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RESEARCH ARTICLE

Aiming Low: A Resident Male's Rank Predicts Takeover Success by Challenging Males in Yunnan Snub-Nosed Monkeys

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In many primate species that form one-male breeding units (OMUs), the threat of a takeover by a bachelor male represents a major challenge to group stability and individual reproductive success. In the case of snub-nosed monkeys, which live in large multilevel or modular societies (MLS) comprising several OMUs that travel, feed and rest together and as well as one or more all male units (AMUs), the process by which rival males challenge resident OMU males for access to females is poorly understood. From September 2012 to October 2013, we recorded 48 cases in which rival males visited an OMU in a MLS of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) inhabiting the Baimaxueshan National Nature Reserve, Yunnan Province, China. In 40 cases, rival males engaged in mild agonistic interactions (approaching, staring, teeth-baring and chasing) but failed to take over the group; we counted these visits as failed takeovers, recognizing that they may nevertheless allow rival males to assess the competitive ability of residents. During eight successful takeovers, however, there was severe physical aggression between challenging and resident males, with serious injuries to participants. We found that neither the number of adult and subadult females in an OMU, the number of non-pregnant, non-lactating adult females in an OMU, nor the rank of a resident male relative to other resident males in the MLS predicted which OMU a challenging male targeted for takeover. However, a resident male's rank significantly predicted whether takeover attempts were successful. Specifically, challenging males were more successful in displacing a lower-ranking resident male than a higher-ranking male. Given that a Yunnan snub-nosed monkey MLS may contain as many as 40 resident and 36 bachelor males, continued research is required to determine the set of factors that enable resident males to maintain high social rank and successfully defend their harems. Am. J. Primatol. 78:974–982, 2016.

Key words: ***Rhinopithecus bieti*; male–male competition; takeover; Elo-rating**

INTRODUCTION

In primate species that form one-male multi-female breeding groups, a resident male attempts to monopolize the reproductive behavior of several adult females by preventing rival males from entering the harem [Dunbar, 2000]. In response, rivals may engage in several alternative behavioral strategies to increase their access to reproductive females. These include aggressively challenging a resident male and taking over his harem [Agoramoorthy, 1994; Swedell, 2000], attracting adult females away from their resident male temporarily [sneak copulations; Roberts et al., 2014] or permanently [female transfer; Qi et al., 2009], or by kidnapping subadult or young adult females through sexual coercion [Pines et al., 2011]. Given that direct encounters between resident and rival males can be extremely aggressive and result in injury or death [Pines et al., 2011; Swedell, 2000], rivals may also engage in an assessment strategy to determine the competitive ability of a resident and the likelihood of

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a successful takeover [le Roux and Bergman, 2012]. This assessment could include the use of third-party information [Silk, 1999] to determine the relative rank, strength, and set of coalitionary relationships among individual males [Gilby et al., 2013; Kitchen et al., 2005; Silk, 1999].

A small number of African papionins and Asian colobines are reported to live in a multilevel society (MLS) in which several one-male harem units (OMUs) travel, feed, and rest together to form a cohesive band [Grueter et al., 2012a,b]. In the case of snub-nosed monkeys (genus *Rhinopithecus*), the band is shadowed or followed by one or more all-male units (AMUs) comprising several adult, subadult, and juvenile males [Grueter and van Schaik, 2010; Kirkpatrick and Grueter, 2010]. AMU members occasionally challenge resident males and attempt to take over their harem. Close spatial proximity between OMUs and AMUs may enable challenging males to monitor social interactions and aggressive contests between resident males and use this information in assessing resident male competitive ability and female fidelity [le Roux and Bergman, 2012]. In the case of golden snub-nosed monkeys (*Rhinopithecus roxellana*), resident males are reported to employ a counter strategy of collective action to expel challenging males from entering their OMUs [Xiang et al., 2014].

