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Male social rank and food competition in a primate multi-level society

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Abstract

Objectives: Social animals often have dominance hierarchies, with high rank conferring preferential access to resources. In primates, competition among males is often assumed to occur predominantly over reproductive opportunities. However, competition for food may occur during food shortages, such as in temperate species during winter. Higher-ranked males may thus gain preferential access to high-profitability food, which would enable them to spend longer engaged in activities other than feeding.

Materials and methods: We performed a field experiment with a breeding band of golden snub-nosed monkeys, a species that lives in a multi-level society in high-altitude forests in central China. We provisioned monkey's high-profitability food during winter when natural foods are limited, and then recorded the times individual adult males spent engaged in different behaviors.

Results: Higher-ranking males spent less time feeding overall and fed on provisioned foods at a higher rate than lower-ranking males. Higher-ranking males therefore had more time to spend on alternative behaviors. We found no significant difference according to rank in times spent moving or resting. However, high-ranking males spend significantly longer on affiliative behaviors with other members of their social sub-units, especially grooming and being groomed, behaviors known to promote social cohesion in primates.

Discussion: We show that preferential access to high-profitability foods likely relaxes time-budget constraints to higher-ranking males. High-ranking males thus spend more time on non-feeding activities, especially grooming, which may enhance social cohesion within their social sub-unit. We discuss the potential direct and indirect benefits to high-ranking males associated with preferential access to high-value food during winter.

KEYWORDS
Rhinopithecus roxellana, social behavior, time budget

1 | INTRODUCTION

Intra-specific competition for food is important for shaping the behavioral interactions among social animals (Janson, 1988; Koenig, 2002). Competitive interactions may determine and/or be affected by the size and social structure of groups (Dunbar, Korstjens, & Lehmann, 2009; Lehmann, Korstjens, & Dunbar, 2007; Snaith & Chapman, 2007; Wrangham, 1980). If valuable food resources are defendable, some individuals or groups of cooperating individuals may be able to prevent other individuals or groups from having access to those resources (Chapais, 1992; Sterck & Steenbeek, 1997; van Schaik, 1989). Additional ecological factors such as food availability and/or food quality may also affect social interactions associated with competition for those food resources (Koenig, Beise, Chalise, & Ganzhorn, 1998). Ecological and social factors will therefore both affect which individuals within groups dominate access to limited food resources, and hence which individuals gain a potential fitness advantage over their less competitive conspecifics.

Competition within groups for resources such as food increases with group size, so group size is often determined when the individual costs of within-group competition equal the benefits of being in the group (Krebs & Davies, 1984). In primates, the importance of competition for food in determining group size varies among taxa (Grueter & van Schaik, 2010; Janson & Goldsmith, 1995). For instance, folivorous species usually occur in small groups that are not generally thought to be the result of within-group competition due to a "superabundance" of food, termed the "folivore paradox" (Snaith & Chapman, 2007). However, competition for food among primate folivores may occur because the availability of "preferred" leaves can be limited in both space and time (Guo, Li, & Watanabe, 2007; Koenig et al., 1998). Additionally, time-budget constraints may limit the affiliations needed among individuals to maintain group social cohesion, that is, the spatio-temporal stability of a group, which may in turn limit group size (Lehmann et al., 2007; Dunbar & Lehmann, 2013; but see also Grueter, Bissonnette, Isler, & van Schaik, 2013). This is because individuals must spend time on essential behaviors such as feeding (Dunbar et al., 2009), which limits the time available to spend engaged in affiliative behaviors, especially grooming (Dunbar & Lehmann, 2013; Lehmann et al., 2007). Moreover, large social groups can consist of several nested smaller sub-groups (Grueter, Chapais, & Zinner, 2012) where individuals mainly associate with the members of their own sub-group (e.g., Ren et al., 2018). In such species, individuals will still need to manage their time-budgets to optimize their food intake and to maintain affiliations with other group members. However, food competition may also occur among smaller sub-groups within the larger group, whereas social affiliations are likely largely confined to within each smaller sub-group.

Mixed-sex primate groups often contain social hierarchies among adult males (Majolo, Lehmann, de Bortoli Vizioli, & Schino, 2012), adult females (He et al., 2013; Majolo et al., 2012; Robbins, Robbins, Gerald-Steklis, & Steklis, 2005) or of both sexes simultaneously (Majolo et al., 2012). Social rank is often positively associated with increased access to food in female primates (Grueter et al., 2016; van

Noordwijk & Schaik, 1987; Vogel, 2005; Whitten, 1983; Wittig & Boesch, 2003; Wrangham, 1981). Food competition has traditionally been examined in female primates because their energetic demands associated with reproduction make access to food the most important fitness determinant (sensu Trivers, 1972). However, there is no reason to assume that males are exempted from feeding competition (e.g., Oelze et al., 2016). When food resources are limiting and/or of variable value, due to increased access to the highest quantity and/or most profitable foodstuffs, it is predicted that higher-ranking individuals will be able to become satiated more quickly and spend less time feeding overall than lower-ranking individuals because they would obtain increased access to the "most" and the "best" foodstuffs. In the presence of limited or variable quality foodstuffs, if higher-ranking individuals spend less time feeding they would have more time for other activities by default. Importantly, this may enable higher-ranking individuals to spend more time engaged in affiliative behaviors such as grooming, which may in turn help maintain social cohesion in their sub-group.

