

Relationships between food provisioning patterns, stress and reproductive parameters of *Rhinopithecus roxellana* (Milne-Edwards, 1870)

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Received: 26. January 2015 / Accepted: 14. July 2015 / Available online: 29. May 2016 / Printed: June 2016

Abstract. Inadequate body condition in wild animals (especially lactating and gestating females) may be caused by intense physiological stress, which compromises reproductive success, thereby reducing population growth rates. Our study troop of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) at the Shennongjia Nature Reserve were subjected to two different food provisioning patterns: (i) an interactive pattern (all family units fed together; 2006–2008) and (ii) an individualistic pattern (family units fed separately; 2009–2012). We postulated that fecal glucocorticoid metabolites (FGM) and birth rates would differ significantly between monkeys subjected to these two feeding patterns. Behavioral ranks were assigned by Dominance Index (DI) values. A Machine Learning (ML) approach was used to assess correlations between behavioral ranks and infant mortality. We collected 841 fecal samples from 12 adults (7♂, 5♀) and monitored survival of infants borne by 16 females in the period 2006–2012. Infant survival rates were 78.26% and 93.10% when the troop was fed interactively and individualistically, respectively. FGM values obtained when provisioning was interactive were significantly higher than when provisioning was individualistic. In cold seasons, FGM values obtained when provisioning was individualistic were much reduced in comparison with interactive provisioning. Low rank among females greatly increased the risk of infant death. Thus, nutritional stress caused by provisioning pattern is a major contributory factor to overall physiological stress in *Rhinopithecus roxellana* females in the Shennongjia Nature Reserve.

Key words: *Rhinopithecus roxellana*, Fecal glucocorticoid metabolites (FGM), Birth rate, Provisioning pattern, Shennongjia

Introduction

Wild animal populations face a variety of stresses generated by their physical environments and the biotic interactions within the communities of which they are members. Although the mechanisms generating stress responses are diverse, the physiological responses are very similar (Sands & Creel 2004). In wild populations of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) seasonal variation in food resources may shift foraging strategies and food preferences (Tie et al. 2010). In well-provisioned groups, variation in provisioning pattern may cause similar shifts (Zhang et al. 2006, Yu et al. 2009a). Furthermore, provisioning patterns shape competition and the imbalance in food distribution among the social units, thereby generating chronic physiological stress. Inevitably, food competition and imbalance lead to dietary deficiencies, and even nutritional stress, at the individual organism level (Pedro & Rutledge 2001, Alejandro et al. 2014). The nutritional stress resulting from long-term food deficiency is the result of

a concatenation of negative influences on the body condition of individual animals, such as retarded physical development, slow recovery from illnesses, and digestive dysfunction (Sapolsky 2005).

Individuals and groups of non-human primates commonly compete for resources (Wrangham & Waterman 1981, Van Schaik 1983, Robinson 1988, Van Schaik & Van Noordwijk 1989, Radespiel et al. 1998, Digby 1999, Koenig 2002). Ranks in hierarchically organized non-human primate societies play an important role in resource distribution (Zhang et al. 2006, Yu et al. 2009a), particularly food resources. The availability of food resources has a great influence on the size and nutritional status of animal populations; these effects have been well studied (Munck et al. 1984, Van Schaik & Van Noordwijk 1989, Piatt & Anderson 1996, Radespiel et al. 1998, Digby 1999, Koenig 2002, Chapman et al. 2006, Li 2005, Piatt & Harding 2007, Kitaysky et al. 2010). High-ranking individuals drive away those of lower rank when the two are feeding together (Scott & Lockard 2006). Because lower-ranking individuals are out-

competed (Thierry et al. 2004) their fecal glucocorticoid metabolites (FGM) levels can be relatively elevated (in comparison with higher-ranking individuals) (Davis & Christian 1957, Manogue 1975, Sapolsky 1985, 1990, 2005, Bercovitch & Clarke 1995, Sands & Creel 2004). Higher-ranking females may dominate those of lower rank (Ren et al. 2000); during the breeding season, low-ranking females have elevated FGM levels resulting from the aggression of dominant females (Cavigelli et al. 2003).