Less is known, however, regarding the set of social, reproductive, and demographic factors that influence the timing and success of male takeovers in snub-nosed monkeys including why a given challenging male targets a particular OMU, and what conditions correlate with takeover success [Ren et al., 2007]. Two key factors that a challenging male might consider in deciding which OMU to target are (i) the number of adult females in a particular OMU, and (ii) the competitive ability of a resident male. For example, an increase in the number of reproductively active females present in an OMU may offer a challenging male the greatest opportunity to increase his reproductive success [Van Hooff, 2000]. It may also be more difficult for a resident male to guard or control the movements of a larger harem, and therefore to defend it from rivals [Muller and Emery Thompson, 2012]. In this regard, female reproductive condition, especially in seasonally breeding species, or the presence of several adult females without dependent offspring (who are therefore likely to return to reproductive condition sooner) might serve as important cues for challenging males to determine which OMU is most attractive or suitable for takeover [Dunbar, 1984]. In addition, the competitive ability of a resident male, as indicated by physical condition, age, and fighting ability, may also have a direct effect on the vulnerability of his OMU to a takeover [Pines et al., 2011; Swedell, 2006]. Specifically, a challenging male might target OMUs that contain older resident males who are past their prime or show signs of deteriorating physical condition resulting from injury or disease.

Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) are an endangered species of Asian colobine endemic to China. The remaining population, estimated to total approximately 2,000 individuals, is confined to high altitude mountain forests on the Tibetan Plateau, within a narrow area between the Yangtze and Mekong Rivers [Liu et al., 2015]. As is the case for other *Rhinopithecus* species, the Yunnan snub-nosed monkey lives in a MLS [Kirkpatrick et al., 1998; Kirkpatrick and Grueter, 2010; Ren et al., 2012] that includes from 5–41 reproductive units (OMUs) and one or more AMUs organized into a band that can contain up to 450 individuals [Grueter and Zinner, 2004; Grueter, 2013; Ren et al., 2012]. OMUs range in size of from 3 to 17, including one adult male, 2–8 adult females, and their offspring. AMUs comprising 5–36 juvenile, subadult, and adult males loosely follow the band [Cui et al., 2008; Grueter and Zinner, 2004; Grueter, 2013].

Given limited information on male takeover events in Yunnan snub-nosed monkeys, we examined social and demographic factors that affect reproductive strategies used by challenging males in targeting and taking over an OMU. Based on data collected during 48 takeover attempts (eight successful male takeovers and 40 failed takeovers), we examined how a rival male's choice of OMUs to target, as well as his success in taking over a targeted OMU, reflected the (i) the total number of adult and subadult females present in an OMU, (ii) the number of non-pregnant and non-lactating adult females present in an OMU, and (iii) a resident male's social rank relative to other resident males in the band.

METHODS

Study Site and Subjects

We conducted this study at Xiangguqing (99°20′ E, 27°30′ N) in the Baimaxueshan National Nature Reserve, Yunnan Province, China. The vegetation in this area is described as mixed conifer and deciduous broadleaf forest (2,500–3,600 m) and subalpine fir forest (3,500–4,000 m). The annual mean daily temperature is 9.8°C with a maximum of 27.7°C in July and a minimum of −9.3°C in January. Annual rainfall is 1,371 mm [Li et al., 2010].

The original Xiangguqing Yunnan snub-nosed monkey MLS studied by Ding and Zhao [2004] included >450 individuals [Ren et al., 2012]. Based on the group's pattern of fission-fusion behavior, the Nature Reserve management decided to split this band [Ren et al., 2012] into a smaller band (provisioned band at Xiangguqing, PX) of ca. ninety-five individuals, including one AMU with approximately

30 males and eight OMUs [Li et al., 2013], and a larger unprovisioned band of more than 360 individuals. Two permanently employed rangers from the Nature Reserve have provisioned the smaller band since May 2008 to enhance monitoring and data collection at close distances. In December 2011, the Nature Reserve management separated approximately 20 subadult and adult males from the PX AMU and returned them to their original unprovisioned band. This management decision aimed to establish a ratio of adult females to adult males (1.5:1) in the PX band was not lower than those reported in other Yunnan snub-nosed monkey populations [adult sex ratio ranging from 2.2:1 to 3.8:1; Grueter, 2009]. At the time of our study the adult female to adult male sex ratio in the PX band was 2.6:1.