We tested these predictions by conducting a field food-provisioning experiment with adult male golden snub-nosed monkeys (*Rhinopithecus roxellana*). This species is particularly suitable to test these predictions for two main reasons. First, *R. roxellana* is one of the few non-human primate species that lives in a multi-level society (MLS; Kirkpatrick & Grueter, 2010; Grueter et al., 2012; Qi et al., 2014, 2017), which consists of multiple small one-male units (OMUs) nested within a larger breeding band (BB) that can consist of over 100 individuals. Each OMU contains a single mature adult male, several adult females (one to seven), and their immature and infant offspring. Young adult males are ejected from the BB by the OMU adult males and form an all-male unit (AMU) that follows the BB (Qi et al., 2014, 2017). OMUs within the BB act in a coordinated way and feed, travel, and rest together. Other than immatures and older infants of both sexes, social interactions among adults are mainly confined within each OMU. While the different OMUs are predominantly in a state of mutual tolerance (a prerequisite for the maintenance of the MLS), competition among OMUs does occur. There is also a distinct male hierarchy that results from dyadic interactions between adult males (Zhang, Watanabe, Li, & Qi, 2008). Such agonistic events often occur due to disputes over food items (Zhao & Tan, 2011), and may also include the participation of some female members of the same OMUs as the competing males (Zhao, Chen, Li, & Romero, 2013). Higher-ranking males, and their associated OMU group members, can therefore be expected to gain preferential access to favored food items, and this may enable higher-ranking males to spend more time on alternative activities, such as engaging in affiliative behaviors with the other members of their OMU (sensu Huntingford & Turner, 1987; Lehmann et al., 2007; Dunbar et al., 2009; Dunbar & Lehmann, 2013).

Second, unlike almost all other primate species, *R. roxellana* lives in a temperate climate. Endemic to central China, *R. roxellana* lives mainly in mixed forests in mountainous regions. Populations are therefore subject to prolonged periods of cold and reduced biological productivity during winter. Although generally described as a

folivorous colobine, the *R. roxellana* diet varies greatly, especially across different seasons (Guo et al., 2007; Hou et al., 2018). Some populations consume lichens year-round (Guo et al., 2007) but during spring and summer their diet tends to be dominated by the young leaves of broadleaved trees, with fruit and seeds (oak acorns and pine seeds) consumed during late-summer/autumn (Guo et al., 2007). During winter in our study area, most food items are absent, forcing a seasonal switch to a very high-fiber diet consisting mainly of twigs, fallen oak acorns, and tree bark (Guo et al., 2007; Hou et al., 2018). This seasonal dietary shift results in a corresponding reduction in available nutrients and an increase in dietary volume due to the high fiber content (Guo et al., 2018). This dietary shift is compounded by increased energy requirements due to often extreme cold and the thermoregulatory demands this creates (Guo et al., 2018; Kronfeld-Schor & Dayan, 2013). Conducting a field experiment provisioning foods of variable value during winter to golden snub-nosed monkeys, thus presents subjects with high-value food resources likely to result in behavioral variation according to both social rank and food value.

We performed a field experiment to enable us to measure the relationships between social rank, food consumption, and time-budgets in OMU adult male *R. roxellana* during winter. This was achieved by first determining OMU adult male social rank and then by provisioning twice daily during winter an *R. roxellana* BB with two different foodstuffs (individual kernels of maize and large chunks of radish) that each likely varied in profitability. We also measured the consumption of naturally occurring foodstuffs, which due to being time-consuming to eat were likely to be less profitable than each of the two provisioned foods. Furthermore, we also measured the behavioral time-budgets of the same OMU adult males.

We made two predictions: (a) Due to preferential access to high-value foods, higher-ranking males will spend less time feeding overall and consume provisioned foods at a higher rate, than lower-ranking males. (b) A reduction in feeding time will enable high-rank OMU adult males to spend longer engaged in other behaviors. Non-affiliative behaviors, such as resting and moving, should be unaffected by rank. However, affiliative behaviors such as grooming likely promote within-group social cohesion. High-rank males will thus spend more time engaged in such behaviors.

2 | METHODS

2.1 | Study site

Our study site is in the Zhouzhi National Nature Reserve (ZNNR, 108°16′E, 33°48′N, elevation: 1,400–2,896 m above sea level), near to the village of Yuhuangmiao, on the northern slopes of the Qinling Mountains, central China. Here, the vegetation varies with altitude from coniferous forests above 2,600 m to mixed coniferous-broadleaf forest between 2,200 and 2,600 m, and deciduous broadleaf forest below 2,200 m (Li, Chen, Ji, & Ren, 2000). According to the China Meteorological Administration (C.M.A., 2012), winter occurs from mid-October to March and summer occurs from mid-May until the

end of August. The average temperature during 2016 was 8.8°C (mean ± *SE*: winter: −3.70 ± 0.25°C; summer: 21.32 ± 0.19°C). Precipitation during 2016 was 590 mm (Weather Transmitter WXT520, Vaisala).

2.2 | Study group

The ZNNR BB has been studied since 2001 and to enable detailed behavioral observations has received food provisioning each winter (as described below). The data we report here were collected between October 14, 2016 and December 10, 2016. Data to establish OMU adult male rank were collected from 14th October to 10th November; all other data were collected from 11th November until 10th December. This time period lies almost exclusively outside of the mating season. During the study, competitive interactions between adult OMU male dyads thus occurred over access to food not adult females. All data recorded to establish rank resulted only from direct dyadic encounters between OMU males, which often involved aggression (see Tables 1 and 2). However, the later-recorded main data set for the focal OMU males resulted from detailed observations of all of their behaviors, especially feeding (in order to test Prediction 1). Such behaviors occurred almost entirely in the absence of direct dyadic interactions between males, including those data associated with competition for food, that is, the times spent feeding and feeding rates. In short, although male rank had largely been previously determined by quantifying the outcomes of aggressive interactions between male–male dyads, the majority of data subsequently recorded did not involve aggression. This is because most data were not recorded during any dyadic interactions between individuals.

Our study BB consisted of 142 individuals, with 14 one-male multi-female OMUs and an associated AMU (34 males including juveniles, sub-adults, and adults) that shadowed the BB. Data were not recorded from the AMU.

We identified BB members by their physical characteristics, such as distinct facial features, scars, color patterns, and body size (Zhang, Li, Wada, Tan, & Watanabe, 2003). Some older individuals could also be recognized by tattoos on their lips applied by previous researchers (Zhang et al., 2003). OMU tenure length varies due to for example the death of an OMU adult male or usurpation by an AMU male. The length of tenure of each OMU adult male at the time of the study was therefore known due to the long-term monitoring of these monkeys.