The two genders of mammals have different responsibilities in reproduction and infant care (Trivers 1972). Females are more likely to be affected by food competition than males (Koenig 2002), especially during parturition and lactation. Adult females are likely to lose infants due to nutritional stress caused by food deficiencies (Trites 1991, Calkins et al. 1998). The effects of nutritional deficiency stress on animal reproductive success and infant survival have been well studied (Cairns 1987, Robbins 1993, Sapolsky 1992b, Liptrap 1993, Dobson & Smith 1994, Murray et al. 1998, Sapolsky et al. 2000, Kitaysky et al. 2007, Oro & Furness 2002, Grosbois & Thompson 2005, Sandvik et al. 2005, Kitaysky et al. 2010). Physiological and nutritional stressors may have many harmful effects on females during breeding and lactation periods (Kennedy & Visness 1992, Wade & Schneider 1992, McNeilly et al. 1994). Physiological stress can impair the reproductive system (Liptrap 1993, Dobson & Smith 1994, Kitaysky et al. 2010) and reduce the survival rate of infants (Oro & Furness 2002, Grosbois & Thompson 2005, Sandvik et al. 2005) of wild animals, thereby impacting population growth rate (Colin et al. 2006). Other factors that influence female primate body condition, such as social bonds (Silk et al. 2003), social ranks and food availability (Van Noordwijk & Van Schaik 1999) may also affect infant survival. Reproductive success rates of individual females are parameters of population dynamic modeling (Robinson 1988, Romero & Wikelski 2000, Colin et al. 2006, Kitaysky et al. 2007, 2010).

Here we report on a study of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) living in a provisioned troop with a territory of 300 km², including a 300 m² feeding area and a 220 km² active area (Yu et al. 2009b). These monkeys have two types of social units: “one male units” (OMUs) and “all male units” (AMUs) (Chen 1989, Kirkpatrick 1995, Ren et al. 2000). Both OMUs and AMUs were provisioned by rangers at the reserve.

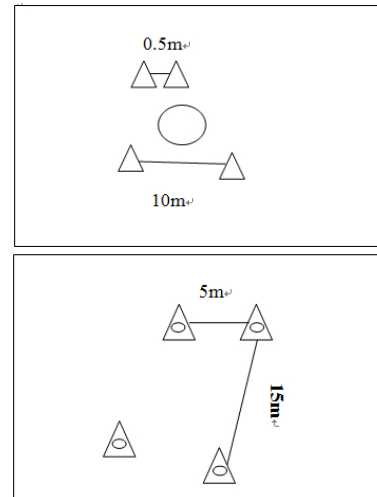


Figure 1. Separation distances between family units fed by interactive and individualistic provisioning (Interactions provisioning pattern. Individualistic provisioning pattern, Note: \blacktriangle - units; \bullet - food piles).

Food was supplied in two provisioning patterns (Fig. 1): when food was supplied in a concentric pattern at a single site prior to 2008, we identified the pattern of provisioning as “interactive” (Yu et al. 2009b); when food was provided separately to each social unit after 2008, we identified the pattern as “individualistic” (Yu 2012). The amount of food supplied to each individual animal was similar between the two provisioning patterns. The provisioning pattern affected dominance behavior during feeding (Yuan et al. 2009); thus, the interactive pattern reduced the distances among units to 0.5–10 m (Zhang et al. 2003). Elevated psychological suppression through eye and body contact frequently escalated to aggressive warning signaling and fierce fighting among units (Zhang et al. 2003, Yu et al. 2009b), which increased physiological suppression among troop individuals. High levels of stress caused by nutritional deficiency and aggressive behaviors can reduce infant survival rates (Trites 1991).

In this study, we used an open-access data approach for transparency and repeatability to assess factors likely to be associated with physiological stress (i.e., FGM) in *R. roxellana* living in the Shennongjia Nature Reserve. We used powerful data searching and Machine Learning techniques (Jochum & Huettmann 2010) to test whether: 1) provisioning patterns affect physiological stress, 2)

nutritional stress caused by provisioning pattern critically affects female physiological stress levels, 3) provision patterns affect the survival rate of infants, and 4) ranks influence the survival rates of infants.