Rangers provisioned the PX study band twice daily (around 9:00 and 17:00 hr) in one of several 30 m × 30 m areas, which are located in nearby forest patches in the valley where the band naturally ranges and feeds. The selection of a provisioning site on a given day depended on the location of the study band. In general the band used the same provisioning site for 2–3 consecutive days and then moved to another part of their range. Rangers scattered approximately 10 kg of lichen (which was changed to bamboo shoots between mid-June and mid-July) and 4 kg of other foods (carrots, apples, or pumpkin seeds) at the provisioning site each day. The quantity of provisioned food was approximately 250 g/individual/day, which represents ca. 18.5% of the amount of food provided daily to captive Yunnan snub-nosed monkeys [1,350 g/individual/day; Zou et al., 1994]. Given that forests surround the provisioned areas, the monkeys consumed both provisioned food and natural food (leaves, buds, lichen, and fruits) every day. After provisioning, band members commonly remained at the provisioning site for an additional 2–3 hr and rested or travelled to other parts of the Xiangguqing Mountains to feed. Additional details of the study band and provisioning process have been published elsewhere [Li et al., 2012, 2013].

Data Collection

PFZ and FX observed the monkeys from September 2012 to October 2013. Observations began at 9:00–9:30 hr and ended at 17:00–19:00 hr on each observation day. Quantitative behavioral data were collected on at least one OMU or AMU on 292 days. Given difficulties in following our study band continuously across rugged mountainous terrain, on average we collected 2.94 ± SD 1.66 hr of quantitative data per day (total 857 hr), with observation periods lasting from 3 min to 5.63 hr (mean ± SD: 1.08 ± 1.03 hr/period). During each observation period, we attempted to collect behavioral information on individuals in all visible OMUs or AMU (range 1–6) that were present. In more accessible parts of the range, we observed the monkeys from a distance of 5–30 m, and we could unambiguously identify all individuals based on body size, hair patterns, scars, facial features, pelage color, and other distinctive physical features [Ren et al., 2011]. In addition, Yunnan snub-nosed monkeys are characterized by extreme sexual dimorphism in body mass and canine size [Grueter and Van Schaik, 2009; Jablonski and Ruliang, 1995]. Therefore, we were able to classify individuals into six sex-age classes: adult males, adult females, subadult males, subadult females, juveniles, and infants [Li et al., 2010, 2012].

Given our focus on male takeovers, we employed an *ad libitum* sampling method to record the start time of a takeover attempt and an all-occurrence sampling method [Altmann, 1974] to record adult male–male social interactions during the entire takeover period. We tracked and recorded the details of the takeover process by scoring the following information on the resident male and the challenging male: time, place, initiator of social interactions, recipient of social interactions, participants, affiliative behaviors, agonistic behaviors, the outcome of each interaction (win, lose, or draw), females' behaviors (stayed or left their original OMU), and demographic changes in each OMU.

In our wild Yunnan snub-nosed monkey band, it was difficult to quantify a males' physical condition accurately based solely on behavioral observations. Therefore, we used a male's social rank as an indirect measure of physical condition and fighting ability [Clutton-Brock et al., 1979], assuming that resident adult males of higher social rank have greater fighting ability. To determine a resident male's social rank, we employed an all-occurrence sampling method [Altmann, 1974] and recorded dyadic agonistic interactions between resident males. We scored aggressive behaviors as staring, threatening, chasing, scratching, fighting and biting. We scored submissive behaviors as crouching, leaving and fleeing. We also scored displacement if, within a maximum period of 1 min (often occurred within a few seconds), an individual left its position in response to the approach (within two meters) of another individual [Zhang et al., 2008a]. The winner of an agonistic interaction was the individual who received submissive behaviors from another individual. The loser of an agonistic interaction displayed submissive behaviors. We scored a draw when neither participant in a dyadic agonistic encounter exhibited submissive behaviors.