2.3 | Study design

The study incorporated the established winter food provisioning program of this BB for three main reasons (see "Data collection" for precise provisioning details). (a) The provisioning of food increased variation in the profitability/value of food items to the monkeys in their otherwise natural environment but only for a limited time period each day. Naturally available foodstuffs during winter are limited to mainly oak acorns (often hidden beneath a layer of snow) and tree

TABLE 1 Dominance interaction matrix showing the numbers of wins and losses between 14 adult male golden snub-nosed monkeys

Male	WF	ST	WX	G3	SQ	BX	ZB	SX	ZD	TB	LZ	XJ	CM	BG
WF	*	5.00	3.00	1.00	4.00	8.00	4.00	1.00	7.00	9.00	4.00	4.00	5.00	4.00
ST	1.00	*	4.00	0.00	2.00	1.00	5.00	4.00	5.00	11.00	12.00	8.00	8.00	2.00
WX	1.00	4.00	*	1.00	3.00	4.00	8.00	1.00	3.00	3.00	3.00	2.00	5.00	3.00
G3	0.00	0.00	1.00	*	2.00	0.00	8.00	2.00	3.00	2.00	3.00	1.00	0.00	1.00
SQ	2.00	1.00	1.00	0.00	*	1.00	1.00	5.00	0.00	4.00	2.00	7.00	3.00	2.00
BX	1.00	0.00	3.00	0.00	0.00	*	4.00	3.00	2.00	5.00	2.00	4.00	5.00	1.00
ZB	0.00	0.00	1.00	1.00	2.00	1.00	*	2.00	4.00	4.00	2.00	1.00	2.00	2.00
SX	0.00	0.00	0.00	0.00	0.00	0.00	2.00	*	1.00	2.00	1.00	2.00	0.00	1.00
ZD	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	*	0.00	0.00	0.00	0.00	0.00
TB	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	*	2.00	1.00	4.00	1.00
LZ	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	*	0.00	4.00	2.00
XJ	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	*	0.00	0.00
CM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	*	0.00
BG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	*

Note: Wins are given in rows and losses in columns.

bark (which requires removal from trees by biting and pulling) (Hou et al., 2018). Both of these natural food items thus require much handling time, and hence will likely have relatively low "profitability" to the monkeys when provisioned food is present. Although these monkeys still compete for natural food items, when this occurs individuals are often distributed in such a manner as to make accurate behavioral observations difficult. For example, individuals may be located in several trees spaced several tens of meters apart. (b) The more clustered spatial distribution of provisioned foods compared with natural foods enables close and accurate monitoring of individuals as they forage. (c) The likely variation in food profitability was predicted to translate to relatively high variation in behavioral responses from individuals associated with food competition, thus potentially reducing the sampling effort required to test our predictions.

2.4 | Data collection

2.4.1 | Food provisioning

This BB has received daily food provisioning each winter since 2001. Each day, the monkeys are provisioned at 10:00 hr and again at 14:00 hr, with a combination of 7.5 kg of small individual kernels of maize (*Zea mays*) that had all been removed from the husk, and 7.5 kg of radish (*Raphanus sativus*) chunks (see Table S1 for descriptive data), an average of 0.21 kg of provisioned food per monkey per day for the entire BB. Maize and radish are both provisioned because these two foods contain nutrients lacking in naturally available winter food (Hou et al., 2018). The food is evenly scattered across a provisioning zone, an area of short grassland (30 m × 30 m) surrounded by mixed forest (Tan, Guo, & Li, 2007). The provisioned foods do not meet the daily energy requirements of the entire BB during autumn-winter (Guo

et al., 2018). Although the energy content per g of provisioned food broadly equates to that of some natural food items consumed during autumn-winter (Hou et al., 2018), ease of access and consumption will likely make provisioned food more profitable than natural foods due to much reduced handling times (Stephens & Krebs, 1987). For instance, after initial removal from the tree, only the inner part of tree bark is consumed. This makes consumption of bark both time consuming and labor intensive for these monkeys.

2.4.2 | Defining OMU adult male rank

We recorded the winner and the loser of all agonistic interactions between any two OMU adult males within and in close proximity to the provisioning zone (*N* = 133; total observation time 84.16 hr). Agonistic interactions were encounters between two males that included threatening and/or physically aggressive behavior. Threatening behavior was determined when one individual (the initiator) leant forward with an open mouth and showed its teeth, while simultaneously staring at another individual (the receiver). Physically aggressive behavior was when one individual (the initiator) chased another individual (the receiver). The initiator almost always made physical contact and grappled with the receiver. When such interactions escalated into fights that ended up involving more participants than only two OMU adult males, data were not included. We used David's score (David, 1987) to estimate dominance ranks for all 14 OMU adult males (Briffa et al., 2013; Gammell, Han, Jennings, & Hayden, 2003). The winner of an agonistic interaction was defined as the OMU adult male that remained at or returned to the location of the contested food item, either provisioned or natural, and continued to feed. The loser was defined as the OMU adult male who moved away and no longer had access to the contested food item. David's score is based on an un-

TABLE 2 Matrix of the proportions of wins and losses of dyadic agonistic interactions between 14 male golden snub-nosed monkeys, and the values for w, w_2, l, and l_2 used to calculate David's scores (DS) and normalized David's scores (NDS) for each individual (de Vries, Stevens, & Vervaecke, 2006)