Materials and methods

Our research was performed at the Dalongtan observation site in Shennongjia National Nature Reserve, Hubei province (31°22'–31°37'N, 110°03'–110°34'E). The site encompasses an area of 800 m² (2160 m above sea level) where the vegetation comprises dense mixed stands of deciduous and evergreen broadleaf and coniferous trees (Zhu & Shu 1999). Canopy density was high. Water was supplied abundantly by 2 rivers and 12 streams (Yuan et al. 2009). The feeding ground (300 m²) of *R. roxellana* was located on the banks of a river flowing through the study area. The mean annual temperature was 11.0–12.2 °C; highest temperatures of ca. 21.2–26.5 °C occurred in July, and lowest temperatures of ca. –5.8 to –3.6 °C in January. The period May–October had moderate temperatures; the period January–December was cold. The annual mean frost-free period was 173 d. For our study, we divided the year into a warm season (May through October), with a mean daily temperature ≥0 °C, and a cold season (November through April) with temperatures <0 °C.

Sample collection

The study extended from 2006 to 2012. We collected 841 fecal samples from 12 Sichuan snub-nosed monkeys at the study site and used infrared distance sensors to measure the distances among the social units. Fecal samples were collected at Dalongtan during two different time periods; i.e., in the warm (July–August) and cold (November–December) months of 2008. During 2008, we collected 620 fecal samples from 10 adults at intervals of 5 days (5♂, 5♀). In the second time period, we again made collections in the warm (June–August, 2011) and cold months (November, 2011–February, 2012). In the period 2011–2012, we collected 207 fecal samples from 11 adult animals (2♂, 9♀) in two social units.

We also recorded the births and deaths of infants borne by 16 females at the Dalongtan observation site in the period 2006–2012, when 52 infants were born. According to the records of the reserve, 23 were born in the interactive provisioning period (2006–2008); five deaths were attributed to stillbirth and disease over 3 yr. Dates of death were as follows: December 26, 2006 (infectious disease; poor health condition), March 11, 2008 (sick, lived for 2 days), March 31, 2008 (stillbirth), April 5, 2008 (stillbirth), April 20, 2008 (sick, lived for 1 day).

Twenty-nine infants were born to the same troop during individualistic pattern provisioning period (2009–2012), and four of these died. Replacement of the alpha male resulted in the killing of two infants in the social unit during April 2012. One infant died during stillbirth (January 19, 2012) and another from disease (April 5, 2012).

Differences in provisioning patterns:

We adopted the interactive pattern for provisioning the *R. roxellana* individuals in Dalongtan prior to 2009. All family units gathered within the feeding area for forage; the units were 0.5–10 m apart. After 2009, the units were fed individually, and were spaced at distances of 5–15 m.

The extraction and determination of cortisol:

Extraction proceeded with the addition of 5 ml of 90 % ethanol to ca. 0.5 g of fresh fecal sample. Samples were vortexed for 30 s, and then centrifuged at 4000 rpm/min for 25 min. The supernatant was recovered, and the pellet was re-suspended in an additional 5 ml of 90 % ethanol in the original tube, vibrated for 30 s, and then centrifuged for 20 min at 4000 rpm/min. Ethanol supernatants were combined, taken to dryness in a water bath at 70 °C, and then re-suspended in 1 ml of methanol. We added 1 ml of diluent (NaH₂PO₄; Na₂HPO₄; NaCl in Milli-Q H₂O; pH = 7.0) and sonicated the mixture for 15 min using an ultrasonic wave device. Samples were stored at –20 °C until analysis.

