (1,549 displacements) and 42 phases for O group (2,258 displacements; Supporting Information Tables S1 and S2).

Several phases were short and had few interactions. For the analysis, we included only those phases for which the number of interactions was higher than the number of relationships. Because structural properties of dominance hierarchies, e.g., transitivity, are only valid for three or more individuals, the four phases with only two males present (three in P group, one in O group) were excluded from certain analyses. In addition, since unknown relationships affect measures of transitivity and steepness (Koenig and Borries, 2006; Klass and Cords, 2011) we only included phases with a sufficient amount of known relationships. For phases with three males, we only included those with 100% known relationships. Phases with 4 or 5 males were included if 80% relationships were known and phases with 6 or 7 males were included with at least 60% relationships known ( $n = 39$  phases total; 11 in P group, 28 in O group).

### Correlates of dominance rank

We assessed dominance ranks for each male during each phase using normalized David's scores (David, 1987; Gammell et al., 2003; de Vries et al., 2006).

David's scores (DS) weight each dyadic success by the unweighted estimate of an individual's overall success, thus taking the relative strengths of other individuals into account.

We note that it could be informative to assess ranks via Elo-ratings instead of David's scores to evaluate the stability of individual males' dominance ranks over time (Albers and de Vries, 2001). However, this is currently beyond the scope of this paper. David's scores provide an advantage because they calculate a measure of relative competitive ability that is directly comparable between group members at a given time (see also: Gammell et al., 2003; de Vries et al., 2006). Furthermore, data selection in the current study followed a strict protocol to minimize unknown relationships and exclude matrices with few interactions (see above). In such instances, results are likely robust and Elo-ratings may not improve the analysis (Neumann et al., 2011). Finally, our goal was to assess hierarchy characteristics (see below) as they relate to various estimates of RHP. David's scores have been suggested to be a better method than ordinal ranking as an estimate of RHP, and have been validated as a cardinal measure of male competitive ability (Bissonnette et al., 2009).

We estimated the ages of all males at the beginning of the study based on physical characteristics. The following age classes were used: 1) subadult male: males that had at least a head-body length of an adult female but had not yet attained the head-body length of an adult male. 2) Young adult male: males that had attained the head-body length of an adult male but were not yet as filled out. It would usually take one year before young adult males had acquired the full adult proportions. Thereafter, we considered them young adult for an additional two years to capture the entire period of maximum physical strength when canines were least worn. Based on males we knew from birth, non-natal young adult males were estimated to be between seven to nine years of age. 3) Adult male: males that had adult proportions and were 10 years of age or older (most of adult life). They also showed some signs of wear on their canines. 4) Old male: males that had adult proportions and had physical signs of aging, e.g., wrinkled skin, ragged fur, and slow movements. The approximate age of the transition from adult to old is unknown.

In addition to these age classes, we achieved a finer resolution by ordering individual males in each group based on their relative ages because we knew which males in a given age class were younger than others. To allow for comparisons across phases that differed in the number of males, we normalized this sequence so that measures varied between 0 and 1. For each phase, the youngest male had a relative age of 0 and the oldest a relative age of 1. Because the number of males varied across phases, for demonstration purposes we grouped the relative ages into five categories (0.0–0.2, 0.21–0.4, 0.41–0.6, 0.61–0.8, 0.81–1.0).

Physical condition was rated visually on a seven-point scale from 1 = meager to 7 = fat, assessing the degree of visibility of shoulder blades, spinal column, ribs, hips and tail bones (Koenig et al., 1997). Individuals were assessed once in the middle of each month. Physical condition data were recorded from August 1993 to June 1997. The majority (74%) of ratings were conducted by a primary observer (C.B.) and three additional observers did the remainder (26%). All observers had been trained by C.B., with periodic interobserver reliability assessments.

We included only months for which all males had been rated ( $n = 28$  phases total, 2 in P group, 26 in O group; the respective phases are identified in the Supporting Information Tables S1 and S2).

### Dominance hierarchy characteristics

For each phase, we determined dominance relationships and hierarchy characteristics with the program MatMan V1.1.4 (de Vries et al., 1993). Relationship characteristics included the directional consistency index (DC index; van Hooff and Wensing, 1987) and the number and percentage of one-way and two-way relationships (i.e., the percent of dyads in which the behavior occurred in one direction only, and in both directions, respectively). The DC index ranges from 0 to 1 and was calculated across all dyads as:  $(H-L)/(H+L)$ , where  $H$  is the number of interactions in the more frequent direction and  $L$  is the number of interactions in the less frequent direction. Thus, a high DC index value indicates high unidirectionality.