Defining Adult Reproductive Status

Yunnan snub-nosed monkeys are strictly seasonal breeders, with a birth peak from March to May. September to November represents the primary mating period [Cui et al., 2006]. Gestation is

approximately 6 months [Huang et al., 2012], and the inter-birth interval is approximately 2 years [Cui et al., 2006] for females whose offspring survive their first year of life. We scored each female as pregnant for the 6 months period prior to her infant's birth date. We scored adult females as non-pregnant if they did not give birth during the birth season of 2013. Our total sample of adult females was 18, seven of which had produced infants in the previous year. For three additional females, we were not able to assess whether they did not conceive or lost their infant prior to birth. During the study period, we observed one stillborn infant on January 3. Two infants were born into the band (one on March 20 and the second on April 8, 2013).

We scored the only adult male in an OMU as the resident male. We referred to a deposed male as a former resident male who had been ousted from his OMU. A challenging male was defined as a male who did not control access to females and engaged in aggressive interactions with resident males. During the course of our observations all challenging males were adults. If a deposed male challenged a resident or if a resident attempted to expand his OMU by acquiring females from other OMUs, we redefined his social status as a challenging resident male.

We often observed challenging males to travel at the periphery of their targeted OMU and continue to shadow the OMU despite being attacked or threatened by its resident male. We defined such challenging behavior as a presumed takeover attempt. We defined a takeover attempt as starting when we first observed an agonistic interaction between a resident male and a challenging male, and ending when the challenging and resident males ceased (for at least 1 week) engaging in agonistic interactions. We scored a successful takeover if the challenging male ousted the resident male and all adult, subadult and juvenile females remained in the OMU or when a challenging male acquired some of the OMUs adult or subadult females for his new harem [Ren et al., 2011; Saj and Sicotte, 2005; Zhao et al., 2011]. We scored a failed takeover if a challenging male was unsuccessful in obtaining at least one adult female via ousting the resident male and occupying his breeding positing in the OMU or by attracting adult resident females to leave their harem. We do not have genetic evidence of paternity, and therefore we were unable to measure the reproductive success of resident and challenging males.

Male Dominance Rank

To investigate a resident male's dominance rank prior to a takeover attempt, we calculated Elo-ratings from the outcomes of a sequence of dyadic aggressive interactions among resident males, with 1000 as the initial value and k set to 100 [Albers and De Vries, 2001; Neumann et al., 2011]. We chose an Elo-rating method because in five takeover attempts the number of resident males and OMUs in the study band was five, which was smaller than the number required in matrix-based methods (at least six individuals are required) to yield significant results [Appleby, 1983]. Elo-ratings are sensitive to sample sizes of as few as two individuals [Neumann et al., 2011]. Also, composition of our study band changed frequently, as new males joined the band and resident males were deposed. The matrix-method requires sufficient interactions to build new matrices after each demographic change, but the Elo-rating method, which is based on an interaction sequence, does not interrupt the rating process. Using this method we could monitor rank changes among resident males at any point in time. For example, we could assess a new resident's rank using Elo-rating based on only two interactions, one interaction with a higher-ranked individual and one interaction with a lower-rank individual, although more interactions increase reliability [Albers and De Vries, 2001]. We assessed males' Elo-rating for our data analyses after they interacted for 1 month. We included ten resident males and 132 interactions in the rating process, with an average of 26.4 interactions for each male. The proportion of draws in the dataset was 4% (Fig. 1). To compare the takeover events during different periods, we followed the methods provided by Neumann and Kulik [2014] to standardize Elo-ratings between the lowest rating 0 and the highest rating 1, and all others being proportionally scaled in between. We used package "EloRating" in the R 3.1.2 to calculate and standardize a resident male's dominance rank [Neumann and Kulik, 2014].