FGM testing method:

We used an enzyme-linked immunoabsorbent assay (EIA) to determine the concentration of FGM. The procedure was initiated by coating plates with cortisol-3 antibody (M344, CalBioReagent) at a working concentration of 1:500 (vol/vol). The plates were kept at 4 °C for 24 h. A standard solution was diluted 1 to 1024-fold in a step-by-step procedure. High- and low-quality controls (binding at 30% and 70%) were prepared from a cortisol-3 HRP solution (C133, CalBioReagent) at a working concentration of 1:10,000 (vol/vol). Extractions were diluted to a concentration of 1:4 (vol/vol). Two wells in each multi-well plate were left as blanks to remove zero disturbances. To the other cells, we added (i) 50 µl of the standard dilution, (ii) controls and (iii) HRP solution. After 1 hour combining at 35 °C, washed plates 3 times with wash solution (NaCl: 43.83 g (Sigma, S9625), Tween 20:2.5 ml (Sigma, P1379), and H₂O: 500 ml). Added 100 µl TMB solution for 15 minutes, then added 50 µl stop solution to each well. Read the plates at 450 nm.

Cortisol-3 antibody (M344, CalBioReagent), standard sample and cortisol-3 HRP (C133, CalBioReagent) are all purchased from CalBioReagents Company; ELISA Plate is NUNC C445101 Bottom Well. Working concentrations are respectively as follows: Cortisol-3 antibody is diluted at 1:500 and cortisol-3 HRP at 1:15,000. The sensitiveness of ELISA Plate is 0.5 ng/ml with 8–15% inter plates and 4–6% inter plate.

Parallelism and recovery rate determination

We tested the validity of the assay by testing serial dilutions of fecal extract against a FGM standard curve ($y = 3.638 - 1.789(X)$; $R^2 = 0.988$, $r = 0.984$; $P < 0.01$). For concentrations in the range 10–500 ng/ml, sensitivity was 50 pg/tube. The buffer blanks were below the limit of sensitivity. The coefficients of variation (CV) within batches were <5%; CV values among batches were <10%. The average recovery rate was 85.19%.

Determination of distance and behavioral monitoring

Infrared sensors were used to measure the intra-unit distances. Data prior to 2009 were obtained from Zhang et al. (2003) and Yu et al. (2009b). Our behavioral sampling procedure followed the methods of Li et al. (2006); we recorded the durations of aggressive (AT) and submissive behaviors (ST) for each individual studied. Animals were observed and the data were compiled for 3 h on every third day through the years 2008, 2011 and 2012. We defined the following as AT: driving away, lunging, chasing, grasping and hitting, wrestling and biting. We defined the following as ST: avoidance, crouching, retreating and fleeing (Yan et al., 2006). The Dominance Index (DI) was calculated as $DI = (\%AT) / (\%ST) \times 100$ for each individual (as a reflection of social rank).

Data processing

For our multivariate Machine Learning analysis, we used the robust TreeNet algorithm (a boosting tree analysis procedure), which described patterns and details of the signals (Cushman & Huettmann 2010, Drew et al. 2011). Unlike other statistical approaches and software, TreeNet allows assessments of statistical interactions (Friedman 1999, 2002). Interactions are problematic for most linear analyses and are currently not well resolved statistically. However, they are inherent in all behavioral and wildlife data, and they are essential components that should be included in any complex analysis. The interactions presented here are two-way and based on classification trees, boosting and bagging (Friedman 2002).

Our FGM data were not normally distributed, and we therefore adopted non-parametric statistical procedures (two-sample Kolmogorov-Smirnov test performed with SPSS ver. 17.0 software). Statistical significance was recognized when $P < 0.05$. We used SigmaPlot 10.0 software to plot the charts.

Ethical note and underlying open access data

This study was fully endorsed by both the Hubei Sichuan Snub-nosed Monkey Research Center and the Shennongjia National Nature Reserve, and received final approval from the Institutional Animal Care and Use Committee (IACUC) at the College of Nature Conservation, Beijing Forestry University. All of the sampling activities were conducted in collaboration with technical staff of the Shennongjia National Nature Reserve. We took particular care to avoid disturbing the animals during fecal sampling and behavioral observations. Thus, we spent about 2 weeks familiarizing the monkeys with our research staff. We wore camouflage clothing to reduce animal stress.