We characterized the degree of linearity of the hierarchy based on the modified Landau's linearity index  $h'$  (de Vries, 1995). A circular, nontransitive triad occurs when A dominates B, B dominates C, but C dominates A. The latter dyad is inconsistent with a linear hierarchy. We employed a two-step test with 10,000 randomizations (default) to assess the significance of the degree of linearity (de Vries, 1995). When the number of individuals is below six, the linearity index cannot reach statistical significance (Appleby, 1983). Therefore, we report significance of the index for only those phases for which it can be tested (i.e., 11 phases with six or more males present). We also report the number and percentage of unknown and intransitive relationships, which were previously shown to affect the linearity index (de Vries, 1995; Koenig and Borries, 2006; Klass and Cords, 2011).

Lastly, we calculated steepness (de Vries et al., 2006) for each phase using the R package Steepness: Testing Steepness of Dominance Hierarchies (Version 0.2, Leiva and de Vries, 2011), available from: <http://cran.r-project.org/src/contrib/Archive/steepness/>. We calculated a dyadic dominance index  $D_{ij}$ , in which the proportion of wins and losses are corrected for the chance occurrence of the observed outcome (de Vries et al., 2006).  $D_{ij}$  was used to calculate the normalized David's score for each individual, with values varying between 0 and  $n - 1$ , where  $n$  is the number of adult males in the group. Normalizing the David's scores allows for a steepness measure to be calculated that varies from 0 to 1. Based on the rank order from the normalized David's score values, individuals received a number ranking (cardinal ranks). Ranked individuals were plotted against their normalized David's scores and ordinary least-squares linear regression was used to find the best-fit straight line. We calculated the steepness measure of the hierarchy as the absolute value of the slope of this line. Following de Vries et al. (2006), we assessed the significance of a hierarchy's steepness through a procedure with 2,000 randomizations (default) that tested the observed steepness against the steepness expected under the null hypothesis of random win chances for all dyads.

### Comparative sample

To assess the degree of despotism of Nepal gray langurs relative to other primates and the proposed link between reproductive skew and differences in dominance

hierarchies, we searched for comparative data among primate multi-male groups. We began with compilations of alpha male paternity (Ostner et al., 2008; Gogarten and Koenig, 2013) and latest publications on this topic and searched for dominance hierarchy characteristics of these populations or groups for which skew was known. In addition to our own study, we found hierarchy values for four chimpanzee (*Pan troglodytes*) groups (from three populations) and one macaque (*Macaca assamensis*) group. In several cases, we used the provided actor-receiver matrices of agonistic behaviors to calculate DCI, linearity, and steepness as described above. We note that in some cases the data for alpha male paternity and hierarchy characteristics did not come from the same time period.

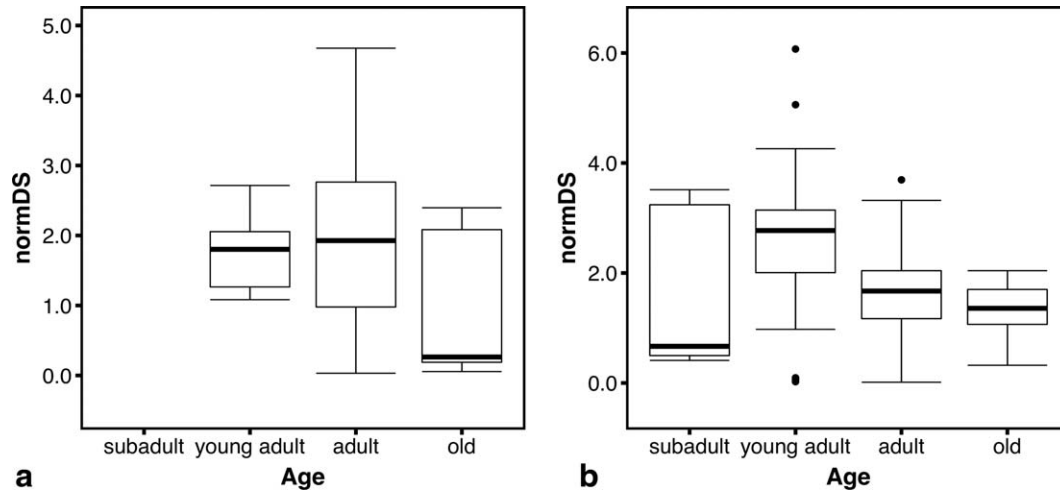
We subsequently searched for additional studies that, while lacking data on reproductive skew, would allow us to increase the sample on dominance hierarchy characteristics. We found an additional nine studies including four cercopithecines (*Cercocebus sanjei*, *Lophocebus albigena*, *Macaca arctoides*, *Macaca sylvanus*), one colobine (*Ptilocolobus tephrosceles*), and two hominoids (three *Pan troglodytes*, one *Pan paniscus*) for a total of 27 groups or populations. Note that the number of cases vary for the different hierarchy characteristics (DCI:  $n = 23$ ; linearity:  $n = 25$ , steepness:  $n = 24$ ).