Statistical Analysis

To explore the set of factors that correlated with the likelihood that an OMU was targeted for takeover and the set of factors that correlated with a successful

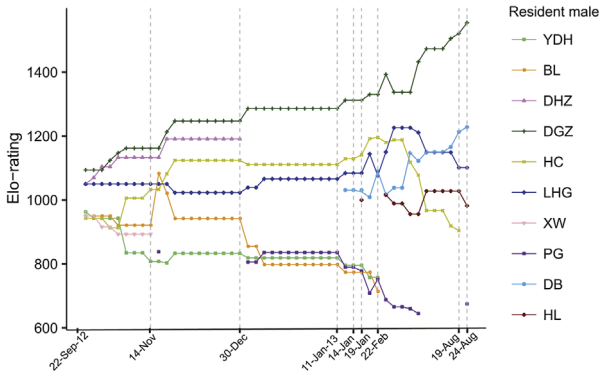

Fig. 1. The rank of resident male relative to other resident male by Elo-rating scores without standardization across 48 male takeover attempts. Vertical lines mark the successful takeovers.

takeover, we analyzed three OMU characteristics: (i) the total number of adult and subadult females in an OMU (i.e., ASF); (ii) the number of non-pregnant, non-lactating adult females in an OMU (i.e., NPLAF), which represents the number of potentially fertile females in the next reproductive period; and (iii) a resident male's rank relative to other resident males in the band (i.e., RMR).

For each takeover attempt, there was one targeted OMU and a median of five OMUs that were not targeted (range = 4–7). Therefore, each takeover attempt included a dataset composed of one targeted OMU (case) and approximately 5 non-targeted OMUs (control; total of 297 lines of data across 48 takeover attempts). To compare the characteristics of the challenged OMU versus those that were not challenged during each takeover attempt (e.g., case:control = 1:5), we utilized conditional logistic regression to identify associated variables [Sun et al., 2011]. We used takeover attempts as strata (e.g., there were 48 strata and approximate six rows of data for each stratum) which allowed us to analyze within-event comparisons between OMUs that were targeted (response: $y = 1$) compared to those that were not targeted ($y = 0$). The number of females (ASF and NPLAF) and RMR were predictors in the model. We conducted this analysis in R 3.1.2, using the *clogit* function in the survival package [Ripley et al., 2015; Therneau, 2015].

To explore factors that correlated with successful takeovers, we used the generalized linear mixed-effects models (GLMMs) with binomial-error distribution and logit link function where the dependent variable was 'successful takeover or not' [1 = success, $N = 8$ takeovers, 0 = failed, $N = 40$; Bolker et al., 2009]. Given that the same OMU and the same challenging male might be included repeatedly within the data set, we included OMU ID and challenging male ID as random effects in the model, whereas we treated OMU characteristics (ASF, NPLAF and RMR) as fixed effects. We used the *glmer* function in the *lme4* package [Bates et al., 2015]. We set significance at 0.05. For parametric data, we reported means and standard deviation (mean ± SD). Otherwise, we used medians and quartiles.

Ethical Standards

All research methods adhered to Chinese legal requirements and complied with protocols approved by the State Forestry Administration of China and the American Society of Primatologists principles for the ethical treatment of primates.

RESULTS

During our observations, the study band contained 42–60 individuals belonging to 5–8 OMUs (3–10 individuals per OMU, with a median of two adult and one subadult female per OMU) and one AMU (6–13 individuals). The AMU contained 2–4 adult, two subadult, and 2–5 juvenile males. Changes in the number of OMUs were the result of the migration of two OMUs from the band and one case in which a resident male successfully usurped the harem of another resident male.