Results

Food resources

In total 202 species of plants were selected as food by *R. roxellana* in the Shennongjia region (Table 1). The seasonal variation in food composition was described by Tie (2009).

FGM levels comparison

Average FGM values were 121.57 ± 2.74 ng/g in the cold seasons and 125.21 ± 3.29 ng/g in the warm seasons when the troop was provisioned in the interactive pattern (2006–2009). Values were not statistically different between cold and warm seasons ($N = 620$, $Z = 1.24$, $P = 0.092$). However, when the monkeys were provisioned in the individualistic pattern, the average FGM values were 27.51 ± 2.67 ng/g in cold seasons and 86.09 ± 5.09 ng/g in warm seasons (2009–2012). The difference was statistically significant ($N = 196$, $Z = 4.542$, $P < 0.001$). The overall FGM levels during interactive pattern provisioning were significantly higher than those during individualistic pattern provisioning ($N = 801$, $Z = 6.889$, $P < 0.001$; two-sample Kolmogorov-Smirnov test) (Fig. 2).

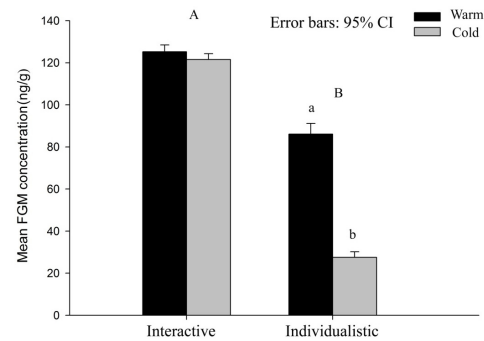


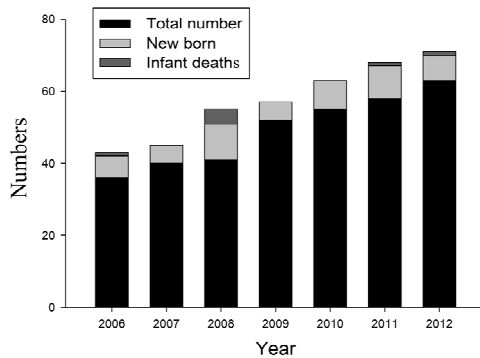
Figure 2. Fecal glucocorticoid metabolite (FGM) levels of monkeys subjected to two patterns of food provisioning in cold and warm seasons. Different lower case letters indicate significant differences between seasons ($P < 0.01$); different upper case letters indicate significant differences between provisioning patterns ($P < 0.01$). (Note: a vs b ($P < 0.01$); A vs B ($P < 0.01$)).

Table 1. Numbers of food types used by Sichuan snub-nosed Monkeys at the Shennongjia Nature Reserve.

Season	Woody plants			Herbaceous plants	Lichens
	Trees	Shrubs	Climbers		
Spring	73	57	21	15	4
Summer	51	56	15	13	4
Autumn	44	40	15	6	4
Winter	9	6	0	0	4
Year-round	91	69	21	17	4

Table 2. Infant births and deaths during the period 2006–2012.

Provisioning pattern	Individual	Infant birth	Infant death	Death rate
Interactive	DaDa	1	1	100 %
	JuZ	2	1	50 %
	LL	1	1	100 %
	HZ	2	2	100 %
Individualistic	HuanHuan	2	1	50 %
	XH	1	1	100 %

**Figure 3.** Total population size, numbers of live births and infant deaths during the period 2006–2012 in the group of Sichuan snub-nosed monkeys at the Dalongtan observation site, Shennongjia Nature Reserve.

Four individuals were re-sampled in this study [YY (♀), DWB (♀), BT (♂) and XX (♂)]. We compared the FGM values of these four individuals between cold and warm seasons with two different provisioning patterns. When the provisioning pattern was interactive, FGM values for females were similar between seasons (YY: $F = 2.880$, $P = 0.109$; DWB: $F = 2.344$, $P = 0.144$). However, when the provisioning pattern was individualistic, FGM values for females were significantly higher in the cold season (YY: $F = 7.847$, $P = 0.007$; DWB: $F = 10.603$, $P = 0.002$) in the period 2008–2011. FGM values for males were seasonally significant different with interactive pattern provisioning (BT: $F = 75.905$, $P < 0.001$; XX: $F = 10.603$, $P = 0.002$) and did not show any difference with individualistic pattern provisioning (BT: $F = 0.723$, $P = 0.398$ [one-way ANOVA]; XX: $U = 866.00$, $P = 0.262$ (Mann-Whitney U test)).