### Statistical analyses

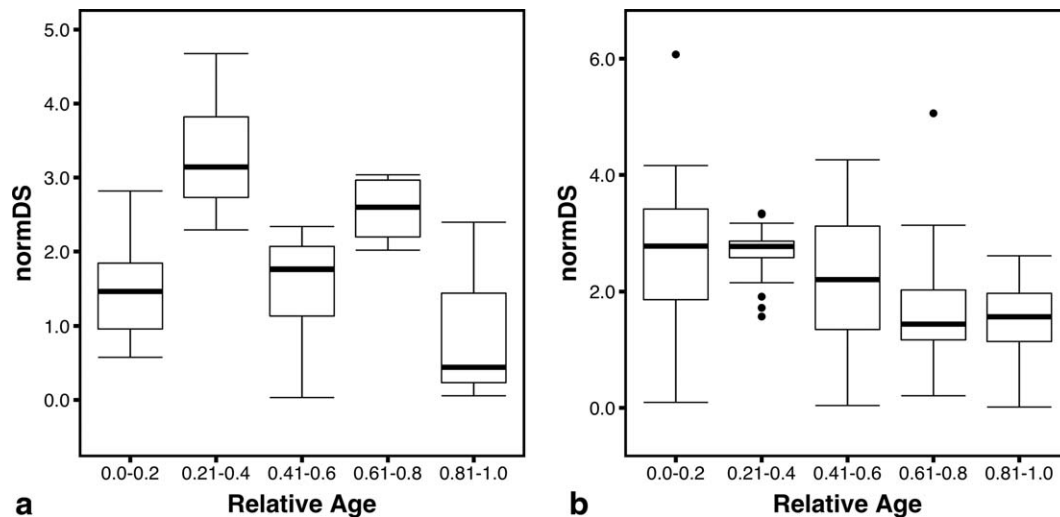
To assess how rank is affected by age and physical condition, we employed linear mixed models (LMMs: McCulloch and Neuhaus, 2001), with normalized David's scores as the dependent variable in each model and age and physical condition included as fixed effects. We included Male ID as a random factor in all models to control for multiple observations of the same individuals. Furthermore, because the maximum value of normalized David's scores depends on the number of individuals present during a given phase, we included the number of males as an additional random factor. Because physical condition data were available for only a subset of the study period, this factor could not be included in a combined model (interaction effect with age). We used the Akaike's Information Criterion (AIC) to compare the goodness of fit for different models. In addition, to examine the significance of each fixed effect, we performed a likelihood ratio test between each full model with the particular fixed effect and a null model that included only the random effects (Crainiceanu and Ruppert, 2004). All statistical analyses were performed in R Version 3.1.3 (R Core Development Team, 2015).

We used Pearson's product-moment correlation coefficient (Sokal and Rohlf, 2012) to examine possible relationships between hierarchy characteristics. To account for potential seasonal influences, each phase was additionally categorized based on whether it was within or outside of the mating season (Borries et al., 2001) assuming stronger competition during the mating season. We performed one-way ANOVAs to assess differences in hierarchy characteristics across seasons. Results were not significant (not reported here) and we did not consider seasonality in the results below.

Because of the small comparative sample, we did not use phylogenetic comparative methods to investigate alpha male paternity and dominance hierarchy characteristics across primates. We also did not correct for



**Fig. 1.** Normalized David's scores in relation to age class in (a) P group and (b) O group. Lines: medians; boxes: inter-quartile range IQR (equals distance between first and third quartiles); whiskers:  $1.5 \times$  IQR; dots: outliers beyond  $1.5 \times$  IQR.



**Fig. 2.** Normalized David's scores in relation to relative age in (a) P group and (b) O group. Lines: medians; boxes: interquartile range IQR (equals distance between first and third quartiles); whiskers:  $1.5 \times$  IQR; dots: outliers beyond  $1.5 \times$  IQR.

repeated measures of the same group. Instead, we describe the general trends apparent in this sample.

## RESULTS

### Correlates of dominance rank

In P group, dominance rank tended to differ with male age ( $\chi^2 = 4.792$ ,  $df = 2$ ,  $P = 0.091$ ), and most high-ranking males were either young adult or adult (Fig. 1a). In O group, dominance rank also differed significantly across male age classes ( $\chi^2 = 56.815$ ,  $df = 3$ ,  $P < 0.001$ ), but here young adult males had the highest ranks, and scores declined with increasing age (Fig. 1b).

