Research Article

Troop Takeover and Reproductive Success of Wild Male Japanese Macaques on Yakushima Island (*Macaca fuscata yakui*)

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Troop takeover is common in one-male primate groups, but there are few reports in multimale groups. Japanese macaques (*Macaca fuscata*) form multimale groups and males commonly join troops at the bottom rank. On Yakushima island, however, where group size is relatively small, entrance into groups at the alpha position is also observed. This paper reports on the general features of troop takeover, on the predictors of takeover events, and on the reproductive success of takeover males. Troop takeovers occurred only in the mating season; nontroop males (NTMs) did not cooperate with each other; former alpha males were rarely expelled from the troop; new alpha males did not commit infanticide; new alpha male tenure in the group was usually less than two years. Logistic regression analysis showed that the number of NTMs associating with a troop predicted the occurrence of troop takeover. Paternity discrimination revealed that 33.3% (3/9) of takeover males succeeded in siring offspring. Contrary to this low success rate, binary logistic regression analysis revealed that the takeover males can expect higher reproductive success compared to troop males. Entering a troop and out-competing the alpha male is one of many available strategies to attain reproductive success in male Japanese macaques.

1. Introduction

Male macaques migrate from their natal groups as they mature, often migrating among nonnatal groups several times during their lives. This behavior may increase the probability of attaining high rank and mating opportunities [1–4]. Group takeover is usually observed in one-male groups, but also sometimes in multimale groups (Japanese macaques: [5, 6]; long-tailed macaques: [3]; capuchin monkeys: [2]; Hanuman langurs: [7]). Male migration, including troop takeover, is usually concentrated in the mating season, although in long-tailed macaques migration can occur in any period [3]. It is often reported that new males kill infants during or after troop takeover [8, 9], increasing the probability of future matings. Resident males, including former alpha males, often defend infants from intruder males, especially when they are likely to be their offspring [10, 11].

In Japanese macaques, intertroop movement is observed in the mating season. It is common for males to enter troops peacefully (i.e., without aggression), assuming low status in the existing dominance hierarchy [12–16]. However, in Ya-kushima, many males visit adjacent troops as nontroop male, (NTMs) during the mating season, and mature NTMs at the peak of physical strength enter troops aggressively. The number of NTMs varies depending on the troop and year, and sometimes NTMs contribute up to 30%–40% of a troop's total copulations [5, 14]. Troop takeovers usually involve such mature intruder males and troops with small numbers of resident males, whereas young males tend to move into troops with many resident males [17]. Current alpha males and other troop males often attempt to expel intruders from the troop, which can result in serious injury to both parties [5]. Thus, entering as a dominant male poses some risk, so it is expected that the takeover strategy also provides some benefit, such as increased reproductive success.

In this study, our first objective is to describe the general feature of troop takeovers in this population. Previous studies on Japanese macaques showed that nontroop males

(NTMs) usually enter troops after most of the troop females have already conceived, suggesting that males might fail to impregnate the females during the mating season [18, 19] but see [20]. If a male is unable to find receptive females in the troop, he may commit infanticide so that lactating females would begin cycling again. However, only one case of infanticide has been reported in this population [21]. Another important factor is the tenure of the alpha male. Usually, the male macaques shift between troops throughout their lives. If a male remains in a troop as an alpha male for many years after takeover, it might ensure high reproductive success. The average male tenure of the Yakushima population is believed to be around 2 to 3 years [5].

We also examine predictor variables that may influence the probability of troop takeover (number of troop males, number of troop estrous females, and number of NTMs), using logistic regression analysis. Finally, we examine the reproductive success of takeover males using noninvasive collection of DNA samples, and we compare the reproductive success of takeover males to that of low- and high-ranking resident males.

2. Method

2.1. Study Site and Subjects. The study site is located on the western coast of Yakushima Island (30°N, 130°E), Japan. The investigation was conducted on 4 troops, referred to as troops B, NA, E, and Momoe. Habituation and long-term research on these troops began on 1992, 1994, 2003, and 2000, respectively [22–24] (Hayakawa; unpublished data). The troops inhabit a coastal broadleaf evergreen forest, which lies 0–350 m above sea level [15, 25]. The population is characterized by many small troops with overlapping home ranges [26, 27]. Solitary floaters are rarely seen in the nonmating season, and the sex ratio of troop members is nearly 1 : 1 in this population, so most males are considered to belong to troops. And these NTMs are also believed to belong to certain troops. Many of these NTMs leave the troop within a few days and then are believed to enter another group or previous group by the end of mating season by losing a fight with troop males or for unknown reasons [5, 14, 26].