Male	WF	ST	WX	G3	SQ	BX	ZB	SX	ZD	TB	LZ	XJ	CM	BG	w	w_2	DS	NDS
WF	*	0.83	0.75	1.00	0.67	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	12.14	62.67	71.32	11.59
ST	0.17	*	0.50	0.00	0.67	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	10.33	42.64	47.94	9.92
WX	0.25	0.50	*	0.50	0.75	0.57	0.89	1.00	0.75	1.00	1.00	1.00	1.00	1.00	10.21	43.97	43.84	9.63
G3	0.00	0.00	0.50	*	1.00	0.00	0.89	1.00	1.00	0.67	1.00	1.00	0.00	1.00	8.06	40.81	41.44	9.46
SQ	0.33	0.33	0.25	0.00	*	1.00	0.33	1.00	0.00	1.00	1.00	1.00	1.00	1.00	8.25	34.88	29.92	8.64
BX	0.11	0.00	0.43	0.00	0.00	*	0.80	1.00	1.00	1.00	1.00	1.00	1.00	1.00	8.34	25.92	21.70	8.05
ZB	0.00	0.00	0.11	0.11	0.67	0.20	*	0.50	1.00	0.80	1.00	1.00	1.00	1.00	7.39	19.69	5.74	6.91
SX	0.00	0.00	0.00	0.00	0.00	0.00	0.50	*	1.00	1.00	1.00	1.00	0.00	1.00	5.50	12.48	−6.00	6.07
ZD	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	*	0.00	0.00	0.00	0.00	0.00	5.20	7.75	−22.82	4.87
TB	0.00	0.00	0.00	0.33	0.00	0.00	0.20	0.00	1.00	*	0.67	1.00	1.00	1.00	2.13	1.89	−35.86	3.94
LZ	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	*	0.00	0.80	1.00	0.20	0.43	−40.41	3.61
XJ	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	*	0.00	0.00	1.00	0.25	−42.33	3.48
CM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	*	0.00	0.25	2.55	−45.08	3.28
BG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	*	0.00	0.00	−53.45	2.68
l	0.86	1.67	2.79	1.94	3.75	3.66	5.61	6.50	8.75	7.80	8.87	9.00	7.80	10.00				
l_2	2.63	3.36	7.55	5.48	9.46	8.90	15.72	17.48	39.14	27.97	31.02	34.58	33.23	43.45				
OMU ♀	6	4	3	5	7	4	3	6	3	4	4	4	5	1				

Note: Data are presented in ranked order top-to-bottom by row according to DS and NDS values. OMU ♀ = N adult females within each OMU.

weighted and a weighted sum of an individual's dyadic proportion of wins combined with an un-weighted and a weighted sum of its dyadic proportions of its losses. Thus, defeating a higher-ranking individual is weighted more heavily than defeating a lower-ranking individual (de Vries et al., 2006). The data matrixes used to calculate David's scores for the 14 OMU adult males are presented in Tables 1 and 2.

After assigning rank, we used the top five and the bottom five ranked OMU adult males as focal animals to record their food consumption and activity budgets. This was due to the logistic constraints of having to gather enough data from individual monkeys by subsequently following and recording all of their daily activities on multiple days (see below).

2.4.3 | Focal sampling

Each morning, two of the 10 adult males were randomly selected for observation using focal sampling. Recording of each focal individual on each day began at 08:00 and ended at sunset (approximately 18:00) and was conducted by one of two observers. Two monkeys were thus observed per day. The distance between each of the focal monkeys and the observers was on average ~5 m and ranged from 0.5 to 40 m. Each of the 10 adult males had its behavior recorded for 1 to 5 days, resulting in a total monitoring time of 213 hr for the five highest ranked OMU males (mean ± *SD* = 10.13 ± 0.49 hr per day) and 211 hr for the five lowest ranked OMU males (mean ± *SD* = 10.06 ± 0.37 per day). To minimize recorder bias both observers made preliminary studies to standardize the recording method. Furthermore, when an individual was selected for observation on multiple days it was ensured that data were recorded by different observers on different days.

We recorded the durations of seven behaviors (Table 3). The time duration of each behavioral bout conducted by each focal individual on each day's sampling was recorded with a stopwatch. Multiple bouts were thus made for each behavior on each day for each focal individual. The time spent on each behavior was summed for each focal individual, for example, the times spent feeding on each of multiple food items were added together to produce the time spent feeding that day for the focal individual.

2.4.4 | Food mass, food type, and energy content

All food items (both provisioned and natural) were recorded and the amount consumed estimated using previously described methods (Guo et al., 2018; Hou et al., 2018; see also online Supplementary Material). We estimated the nutrient contents of provisioned and natural foods using established methods (Rothman, Chapman, & Van Soest, 2012; see Supplementary Material). Natural foods were widely available at the periphery of the provisioning zone and beyond. We measured the mass and energy (kJ) of all food items. This was accomplished by recording the specific plant part and plant species consumed and cross referencing with existing data on the nutritional content of foods consumed by this same BB (Hou et al., 2018). Because we collected data for the food

TABLE 3 Detailed descriptions of the seven separate behaviors recorded during the daily focal sampling of 10 adult male golden snub-nosed monkeys

Behavior	Description
Feeding	The monkey actively picked or picked-up, manipulated, put in its mouth, chewed and then swallowed an individual food item.
Moving	An OMU male was moving on the ground or in a tree not for the direct purpose of obtaining a food item. Therefore, when an OMU male was moving between food items while feeding, the time spent doing so contributed to its feeding time that day
Resting	An OMU male was stationary for at least 1 min or was sleeping. This was thus largely the time the OMU male spent between other activities.
Grooming	The OMU leader male systematically picks-out small objects (e.g., dirt or parasites) from the hair and/or the skin of another individual (usually an adult female) from the same OMU, using its fingers and/or teeth. Any parasites removed are either put into the mouth and eaten by the groomer if removed by the fingers or eaten directly if removed by the teeth
Being groomed	An individual (usually an adult female) from the same OMU systematically picks-out small objects (e.g., dirt or parasites) from the hair and/or the skin of the OMU leader male, using its fingers and/or teeth. Any parasites removed are either put into the mouth and eaten by the groomer if removed by the fingers or eaten directly if removed by the teeth
Mating	The OMU leader male grabs an adult female with his arms and pulls her towards him so his belly touches her back. He then inserts his genitalia into her vagina and begins to twitch. Mating is deemed to end when the couple separate.
Embracing	The OMU leader male holds another individual (usually an adult female) from the same OMU in its arms face-to-face or face-to-back in an unaggressive and non-threatening manner. Alternatively, the OMU male was the recipient of the same behavior from another individual (usually an adult female) from the same OMU.

Note: Non-affiliative behaviors: feeding, moving, and resting. Affiliative behaviors: grooming, being groomed, mating, and embracing.

items eaten and the amount of each food item eaten, we could then calculate for each focal monkey the food mass eaten and the energetic intake per hour of observation. On average, provisioned foods contained significantly more energy than natural foods (see Supplementary Material) and because they were larger, each piece of radish contained more energy than each kernel of maize (Table S1).