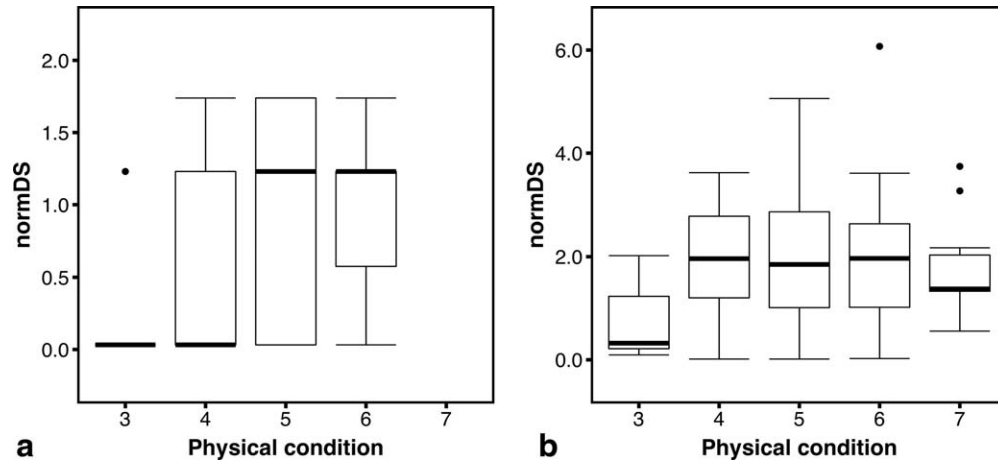
Dominance rank significantly depended on relative age in P group ( $\chi^2 = 6.920$ ,  $df = 5$ ,  $P = 0.009$ ) as well as O group ( $\chi^2 = 28.024$ ,  $df = 5$ ,  $P < 0.001$ ). In P group, normalized David's scores were highest for the males in the second relative age category, i.e., relatively young but not the youngest (Fig. 2a). In O group, normalized

David's scores were highest for the youngest males in the group (Fig. 2b).

Dominance rank was influenced by physical condition in both P group ( $\chi^2 = 4.067$ ,  $df = 1$ ,  $P = 0.044$ ) and O group ( $\chi^2 = 10.577$ ,  $df = 1$ ,  $P = 0.001$ ). In P group, males with the two best physical condition scores (rating of 5 and 6) had the highest normalized David's scores (Fig. 3a). In O group, males in better condition (rating of 4, 5, and 6) had higher normalized David's scores, but the scores for the males in the best physical condition (rating 7) were lower (Fig. 3b). For both P group and O group, male group size had a significant effect in all analyses of age, relative age, and physical condition, with larger groups having higher David's scores ( $P_s < 0.001$ ).

### Dominance hierarchy characteristics

**Nepal gray langurs.** P group averaged a DC index of 0.887 (range: 0.625–1.000, Table 1; Supporting Information



**Fig. 3.** Normalized David's scores in relation to physical condition in (a) P group and (b) O group. Lines: medians; boxes: interquartile range IQR (equals distance between first and third quartiles); whiskers:  $1.5 \times$  IQR; dots: outliers beyond  $1.5 \times$  IQR.

**TABLE 1.** Male dominance relationships and hierarchy characteristics for the two study groups

	P group	O group
Mean number of males	$3.15 \pm 1.43$	$4.07 \pm 1.27$
Total number of males (range)	2–7	2–8
Number of phases analyzed	11	28
Mean duration of phases (days)	130.3	48.9
Mean number of interactions (per phase)	127.2	74.4
Unknown relationships (%)	$10.6 \pm 15.7$	$10.8 \pm 13.2$
One-way relationships (%)	$53.3 \pm 30.4$	$78.1 \pm 19.2$
Two-way relationships (%)	$36.1 \pm 36.6$	$11.1 \pm 18.0$
Intransitive relationships (%)	$0.0 \pm 0.0$	$1.4 \pm 2.9$
DC index	$0.887 \pm 0.112$	$0.966 \pm 0.050$
$h'$	$0.924 \pm 0.136$	$0.809 \pm 0.240$
Steepness	$0.670 \pm 0.221$	$0.650 \pm 0.230$

Given are average characteristics  $\pm$  standard deviation across 11 (P group) and 28 (O group) phases analyzed when groups had at least three males and a minimum percentage of known relationships. Mean number of males is calculated as an adjusted mean weighted by phase duration. For details on data selection and calculation of hierarchy characteristics, see the Methods section.

DC index: directional consistency index;  $h'$ : modified linearity index. Values for each phase separately are given in the Supporting Information Tables S1 and S2.