This study covers a 6-year period for troop B, 5 years for troop NA, and 1 year for each troops E and Momoe, with some observation gaps in each data set. The study troops were monitored with respect to their membership size at least twice a year, during the mating season (Sep–Jan) and the nonmating season (Feb–Aug). During the mating season, observations are focused on the mating behavior of the members and on monitoring the NTMs. Behavioral sampling procedures varied over the period and troopsfor each distinct project. Troop B: Ad libitum sampling (1996) and focal animal sampling (1997 and 2003). In 1999 and 2000, behavioral data are not collected; however, female's estrous condition and her mating partner and visiting NTM were recorded; Troop NA: Focal animal sampling (1997 to 2000 and 2003); Troop E: Focal animal sampling (2003); Troop Momoe: Focal animal sampling (2003). For further details and the results of each project, see previous reports [6, 28].

Troop males are defined as males that have been observed in the troop from the previous nonmating season, and NTMs are defined as males that did not belong to the target troop in the previous nonmating season and first interacted with the troop after the onset of a mating season [20, 24]. Many NTMs are merely visitors who remain near the troop for only a few days to several weeks and then just disappear. Some NTMs dominate troop males and exhibit behavioral patterns that researchers term the "alpha-male attitude"; this attitude includes shaking trees while giving barking vocalizations and displaying aggressiveness toward the troop males [13]. Many of these males become the new alpha male of the troop, but some of them disappear before the end of the mating season [5, 6]. In this study, these males who showed "alpha-male attitude" were also classified as NTMs.

In this research, we defined troop takeover as those cases in which males (1) visited the troop over a minimum of 20 days continuously or intermittently, (2) showed aggressive behaviors, such as branch shaking with vocalizations, staring at or chasing group males, and mounting group members in the center of the group, and (3) received submissive behaviors from the majority of troop males, including the alpha male.

2.2. DNA Isolation, Quantification, and Microsatellite Genotyping. Paternity data on this population has been reported previously [20, 21, 28]. Additional paternal discrimination was carried out for infants who were born in 2004 in the three troops which were taken over by NTMs. Samples were collected from the infants and their mothers, all the males of the troops under study, and 20 NTMs (22.5% of all the observed NTMs) who interacted with troop females. DNA from adult males was extracted mainly from the semen of masturbating individuals or from semen that had dropped to the ground after copulation. DNA from mothers were mainly extracted from menstrual blood. DNA was extracted from the tissue sample of one infant who died two days after birth. The remaining individuals' DNA was extracted from multiple samples of urine, feces, and hairs (plucked by themselves or by groomers). Fresh samples were placed in 25 mL tubes containing absolute alcohol and stored at 4°C until extraction.

Genomic DNA was extracted using a QIAmp DNA stool kit and QIAmp DNA mini kit (Qiagen, Chatsworth, Calif) in accordance with the manufacturer's instructions. DNA from single shed hairs was extracted using an ISOHAIR kit (Nippon gene). Semen and tissue samples were cut into small pieces and combined with 250 μL of STE buffer (0.1 M NaCl, 10 mM Tris and 1 mM EDTA pH 8.0), 30 μL of 10% sodium dodecylsulfate, and digested with proteinase K (20 μL of 5 mg/mL) at 55°C for 2 hours. For semen samples, DTT (dithiothreitol, final concentration, 0.6 mg/mL) was added prior to proteinase K digestion. For both tissue and semen, digestion was continued for 2 hr or until complete. After this step, a standard phenol-chloroform procedure for DNA extraction was performed.

Eight microsatellite loci were used in the PCR (D5S1470, D1S533, D12S67, D6S493, D5S820, D6S501, D19S582, and

Locus	Allele	N	H (obs)	H (exp)	HW
D5S1470	8	94	0.787	0.717	NS
D1S533	6	105	0.733	0.73	NS
D12S67	8	109	0.734	0.755	NS
D6S493	7	108	0.731	0.687	NS
D5S820	6	104	0.76	0.752	NS
D6S501	6	101	0.743	0.752	NS
D19S582	4	106	0.726	0.738	NS
D10S611	7	103	0.738	0.698	NS

N indicates the number of individuals typed; H (obs) and H (exp) indicate the observed and expected heterozygosities. HW refers to deviation for Hardy-Weinberg equilibrium, and NS stands for nonsignificant.