Male Takeovers

We observed 48 takeover attempts involving seven challenging males and ten resident males. The median duration of a takeover attempt was 1 day (IQR: 1–2), and ranged from 1 to 10 days ($N = 48$). Eight of these were successful, resulting in a change in the resident male. Successful takeovers occurred in January ($N = 3$), February ($N = 1$), August ($N = 2$), November ($N = 1$), and December ($N = 1$). No successful takeovers occurred during the birth peak (March–May) and only one case occurred during the mating peak (from September to November).

In six of eight successful takeovers, all females of the targeted OMU abandoned the original resident male and followed the new one. In the remaining two cases only a portion (4/7 and 1/3) of the resident adult, subadult and juvenile females in the OMU followed the new resident male. We did not observe any aggressive or herding behavior by the resident male or by challenging males toward females during takeover attempts. There were no infant losses associated with any of these successful takeovers.

Male–Male Interactions During Takeovers

During the 40 failed takeovers, we observed 76 agonistic interactions between resident and challenging males (median = 1, IQR = 1–2 agonistic interactions for each failed takeover). These almost exclusively involved mild forms of aggression (99%; approaching, staring, teeth-baring, and limited chasing). In only one instance did a challenging male attack and bite a resident male during a failed takeover.

During a successful takeover, we observed a median of 3 (IQR = 2–5) agonistic interactions between the resident and challenging males. Of the 25 agonistic interactions observed, 15 involved mild forms of aggression and the remaining 10 cases resulted in direct physical encounters (e.g., fights). We observed severe aggression between resident males and challenging males in four cases and inferred severe aggression based on injuries in two other successful takeovers. Thus, in contrast to male–male interactions during failed takeovers, successful takeovers more commonly involved highly aggressive encounters.

We did not observe resident males acting collectively to defend their OMUs against challengers. In addition, adult females did not participate in takeover

attempts in support of either their resident or the challenging male. Rather, during attempted takeovers, females stayed at their feeding or resting sites and watched. Resident males returned to their females after chasing the challenging male away.

Factors Predicting a Takeover Attempt

A conditional logistic regression model including ASF, NPLAF, and RMR as predictors of the identity of the OMU targeted by challenging males did not differ significantly from a null model (predictors absent; likelihood ratio test: $\chi^2 = 0.55$, $P = 0.91$). All predictors had no significant effects: (i) ASF: OMUs that were targeted for takeovers (median = 3, IQR = 3–4) versus those were not (median = 3, IQR = 3–5; Wald tests: odds ratio = 0.94, $Z = -0.44$, $P = 0.66$); (ii) NPLAF: targeted OMUs (median = 1, IQR = 1–2) versus non-targeted OMUs (median = 1, IQR = 1–2; Wald tests: odds ratio = 0.94, $Z = -0.31$, $P = 0.76$); (iii) RMR: targeted OMUs (median = 0.54, IQR = 0.10–0.79) versus non-targeted OMUs (median = 0.55, IQR = 0.11–0.75; Wald tests: odds ratio = 0.81, $Z = -0.41$, $P = 0.68$).

Factors Predicting a Successful Takeover

A GLMM including ASF, NPLAF, and RMR as predictors differed significantly from a null model (likelihood ratio test: $\chi^2 = 8.33$, $P < 0.05$). Neither ASF (GLMM: $\beta \pm SE = 0.04 \pm 0.31$, $Z = 0.13$, $P = 0.90$) or NPLAF ($\beta \pm SE = -1.39 \pm 0.75$, $Z = -1.85$, $P = 0.06$) predicted takeover success (Fig. 2). However, a resident male's rank relative to other resident males in the band (RMR: $\beta \pm SE = -2.96 \pm 1.46$, $Z = -2.03$, $P < 0.05$) was a significant factor. A challenging male decreased his odds of takeover success by 5.20% with a one-step increase in RMR (Fig. 2). These results indicate that challenging males were most successful in taking over the OMU of a lower-ranking resident male and least successful in taking over an OMU of a higher-ranking resident male.