2.4.5 | Data analysis

We used linear mixed models (LMMs) to measure the effects of OMU adult male rank, which was included as an explanatory fixed factor

(either high or low). Actual rank: 1–5, 10–14 was not included as a continuous covariate, because we did not have data for the males of the ranks 6–9. Using the "ranks-of-ranks" as a continuous explanatory variable or a factor consisting of 10 groups would also complicate the results interpretations and graphical representations of rank by food type interactions.

For prediction 1, we used two models (Table 4.) each of which included as the response variable either: (a) the proportion of all daily recorded time spent feeding or (b) the rate of food consumption (g per hour feeding time). In addition to "rank," "food type" (either provisioned or natural) was also included as an additional fixed factor, which enabled the quantification of any disproportionate effects of rank on different food types by the inclusion of a rank by food type interaction in each statistical model.

For prediction 2, we built seven models (Table 5). To extract maximum information from our data, we analyzed each behavior recorded separately by using the proportion of all daily monitored time the monkeys spent on each behavior as a response variable in a separate statistical model. We also partitioned different behaviors into those that could be interpreted as "affiliative" or not. The non-affiliative behaviors were moving and resting; the affiliative behaviors were: grooming other individuals within the OMU (usually one of the adult females), being groomed by other members of the same OMU (usually by one of the adult females), embracing, and mating (Table 3). The first affiliative behavior model used as the response variable the proportion of all daily monitored time monkeys spent engaged in affiliative behaviors, defined as the sum of the times monkeys spent engaged in each of the four affiliative behaviors. We then built four individual models for each affiliative behavior (the proportion of all monitored time spent engaged in the specific activity) as the response variable. (Feeding was tested for Prediction 1.)

For all models involving proportional response variables we used the proportion of time spent on the behavior under scrutiny of the total monitoring time for that day (arcsine square-root transformed) in

TABLE 4 Results of two linear mixed-model (LMM) testing our predictions for trends in feeding

Feeding time	MS	DF	F	p
Rank	0.0070	1,78	3.345	.07
Food	0.777	1,78	372.92	<.0001
Females	0.000	1,78	0.0003	.98
OMU age	0.0004	1,78	0.189	.66
Rank × Food	0.150	1,78	71.91	<.0001
Food mass rate	MS	DF	F	p
Rank	0.287	1,78.72	4.89	.0299
Food	3.469	1,58.77	59.10	<.0001
Females	0.012	1,71.60	0.195	.659
OMU age	0.015	1,76.12	0.253	.616
Rank × Food	1.324	1,58.77	22.55	<.0001

Note: Response variables are given above each sub-table; explanatory variables are given in bold.

order to control for variation in the total monitoring times on different days. For food intake rates, data required log transformation. After transformation, all response variables concurred with the heteroscedasticity and error variance distribution requirements underlying linear models. We did not use generalized linear mixed models (GLMMs) with a binomial error structure for proportional data because our time data were in hours so did not meet the requirements for data to be integers for this type of analysis.

To remove the effects of pseudo-replication (Briffa et al., 2013), we also included in each model as a random factor "male id" because measurements were made from most of the same 10 OMU adult males on more than 1 day. For models testing prediction 1, because each male ate both provisioned and natural foods on each day it was monitored (see below) we included as an additional random factor "day." The presentation of the ANOVA tables (Tables 4 and 5) and summary results (Tables S2–S9) for each model thus control for any unmeasured variance according to these random factors All models had variance inflation factors (VIFs) of between 1 and 4, showing that multicollinearity between explanatory variables was unlikely to have strongly affected our results. All models were compared to the appropriate null model (Crawley, 2007; for model comparisons see Tables S2–S9 in the online Supplementary Materials).

All models testing both predictions included as explanatory covariates "female number" (the number of adult females in the focal adult male's OMU) and "tenure." "Female number" was included because females may assist (possibly indirectly without becoming directly involved) OMU males in competitive interactions with other OMU males (Zhao et al., 2013). Tenure was used as a proxy for OMU stability/cohesion, under the premise that OMU long-term stability is, at least in part, the result of successful competition for resources and/or a high degree of group (in this case OMU) social cohesion.

We also tested for differences between high- and low-ranking males in the number of adult females within OMUs, and the length of male OMU tenure using *t*-tests.

All statistical tests were performed using R 3.5.2. (R-Core Team, 2018), either using the base package or with the additional package "lmerTest" (Kuznetsova, Brockhoff, & Christensen, 2017).

3 | RESULTS

3.1 | Prediction 1: Higher-ranking males will spend less time feeding overall but consume provisioned foods at a higher rate than lower-ranking males

Our results generally support this prediction. Higher-ranking males tended to spend on average approximately 22% less time feeding overall than lower-ranking males (Figure 1a; Table 4). A significant rank by food-type interaction (Table 4; see also Table S2) reflected the clear trend that higher-ranking males spent longer feeding on provisioned foods and less time on natural foods than lower-ranking males (Figure 1a).

TABLE 5 Results of seven linear mixed models that each explain variation in one OMU leader male behavior

	All affiliative behaviors					Embracing			
	MS	DF	F	p		MS	DF	F	p
Rank	0.0159	1,38	8.944	.0049	Rank	0.00176	1,4.96	2.36	.186
Females	0.00058	1,38	0.326	.572	Females	0.00016	1,8.58	0.21	.659
Tenure[a]	0.0083	1,38	4.670	.037	Tenure	0.00032	1,4.42	0.433	.543
b ± SE[a]			t						
−0.012 ± 0.005			−2.16						

	Grooming other individuals within an OMU					Moving			
	MS	DF	F	p		MS	DF	F	p
Rank	0.0063	1,4.76	11.06	.0025	Rank	0.0021	1,4.54	1.627	.264
Females	0.00082	1,8.16	1.44	.264	Females	0.000028	1,7.90	0.022	.885
Tenure	0.0000005	1,4.55	0.009	.929	Tenure	0.000613	1,4.20	0.485	.523