D10S611). The calculated and observed heterozygosities of 8 microsatellite loci are shown in Table 1, and the probability of exclusion was 0.995 for the second parent (assuming that the first parent was correctly assigned). Each PCR product was purified by ethanol precipitation to remove nucleotides, primers, salts, and proteins. The 5′ ends of the forward primers were labeled with a fluorescent color, the amplification products were separated using capillary electrophoresis (ABI 310), and allele sizes were determined relative to an internal size standard. Polymerase chain reaction amplification for urine and fecal-derived DNA was repeated independently 3–7 times [29] whenever possible to check for genotyping errors such as allelic drop out.

Comparison of the infant and maternal genotypes allowed for the deduction of the paternal allele(s). Males whose alleles did not match the deduced paternal allele(s) were excluded as paternity candidates. When all candidate fathers except one were excluded, the remaining male was assumed to be the likely father. In cases in which all the candidate males were excluded, it was assumed that the father was probably an NTM whose DNA sample we failed to collect. Furthermore, the parentage likelihood was calculated using the program CERVUS 2.0 (Trisran Marshall, Edinburgh, UK; [30]). The allele frequencies of the entire population were used to compute the paternity exclusion probabilities, and the assigned fathers were required to have values of 90% or greater. For further details, see our previous reports [20, 21, 28].

2.3. Statistical Analysis. We used binary logistic regression to test troop composition, and the number of NTMs affect the occurrence of troop takeover. The occurrence of takeover (yes/no) was the dependent variable, and the number of NTMs, troop males, and estrous females were independent variables. To detect multicollinearity between the independent variables, diagnostic statistics were examined via linear regression analysis. The variance inflation factors (VIF) determined were 1.818 (NTMs), 5.373 (troop males), and 4.638 (females). Values exceeding 10 are often considered to indicate multicollinearity. Based on our results, we concluded that there was no multicollinearity between the independent variables.

We also used binary logistic regression to test between the category of candidate fathers and the success of infant siring (yes/no). The infant siring (yes/no) was the dependent variable, and the category of candidate fathers (higher-ranking troop males, lower-ranking troop males and takeover males) and the number of infants born were independent variables.

3. Results

3.1. Features of Japanese Macaque Troop Takeover. All observed troop takeovers on Yakushima Island ($n = 7$) across 4 troops (1996–2003) occurred during the mating season (Table 2). Although multiple nontroop males (NTMs) appeared around the troop in the seasons when troop takeover occurred, no coalition of takeover males was observed. For example, successive troop takeovers by different NTMs occurred in troop B in 1996 and 2000. The two successive takeover males were never observed to cooperate in defeating the current alpha males and behaved aggressively toward each other. In both cases, the male who intruded later overcame the one who had intruded first.

When NTMs successfully took over a troop and assumed the alpha position, the 7 former alpha males never left the troop during the concurrent mating season. Although 2 of these previous alpha males suffered severe wounds during the mating season (usually the aggressor was unknown), they remained in the troop in the beta or gamma dominance position. During takeover mating seasons, there were few or no unweaned infants, and there was no directly observed infanticide. Circumstantial evidence for infanticide by NTMs was also lacking, as there were no infant disappearances during takeover mating seasons.

3.2. Determinants of Japanese Macaque Troop Takeover. Univariate binary logistic regression analyses revealed that the number of NTMs significantly predicted the occurrence of troop takeover but that the number of troop males and the number of estrous females did not (Table 3). To test for the independent effects of each variable, bivariate analyses were conducted, but, in these analyses, no significant results emerged. However, when controlling for the effects of the number of troop males and estrous females, the effect of the number of NTMs on takeover likelihood remained close to statistical significance. Also, after controlling for the number of estrous females, the effect of the number of troop males on takeover likelihood also approached statistical significance. For this Yakushima Island data set, the number of NTMs had the strongest effect on troop takeover, the number of troop males had a negligible effect, and the number of estrous females had no discernable effect on the likelihood of troop takeover.

All males that took over troops appeared when most of the troop females had not yet conceived (Table 4), and mating between nontroop takeover males and troop females was often observed, indicating that the males had reproductive opportunities.

Table 5 reveals that the tenure of takeover males in the alpha position was short, usually ranging from one season to 2 years, with one outlier tenure length of 4 years. One

Table 2: The composition of the target troops.