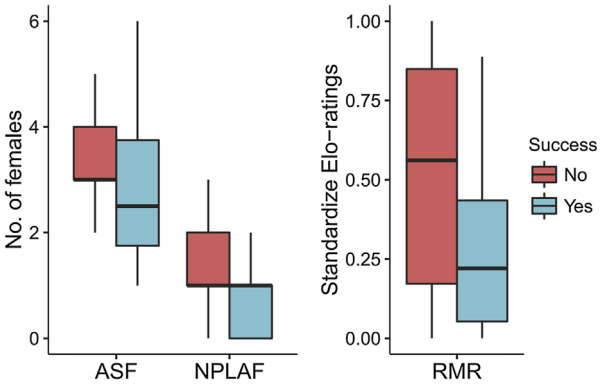

Fig. 2. The number of females and resident male rank in OMUs that were successfully taken over versus those that were not successfully taken over. NPLAF refers to the number of non-pregnant, non-lactating adult females in an OMU. ASF refers to the number of adult and subadult females. RMR refers to a resident males' social rank relative to other resident males in the band.

DISCUSSION

Our results showed that rival males interact with OMU males in two main ways. Challenging males engaged in low risk, mildly aggressive encounters with resident males during failed takeovers that may allow them to assess the resident male competitive ability. In addition, challenging males engage in highly aggressive encounters with resident males that often result in a successful takeover of the harem. We found that the relative rank of a resident male was the strongest predictor of whether challenging males could successfully displace him and become the OMU breeding male. Our results also indicated that the size, composition, or breeding status of females predicted neither the choice of which resident to challenge nor the likelihood of a successful takeover. In this regard, our results support the findings of Yao et al. [2011] who reported no differences in the number of adult and subadult females within OMUs that were taken over and OMUs that were not taken over in golden snub-nosed monkeys.

Assuming that relative rank is an index of male condition or competitive ability, challenging males may incur a lower risk of injury when taking over the OMU of a relatively low-ranking resident male. Moreover, the females of a lower-ranking resident male may be more likely to join the challenging male, especially if this increases priority access to resources at contested feeding sites. In line with observations on golden snub-nosed monkeys [Zhang et al., 2008a], female Yunnan snub-nosed monkeys who reside in OMUs of low ranking resident males leave a feeding or resting site if their resident male loses an agonistic interaction against another resident male [unpublished data].

In 6 of 8 successful takeovers in our study, all females followed the new resident male, whereas in two instances 43–67% of females remained with their original resident male. In keeping with observations on golden snub-nosed monkeys, we did not observe any coercive behavior such as aggressive herding by resident or challenging males towards females [Qi et al., 2009]. Therefore females appear to engage in mate choice, and decide either to leave or stay. This behavior could influence the outcome of male takeovers. In golden snub-nosed monkeys, females voluntarily transfer to other OMUs [Qi et al., 2009], sometimes following the replacement of a resident male [Guo et al., 2015]. For adult females with dependent offspring, changing allegiance to a new resident male might increase the risk of

infanticide [Palombit, 2012] whereas remaining with her resident male may result in enhanced protection for her infant.

There was one case in our study in which an OMU resident male successfully took over another harem in the band. Generally, in snub-nosed monkeys, resident males are overthrown either by an adult AMU male [Yao et al., 2011] or an adult solitary male [Qi et al., 2009]. Although some adult males with harems are deposed males [e.g., lone males whose harems were previously taken over; Zhao and Li, 2009], it is rare for a resident male to oust another resident male to expand his harem. One such case was documented in hamadryas baboons [*Papio hamadryas*; Swedell, 2000], and two suspected cases have been observed in golden snub-nosed monkeys [Zhang et al., 2008b]. In these suspected cases, two OMUs appeared to have merged to form a single OMU with one of the resident males disappearing [Zhang et al., 2008b]. Although taking over an OMU is one strategy used by bachelor and resident adult male snub-nosed monkeys to increase their reproductive success, an alternative strategy may be to sneak copulations with females from several OMUs in the band [Guo et al., 2010; Zhao et al., 2005].