	Being groomed by other OMU individuals					Resting			
	MS	DF	F	p		MS	DF	F	p
Rank	0.0056	1,38	4.038	.05	Rank	0.00038	1,6.34	0.78	.410
Females	0.000003	1,38	0.0002	.99	Females	0.00023	1,10.09	0.47	.507
Tenure[b]	0.0094	1,38	6.72	.014	Tenure	0.00123	1,6.32	2.55	.159
b ± SE[b]			t						
−0.0125 ± 0.0048			−2.592						

	Mating			
	MS	DF	F	p
Rank	0.000031	1,6.12	0.264	.626
Females [c]	0.0011	1,9.70	9.092	.013
Tenure	0.00031	1,6.14	2.655	.153
b ± SE[c]			t	
0.0063 ± 0.0021			3.015	

Note: Where any of the two continuous covariates are significant, that is, the number of adult females in each OMU (Females) and the tenure length of each OMU leader male (OMU age), the corresponding beta coefficients (b ± SE) and t values are presented.

Higher-ranking males had a higher overall rate of food consumption (food mass consumed per hour feeding time) than lower-ranking males (nearly two-fold), with provisioned foods being consumed by all individuals at a higher rate than natural foods (over two-fold; Figure 1b). A significant rank by food-type interaction showed that higher-ranking males consumed provisioned food at a significantly higher rate than lower-ranking males;
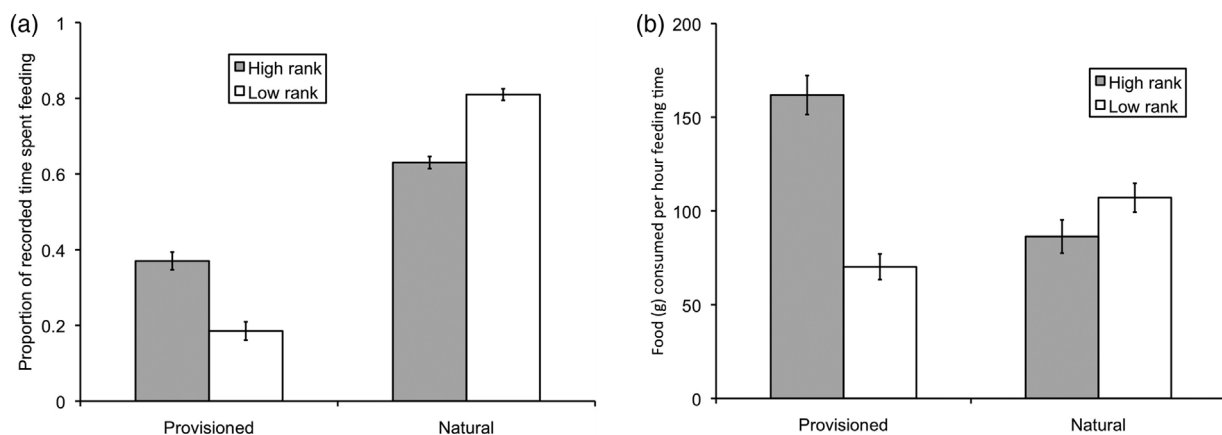

FIGURE 1 Mean ± *SE*, (a) proportion of recorded time that focal males spent feeding and (b) the rates (g per hour) at which focal males consumed, either provisioned or natural food items according to social rank

lower-ranking males had a higher rate of natural food consumption than higher-ranking males (Table 4; Figure 1b.; see also Table S3).

3.2 | Prediction 2: Rank will not affect non-affiliative behaviors but higher ranking OMU adult males will spend more of their daily time budgets engaged in affiliative behaviors, especially grooming, than lower-ranking males

The proportion of time spent engaged in the two non-affiliative behaviors, moving and resting, were not significantly affected by OMU social rank, the number of females within OMUs nor by OMU tenure length (Table 5).

As predicted, higher-ranking adult males spent approximately 50% more of their time engaged in affiliative behaviors than did lower-ranking males (Figure 2a; Table 5). This was offset slightly by a weak (i.e., the coefficient or "slope" was small) negative relationship between tenure duration and the time spent engaged in affiliative behaviors (Table 5). This was probably due to higher-ranking males

having longer tenures (mean ± SE = 4.29 ± 0.36 years) than lower-ranking males (2.86 ± 0.55 years; t-test - t_{12} = 2.17, p = .05).

When behaviors are examined individually, it is clear that the time OMU adult males spent grooming explains much of the rank differences in the overall time spent on all affiliative behaviors. Higher-ranking males groomed other OMU members (mainly the adult females) for significantly longer (approximately four-fold) as a proportion of all time per day than lower-ranking males (Figure 2b; Table 5). The proportion of all time a higher-ranking adult male spent being groomed by other members of his own OMU (mainly the adult females) was significantly higher than for lower-ranking males (approximately 20% longer; Figure 2c; Table 5). The proportion of their time budget males spent being groomed by other members of their OMU also increased with tenure length (i.e., the coefficient or "slope" was positive; Table 5).