Table S1) despite a relatively low number of one-way relationships (mean: 53.3%) and a correspondingly high number of two-way relationships (mean: 36.1%). In particular, two phases (18, 19) had 100% two-way relationships. The percent of unknown relationships averaged 10.6% (range: 0.0–40.0%), including seven phases (4–6, 12, 17–19) with 0% unknown relationships. The linearity index  $h'$  averaged 0.924 (range: 0.629–1.000). High linearity was expected given the absence of intransitive relationships ( $n = 0$ ). There was a significant negative correlation between the value of  $h'$  and the percent of unknown relationships ( $r = -0.95$ ,  $P < 0.001$ ,  $n = 11$  phases) and in three phases for which all relationships were known, the linearity index was 1.000. Of the three phases with six or more males that were assessed for significance of the linearity index, one (phase 10) showed a trend ( $h' = 0.732$ ,  $P = 0.094$ ,  $n = 7$  males). P group had a mean hierarchy steepness of 0.670 (range: 0.277–0.888).

O group had a mean DC index of 0.966 (range: 0.822–1.000, Table 1; Supporting Information Table S2). It had a mean of 78.1% one-way relationships and 11.6% two-way relationships. The percent of unknown relationships averaged 10.8% (range: 0.0–40.0%) and that of intransitive relationships 1.4% (range: 0.0–10.0%). O group hier-

archies varied greatly in linearity (range of 0.304–1.000), with a mean  $h'$  of 0.809. The value of  $h'$  was significantly negatively correlated with the percent of unknown relationships ( $r = -0.90$ ,  $P < 0.001$ ,  $n = 28$  phases) as well as with the percent of intransitive relationships ( $r = -0.68$ ,  $P < 0.001$ ,  $n = 28$  phases). In all 14 phases for which all relationships were known, the linearity index was 1.000. Only one (phase 37) out of eight phases that could be tested for significance had a significant linearity index ( $h' = 0.833$ ,  $P = 0.010$ ,  $n = 8$  males). O group had a mean hierarchy steepness of 0.650 (range: 0.234–0.976).

**Comparative sample.** Alpha male paternity in the comparative sample ranged from 73.9 to 29.0%, and appears to decrease with increasing number of males in the group (Table 2). DC index values were high regardless of alpha male paternity. While the highest alpha paternity (our study population and chimpanzees from the Tai Forest) was associated with rather high linearity and steepness, even the very low reproductive skew of Assamese macaques was associated with high linearity and steepness. Thus, in the available sample there

TABLE 2. Alpha male paternity and dominance hierarchy characteristics in primate multi-male groups

Species	Study site	w/p	Alpha male paternity (%) <sup>a</sup>	N adult males (paternity)	Reference (paternity)	Group name	N adult males (dominance)	DC index	h'	Steepness	Behavior	Reference (dominance)
<i>Semnopithecus schistaceus</i>	Ramnagar, Nepal	w	73.9	3.8	Gogarten and Koenig (2013)	P	2-7	0.89	0.92	0.67	Displacements	Present study
<i>Pan troglodytes</i>	Tai Forest, Ivory Coast	w	66.7	3	Table 1 <sup>b</sup> , Boesch et al. (2006)	O	2-8	0.97	0.81	0.65	Displacements	Present study
						North Community 1996-1999	3	1.00	1.00	0.94	Pant-grunts	Calculated from Wittig and Boesch (2003)
		w	55.6	6-7	Table 1 <sup>c</sup> , Boesch et al. (2006)	North Community 1993	5	0.98	0.95	0.59	Pant-grunts	Calculated from Boesch and Boesch-Achermann (2000)
<i>Pan troglodytes</i>	Mahale Moun-tains National Park, Tanzania	w	45.5	?	Inoue et al. (2008)	M 1985	10	1.00	0.62	0.23	Pant-grunts	Calculated from Hayaki et al. (1989)
						M 1992	9	0.99	0.82	0.53	Pant-grunts	Calculated from Nishida and Hosaka (1996)
						M 2011	10			0.30	Aggression	Kaburu and Newton-Fisher (2015)
<i>Pan troglodytes</i>	Budongo Forest Reserve, Uganda	w	30.8	14.5	Gogarten and Koenig (2013)	Sonso 1994/95	12	1.00	0.71	0.27	Pant-grunts	Calculated from Newton-Fisher (2004)
						Sonso 2003/04	8			0.70	Aggression	Kaburu and Newton-Fisher (2015)
<i>Macaca assamensis</i>	Phu Khieo Wildlife Sanctuary, Thailand	w	29.0	9-15	Sukmak et al. (2014)	AS 2006/07	12	0.98	0.89	0.51	Submission	Ostner et al. (2011)
<i>Ptilocolobus tephrosceles</i>	Kibale National Park, Uganda	w				AS 2007/08	8	0.91	0.92	0.69	Submission	Ostner et al. (2011)
		w				CW 1975	3	0.92	1.00	0.87	Aggression and displacements	Calculated from Struhsaker (1975)
		w				CW 1985	3	0.96	1.00	0.88	Aggression and displacements	Calculated from Struhsaker and Leland (1985)
<i>Lophocebus albigena</i>	Kibale National Park, Uganda	w				CC 2006	4	0.48	1.00	0.57	Decided agonistic bouts	Calculated from Arlet and Isbell (2009)
		w				CC 2007	4	0.57	0.90	0.55	Decided agonistic bouts	Calculated from Arlet et al. (2011)
		w				BT1 2007	4	0.31	0.70	0.27	Decided agonistic bouts	Calculated from Arlet et al. (2011)
		w				LC 2006	4	0.25	0.81	0.38	Decided agonistic bouts	Calculated from Arlet and Isbell (2009)