Survival rate of newborn monkeys

During the period 2006–2012, 52 infants were born at the study site. Five died during interactive pattern provisioning and two during individualistic pattern provisioning (Table 2). Eighteen adult females at the study site mated in the period till the

end of 2008. The same proportion of females mated in the later period till the end of 2012. The monkey population grew from 45 in 2006 to 65 in 2012 (Fig. 3). The average survival rate of infants was 78.26% with interactive pattern provisioning (2006–2008) and 93.10% with individualistic pattern provisioning (2009–2012).

Rank of female individuals

We used the DI values for 2008 to construct a dominance hierarchy for the female monkeys in all OMUs (Table 3) (Yu et al. 2009b). Adult females that lost infants had the lowest rank within their units. The units they belonged to were lower than in the ones where no infants died. The relationship between behavioral rank, FGM and the number of infant deaths is depicted in Figure 4. Infant deaths were elevated among females of low rank and when FGM values exceeded 200 units. FGM values between 40 and 200 units were negatively correlated with infant death. Table 4 presents two-way interactions between factors (based on classification trees). Rank in the dominance hierarchy had the highest importance value.

Discussion

When subjected to the interactive provisioning pattern, family units of the monkeys were forced to circle and compete for food at distances of 0.5–10 m. This provisioning pattern led to an imbalance in food distribution due to rank differences. Individuals fought for sufficient food, and aggressive behaviors were clearly observable (Yu et al. 2009b). In the wild, the distances between Sichuan snub-nosed monkey troops are always 10–50 m, and aggressive behaviors are seldom observed (Lu 2007, Yu et al. 2009b). Complete visual exposure to other family units during feeding may promote physical conflict. Frequent fighting and warning behaviors occur as a consequence of competition for resources, particularly during reproductive seasons (Zhang et al. 2003, Yu et al. 2009b). How-

Table 3. Dominance hierarchy ranks of members in each family unit of Sichuan snub-nosed monkeys at the Dalongtan observation site, Shennongjia Nature Reserve.

Ranks	Interactive pattern			Individualistic pattern		
	HTUnit ^a (DI)	CM Unit (DI)	BT Unit (DI)	XX Unit (DI) (Yu Yang, 2012)	DDUnit (DI) (Yu Yang, 2012)	DY Unit (DI)
1	HT (0.50 ± 0.12)	CM (0.50 ± 0.09)	BT (0.47 ± 0.12)	XX (1.00 ± 0.00)	DD (0.99 ± 0.14)	DY (0.97 ± 0.12)
2	LN (0.34 ± 0.29)	JJ (0.41 ± 0.12)	TT (0.44 ± 0.17)	NN (0.83 ± 0.17)	JJ (0.77 ± 0.18)	HuHu (0.86 ± 0.21)
3	HuHu (0.34 ± 0.21)	JZ* (0.35 ± 0.49)	DWB (0.44 ± 0.17)	LL (0.62 ± 0.20)	LN (0.56 ± 0.21)	HuanHuan* (0.58 ± 0.13)
4	GP (0.31 ± 0.29)	HZ* (0.25 ± 0.25)	XWB (0.43 ± 0.17)	BB (0.51 ± 0.21)	YinYin (0.48 ± 0.22)	XH* (0.45 ± 0.20)
5	HuanHuan (0.29 ± 0.18)		YingYing (0.38 ± 0.23)	TianTian (0.33 ± 0.21)	XL (0.20 ± 0.20)	
6	QQ (0.27 ± 0.26)		NN (0.36 ± 0.24)	WF (0.16 ± 0.12)	GG (0.00 ± 0.00)	
7	HuiHui (0.25 ± 0.29)		HH (0.35 ± 0.25)	HongHaier (0.04 ± 0.04)		
8	BB (0.17 ± 0.25)		DaDa* (0.34 ± 0.24)			
9	DouDou (0.17 ± 0.29)		WF (0.29 ± 0.27)			
10	YinYin (0.14 ± 0.24)		LL* (0.25 ± 0.29)			
11	TianTian (0.06 ± 0.18)		XL (0.10 ± 0.22)			