(a) B troop

Year	Troop takeover	Num of troop males	Num of troop females	Num of NTMs
1996	Yes	6	7 (4)	13
1997	No	7	6 (5)	5
1998	No	5	5 (3)	0
1999	Yes	0	2 (2)	4
2000	Yes	2	4 (3)	4
2003	No	2 (4)*	3 (3)	10

*Two males who moved with females in the previous nonmating season were never found in B troop during the mating season; however, they were again found in the troop after the mating season was over.

(b) NA troop

Year	Troop takeover	Number of troop males	Number of troop females	Number of NTMs
1997	No	15	15 (11)	0
1998	No	12	13 (6)	0
1999	Yes	7	6 (6)	11
2000	No	7	7 (4)	2
2003	Yes	1	5 (4)	13

(c) Momoe troop

Year	Troop takeover	Number of troop males	Number of troop females	Number of NTMs
2003	Yes	4	6 (6)	10

(d) E troop

Year	Troop takeover	Number of troop males	Number of troop females	Number of NTMs
2003	Yes	7	8 (8)	17

Table 3: Contribution of the variables (B), standard error (SE), and significance (P) of binary logistic regression model concerning the occurrence of troop takeover.

Independent variable		B	SE	P
Univariate analyses				
Number of NTMs		0.356	0.178	0.045*
Number of troop males		−0.335	0.217	0.124
Number of estrus females		−0.113	0.242	0.640
Bivariate analyses				
	Controlling for:			
NTM	Troop males	0.345	0.201	0.087
	Estrous females	0.386	0.206	0.061
Troop males	NTMs	−0.372	0.321	0.248
	Estrous females	−0.969	0.502	0.054
Estrous females	NTMs	−0.330	0.553	0.537
	Troop males	1.227	0.780	0.116

*$P < 0.05$.

male was expelled, and 2 males were supplanted by other NTMs. Both the supplanted males remained in the troop as beta male for at least 1 more year. The remaining four males

disappeared from the troop for unknown reasons (one might have died during the period of mass mortality).

3.3. Reproductive Success of Japanese Macaque Takeover Males. We compared the number of offspring sired by takeover males to that sired by high-ranking and low-ranking troop males (Table 6). Five offspring were not included in the analysis because we failed to collect sufficient samples to test their paternity. The number of high-ranking males was determined annually by the average number of receptive females in each troop: if the average number of estrous females was below 1.5, then only the alpha male was considered dominant, and if the average was 1.5 or above, then the number of high ranking males was increased to two (alpha and beta males). Six of nine infants were assumed to be sired by NTMs whose DNA samples we failed to collect, because all the candidate fathers (including 20 NTMs) were excluded by the analysis.

The result is that 3 of the 9 (33.3%) takeover males succeeded in siring infants, while 4 of the 19 (21.1%) high-ranking troop males and 8 of 56 (16.0%) low-ranking troop males did so. Step-wise logistic regression analyses revealed that the factor "Category of candidate fathers" and the factor "Number of infants" are the significant factors predicted sire-hood (Table 7). The factor "Category of candidate father (1)" divides takeover males from other males, and "Category of candidate father (2)" divides high-ranking males from other males. The analysis showed that only "Category of candidate father (1)" is significant, so takeover males can expect higher reproductive success than males in other categories.

4. Discussion

4.1. Features of Japanese Macaque Troop Takeover. Troop takeover only occurred in the mating season, consistent with the idea that such actions are part of a reproductive strategy. Once appearing in the troop, NTMs rapidly established high rank (Table 4). Although takeover males were sometimes attacked by coalitions of troop males, such attacks never succeeded in expelling the intruder from the troop.

A newly dominant male could benefit from committing infanticide when he has not possibly sired the infant and very likely to sire the next. However, the only observed infanticide in this population involved a troop male who recently rose in rank, not a male who took over the troop [21], and there was no direct observation of infanticide, attempted infanticide, or indirect evidence of infanticide by takeover males. There are several reasons why takeover males may not use infanticide as a reproductive tactic. First, NTMs entering a troop encountered few unweaned infants (Table 2), so the opportunities may have been few. Second, takeover males have immediate competing interests, namely, following and consorting with estrous females. Females show prolonged estrous [31] and often try to mate with multiple males, so dominant males spend a great deal of time mate guarding. Third, resident males may prevent infanticide. In Japanese macaques, infanticide, though rarely observed, is most likely to occur when there are no resident males to defend the infant against attacks [10].

TABLE 4: Factors associated with troop takeover.