The proportion of time spent mating within an OMU did not differ between higher- and lower-ranking adult males but was positively associated with the number of adult females in the same OMU (Table 5). The numbers of females within the OMUs of higher-ranking (4.86 ± 0.55) or lower-ranking adult males (4.14 ± 0.67) did not differ (t-test—t_{12} = 0.82, p = .43).
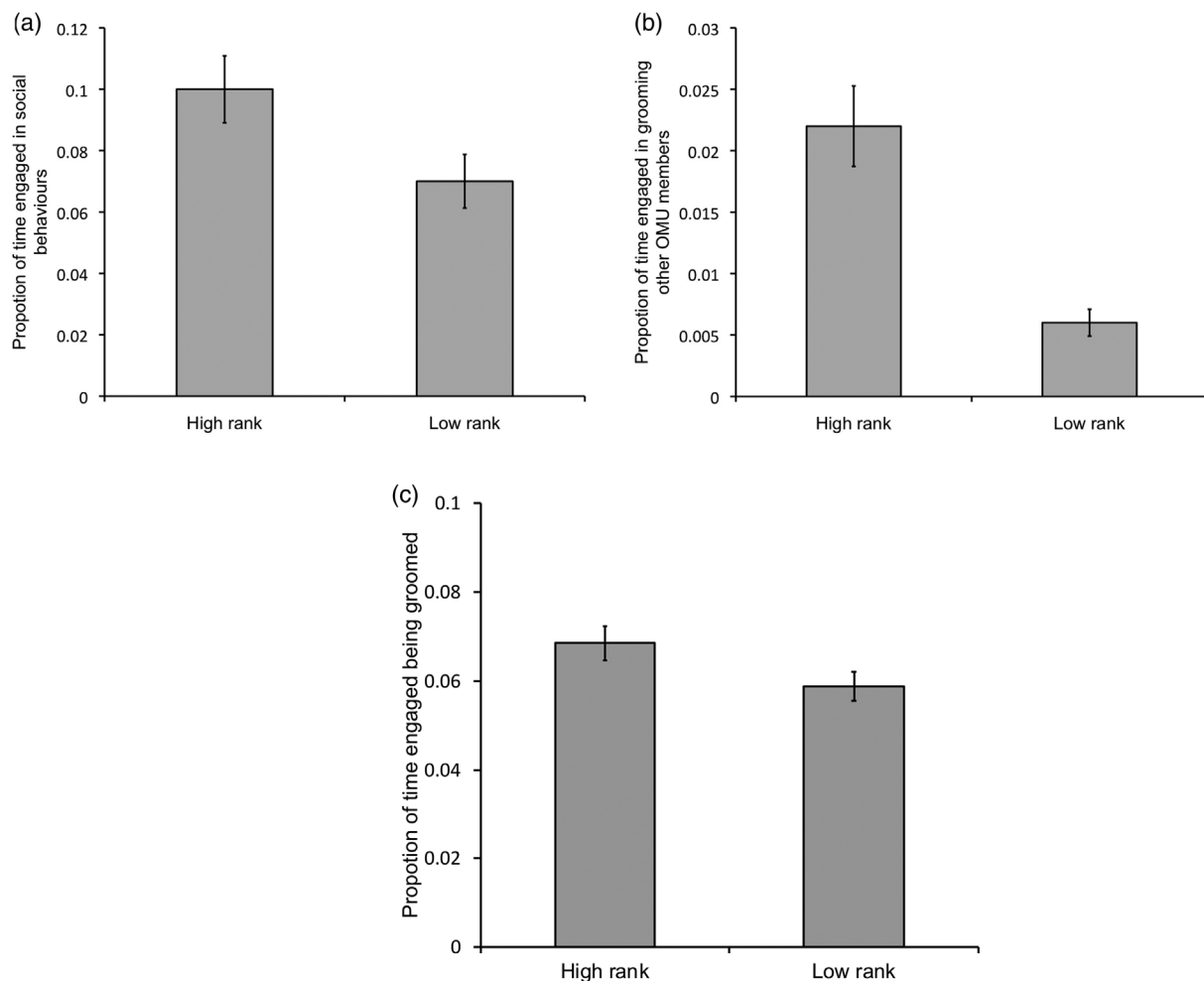

FIGURE 2 Mean ± SE, (a) proportion of recorded time that focal males spent engaged in socially affiliative behaviors, (b) grooming other members of their own OMU, and (c) being groomed by other members of their own OMU, according to social rank

The proportion of their daily time budgets OMU adult males spent embracing, or being embraced by, other members of their own OMU was not significantly affected by their social rank, the number of females within their OMU nor their OMU tenure length (Table 5).

4 | DISCUSSION

We tested the effects of social rank on competition for food among male *R. roxellana*. Consistent with Prediction 1, higher-ranking males spent less time feeding overall and consumed provisioned food at a higher rate, than lower-ranking males. Higher-ranking males also spent more time feeding on provisioned foods and less time on natural foods, than lower-ranking males. Consistent with Prediction 2, higher-ranking OMU adult males spent more time engaged in affiliative behaviors with other OMU members, especially grooming and being groomed. As predicted, the time adult males spent on non-affiliative behaviors, moving or resting, was unaffected by social rank.

Our results show that in *R. roxellana*, high OMU adult male social rank confers preferential access to food, which is consistent with previous findings showing that contest competition among females can be mediated by rank (Janson, 1988; Janson & van Schaik, 1988; Koenig, 2002; van Schaik, 1989). In other primate species, there is evidence of rank affecting foraging success among groups. For instance, black-and-white colobus (*Colobus guereza*) groups that initiate and win between-group encounters (high rank) often feed in the same areas in which losing groups (low rank) had previously fed. Groups can be ranked in a linear dominance hierarchy, with group rank inversely related to the quantity and quality of food in groups' core areas (Harris, 2006; Harris, Chapman, & Monfort, 2010). In tufted capuchins *Sapajus nigritus*, dominant groups are better at defending their core area, and may thus have higher per capita access to food (Scarry, 2013). There is also evidence of competition for food among OMUs within this same *R. roxellana* BB (Zhao & Tan, 2011) but the effects of rank are unknown. Overall, we show that social rank among adult males can affect access to high-quality food within this MLS.

In the *R. roxellana* MLS, within a particular OMU, the females and juveniles almost always forage in close proximity to the adult male (Guo, Huang, Ji, Garber, & Li, 2014). The whole OMU may thus attain the rank-based foraging privileges as their OMU adult male by default. In the context of the *R. roxellana* MLS, the adult OMU males may thus obtain both direct that is, material, and indirect that is, reproductive, benefits from preferential access to foodstuffs. High-ranking males clearly benefit directly from increased access to foods during winter when there is limited food availability. Additionally, males may benefit directly if increased access to food during winter results in the adult females of their OMU being more likely to give support to the OMU male during and/or after agnostic interactions with other OMU males (sensu Fashing, 2001; Zhao et al., 2013, 2015). Importantly, males can also benefit indirectly via at least two not necessarily mutually independent mechanisms. First, adult females may obtain increased nutrition to invest during the following spring in offspring fathered by the OMU male. Second, there may be increased winter survival of juveniles that are the offspring of the OMU adult male. Surviving male offspring may also benefit their fathers in the future by forming coalitions to defend females (sensu Fashing, 2001), from attempted OMU take-overs and/or by successfully taking-over existing OMUs (Qi et al., 2017). It can therefore be predicted that adult OMU male lifetime reproductive success is correlated positively with social rank via such mechanisms. Further research is needed to test this hypothesis, work that would increase the general understanding of the nature of MLSs in nature.