TABLE 2. Continued

Species	Study site	w/p	Alpha male paternity (%) <sup>a</sup>	N adult males (paternity)	Reference (paternity)	Group name	N adult males (dominance)	DC index	h'	Steepness	Behavior	Reference (dominance)
	Kibale National Park, Uganda	w				MK 2006	5	0.64	1.00	0.72	Decided agonistic bouts	Calculated from Arlet and Isbell (2009)
	Kibale National Park, Uganda	w				LC 2007	5	0.21	0.75	0.18	Decided agonistic bouts	Calculated from Arlet et al. (2011)
	Kibale National Park, Uganda	w				BT1 2006	9	0.56	1.00	0.67	Decided agonistic bouts	Calculated from Arlet and Isbell (2009)
<i>Cercocebus sanjei</i>	Udzungwa Mountains National Park, Tanzania	w				Njokamoni	4-6	0.94	0.84		Aggression	Mwamende (2009)
<i>Pan paniscus</i>	Salonga National Park, DR Congo	w				unnamed	5	0.88	1.00	0.90	Decided agonistic bouts	Calculated from Surbeck et al. (2011)
<i>Macaca arctoides</i>	Wat Tham Khaeo Daeng, Thailand	p				unnamed	9 <sup>d</sup>	0.89	0.71	0.58	Decided agonistic bouts	Richter et al. (2009)
<i>Pan troglodytes</i>	Kibale National Park, Uganda	w				Kanyawara 1998	11	0.97	0.82	0.53	Pant-grunts and decided agonistic bouts	Calculated from Muller and Wrangham (2004)
<i>Pan troglodytes</i>	Kibale National Park, Uganda	w				Kanyawara 2009/10	12 <sup>e</sup>	0.83			Pant-grunts and decided agonistic bouts	Georgiev (2012)
<i>Macaca sylvanus</i>	Affenberg Salem, Germany	p				H	23	0.92	0.78	0.53	Decided agonistic bouts	Berghänel et al. (2010)
<i>Pan troglodytes</i>	Kibale National Park, Uganda	w				Ngogo	24	0.94			Pant-grunts	Muehlenbein et al. (2004)

Table sorted by alpha male paternity or number of males (if alpha paternity was unavailable). w/p: w, wild and unprovisioned; p, provisioned or captive. DC index: directional consistency index; h': modified linearity index. The column "Behavior" denotes the behaviors used in actor-receiver matrices to describe dominance hierarchy characteristics. In some chimpanzee studies multiple matrices with different behaviors were available. To increase comparability across populations we used data for pant-grunts if possible.

<sup>a</sup> Alpha paternity only available for the population or multiple mating seasons except when noted.

<sup>b</sup> Alpha paternity 1995 to 1997 corresponding to n adult males of dominance data reported in Wittig and Boesch (2003).

<sup>c</sup> Alpha paternity 1989 to 1994 corresponding to n adult males of dominance data reported in Boesch and Boesch-Achermann (2000).

<sup>d</sup> Includes two subadult males (Richter et al., 2009).

<sup>e</sup> Includes three late-adolescent males (Georgiev, 2012).

seems to be no apparent link between reproductive skew and hierarchy indices.

In the overall sample of dominance hierarchy characteristics, linearity values were generally high between 0.62 and 1.00 (mean: 0.87), while DC index and steepness were more variable (DC index: 0.21–1.00, mean: 0.79; steepness: 0.18–0.90, mean: 0.57; Table 2). The scores for the Nepal gray langurs ranged above the mean for DC index and steepness, or above and below the mean for linearity (Table 2).