* Individuals who lost infants; ^a, units are identified by the dominant individual (e.g., HT); DI, dominance index; individuals are identified by either two upper case letters or by their names (e.g., HT and HuHu)

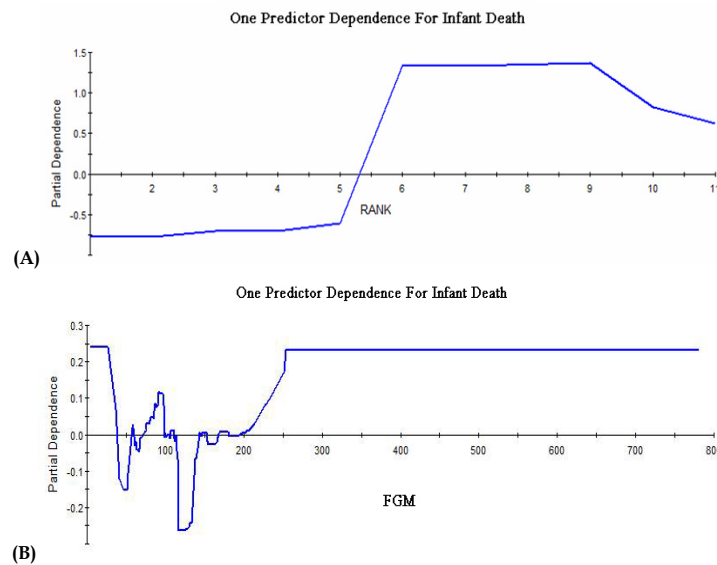


Figure 4. Relationship between numbers of infant deaths, dominance ranks of females and fecal glucocorticoid metabolites (FGM) determined by the TreeNet algorithm (Note: A: Rank was classified from 1 to 11; 1 means highest rank and 11 means the lowest rank. The death of infants increased with the rank reduced; B: Number of infants death increased with the FGM levels increased).

Table 4. Two-way interactions calculated by the TreeNet algorithm (Friedman 1999, 2002).

Factor	Importance Value
RANK	51.70
UNIT	24.85
FGM	16.82
SEASON	5.70
PROVISION PATTERN	0.31

RANK, female position in the dominance hierarchy (see Table 3); UNIT, family unit, FGM, fecal glucocorticoid metabolites; SEASON, cool and warm periods of the year; PROVISION PATTERN, interactive vs. individualistic pattern provisioning

ever, these phenomena have rarely been observed in wild troops (Lu 2007).

The individualistic provisioning pattern promoted wide spacing between family units, each of which had an independent feeding space. Eye, physical contact and aggressive behaviors decreased greatly during feeding. The overall stress levels of the whole troop and the family units were reduced compared to levels measured when provisioning was interactive.

We found that environmental factors (e.g., temperature and habitat quality) were unrelated to high FGM values in cold seasons. The interactive provisioning pattern caused an imbalance in food distribution between high- and low-ranking individuals. Artificial provisioning is the only mechanism that provides adequate food supplies for these wild monkeys during winter when food resources are limited (Table 1) (Li 2006, Tie et al. 2010). When the troop was interactively provisioned, low-ranking individuals found it difficult to obtain sufficient food within the 300-m² area available at Dalongtan. Shortages of food promoted fierce competition for resources and increased the FGM level of the entire troop, causing high levels of chronic stress in pregnant and lactating individuals. Mortality is high and the birth rate is low among monkeys at Shennongjia during winter (Li et al. 2005).