When lower-ranking males gain access to high-profitability provisioned foods, they would be expected to eat quickly if there was a high likelihood of being displaced by a higher-ranking competitor. Higher-ranking males consuming provisioned foods at a higher rate than lower-ranking males is thus to some extent counter-intuitive. However, this can be explained by the two types of provisioned foods, large chunks of radishes and small, individual kernels of maize, probably having different handling times and thus different profitabilities to individuals (Stephens & Krebs, 1987). On average, radish pieces are ~65× the mass (25.59 vs. 0.394 g) and ~100× the volume (31.75 vs. 0.31 ml) of maize kernels (Table S1). Although radish has a much higher water content than maize (~79 vs. 14% [maize is dried for storage after harvesting]) and the caloric content per dry unit mass is similar (radish—15.21 kJ/g; maize—14.6 kJ/g), each radish chunk still has on average ~16× the energy value as a single maize kernel. Adult males pick-up individual radish chunks from the ground and eat each one by taking two or three bites; maize kernels are also usually picked-up individually and then eaten whole one-at-a-time and only rarely eaten collectively (S. J. He, personal observations). It will therefore likely take longer to search for and then consume the 16 kernels of maize required to match the nutritional gain from eating a single chunk of radish. Even though there is little overall nutritional difference between the maize and radish (Hou et al., 2018), if the radishes are eaten pre-dominantly by high-ranking males this would, at least partially, explain why high-ranking males have higher feeding rates than lower-ranking males and why this is especially pronounced for the provisioned foods.

High-ranking OMU adult males spent more of their time grooming, and to a lesser extent being groomed by, the adult females of their own OMUs. Grooming is a behavior known to be important for maintaining social cohesion in primate groups (Dunbar et al., 2009; Dunbar & Lehmann, 2013; Lehmann et al., 2007). Because higher-ranking OMU males spent less time overall feeding than lower-ranking OMU males, they traded-off time to spend on affiliative behaviors that may in turn enhance social cohesion within their OMU. Males did not use this extra time to spend on the non-affiliative behaviors we recorded, moving and resting. Moreover, we also show that higher-ranking males had significantly longer tenures than lower-ranking males, supporting the predicted positive relationship between social cohesion and current social rank at the OMU level.

The large difference in the time adult males spent grooming other OMU members (almost always the adult females) suggests that this was the main driver of rank differences in the time males spent overall on affiliative behaviors. Although significant, there was a much smaller

difference between ranks in the time the same males were groomed by the females (Figures 2b,c). This suggests that the high-ranking males were proactive in using at least some of their "free," non-feeding time to groom the adult females of their OMU, and they were doing this in preference to alternative activities. In addition to potentially facilitating within-OMU social cohesion, high rates of grooming within high-ranking OMUs may also confer additional benefits to the adult OMU members. For example, grooming has been shown to alleviate stress in social primates (e.g., Wittig et al., 2008). Because male rank had less of an effect when females groomed the males than vice-versa (Figure 2b,c) females are thus more likely to be the recipients of grooming so will incur fewer overall costs of grooming than males. Therefore, the females within the OMUs of high-ranking males may incur more benefits of increased grooming time than males. Moreover, these trends may be context dependent. For instance, females may be more likely to groom males that have just been involved in a fight with another OMU or an AMU male but further work is needed to clarify if this occurs and how social rank may play a role (see Zhang, Zhao, & Li, 2010; Zhao et al., 2015).

As predicted, we found no effect of rank on the amount of time males spent engaged in non-affiliative behaviors. However, although the study was conducted outside of the mating season and little time was spent mating, we still detected a slight but significant positive correlation between the time spent mating and the number of females within OMUs (Table 5). This suggests that any mating was contained within OMUs. In other words, the adult OMUs were unlikely to have been involved in extra-pair copulations (EPCs) even though EPCs are common during the mating season (Zhao, Li, Li, & Wada, 2004). Alternatively, the mating we observed likely served a non-reproductive function (Dixson, 2012). Nevertheless, our finding gives added support that our main results reflect male–male competition for food not mates.

In summary, within the *R. roxellana*, MLS competition for food between adult males appears to be mediated, at least in part, by their social rank, with higher-ranking males spending less time feeding and consuming high profitability provisioned foods at higher rates than lower-ranking males. Higher-ranking males spend relatively more time exhibiting socially affiliative behaviors, especially grooming the adult females of their OMU, and have presided over their OMUs for longer, than lower-ranking males. This suggests that the OMUs of higher-ranking makes may be more socially cohesive than those of lower-ranking males. We suggest that high-ranking males may benefit both through increased access to high-profitability food during winter food shortages and due to increased numbers of offspring. This may thus give all members of a higher-ranking OMU an advantage during competition for food during winter.

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AUTHOR CONTRIBUTIONS

Songtao Guo: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; supervision; writing-original draft; writing-review and editing. **Shu-jun He:** Data curation; formal analysis; investigation; methodology; writing-original draft; writing-review and editing. **He Zhang:** Data curation; writing-original draft. **Rui-feng Bai:** Methodology. **Si-Meng Zhang:** Data curation; methodology. **Rong Hou:** Data curation; investigation. **Cyril Grueter:** Conceptualization; writing-review and editing. **Colin Chapman:** Conceptualization; writing-review and editing. **Derek Dunn:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; writing-original draft; writing-review and editing. **Baoguo Li:** Conceptualization; funding acquisition; supervision; writing-review and editing.

ETHICS STATEMENT

The study was approved by the Ethical Committee of Northwest University and adhered to the Ethical Regulations of the China Primatological Society, and the laws of the People's Republic of China.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding authors upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.