## DISCUSSION

Male rank appeared to be primarily determined by age and to a lesser degree by physical condition, suggesting that young males are in their prime, allowing them to reach the top of the hierarchy. This resulted in the inverted U-shaped age-dominance relationship predicted by RHP (Parker, 1974). As expected, the hierarchy in male Nepal gray langurs followed predictions of a despotic system, which is in line with the relatively high alpha male paternity in this population (Gogarten and Koenig, 2013; but see below).

### Correlates of dominance rank

The relationship between dominance rank and age generally formed an inverted U-shape, starting low in subadults, rising to the highest rank in young adult and adult individuals, and declining with old age. As predicted, rank followed an RHP-related pattern, presumably reflecting age-related changes in an individual's fighting ability; a pattern found in multiple species of cercopithecines and hominoids (van Noordwijk and van Schaik, 1985; Boesch and Boesch-Achermann, 2000; Alberts et al., 2003; Setchell et al., 2006; see also Introduction). This result was further supported by the fact that the relatively youngest adult individuals were at the top of the hierarchy.

Interestingly, the relationship between age class and rank varied between study groups. While adult males in P group were often of higher rank, it was the young adults in O group that attained highest ranks. Two explanations could potentially account for this difference. First, it has been suggested that the probability of a hierarchy correlating perfectly with RHP may be low unless group size is small (Mesterton-Gibbons and Dugatkin, 1995). However this explanation is unlikely because the smaller P group (mean: 3.15 males, range: 2–7) followed an RHP pattern less clearly compared with the larger O group (mean: 4.07 males, range: 2–8).

Alternatively, between-group variation may be related to differences in group composition and the resulting age structure. In a re-analysis of age and rank data in male macaque species, Sprague (1998) demonstrated the influence of demographic composition on the relationship between age and rank, illustrating how age-rank correlations can be masked in groups with limited age range, or in those that include many newly arrived males. In male Nepal gray langurs at Ramnagar, secondary dispersal is common and male residency averages only 11.7 months (Borries, 2000). Frequent immigration is likely a strategy for attainment of high rank, as it has been previously shown that 75 to 80% of alpha males gained the position immediately after immigration (Borries et al., in press). Such frequent dispersal makes group composition and age structure likely to vary between groups as well as within a group over time. For example, P group

changed in size and composition considerably, with phase 10 containing seven males (one young adult, four adults, two old adults) and phase 19 containing three males (three adults only; Supporting Information Table S1). Importantly, over the entire observation period, this group only rarely contained young adult males and never subadult males. Thus, although other factors can affect aspects of dominance relationships (e.g., Setchell et al., 2006), the difference between these two groups is likely the result of more frequent immigrations and the presence of young adult males in O group.

In addition, predictions based on an RHP-related pattern of dominance rank somewhat held for male physical condition in both groups. This relationship between male condition and rank, with low-ranking males being in poorer condition, has been documented in several primate taxa (e.g., long-tailed macaques: van Noordwijk and van Schaik, 1985; rhesus macaques, *Macaca mulatta*: Bercovitch and Nürnberg, 1996; Barbary macaques, *Macaca sylvanus*: Bissonnette et al., 2009). However in Nepal gray langurs, although low rank was associated with lower physical condition scores, males did not need to be in the best physical condition to achieve high rank. This may indicate that a threshold condition exists above which nutritional condition becomes less important, suggesting that greater fighting ability is not only about being bulky. Indeed, young adult males had already reached full adult stature and were able to attain high rank, but they still remained more slender than adults. Similar to our study, a lack of a clear relationship between body size and dominance has also been shown in male chacma baboons (*Papio ursinus*: Kitchen et al., 2003) and male mandrills (Setchell et al., 2006).

Another explanation for our finding may be the subjective nature of our assessment. Although body condition scoring by visual evaluation can still provide reliable measures as long as interobserver variation is low (Clancey and Byers, 2014), less subjective measures should be preferred. In recent years, C-peptide, a urinary metabolite produced in equimolar ratio to insulin, has been measured as a non-invasive indicator of energetic status (Sherry and Ellison, 2007) and could perhaps provide a better understanding of how physical condition influences male rank. For example in rhesus macaques, C-peptide of dominant males declined during the mating season (Higham et al., 2011), suggesting that a clear relationship between status and condition may be obscured by energetic costs suffered by maintaining high rank. Thus, while body condition contributed to a male's ability to attain high rank in the study population, other factors (in addition to age/RHP) may also influence the outcome of dominance interactions.

### Dominance hierarchy characteristics

Pairwise relationships of males were relatively consistent, with a mean DC index of 0.887 for P group and 0.966 for O group. These values are higher than those reported for many other primate species (Table 2), which range between 0.21 and 1.00. While no particular numerical value exists for despotism, such consistent dyadic dominance relationships suggest rigid rank relationships between individuals.