Troop	Year	Male	Date he was first consorting with a troop female	Date the alpha male first showed submissive behavior	Fate of the alpha male	Number of estrous females	Infants born	Infants conceived after his appearance	Number of unweaned infants
B	1996	PE MR	17th October 5th November	24th October 9th November	Stayed	4	1	1 1	2
NA	1999	BT	No data	No data	Stayed	6	3	1	0
B	1999	MS	No data	No data	*	2	1	1	0
B	2000	AO MA	No data No data	No data No data	Stayed	3	1	1 1	0
NA	2003	MD	26th October	4th November	Stayed	5	3	2	1
Momoe	2003	TR	25th October	5th November	Stayed	5	2	1	0
E	2003	MN	14th October	15th October	Stayed	8	6	5	0

* All resident males had left the troop before MS appeared in the troop.

TABLE 5: Tenure of takeover males in the alpha position.

Troop	Male	Time of appearance	Time of his leaving	Reason he lost his tenure	Tenure as top-dominant male	Number of siring infant
B	PE	1996 October	1996 November	Another takeover	Part of one season	0
B	MR	1996 October	1998 August	Presumably died	2 years	0
NA	BT	1999 October	1999 November	He left voluntarily	Part of one season	0
B	MS	1999 October	2001	Another takeover	1 year*	0
B	AO	2000 October	2002	Another takeover	Part of one season*	0
B	MA	2000 October	2002	Another takeover	2 years	1
NA	MD	2003 November	2004	?	1 year	1
Momoe	TR	2003 November	2004 or 2005	?	1 year or 2 years	0
E	MN	2003 October	Still in the troop in 2009	Another takeover	4 years	2

TABLE 6: Reproductive success of takeover males.

Year	Troop	Troop takeover	Average number of estrous females per day	Infants born (paternity decided)	Number of male siring offspring			
					High-ranking troop male[c]	Low-ranking troop male[c]	NTM	Takeover
1996[a]	B	Yes	1.53	1 (1)	0 (2)	0 (4)	1	0 (2)
1997[a]	B	No	1.73	3 (2)	1 (2)	0 (5)	1	—
1998[a]	B	No	No data	0	0 (1)	0 (4)	0	—
1999[a]	B	Yes	No data	1 (1)	—	—	1	0 (1)
2000[a]	B	Yes	No data	1 (1)	0 (1)	0 (1)	0	1 (2)
2003	B	No	0.52	0	0 (1)	0 (1)	0	—
1997[b]	NA	No	2.42	11 (9)	2[d] (2)	3 (13)	3	—
1998[b]	NA	No		0	0 (2)	0 (10)	0	—
1999[a]	NA	Yes	1.77	3 (2)	0 (2)	1 (5)	1	0 (1)
2000[a]	NA	No	1.28	1 (1)	0 (2)	1 (5)	0	—
2003	NA	Yes	1.63	3 (2)	1 (1)	0 (0)	0	1 (1)
2003	E	Yes	2.13	6 (5)	0 (2)	1 (5)	2	1[e] (1)
2003	Momoe	Yes	1.39	2 (2)	0 (1)	2 (3)	0	0 (1)
Total				32 (26)	4 (19)	9 (56)	9	3 (9)

[a]Data are from Hayakawa 2008. [b]Data are from Soltis et al., 2000, 2001. [c]The number in parenthesis shows the number of candidate fathers. For example, in 1996, the number of high-ranking troop males was two, but the number of high-ranking males successfully siring offspring was zero. [d]One of the high ranking male succeeded in siring two offspring. [e]Take over male succeeded in siring two offspring.

TABLE 7: Contribution of the variables (B), standard error (SE), and significance (P) of binary logistic regression model concerning the success of infant siring.

Independent variables	B	SE	P
Category of candidate father			.061
Category of candidate father			
(1)	1.834	.906	.043*
(2)	0.882	.760	.246
Number of infants born	.223	.078	.004*

$P < 0.05$. The factor "Category of candidate father (1)" divides takeover males from other males, and "Category of candidate father (2)" divides high-ranking males from other males. The analysis showed that only "Category of candidate father (1)" is significant.

4.2. Determinants of Japanese Macaque Troop Takeover. The number of NTMs associating with a troop was the main predictor of troop takeover. This was the case despite the fact that NTMs did not cooperate with each other during takeovers. The number of NTMs may positively influence the probability of takeover because (1) the higher the number of males in the NTM group, the greater the probability that one of them will outrank the alpha male, (2) NTMs may be drawn to groups with relatively weak alpha males, or (3) large groups of NTMs who independently attack the troop may wear down resident males from their repeated efforts, even though only one of them takes over the troop at a time.