When the provisioning pattern was individualistic, FGM values were significantly different between warm and cold months of the year (Fig. 2). The breeding seasons overlapped with the warm season. During the breeding seasons, males fought for mating opportunities. The entire troop was influenced by this fierce competition, which was correlated with significant increases in FGM values. When adequately provisioned, the monkeys were more peaceful during the cold seasons. However, when the monkeys were provisioned in the

interactive pattern, members of the troop competed for food in the cold season and FGM values of the entire troop were as high as those in the breeding (warm) seasons.

Rank was the most important factor influencing infant death rates. High-ranking individuals had more opportunities to access food resources and drove away those belonging to inferior rank (Ren et al. 2003, Zhang et al. 2003, Yu et al. 2009a). A study on king colobus (*Colobus polykomos*) showed that competition among female individuals is correlated with food resource availability (Korstjens et al. 2006); thus, during the breeding season the FGM levels of lower-ranking females were elevated because they were exposed to more aggression (Cavigelli et al. 2003). Koenig (2002) pointed out that in top-down hierarchical societies of non-human primates lower-ranking individuals are inferior in the competition for resources and breeding opportunities. Losing the competition for resources can elevate the FGM levels of lower-ranking individuals (Davis & Christian 1957, Manogue 1975, Sapolsky 1985, 1990, 2005, Berco-vitch & Clarke 1995, Sands & Creel 2004). Shortages of food intensify the nutritional stress of low-ranking individuals (Wrangham 1980, Whitten 1983, Thierry et al. 2004), thereby increasing physiological stress and degrading body condition. Chapman et al. (2006) showed that nutritional deficiency is the main cause of population declines in colobus monkeys (*Procolobus rufomitratus*). Trites and Donnelly (2003) found that Steller's sea lions (*Eumetopias jubatus*) experienced nutritional stress when food supplies were deficient, with consequent reductions in the birth rate.

Low-ranking adult female Sichuan snub-nosed monkeys may suffer stillbirth during parturition due to food deficiencies and stress. Chronic stress can damage the reproductive system (Abbott 1997, Carlstead & Brown 2005, Alejandro et al. 2014) and decrease the survival of offspring (Oro & Furness 2002, Grosbois & Thompson 2005, Sandvik et al. 2005). A low stress level guarantees a high offspring survival rate and promotes population growth (Colin et al. 2006). Feeding provision patterns have a direct influence on food distribution among individuals. When the distribution is highly skewed, infants may die of nutritional deficiency and infectious diseases during the lactation period. In our study, infant deaths were restricted to the cold season (November to April), which is the period of the year when females give birth and feed milk to their offspring.

The pattern of food provisioning greatly influenced the survival rate of infants: survival rates were 78.26 % and 93.10 % when the provisioning patterns were interactive and individualistic, respectively. Thus, the death of infants was closely related to the peak of physiological stress imposed by the different feeding patterns.

Conclusions

Based on our analysis we conclude that: 1) the survival rate of infants increased from 78.26 % with interactive pattern provisioning to 93.10 % with individualistic pattern provisioning; 2) interactive pattern provisioning caused increases in the troop FGM levels compared to individualistic pattern provisioning (Interactive pattern provisioning intensified aggressive behaviors, and exacerbated imbalances in food distribution during cold seasons, thereby increasing levels of food deficiency and physiological stress. Individualistic pattern provisioning reduced conflict and competition among family units and individuals to some degree, which in turn reduced physiological stress); 3) Female rank markedly influenced infant death rates. Low-ranking female individuals suffered severe nutritional stress, especially in cold seasons when food was provided by interactive provisioning, and often lost new-born infants in consequence; 4) Nutritional stress increased overall physiological stress in females during cold seasons.

Acknowledgments. Funding for this project was provided by the Special Fund for Forestry Scientific Research in the Public Interest, Chinese Ministry of Science and Technology (No. 201004054). We thank the Shennongjia National Nature Reserve at Hubei Province China for allowing us to pursue our research on their site; we also thank Liao Mingyao, Zhao Benyuan and Yang Jinglong for their assistance, and Zhang Dong and Eric Isai for editing and providing advice on the manuscript.

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