As expected, linearity was also generally high for P and O group, averaging 0.924 and 0.809, respectively. Although data are limited on dominance hierarchy

characteristics for male colobines, this is in line with linear hierarchies described in male ursine colobus monkeys (*Colobus vellerosus*: Teichroeb and Sicotte, 2008). Linearity of the dominance hierarchy reported here was lower than in groups of red colobus (*Ptilocolobus tephrosceles*), the only colobine for which comparative values of hierarchy characteristics were available (Table 2). With an average steepness of 0.670 for P group and 0.650 for O group, male Nepal gray langur hierarchies were steeper than the hierarchies of most other male primates. Interestingly, steepness values for male red colobus hierarchies were even higher (Table 2). Still, the steepness values were clearly lower than those for male bonobos and some chimpanzee groups. Unlike langurs and macaque species, bonobos and chimpanzees exhibit male-philopatry (Koenig and Borries, 2012), which can promote maternal support in agonistic interactions, thus potentially providing a different context for social relationships (Surbeck et al., 2011; Markham et al., 2015). But given the effects of group size and unknown relationships on both steepness and linearity (Mesterton-Gibbons and Dugatkin, 1995; Koenig and Borries, 2006; Klass and Cords, 2011), it is hard to directly compare results across species and populations or even groups. Moreover, the data currently available in the literature are biased toward the genus *Pan* and more data on other species and comparative work is clearly needed.

Overall, these results suggest a rather strong despotism in male Nepal gray langurs. In addition, it seems noteworthy that there was considerable variance in hierarchy characteristics across the study phases, possibly indicating unresolved, unstable relationships in some phases and resolved and stable relationships in others. Several factors could have influenced this instability in social structure. First, competitive asymmetries may be temporarily dynamic depending on the context of contests. For example, increased group size has led to decreased rank stability in savannah baboons and mandrills (Alberts et al., 2003; Setchell et al., 2006). In our sample, we could detect four rank changes in otherwise demographically stable phases (see Methods). Male group size at the time of the change was three in P group and ranged from three to seven in O group (see Supporting Information Tables S1 and S2). While these are only four examples, they nevertheless suggest that male group size likely did not affect the stability of the relationships. More probable, variance may be due to missing data, as linearity and steepness negatively correlated with the number of unknown relationships. Taking these effects into account and considering only periods for which all relationships were known, both P and O group hierarchies had a linearity of 1.000. These periods also maintained higher steepness values, indicating that for phases for which all relationships are known, dominance relationships suggest an even more despotic system.

These findings for Nepal gray langurs seem to generally support the proposed link between reproductive skew and despotism (van Schaik, 1989). In the study population, a high reproductive skew of 73.9% alpha paternities was associated with despotic (i.e., unidirectional, linear, and steep) hierarchies. On a broader scale, the situation is more complex. While variation in reproductive skew among male primates is often driven by variation in the monopolizability of receptive females (priority-of-access model, Altmann, 1962), monopolization is also influenced by factors such as female group size, female reproductive synchrony, and the number of

competitors (Ostner et al., 2008; Gogarten and Koenig, 2013). Thus, even if hierarchies are despotic, skew might still be low. This is also apparent in the admittedly small, comparative sample in which alpha paternity was associated with male group size, but did not seem to have any clear association with hierarchy indices. For example, Assamese macaque males have rather despotic hierarchies, but alpha paternity reached only 29% (Table 2). In Assamese macaques, monopolization potential is likely reduced by a high number of males in the group (Gogarten and Koenig, 2013) combined with a short conception season (Fürtbauer et al., 2010) and high overlap in female receptivity (Fürtbauer et al., 2011). Thus, social despotism might be associated with reproductive despotism (as predicted), but reproductive despotism may be affected by additional factors.

In sum, we found that dominance ranks among male Nepal gray langurs correlated with age, demonstrating a pattern of rank acquisition that is dependent on individual resource holding potential. Low rank was associated with poor physical condition; however, high-ranking males did not generally achieve the highest physical condition ratings, indicating that factors other than individual competitive ability may be at play in determining dominance rank. More studies on rank acquisition and rank dynamics in primate multi-male groups are clearly necessary. Our analyses furthermore revealed a despotic social system among the males in the study groups. This matches previous work demonstrating strong bias in paternity toward alpha males within multi-male groups (Launhardt et al., 2001; Gogarten and Koenig, 2013). However, on a broader scale the link between hierarchy characteristics and reproductive skew appears to be weak. The limited sample size, however, necessitates more comparative work to explore this link further.

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