Another possibility is that the occurrence of troop takeover itself leads to the increased number of NTMs, because the number of NTMs includes those who visited after the occurrence of troop takeover. When the troop is taken over, it become less cohesive because (1) the takeover male often copulates on the periphery of the troop, perhaps to prevent cooperative aggression by troop males [6], and (2) takeover males cannot make affiliative relationship with nonestrous females or other troop males, and this results in troop members moving in separate groups [5, 24]. This lack of cohesiveness may attract NTMs who can easily approach estrous females and may sometimes lead to a second troop takeover.

Our analysis failed to show that the number of troop males affects the occurrence of troop takeover. However, previous studies indicate that the number of troop males negatively correlates with the number of NTMs on a daily basis [6], and troop takeover tends to occur in the troops with small numbers of troop males [17]. Furthermore, in the main island of Japan where troop size is much bigger than Yakushima, troop takeover is rarely observed. So, these results should not be construed as evidence that the number of troop males generally has no effect on takeover. First, the association was in the expected direction (the few males in the troop the more likely a takeover), and when controlling for the number of estrous females, the relationship approached significance (Table 3). Second, since troop size on Yakushima Island is generally small, there may not have been enough variation in the number of troop males across groups and years to observe a discernable effect of troop male number on troop takeover (floor effect). Third, the effect of the number of troop males on troop defensibility may have been diminished if some resident males sought mating opportunity on the periphery [6] or if some resident males were not physically mature enough to compete with challenger males.

4.3. Reproductive Success of Japanese Macaque Takeover Males. The result showed that 3 of the 9 (33.3%) takeover males succeeded in siring infants. The logistic regression analyses revealed that takeover males can expect higher reproductive success than males of other categories. But the success rate is smaller compared to that of other species [2, 3, 8]. Why did these males not have higher reproductive success? First, as the logistic regression model indicated, a male's success of siring an infant depends on the number of infants born. Troops with fewer males would be easier to takeover because a small number of males implies less defensibility by troop males [5, 17]. However, at the same time, it also indicates that the number of estrous females in the troop is small because the sex ratio of this population is nearly uniform. Thus, it is assumed that the males could not sire many infants due to the small size of the troops.

Second, takeover males often mate with estrous females in the periphery of the troop [6], probably thereby avoiding the troop males' aggression. However, taking a female to the periphery of the troop also increases the chances that those females will meet other novel NTMs and also causes decreased cohesiveness of the target troop. Estrous females sometimes leave the troop temporarily and meet with NTMs or low-ranking males in locations where they cannot be detected by other males. These promiscuous behaviors of females are considered as a counterstrategy against infanticide and cause difficulties for males to monopolize estrous females.

If a male retains his dominant status for a long period, he could increase the possibility of enjoying high reproductive success, but this was not the case. The main reason that a usurping male loses the top dominance so quickly is another troop takeover (Table 5). Considering the cost of the time and energy to take over the troop, it seems strange that usurping males lose their tenure so quickly. However, in this population, maintaining high rank does not guarantee high reproductive success. Given the presence of a challenger trying to enter his troop, the alpha male must choose whether to take the risk of receiving severe wounds or to turn over his alpha position. The takeover strategy appears to be a short-term, high-risk strategy for prime males to gain immediate chances of siring a few offspring which may provide more reproductive opportunities than entering gradually and peacefully at the bottom of the hierarchy, remaining as a NTM, or rejoining his previous troop.

4.4. Comparison to Takeovers in Other Multimale Groups. Troop takeover has been observed in several multimale primate groups [2, 3, 8, 17]. With the exception of the Japanese macaque, alpha status confers clear reproductive benefits in the above species, which drives males to challenge troop takeover. This study and previous research into the relationship between male dominance rank and reproductive success

in Japanese macaques have yielded mixed results [20, 28]. This may be one reason that troop takeover is relatively rare and opportunistic in this species.

Another remarkable feature of Japanese macaque takeovers is that NTMs do not cooperate. In white-faced capuchins, on the other hand, 4 of 7 (57%) takeovers involved multimale, cooperative invasions. In most of these cases, invaders matched or outnumbered resident males. Larger numbers of cooperating intruders should increase the likelihood of troop takeover, but it also increases within group competition after takeover. Further investigation will be needed to account for the variability in takeover strategies within and across primate species.

Acknowledgment

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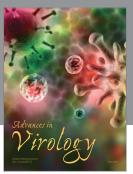
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