Successful takeovers were characterized by higher levels of aggression between residents and challengers than failed takeovers, resulting in severe injuries to participants. Life-threatening injuries associated with male intrasexual reproductive competition have also been reported in other primates including golden snub-nosed monkeys [Ren et al., 2007; Yao et al., 2011], geladas [*Theropithecus gelada*; Dunbar, 1984], white-headed leaf monkeys [*Trachypithecus leucocephalus*; Zhao et al., 2011] and hanuman langurs [*Semnopihtecus entellus*; Sugiyama, 1964]. In contrast, during failed takeovers, challenging males engaged in mildly aggressive low-risk encounters with resident males. These interactions may best be interpreted as a form of direct rival assessment whereby challengers identify males whose competitive ability is lower than theirs and gauge the likelihood of being successful in acquiring a harem.

Challengers may also rely on morphological indicators of male competitive ability and status to directly assess the odds of winning an encounter with a resident male. Such proxies for a contestant's fighting ability and quality include body size/mass [reviewed by Arnott and Elwood, 2009] and coloration, respectively [Bergman et al., 2009]. For example, facial red coloration in male mandrills (*Mandrillus sphinx*) is positively correlated with rank and males appear to use coloration as a cue to assess individual differences in competitive ability [Setchell and Wickings, 2005; Setchell et al., 2008]. Similarly, chest redness of male geladas [Bergman et al., 2009] and lip redness, a conspicuous feature of male Yunnan snub-nosed monkeys [Grueter et al., 2015], seem to be indicators of male social status as resident males scored higher on redness than AMU males. In the case of Yunnan snub-nosed monkeys, however, it is unknown if male dominance among different OMUs influences skin coloration.

Challenger males may also make use of *indirect* methods to assess rivals prior to a takeover. le Roux and Bergman [2012] examined there possible ways of indirect rival assessment by bachelors in gelada multilevel societies; these are (in order of increasing cognitive complexity) monitoring the frequency of fights between OMU males to identify unstable OMUs [le Roux and Bergman, 2012], attending to competitive signaling bouts between unit leaders to gain information on their quality, and eavesdropping on relationships between leader males and their females to identify weak bonds. We did not collect the requisite data to determine the assessment strategies used by snub-nosed monkey males to gauge the likelihood of success in advance of challenging a resident male. Additional contextual data on whether bachelors observe inter-OMU agonistic interactions and remember previous interactions with particular resident males during takeover attempts are needed.

In MLS in which several OMUs and AMUs travel, feed, and rest together to form a cohesive band, the close proximity among units facilitates the acquisition of information about resident males. By contrast, in one-male, multi-female species [e.g., blue monkeys, *Cercopithecus mitis*; Roberts and Cords, 2015] in which different one-male groups have separate home ranges it might be more difficult or energetically costly for bachelors to track more than a single group [Jones and Bush, 1988]. Therefore, complex ways of indirect rival assessment can be envisaged for primates living in a MLS. However, MLS are typically very large (one Yunnan snub-nosed monkey band contained more than 450 individuals [Ren et al., 2012]) which may present a cognitive challenge for males to individually recognize, evaluate, and score interactions among coresiding contemporaries [Bergman, 2010]. Thus some indirect rival assessment strategies such as observing OMU holder-female interactions are probably beyond the cognitive scope of these primates. They may, therefore, rely on simpler (cognitively less taxing) ways of rival assessment (see also le Roux and Bergman [2012]).

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